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Ecological Studies of Wolves on Isle Royale, 2019-2020

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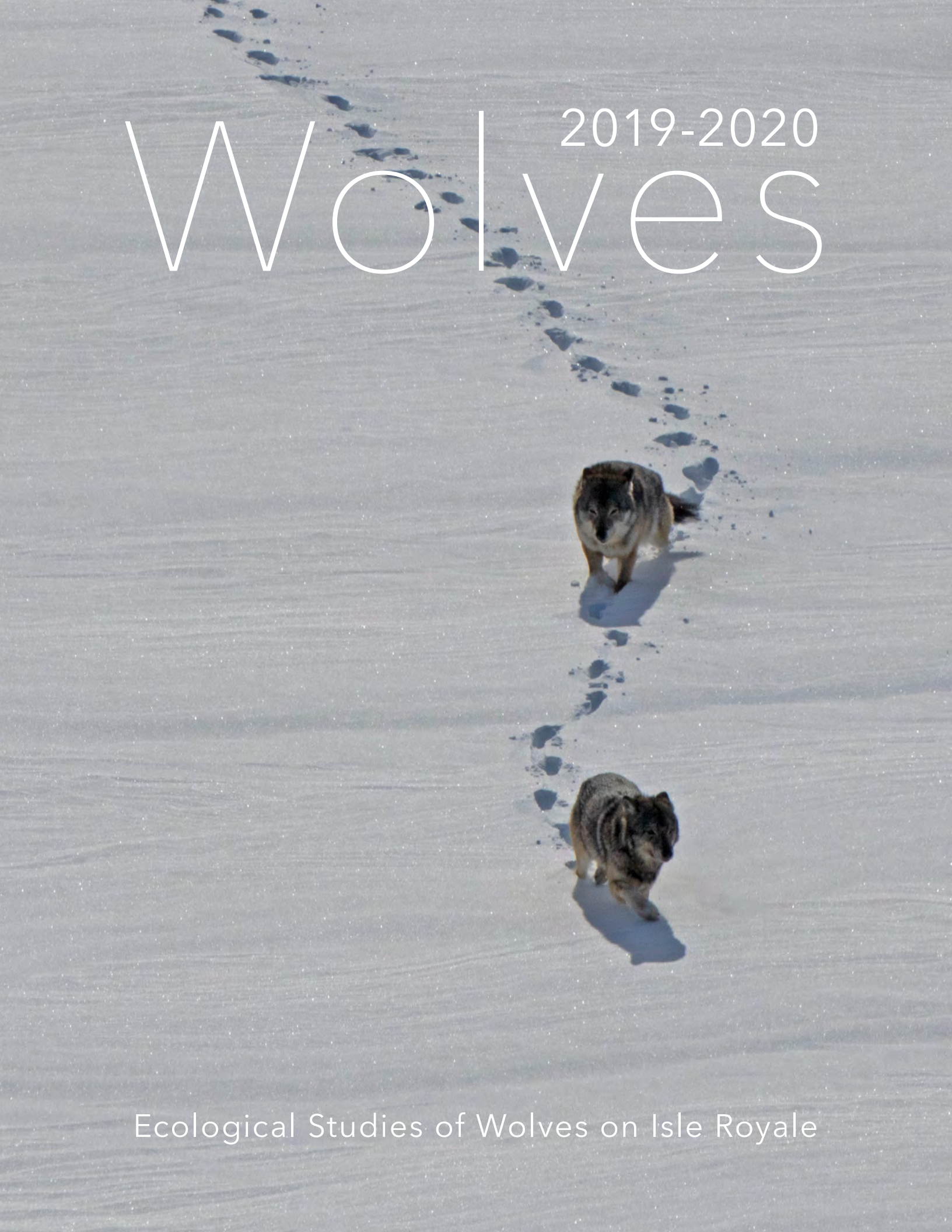
Wolves 2019-2020



Ecological Studies of Wolves on Isle Royale

> What escapes the eye ... is a much more insidious kind of extinction: the extinction of ecological interactions.

D.H. Janzen, 1974

Ecological Studies of Wolves on Isle Royale

Annual Report 2019-2020

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April 2020

Front cover photograph: The final survivors of the native wolf population on Isle Royale, F193 (front) and M183, February 2019.

Support and Contributions

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Team IA–Michael George (leader), Sumit Dongre, Seth Shannon, Tyler Shannon, Peter Wegner, and Lada Zednik
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Team IC–Joe Olenik (leader), Erik Freeman, Hal Hanson, Mike LaMotte, Stuart Portoghese, and John Warming
Team ID–Wayne Shannon (leader), Ron Eckoff, Larry Fuerst, Nancy Moran, and Ron Porritt
Team I auxiliary–Bob and Jenny Bollinger
Team IIA–David Conrad (leader), Mark Kanitz, David Snoek, and Dan Dunleavy
Team IIB–Clay Ecklund (leader), Erik Freeman, Ryan Talbot, and Patrick Huver
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Team IVC–Jason Duetsch (leader), Trevor Edmonds, Hal Evensen, and Ted Lind
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Moosewatch for Teachers II–Karen Bacula (leader), Kari Keith, Amanda Meek, and Deborah Yats

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The results reported here are preliminary and, in some cases, represent findings of collaborators; please do not cite without consulting the authors. Specifically, data on wolf movements from GPS collars was provided by the National Park Service (NPS) and is used here by permission. For further details see: *Romanski et al. (2020) Wolves and the Isle Royale environment: restoring an island ecosystem 2018-2020, National Park Service, Isle Royale National Park, Houghton, MI.* Hereafter this report is cited as *NPS 2020.* The views expressed here do not necessarily reflect those of the NPS or the US National Science Foundation.

Ecological Studies of Wolves on Isle Royale

SUMMARY

Over the past year, the National Park Service (NPS) continued its efforts to restore wolf predation on Isle Royale by translocating four wolves from Michigan. By early March 2020, the wolf population was likely composed of 12 wolves, but could be as many as 14 wolves. This is a slight decline from March 2019 when there had been 15. Annual mortality rate was high (approximately 40 percent), and many of the mortalities were attributable to wolves killing other wolves. A pup is likely to have been born in April 2019. The origin of an non-collared adult is not known—it could be a natural immigrant or a translocated wolf that lost all tags.

The wolf population appears to be organizing itself into four social groups, each of which displayed signs of courtship or readiness to mate. Two of the groups defended secure territories, and two groups seem to have less secure territorial claims. One of the groups with a secure territory consisted of a bonded male-female pair that are closely related.

The estimated abundance of moose declined, by 9 percent, from 2,060 to 1,876, between February 2019 and February 2020. Longer-term trends in the population and statistical uncertainties associated with any particular estimate allow one to reasonably infer that the population had increased greatly over an eight-year period (2011–2019) and during the past year the population has declined slightly or remained about the same. In mid-March, 25 moose were outfitted with GPS collars so that their movements and behavior can be monitored, adding to the 20 moose radio-collared in 2019.

For more information, go to: **www.isleroyalewolf.org** and "Wolves and Moose of Isle Royale" (Facebook).

PERSONNEL AND LOGISTICS

In summer 2019, 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 Christian Stevens, Eli Paulen, Emily Stern and Amelia Cole did widespread fieldwork on moose-balsam fir interactions, and additional fieldwork was carried out by Isabella Evavold and Tom Offer-Westort. Leah Vucetich also led a number of people working in the lab, especially Grace Parikh, Zach Merrill, John "Moose" Henderson, Tanner Barnes, Erin Brooks, Otti Brueshaber, Rachel Christensen, Tori Engler, Kady Gehrke, Allie Johnson, Eli Paulen, America Parker, Jayme Randolph, Joellen Saugrich, Christian Stevens, Noah Yacks, and Carly Zielinski.

During the course of the summer field season, many park staff, other researchers, 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 2020, the annual Winter Study was conducted during 21 January to 10 March. The winter fieldwork was led by John Vucetich, Sarah Hoy, and Rolf Peterson, with key contributions provided by pilots Don L. Murray (UpNorth Aerials, Two Harbors, Minnesota) during 21 January to 10 February and 19 February to 7 March and Don E. Glaser (Arctic Wings, Willow, Alaska) during 9 to 17 February. Ky and Lisa Koitzsch provided daily fieldwork on skis to collect data on moose and balsam fir. NPS staff Marcus Tanskanen and John Boyle provided important logistical assistance throughout the Winter Study, as well as Mark Romanski and Lynette Potvin during mid-February, and Helen DeMarsh and Elizabeth Orning assisted with telemetry data. Corey Process (NPS) and Robert Glaser provided ground transportation on the mainland.

An effort to radio-collar moose was initiated on 10 March, headed by Sarah Hoy (MTU), Mark Romanski (Division Chief of Natural Resources, Isle Royale National Park), Seth Moore (Director of Biology and Environment, Grand Portage Band of Lake Superior Chippewa), and Tiffany Wolf (DVM and Assistant Professor from the University of Minnesota). This effort was greatly aided by Lynette Potvin (NPS), Michelle Verrant (wildlife veterinarian, NPS), Bryce Olson (private consultant, Ressurs LLC), Nicholas Thompson (NPS pilot who flew a fixed-wing

aircraft provided by Voyageurs National Park), Jerrold Belant (Professor, State University of New York College of Environmental Sciences and Forestry [SUNY ESF]), Andrew Miller (private contractor) and the following crew from Helicopter Wildlife Services (Heliwild): Harry Hensberg (pilot), Roy Hensberg, and Justin Thompson.

WOLF POPULATION

By early March 2020, the wolf population was likely composed of 12 wolves, but could have included as many as 14 wolves (Figure 1). Between September 2018 and September 2019, the NPS implemented a plan to restore wolf predation on Isle Royale by translocating a number of wolves from the mainland and Michipicoten Island (in eastern Lake Superior) to Isle Royale. All of the translocated wolves were outfitted with GPS-enabled radio-collars so that their movements can be monitored remotely. All wolf GPS data referred to throughout this report were provided by NPS (NPS 2020). Those translocation efforts have importantly influenced wolf abundance over the 19-month period from September 2018 to March 2020. The sequence of key events is:

Aug 2018: The population consists of two island-born wolves, male (M183) and female (F193).

Sept 2018–March 2019: Four wolves were brought to the island from Minnesota, three from near Wawa, mainland Ontario, and eight from Michipicoten Island. By early April 2019, one of those wolves died, and one left the island on an ice bridge. In March 2019, the population included 15 wolves. Details of events up to March 2019 are reported in the 2018–2019 Annual Report.

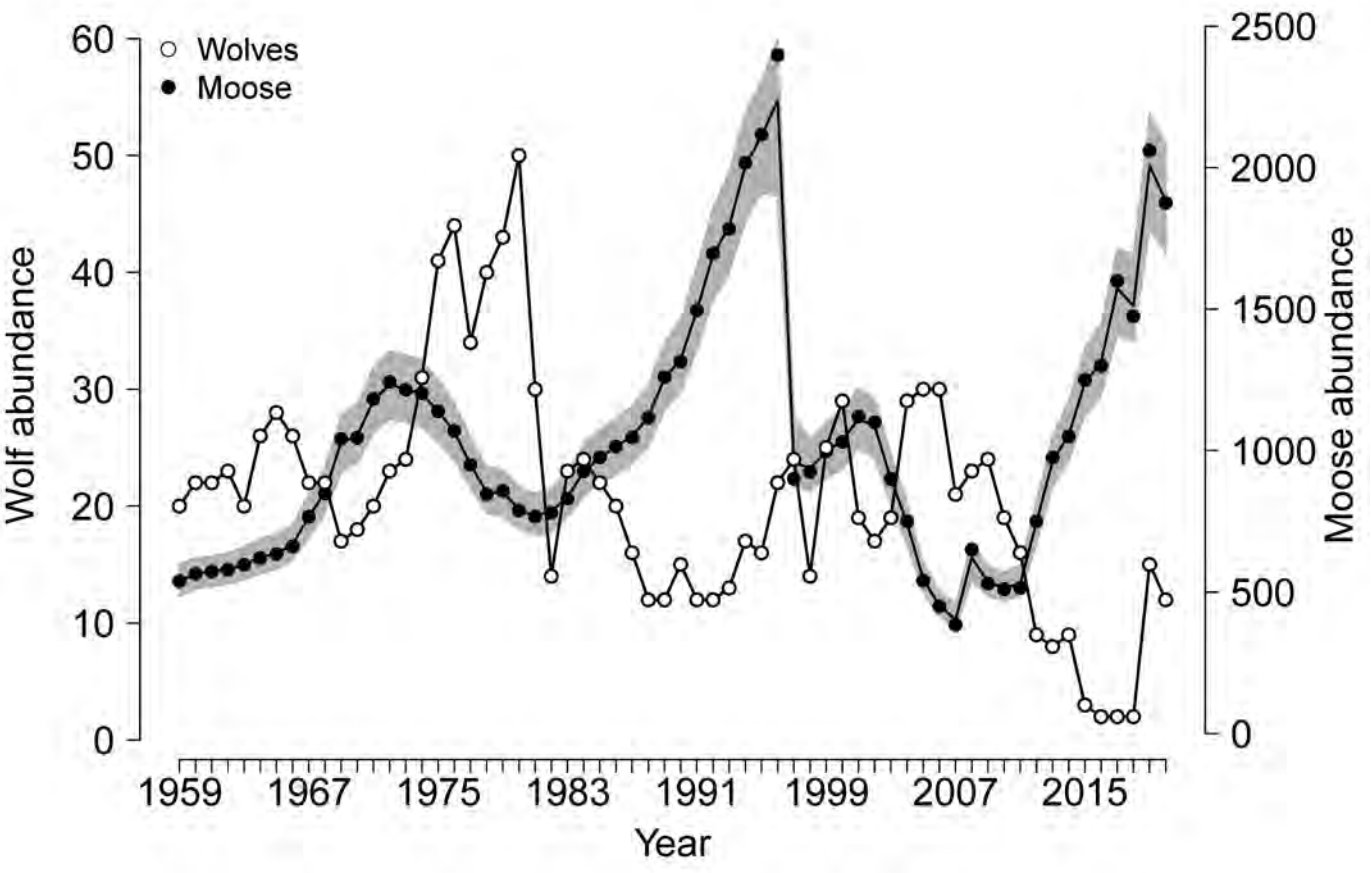


Figure 1. *Wolf and moose fluctuations in Isle Royale National Park, 1959–2020. Wolf abundances (open circles) were based on aerial surveys conducted from January to March. The sudden increase in wolf abundance in 2019 is the result of wolves being translocated by the National Park Service. Moose abundances (filled circles) during 1959–2001 are based on population reconstruction from the recoveries of dead moose, and estimates from 2002 to 2020 are based on aerial surveys. The second set of moose abundances (lines) and confidence intervals (shaded area) are results of a Bayesian state-space model that takes account of density dependence and age structure, as well as sampling error (Hoy et al. 2020,* Functional Ecology*). By contrast, confidence intervals reported in the main text emphasize sampling error associated with aerial surveys.*

31 March 2019: A male wolf, which had been translocated from Wawa, died after being on Isle Royale for approximately six weeks.

April 2019: A pup may have been born on Isle Royale (see details below).

July 2019: The GPS collar worn by 9M (from Michipicoten) was found and recovered by NPS, separated from 9M. Since that time there has been no definitive evidence on the status of this wolf (NPS 2020).

Sept 2019: Four wolves were translocated from Michigan to Isle Royale. One died within 48 hours of release. A Minnesota-born female wolf died after being on Isle Royale for approximately 12 months.

Oct 2019: M183 died after sustaining injuries from other wolves. He was the last male to live on Isle Royale prior to the reintroductions of 2018 and is believed to have been 11 years of age (he is shown on the front cover in a photo from 2019, following his daughter, F193).

Jan 2020: NPS data indicate that three wolves died: a Michigan-born female (18F), a Michipicoten-born male (10M), and a female from mainland Ontario (5F). At least two (18F and 10M) were killed by wolves (NPS 2020).

***ca.* 3 Feb 2020:** A male wolf from Michipicoten (13M) lost his GPS collar (when the collar's release mechanism was triggered), after which his movements could no longer be monitored.

Feb-March 2020: Two non-collared wolves were seen together on five different days. The identity of these two wolves is key to understanding how many wolves are in the population.

The two non-collared wolves differ significantly in size. Images of the wolves' behavior and documentation of other observed interactions between these wolves were shared with experts whose judgment is that the non-collared wolves in Figure 2 are likely a pup and adult (see Appendix for details).

It is also significant that neither wolf in Figure 2 has an ear-tag, because tags were affixed to each ear of every wolf translocated to Isle Royale as part of the NPS translocation program. Ear-tags are conspicuous and are nearly always visible in images of wolves that wear ear-tags. Furthermore, it is rare for an ear-tag to fall out, let alone for both ear-tags to fall out on a single wolf. All of the translocated wolves that were photographed at close range during the 2020 Winter Study had both ear-tags that were clearly visible. For those reasons, the larger (adult) wolf is unlikely to be 9M (more discussion below) or 13M, which were affixed with ear-tags when they were translocated from Michipicoten and had lost their GPS collars by the time the two non-collared wolves in Figure 2 were observed.

The only known wolf on Isle Royale that was never affixed with ear-tags is female F193 who was born on Isle Royale nine years ago. However, F193 is unlikely

Figure 2. *A surprise this winter is evidence that a pup may have been born on Isle Royale in spring 2019 and that pup associated with an adult wolf of unknown origin (see text). The putative pup and adult, both non-collared, were photographed at Houghton Ridge on 24 February 2020 (left panel, the putative pup is the upper wolf). These wolves are also shown with the radio-collared female, 14F, at Houghton Ridge on 6 March 2020 (right panel), where the putative pup is to the right of 14F.*

to be the adult wolf pictured in Figure 2, because her pelage (as documented in photos from previous years) is inconsistent with the pelage of the adult depicted in Figure 2. In particular, F193 lacks markings around the eyes and displays markings on her front legs that are inconsistent with the appearance of either of the wolves pictured in Figure 2. Furthermore, Figure 2 shows the non-collared adult beside 14F. Those two wolves are approximately the same size, which is significant because evidence indicates that F193 is a small wolf (Figure 3) and 14M is a large wolf (as documented in our field notes from Winter Study 2020).

The conclusion to draw from these observations is that the non-collared adult in Figure 2 is not easily accounted for among the wolves known to be on Isle Royale. One possibility is that a non-collared wolf arrived at Isle Royale by walking across an ice bridge in February 2019. This possibility is also supported by observations reported in the 2018–2019 annual report which describes extensive tracks from what appear to have been at least three wolves that did not belong to other wolves known to be in the population at that time. Alternatively, if loss of *both* ear-tags is assumed, then the wolf could be 9M, who shed his collar in July 2019. If the population is currently composed of one or more wolves that arrived to Isle Royale on their own last year, and if any of those wolves become reproducing members of the population, then their presence is likely to be detected through the analysis of DNA extracted from scats collected in 2020 and future years. These analyses will be a collaborative effort involving geneticist K. Brzeski (MTU), J. Belant and the NPS.

Figure 3. *The last two island-born wolves to survive on Isle Royale before other wolves were translocated to Isle Royale by the National Park Service (photograph taken winter 2019). The male, M183 (rear), died in October 2019 after sustaining injuries during a conflict with other wolves. The current status of the female, F193 (front) is unknown, and she has not been observed since February 2019.*

To summarize, 19 wolves were translocated to the population of two island-born wolves. Of these 21 individuals, the fate of 19 is known: one wolf left the island (3F), eight wolves died (4F, 5F, 18F, 20F, 8M, 6M, 10M, M183), one (13M) wore a collar until approximately 3 February, which indicates he was alive at least until then, and nine wolves wore functioning radio-collars, which confirmed that they were alive as of March 2020 (1F, 11F, 14F, 15F, 7M, 12M, 16M, 17M, 19M). Thus, of those 19 wolves, at least 10 were alive during the Winter Study.

The status of two wolves, F193 and 9M, is uncertain because neither wolf wears a radio-collar, nor was either observed during the winter field season. Nevertheless, several observations regarding F193 make her death plausible. First, she is nine years old, which is relatively old for a wild wolf. Second, since her long-time partner (M183) died in October 2019, she may have been socially disadvantaged in a way that made her vulnerable to being killed by other wolves, and such killings were common in late 2019 and early 2020. Lastly, if F193 were alive and had associated with one of the collared wolves there is a relatively high chance that we would have seen her. With respect to 9M, we found no evidence of his presence during the 2020 Winter Study (as documented in our field notes from Winter Study 2020). While these considerations about 9M and F193 are relevant, the status of both wolves during the 2020 Winter Study was unknown.

The preceding account indicates that the wolf population consists of 10 wolves whose identities are known, two non-collared wolves (i.e., the putative pup and adult in Figure 2), and possibly two other wolves (F193 and 9M, both non-collared) whose status is unknown. This means there are likely 12 wolves, though possibly 14. If the two wolves whose fate is unknown (9M and F193) are still alive, then we are likely to discover them in the future through the analysis of DNA from scats. In any case, the population consists of at least four females and six males (1F, 11F, 14F, 15F, 7M, 12M, 13M, 16M, 17M, 19M).

The difficulty in concluding the precise number of wolves with complete certainty is importantly attributable to the wolves' use of habitat. In most years, Isle Royale wolves spend significant time traveling and resting on shorelines and lakes where they are easily observed and counted. This year most wolves spent nearly all of their time in thick forest cover where they were difficult to observe. Furthermore, they usually rested some distance from sites where they'd killed moose, in contrast to the more common situation at Isle Royale, where wolves typically rest in the immediate vicinity of kill sites. Such furtive behavior is common in mainland populations, where secretiveness reduces the risk of being killed by humans. Some of the wolves had been captured using helicopters, so avoidance of aircraft may have been learned. The secretive behavior may also represent wolves' wariness for being detected by other hostile wolves. Hostility is evidenced by the high rate at which wolves killed other wolves (see below).

Social Organization

Prior to January 2020, and as reported in a 20 December 2019 NPS press release, GPS collars indicate that only a single group (of three wolves) had begun to coalesce. By March 2020, four social groups seemed to have formed. Two of these groups seem to have established territories (see upper map, inside-back cover, GPS data provided by NPS):

- A trio consisting of a Minnesota-born female (1F) and two males from Michipicoten (7M, 13M). This trio secured a territory on the western half of Isle Royale, where they killed 10 moose during the winter field season. The trio tracked other wolves in the western half of this island during the winter field season. In early February, 13M may have been the target of aggression from another wolf, as indicated by bloody tracks at a site near Long Point. GPS data indicates that the only other collared wolves in that area, at that time, were his packmates 7M and 1F (NPS 2020). From the time of that event onward, 13M was difficult to monitor. The conflict coincided with 13M losing his collar, when the collar's release mechanism was triggered. On three occasions after these events, we observed 1F and 7M, but not 13M. However, on 23 February we observed the tracks of three wolves suggesting 13M may have rejoined this group.
- A male-female pair (12M, 15F) that were both born on Michipicoten Island and are close relatives. Genetic analyses to be conducted later this year by K. Brezski (MTU) and collaborators will provide more insight. This pair secured a territory on the eastern half of Isle Royale (upper map, inside back cover), where they killed seven moose during the winter field season. On 22 February, we observed raised-leg urinations left by this pair on the south shore of Linklater Lake, confirming their territoriality.

Two other social groups were identified during the winter field season, but their territorial claims seemed less secure, based on winter observations and GPS data provided by NPS (see lower map, inside back cover):

- One of these groups formed in late January and consists of a female (11F) translocated from Michipicoten and a black male (16M) from near Wawa, mainland Ontario. The movements of this pair were largely concentrated along the north shore of Isle Royale at the west end of the island. On six occasions during the winter field season, this pair swam to smaller islands off Isle Royale's southwestern shore. These wolves killed at least two moose and fed from at least three kills made by other groups.
- The other group was identified in late February and included three wolves: a female from Michipicoten (14F) and two non-collared wolves, including the putative pup (Figure 2). Wolf 14F tended to be on one of two peninsulas not often frequented by territorial groups—either the small peninsula just south of Conglomerate Bay on the island's eastern end or on one formed by Houghton Ridge at the island's western end.

The remaining wolves in the population include two mainland Michigan males (17M and 19M) that appeared to live alone during the study, scavenging kills from other groups and generally staying clear of other wolves. Wolf 17M is likely to have been attacked by 12M and 15F on 20 February at the east end of Isle Royale. Evidence of the attack were marks in the snow indicative of a significant skirmish near Sargent Lake. Observations suggest that all three wolves were likely at the same time and place of the event. Afterward, GPS data suggests that 17M remained very near that location for several days, suggesting that he might have been injured, and then he moved abruptly to the other end of the island. On 6 March, we observed 17M and 19M at different locations in the western portion of Isle Royale, indicating that they were still living alone by the end of the winter field season.

Figure 4. *The social-bonded pair of wolves with a secure hold on a territory in the western portion of Isle Royale (see map inside back cover). The male (7M) is on the left, and the female (1F) is on the right, 4 March 2020.*

Courtship and Related Observations

We observed evidence consistent with potential mate formation in four social groups:

4 February: On the shore of Siskiwit Bay, 7M was observed sniffing the genital area of 1F while she stood in place with an erect tail.

4 March: Between Lake Desor and Washington Harbor, 7M and 1F were observed exhibiting friendly behavior between each other, as is typical of a bonded pair (Figure 4).

24 February: On Houghton Ridge, 14F and the non-collared wolves were observed near a wolf bed with estrous blood.

29 February: Near Hay Bay, 11F was observed play-soliciting from 16M in a manner indicative of courtship (Figure 5).

29 February: Near Sargent Lake, 15F (bonded with 12M) left estrous blood in her bed.

These early developments in social organization and territoriality have compelling implications for the future genetics of this population. One significant circumstance is that one of the bonded male-female pairs (12F, 15M) with an established territory are closely related wolves from Michipicoten. Furthermore, of the two groups that have less secure territorial claims (lower map on inside back cover), one or possibly both consist of genetically unrelated individuals. More generally, the males in the population represent three lineages (Michipicoten, mainland Ontario, Michigan) and the females represent two (Minnesota, Michipicoten). If the population includes wolves that arrived on their own (see above), then those wolves may represent an additional lineage. If female F193 is alive, then an Isle Royale lineage is present. In any case, any pups born in 2020 will have at least one parent originating from Michipicoten Island. Analyses to be conducted later this year by geneticists will provide more insight.

Population Losses

Over the last 12 months (March 2019–February 2020) there was significant mortality. In particular, the annual mortality rate was approximately 40 percent. If the two wolves whose fate are unknown (9M, F193) are also dead, then the mortality rate would be 46 percent. By comparison, the long-term, mean annual mortality rate (excluding the period before pups are nine months old) for Isle Royale wolves is 26 percent (±3 percent SE). During the past 12 months,

Figure 5. *The social-bonded pair of wolves with a tenuous hold on a territory in the western portion of Isle Royale (see map inside back cover). The gray female (11F) displays play-bow behavior toward the black male (16M) near Hay Bay, 29 February 2020.*

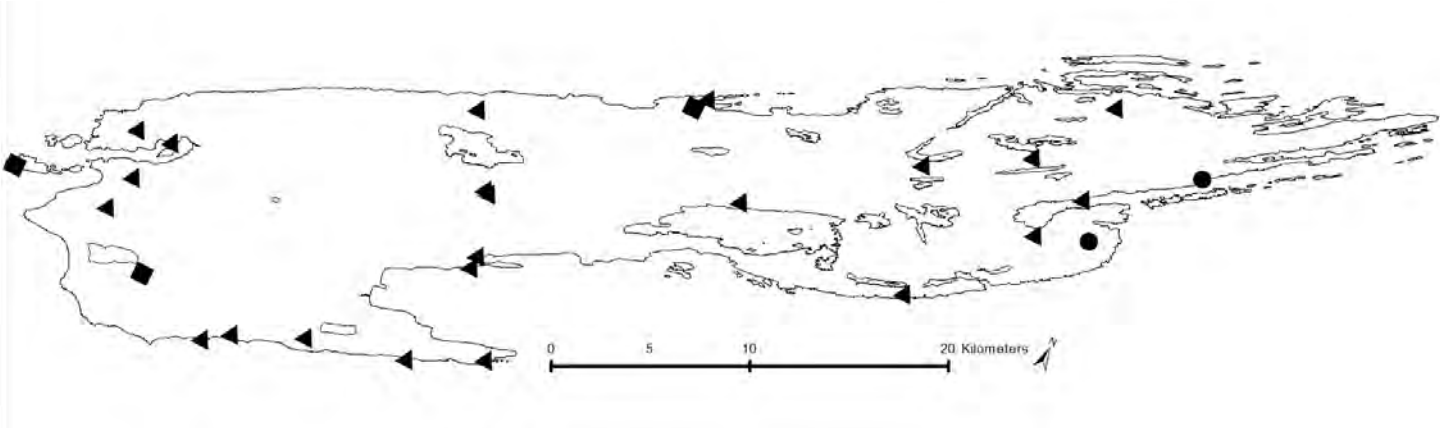


Figure 6. *Sites where wolves fed on moose carcasses during the 2020 winter field season. Triangles are moose killed by wolves during Winter Study, squares are moose probably killed by wolves before Winter Study, and circles are carcasses of moose where wolves fed, but were unlikely to have been killed by wolves.*

wolves killing other wolves (also known as intraspecific killing) was the most common cause of mortality, accounted for four (M183, 4F, 18F, 10M) and possibly five (5F) deaths (NPS 2020).

Since the NPS translocation efforts began in September 2018, 20 wolves were captured and deemed fit for release on Isle Royale. Of those 20 wolves, eight died and one (3F) left by crossing an ice bridge. Of the eight wolves that died, two females (2F, 20F) perished during or immediately after being captured or translocated. Two males (8M, 6M) died within six weeks of being translocated, and the cause of death is not known. However, both wolves appeared healthy when released and there was no evidence that either was killed by other wolves.

Only one of the eight wolves translocated from Michipicoten has died. By contrast, seven of the 11 wolves which arrived from other mainland sites have died (NPS 2020). That outcome is noteworthy for two reasons. First, some of the Michipicoten wolves were in poor condition when they were translocated. Second, the eight wolves translocated from Michipicoten in March 2019 were all closely related, whereas wolves from other mainland sites were translocated with fewer packmates or no packmates at all.

Carcass Utilization Rates

The per-capita rate of prey acquisition (sometimes equated with the per-capita kill rate) is a statistic that describes the rate at which a predator acquires food. That statistic is calculated as the number of carcasses from which the wolves fed, divided by the number of wolves, divided by the number of days over which the carcasses were acquired. This winter we observed 12 wolves feeding on 24 moose carcasses during 48 days from 18 January–5 March (Figure 6). Of those 24 moose, 22 were killed by wolves and two likely did not die of predation, but were scavenged. One of the scavenged moose died during winter study as indicated by our having discovered it atop the snow before any wolf had begun feeding from it. The other scavenged moose died in early winter, as indicated by 14F having dug it out from beneath the snow and by the carcass being partially decomposed. We also found the remains of four moose that were probably killed by wolves before the start of winter study. Kill sites will be examined during summer fieldwork.

Those observations indicate that this year's rate of prey acquisition is 1.27 moose per wolf per month. That rate is 1.8 times greater than the long-term average rate of 0.7 (±0.04 SE) observed between 1971 and 2011 (the period prior to the wolf population's recent collapse). As such, it is reasonable to conclude that the wolves are well fed.

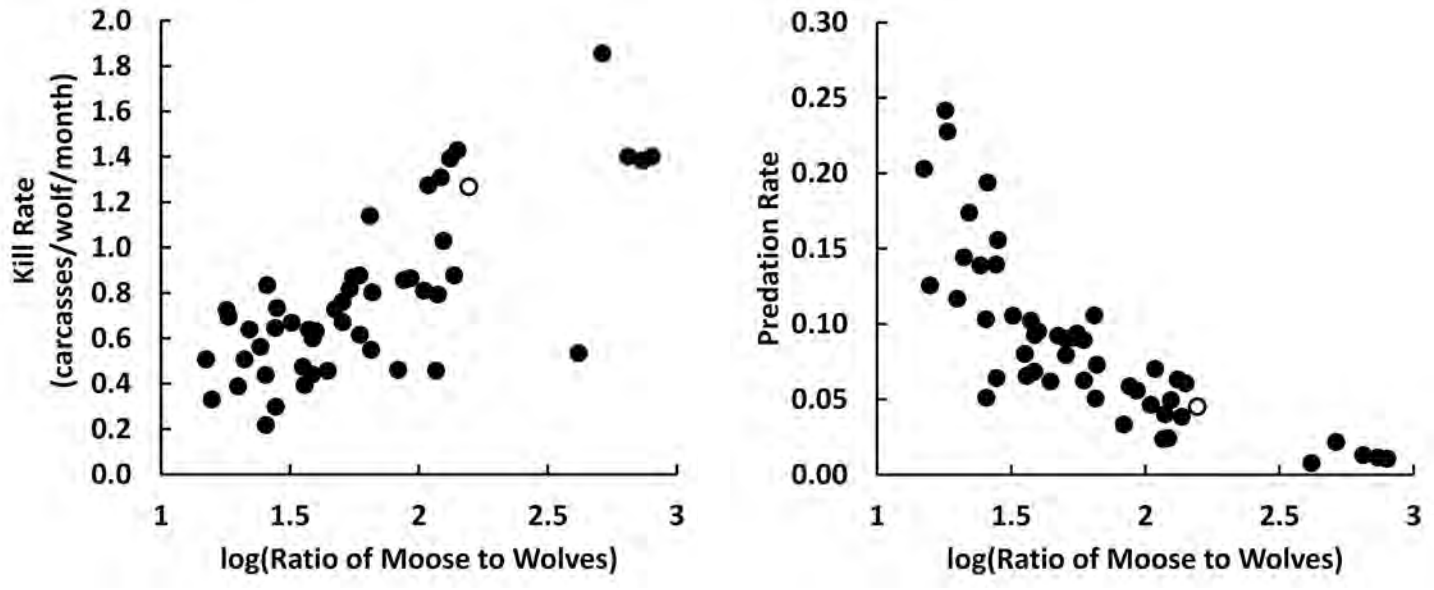


Figure 7. *The ratio of wolves to moose in relationship to the rate at which wolves acquired prey on a per-capita basis (i.e., kill rate, left panel) and the proportion of the moose population killed by wolves (i.e., predation rate, right panel) for the period,1971–2020. Open circles indicate the observation for 2020. The rate of prey acquisition includes the number of moose killed by wolves, plus those scavenged.*

While this rate is higher than the long-term average, it is within the range of rates that one would expect, given the ratio of moose to wolves on Isle Royale (Figure 7, left panel). A higher than average rate is also expected because most wolves presently live in small groups, which tend to lose a larger portion of their kills to scavengers and kill at higher per-capita rates than wolves in larger groups (Vucetich et al. 2004; Animal Behaviour, 67:1117).

Last year's annual report included a typo. Specifically, it stated that 4F is the identity of a wolf that left Isle Royale by crossing an ice bridge. The correct identity for that wolf is 3F.

MOOSE POPULATION

The 2020 moose census (conducted during 26–30 January) resulted in an estimated abundance of 1,876 moose (Figure 1). The 80 percent confidence intervals on this estimate are [1,578, 2,185], and the 90 percent confidence intervals are [1,438, 2,368]. Moose density was lowest in central Isle Royale (1.8 moose/km^2) and greater at the two ends of the island (5.2 moose/km^2, Figure 8).

The estimate is based on a sightability correction factor of 58 percent, which is based on tests performed with collared moose. On 19 occasions we searched

Figure 8. *The density of moose on Isle Royale during winter 2020 was lower in the central portion of Isle Royale and higher in the eastern and western portions of Isle Royale (shaded). Estimates are based on aerial surveys of 91 plots that comprised 17 percent of the main island area.*

for collared moose using the same flight plan used for estimating moose abundance, i.e., flying circles and covering a square kilometer in a 10–15-minute period. Of those 19 tests, we observed the collared moose on 11 occasions (11/19 = 0.58). In four instances (i.e., in half of the "misses") we were unable to observe the collared moose even when guided by a telemetry signal. For context, sightability was assumed to be 0.49 in 2019.

The sightability of moose was influenced by snow conditions. In February snow was somewhat deeper than average and snow density was much greater than typical. Those conditions are associated with moose spending more time in habitats where snow cover is less. Those habitats include coniferous forests with thick canopies where moose are difficult to detect.

This winter's estimated abundance (1,876 moose) is 9 percent lower than last winter's estimate (2,060 moose). However, a Bayesian model that estimates moose abundance by taking account of density dependence, age structure and sampling error, suggests that 2,060 is a slight overestimate of last year's abundance (Figure 1) and that the decline in moose population is less than 9 percent. Nevertheless, moose abundance is still estimated to have increased by 19 percent each year, on average, during the previous eight years (2011–2019). Taking account of statistical uncertainties, it is reasonable to infer that the population grew rapidly for a number of years and has now leveled off or declined slightly.

In 2020, 11.2 percent of the 250 moose counted on the 91 survey plots were calves. Using general methods for calculating confidence intervals for proportions, the 90 percent confidence intervals for that observation are 7.9 percent and 14.5 percent. This is the second consecutive year of below-average recruitment, which is consistent with the moose population having stopped increasing or having started to decrease over the past year (Figure 9).

The impact of predators on a prey population is indicated by predation rate, which is the proportion of the moose population 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).

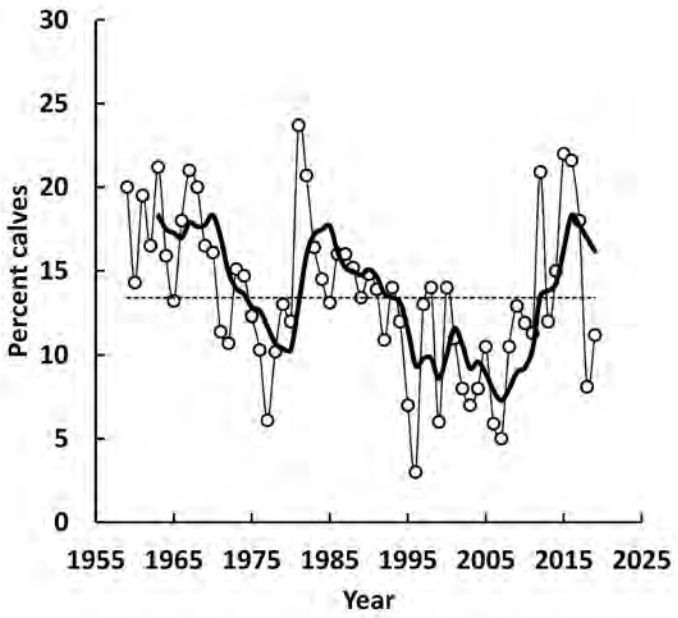


Figure 9. *Long-term trends (1959–2020) in the percentage of the total moose population that are eight-month-old calves. The 50-year average (13.4 percent) is marked by the dashed line, and the thicker line represents the five-year moving average.*

This year, calculations indicate a predation rate of 4.5 percent (Figure 7, right panel). For context, this is the highest predation rate observed since 2011. However, this year's predation rate of 4.5 percent is still well below the long-term average predation rate of 9.9 percent (±0.8 SE) observed between 1971 and 2011 (the period prior to the wolf population's recent collapse). When the ratio of wolves to moose is very low, as it was this winter (i.e., 12:1876), then predation rate is determined largely by the ratio, rather than the kill rate. Thus, even with a relatively high estimate of kill rate, predation rate is still very low. We expect the predation rate to remain relatively low until there is a considerable increase in the ratio of wolves to moose.

Each spring and summer many moose feed on aquatic plants in Lake Ojibway. The lake had been held by a beaver dam first built in the 1950s. In November 2017, the beaver dam blew out and Lake Ojibway has been draining ever since, exposing an increasingly large area of deep mud (Figure 17 in 2018–2019 Annual Report). Moose accustomed to feeding there have continued to do so. During summer 2019, we

Figure 10. *A bull moose mired in mud at Lake Ojibway, on 29 May 2019. He was unable to free himself and died soon after being found. A necropsy revealed that the bull was approximately 10–12 years old and in poor condition. The bull had previously broken both mandibles (most likely from a fall some weeks before) and had not recovered from the injury. That injury would have severely impacted his capacity to forage.*

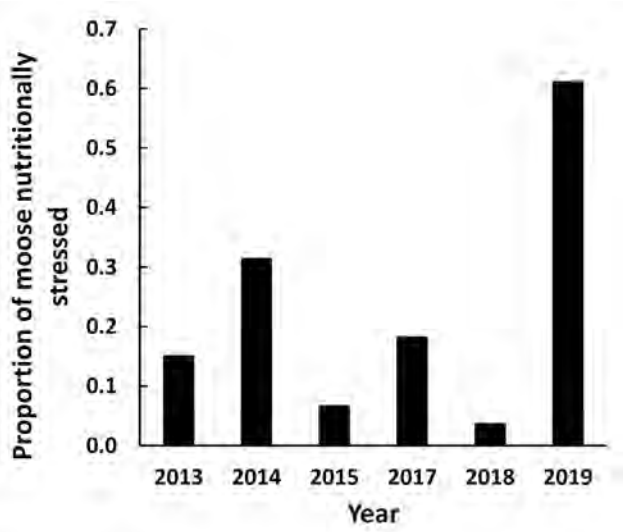


Figure 11. *The proportion of nutritionally stressed moose as indicated by the chemistry of urine collected from yellow snow. Specifically, the graph shows the proportion of moose whose ratio of urinary nitrogen to creatinine (UN:C) exceeded 3.5, which indicates starvation in ungulates. For details, see Parikh et al. 2017* (Oikos).

discovered that four moose had died after becoming stuck in the mud at Lake Ojibway (Figure 10), including one from summer 2018.

Each year, we gain important insights about the health of the moose population by collecting urine and fecal samples deposited by moose in the snow and analyzing those samples for a range of different biomarkers. For example, we analyze snow urine samples for the ratio of urinary nitrogen to creatinine. That ratio is an indicator of the extent to which moose are metabolizing their muscles tissue, which is an indication of being nutritionally stressed. Most of the samples collected last winter (February 2019) had very high ratios (Figure 11), suggesting higher-than-average nutritional stress. That result is consistent with several other observations. First, moose abundance has been higher than average for about seven years, indicating higher competition for food. Second, balsam fir (a primary source of winter forage for moose) has been exhibiting signs of extreme browsing pressure, which is a consequence of several consecutive years of high moose abundance. Third, last winter (2018–2019) snow was unusually deep and uncompacted, which increases the energetic cost of movement. Those conditions all tend to have an adverse effect on the nutritional condition of moose.

We have monitored the severity of winter tick infestation for moose since 2001 by photographing moose in spring, digitizing each side profile and calculating the proportion of hair loss. There is considerable variation in the extent of hair loss observed between individuals within a given year, and also among years (Figure 12).

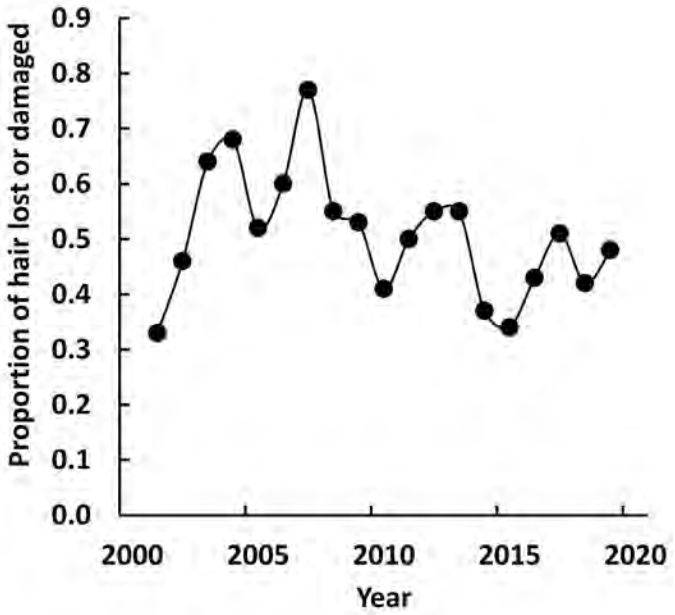


Figure 12. *Photographs of moose in spring provide annual information on the extent of hair loss caused by winter ticks. Graph shows the average extent of hair loss for moose in the Isle Royale population each year, over the last 19 years (2001–2019).*

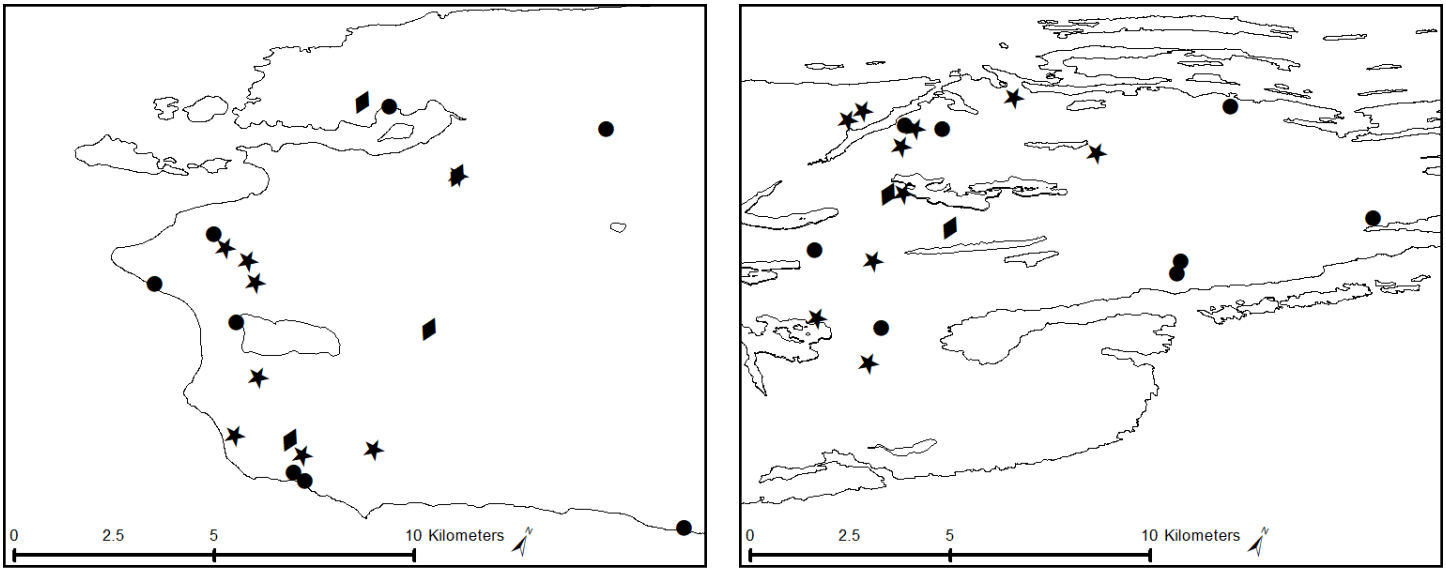


Figure 13. *The locations of GPS-collared moose on 13 March 2020 at the east end (right panel) and west end (left panel) of Isle Royale. Moose collared in March 2020 are represented by stars (cows) and diamonds (bulls). Cows collared in 2019 are circles. (No bulls were collared in 2019.)*

In sum, it seems that moose demography is largely driven by depleted forage and a more severe winter than average in 2018–2019. Wolf predation is beginning to have a minor influence on moose demography, primarily on moose recruitment rates given the strong tendency for wolves to prey on calves rather than adults.

Collared moose

In February 2019 a new collaboration began that involved outfitting 20 cow moose with GPS-enabled radio-collars. We advanced that project by collaring another 25 moose (19 cows and six bulls) during 10–12 March 2020, with funding for the collars this year provided by the National Parks of Lake Superior Foundation, the National Park Service, and the Grand Portage Band of Lake Superior Chippewa (Figure 13). The collaring efforts were led by Sarah Hoy, Rolf Peterson, and John Vucetich from MTU, in partnership with Mark Romanski and Lynette Potvin from NPS, Seth Moore, director of biology and environment for Grand Portage Band of Lake Superior Chippewa, and Tiffany Wolf from University of Minnesota.

The collars record each moose's location every 30 minutes, and those data are periodically uploaded via satellite to an online database, allowing us to track each animal's movements remotely. Each collar is also equipped with sensors that record intensity of movement and ambient temperature every five minutes (Figure 14).

Figure 14. *A bull on Beaver Island (left) and a cow near Rainbow Point (right), each recently fitted with a GPS enabled radio-collar.*

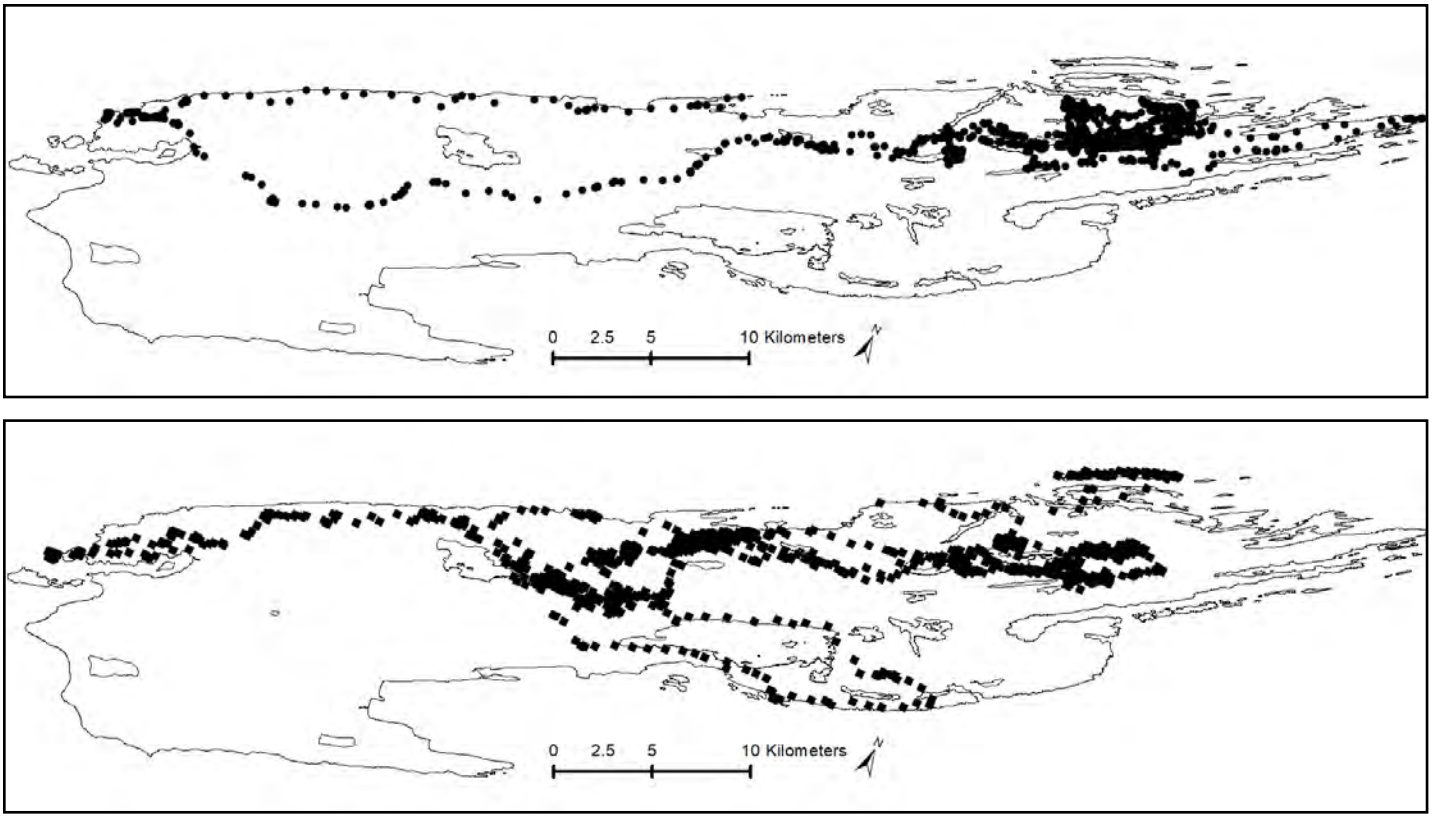


Figure 15. *The extensive movements of two collared moose in June and July 2019. See* ***Collared Moose*** *for details.*

An important aim of this project is to help the NPS assess the influence of predation as it is restored. Other aims include advancing our understanding of how activity levels and habitat selection are related to a moose's nutritional condition, various aspects of their diet, and temperature. The data collected through this project will also be valuable for comparing the moose of Isle Royale National Park with mainland moose on the reservation lands of the Grand Portage Band of Lake Superior Chippewa, which sits on the northwest shore of Lake Superior.

During the past year, we collected movement and activity data from most of the moose collared in winter 2019. However, one collar failed in May 2019, three failed in February 2020, and two more failed in April–May 2020. All of the moose wearing failed collars were known to be alive during January–March 2020.

Over the last year, several collared moose made significant movements. For example, in July 2019, one moose (ISRO-2019-18) traveled from just west of Lane Cove (east end) to the North Gap (west end) and then returned (Figure 15, upper panel). During June and July 2019, another moose (ISRO-2019-19) traveled between Amygdaloid Island, at the east end of Isle Royale, and John's Island at the far west end. (Figure 15, lower panel). Three other individuals made similarly large movements across the island over the past year. In December 2019 and January 2020, four moose abruptly departed from their usual locales after the pack of three wolves at the west end of the island moved through the area (NPS 2020). After traveling 10–20 km to the east, the four moose returned to their formerly used areas over a period of two weeks to two months.

Of the 16 moose collared in 2019 that were still transmitting in January and February 2020, 15 of them were tracked by winter study's ground crew, Ky and Lisa Koitzsch. They were tracked to determine which moose were raising calves and to collect urine (yellow snow), fecal pellets samples. We also collect samples of balsam fir from saplings that the collared moose had fed on. The fir samples will provide insights about forage quality. The pellet and urine samples will be analyzed to determine each individuals' diet and to assess biomarkers of the individuals' condition. Ultimately, these data will answer questions about relationships amongst habitat selection, foraging

behavior, and individuals' body condition, as well as how those relationships affect survival and reproductive success. Interestingly, of the 15 collared moose tracked this winter, four were raising a single calf and another cow had twins.

Of the 25 moose collared in early March 2020, 24 were still alive by late April and one individual's status is unknown due to collar failure shortly after deployment. Importantly, none of the collared moose died during the first year of monitoring.

VEGETATION

Balsam fir is the primary forage for moose during winter. Fir typically comprises about 50 percent of a moose's winter diet, but can comprise as much as 80 percent, or as little as 20 percent. Over the last century there has been a dramatic decline in the number of mature fir trees across Isle Royale. Consequently, 479 mature balsam fir trees were tagged along a 10-mile transect (representing a 10-ha area) at the west end of the island in 1988. By spring 2019, only 21 (4 percent) of these tagged trees remained. This decline in mature trees is significant because canopy trees are needed to produce seeds for the next generation of fir trees.

Moose browsing is one factor contributing to this dramatic decline in mature fir because browsing had largely eliminated the regeneration of fir trees over the past 100 years at the west end of Isle Royale. However, between 2000 and 2010, heavily browsed and stunted balsam fir on the island's west end started to grow unimpeded by moose browsing. This corresponds to the period of lowest moose density in the past half-century. By 2017 there were more than 500 newly emerging fir trees (>175cm in height) along the same 10-mile transect where mature fir trees are monitored. Those emerging fir trees have been tagged and their growth is monitored each spring.

Over the last three winters, intense moose browsing is now beginning to reverse the fir dynamics observed prior to 2017. The impact of moose browsing on the island's vegetation was extremely high this past year (Figure 16). Data collected this winter by Ky and Lisa Koitzsch indicates that moose had eaten virtually 100 percent of the new growth from 2019 that was

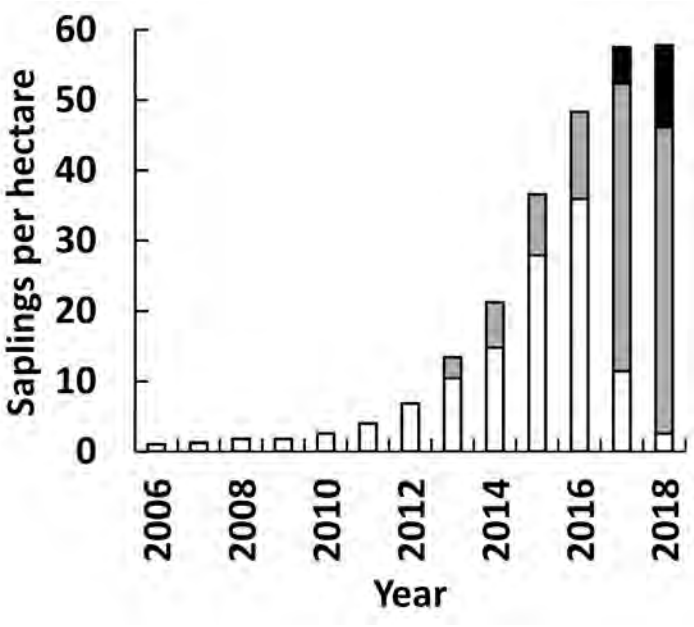


Figure 16. *When balsam fir saplings grow to a height of 175cm, their main growing stem (terminal leader) is on the cusp of being out of reach for a moose and that tree may escape and grow into the canopy. The number of fir saplings >175cm on the western portion of Isle Royale increased dramatically up to 2016 (white bars). However, from 2013 to 2018 there was a dramatic increase in the number of these saplings whose terminal leader had been browsed by moose in a manner that would have arrested their height growth (gray bars). The proportion of those saplings whose stems had been broken by moose, which is a severe setback to height growth, is shown by the black bars. These saplings were sampled along a transect that coincides with the Huginnin Trail.*

Figure 17. *The impact of moose browsing on balsam fir has been severe in recent years. The lower panel shows a small stand of fir saplings on Beaver Island in 2020. The upper panel shows the same stand from the same approximate perspective, one year earlier in 2019. For context, arrows point to the same tree. Credit: Ky Koitzsch.*

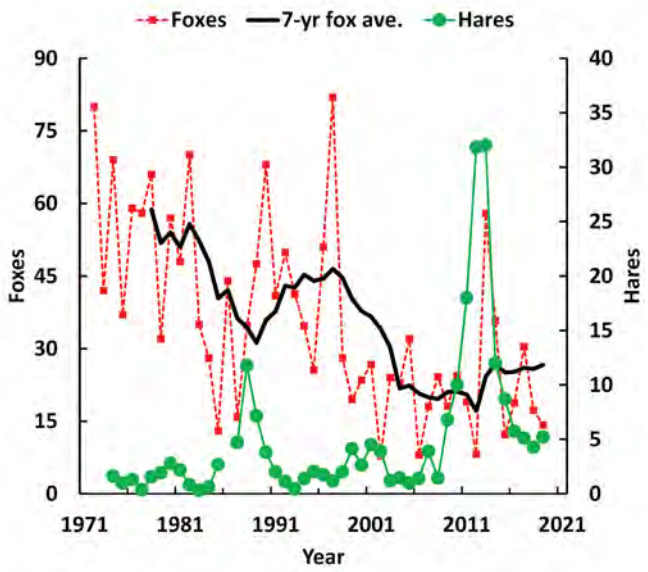


Figure 18. *Indices of abundance for red foxes and snowshoe hares on Isle Royale, 1974–present. The hare index is the number of hares seen per 100 km of summer hiking. The fox index is the number of foxes seen from the plane during Winter Study, the sum of the maximum number seen at kills and the number seen otherwise per 100 hours of flight time.*

detectable above the snow surface (Figure 17). The future status of balsam fir on the west end of Isle Royale is critically dependent on the growth and survival of new regenerating trees as 96 percent of the mature canopy trees on the west end have died in the past 30 years, based on mature trees tagged in 1988. The fate of regenerating fir saplings will depend on how quickly moose abundance declines in upcoming years.

OTHER WILDLIFE

During winter 2020, the tracks of marten were observed in the Huginnin Cove area, Windigo, and Feldtmann Ridge. Marten sign was not observed between 1959 and 1990; however, since 1991, marten sign has been observed every year but three.

Winter observations of red foxes were similar to last year (Figure 18). Their primary prey, snowshoe hares, have remained at a similar level of abundance over the last three years (Figure 18). In the near-term future, foxes are expected to fare slightly better than in previous years, due to the recovering wolf population providing moose carcasses that foxes can scavenge.

The beaver population has increased dramatically since 2012 (the period after the wolf population had collapsed, but before wolves were relocated). An

aerial count of active beaver colonies could not be completed in October 2019 because of bad weather and will be scheduled as soon as feasible. As predation rates on beaver increase, one of the likely effects is a reduction in the number of active colonies or a reduction in the number of beavers living in each beaver colony.

WEATHER AND ICE

The winter of 2020 was noteworthy for particularly low levels of ice cover (<20 percent) on Lake Superior. Most of Lake Superior's ice at Isle Royale was confined to bay areas and there was no formation of an ice bridge connecting Isle Royale to the mainland. High winds during January and February limited the number of days that aerial surveys could be conducted. Temperatures remained below freezing for the majority of days during winter study (Figure 19). Snow was somewhat deeper (average 26 inches) and snow density was much greater than typical during winter study (Figure 19). Throughout winter study, deep and dense snow tended to restrict moose to areas with thick conifer canopy where the snow was less deep. Despite the lack of ice cover and cold temperatures, two wolves (11F and 16M) made several trips to small islands off the southwestern end of Isle Royale during the winter study.

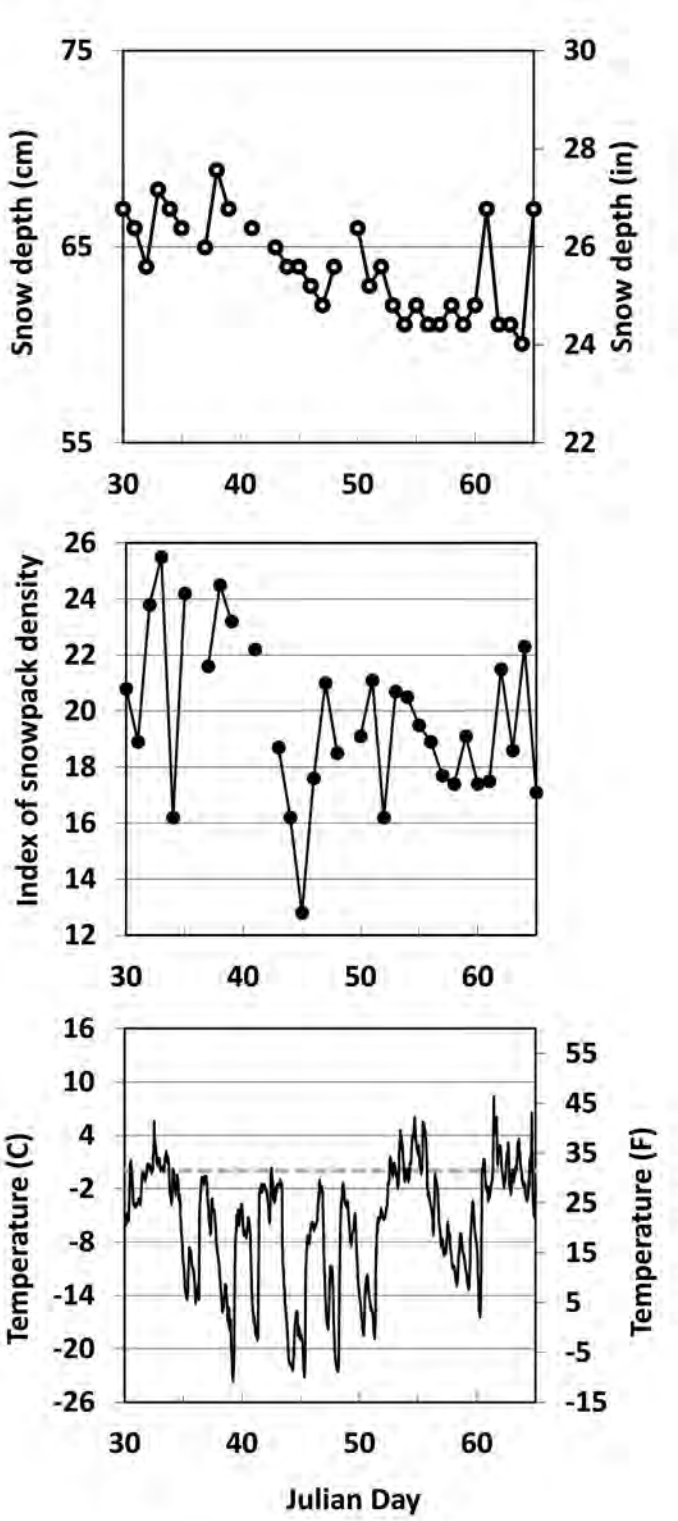


Figure 19. *Daily snow depth (top), daily snowpack density (middle), and temperature (30-minute intervals, bottom) during the 2020 Winter Study on Isle Royale. Density was estimated as the "Rammsonde hardness" value calculated using a penetrometer. Dashed line in the lower panel indicates freezing point (0°C).*

APPENDIX.

More on the identity of the non-collared wolves.

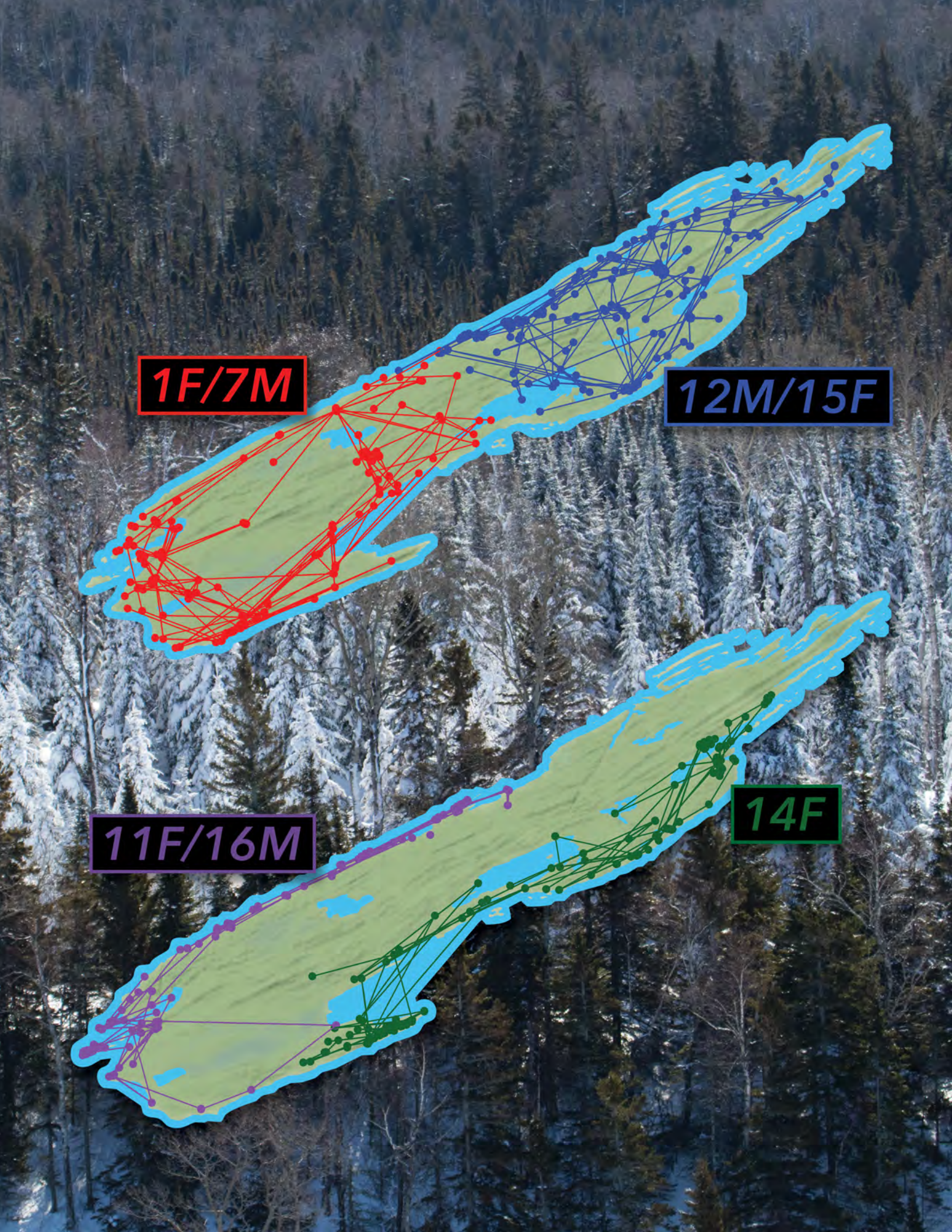
Evidence that the small wolf in Figure 2 is likely a pup includes:

a. The following written account of behavioral interactions including the non-collared wolves in Figure 2:

> *At 14.19 on 4 March 2020, we located collared female W14F using VHF* [radio-tracking] *to a fairly open area of cedar swamp to the east of lake Halloran. At first, we just saw one wolf bedded (call it A) and then we noticed another wolf standing nearby, which then walked up to a third wolf (call it B) that was also bedded about 10 m away from wolf A. The wolf that was walking was noticeably smaller than the other two wolves (wolves A and B). This "smaller wolf", wagging its tail, jumped on the bedded wolf (B). The bedded wolf (B) spun around and pawed at the smaller wolf—it all looked playful and not aggressive. Then the bigger wolf (B) stood up, and the smaller wolf lay down in front of it—still wagging its tail. Then the two wolves (B and the smaller wolf) seemed to go back and forth sparring with each other, but again in a playful manner. After playing for a minute or so, the bigger wolf (B) walked over to the wolf that was still bedded (wolf A). The smaller wolf followed at the back end of wolf B and pulled on its tail. This prompted the first wolf (A) to get up and start slowly walking towards the east. The other two wolves (B and the smaller wolf) started to follow the first wolf (A) still headed in an easterly direction. The wolves were walking at a very leisurely pace through the semi open cedar swamp. The smaller wolf still appeared to be in a playful mood, it kept going up to one of the larger wolves, either getting close up in its face or nipping at its back legs and tail—but all the while the smaller wolf was wagging its tail. The larger wolf seemed tolerant of this behavior. As they were walking (still at a relaxed pace), all in a line, it was very clear that one of the wolves was smaller than the other two. One of the larger wolves bedded down for a minute or so but then they all resumed walking in an easterly direction. We lost sight of those wolves as they headed into thicker vegetation around 14.45.*

b. The above narrative and several images of the non-collared wolves were shared with experts Kira Cassidy and Rick McIntyre (both from the Wolf Project, Yellowstone National Park) and Lori Schmidt (International Wolf Center). Their collective view is that one of the wolves in the images is likely a pup, based on appearance and behavior.

Inside back cover image: GPS locations of wolves defined spatial relationships among wolf groups during midwinter in 2020 (NPS 2020).


1F/7M
12M/15F
11F/16M
14F

Michigan Technological University

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