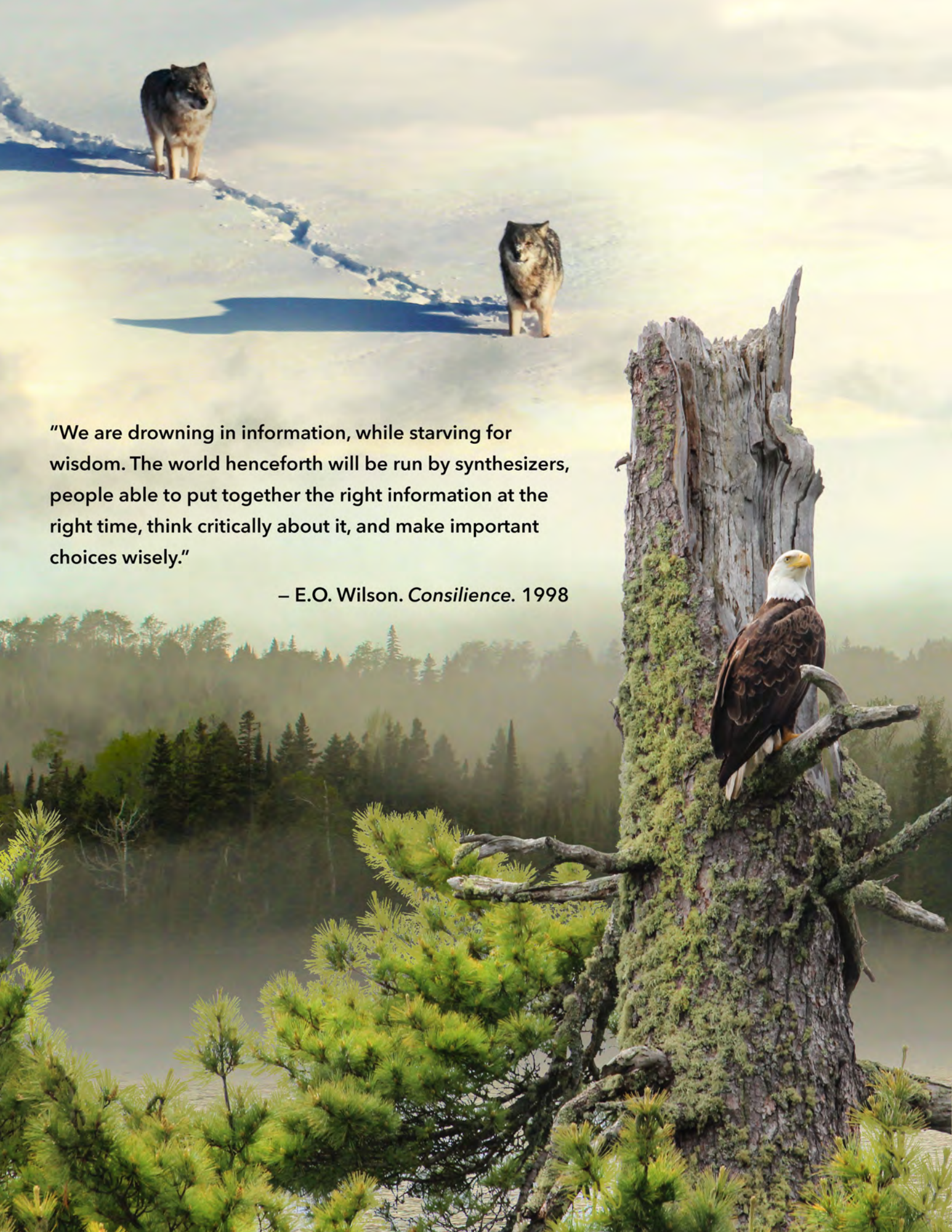Ecological Studies of Wolves on Isle Royale

Wolves

2016-2017

"We are drowning in information, while starving for wisdom. The world henceforth will be run by synthesizers, people able to put together the right information at the right time, think critically about it, and make important choices wisely."

– E.O. Wilson. *Consilience.* 1998

Ecological Studies of Wolves on Isle Royale

Annual Report 2016–17
by
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31 March 2017

www.isleroyalewolf.org and Wolves and Moose of Isle Royale (Facebook)

Ecological Studies of Wolves on Isle Royale

Summary

Between January 2016 and January 2017, the wolf population continued to be comprised of just two wolves (Fig. 1). The wolves are very likely a single male-female pair and closely related to one another. The wolf population is also almost certainly headed for extinction and wolf predation has been effectively absent as an ecological process for the past six years. Moose abundance increased over the past year and is estimated to be 1600 moose. In the absence of predation, moose abundance may double over the next 3-4 years. If that happens, it will be the largest number of moose ever observed during the six decade history of the wolf-moose project. The number of beaver colonies on Isle Royale has also increased dramatically over the past six years, from approximately 100 to almost 300. That increase is also very likely attributable, in large part, to the lack of wolf predation.

Background

Isle Royale National Park is a remote island located about fifteen miles from Lake Superior's northwest shoreline. The Isle Royale wolf population typically varies from 18 to 27 animals, organized into three packs. The moose population usually numbers between 700 and 1,200 moose. The wolf-moose project of Isle Royale, now in its 59th 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
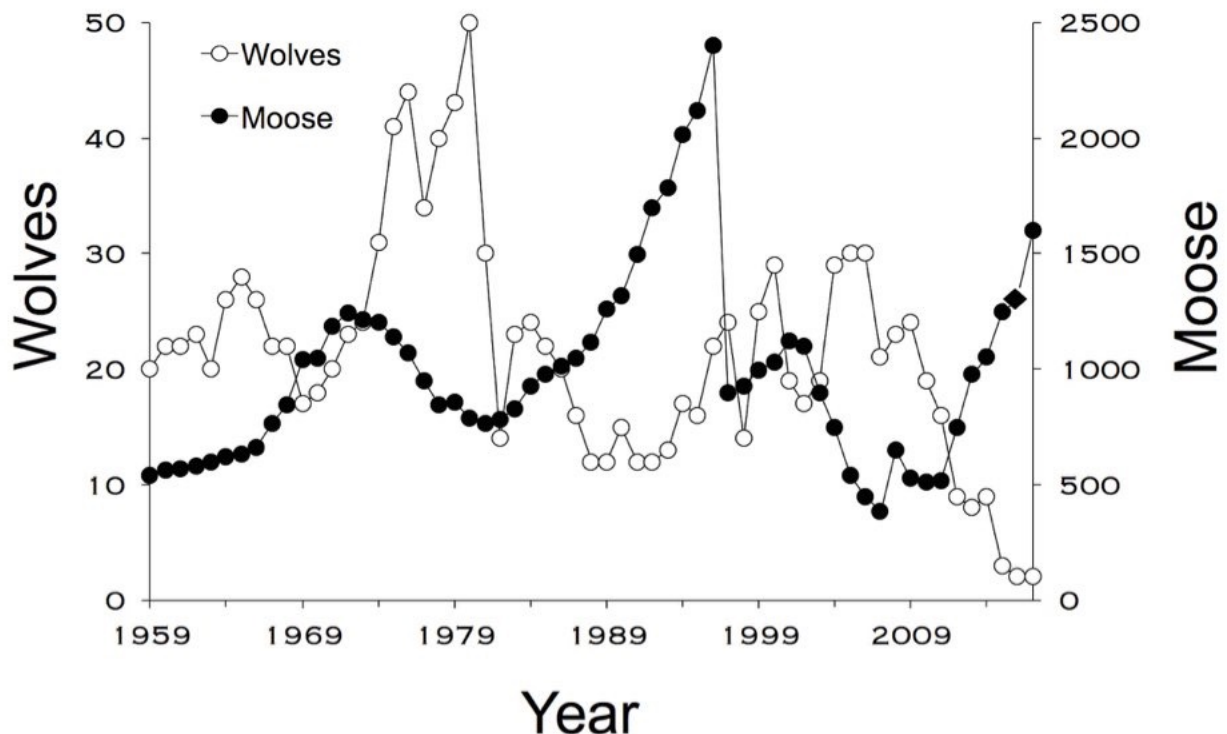

Figure 1. Wolf and moose fluctuations, Isle Royale National Park, 1959-2017. Moose population estimates during 1959–2001 were based on population reconstruction from recoveries of dead moose, whereas estimates from 2002–2017 were based on aerial surveys.

environment. For fifty years, moose abundance fluctuated dramatically, limited only by starvation. Wolves established themselves on Isle Royale in the late 1940s by crossing an ice bridge that connected the island to mainland Ontario. Researchers began annual observations of wolves and moose on Isle Royale in 1958-59.

Isle Royale's biogeography is well-suited for the project's goals. That is, Isle Royale's wolves and moose are isolated, 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 rather simple 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 significant at times. Finally and importantly, human impact is limited in the sense that people do not hunt wolves or moose or manage the forest, the island provides an outstanding venue for ecosystem science.

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 nearly 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 with nature.

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

Personnel and Logistics

In summer 2016, we conducted ground-based fieldwork from early May through mid-October. Rolf Peterson and John Vucetich directed that fieldwork with assistance from Carolyn Peterson and Leah Vucetich. Summer interns Joe Lazzari and Andrew Kalembar ranged widely across the island in May-June, gathering data on moose-balsam fir interactions. Leah Vucetich also led a number of people working in our lab, especially John Henderson, Grace Parikh, Joe Lazzari, and Andrew Kalembar. Post-doctoral researcher Dr. Sarah Hoy has recently joined our efforts to transform field insights from Yellowstone and Isle Royale into scientific publications.

During the course of the year, many park staff and visitors contributed key observations and reports of wolf sightings and moose bones.

In 2017, the annual Winter Study was conducted from January 18 to March 4, led by John Vucetich and Rolf Peterson. Ky and Lisa Koitzsch provided a solid month of daily field work on skis to collect data on moose and fir condition. Pilot Don L. Murray (UpNorth Aerials, Two Harbors, MN) piloted the primary research aircraft for the entire winter study. Pilot Don E. Glaser provided a second aircraft and piloted during 1-11 February. National Park Service staff from Isle Royale National Park, Nathan Hanks and Lynette Potvin, contributed directly to the winter study effort. Bob Glaser, Lynette Potvin (NPS) and Mark Romanski (NPS) provided ground transportation on the mainland.

The Wolf Population

On January 17th 2017, we observed two wolves at the site of a moose carcass on the ice at McCargo Cove. The carcass was that of a moose calf which had been killed, probably one or two weeks earlier. Two weeks later, on February 8th we observed two wolves traveling from Moskey Basin to McCargo Cove (Fig. 2).

A week after that observation, on February 15th, we observed two wolves and their tracks. That day the wolves traveled from Lake LeSage to Horner Island (near Belle Isle campground). Those tracks also led us to discover a site where the wolves had been

Figure 2. In 2017 the two wolves remaining on Isle Royale were this father-daughter pair (who also shared the same mother, so they are half-siblings). The male (front) is eight years old and the female (rear) is six years old. Here they are shown crossing Lake LeSage on February 8, 2017.

Ridge and into Tobin Creek where they killed a moose.

Finally, on February 27th, the two wolves were observed again near their kill on Tobin Creek. This time the female was obviously in estrus and the male courted her incessantly, but to no avail. The female responded to the courtship advances of her father with intense aggression, perhaps an example of incest avoidance behavior that is generally present among animal species.

In addition to those wolf sightings, we also observed fresh tracks of the pair throughout the eastern third of the island plus two additional kills that appeared to have been made during the winter study, near Epidote Lake and Lake Richie.

scavenging from a moose which had most likely starved to death (Fig. 3). The moose had been an old bull with necrotic teeth. The percent fat content of its bone marrow was 12% (normal is >70%) - indicating that it was in a state of severe nutritional depletion at the time of its death. Other signs point to scavenging rather than a predation event: the carcass was buried in old snow and the sternum had not been consumed.

Two days later, on February 17th, we observed two wolves and their tracks. They had traveled from Horner Island, into Duncan Bay, over the Greenstone

The per capita rate of prey acquisition (sometimes known as kill rate) is a statistic that accounts for 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 (2), divided by the number of days over which the carcasses were acquired. This year, the acquisition rate included four predated moose and one scavenged carcass. If those carcasses were acquired between early January (say, January 7th) and March
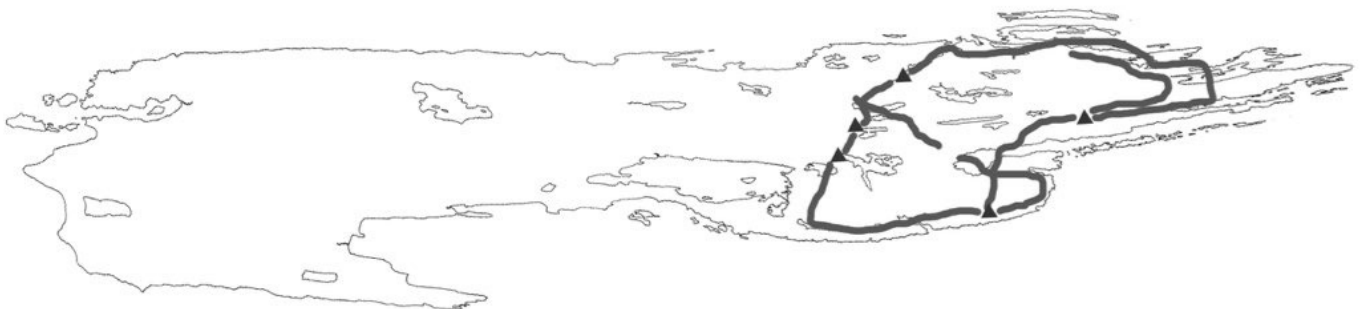
2017 Wolf Travels

Figure 3. The remaining wolf pair remained in its usual territory at the east end of Isle Royale during the Winter Study of 2017. They fed from five moose carcasses, including one adult male that probably starved to death plus four moose that they probably killed.
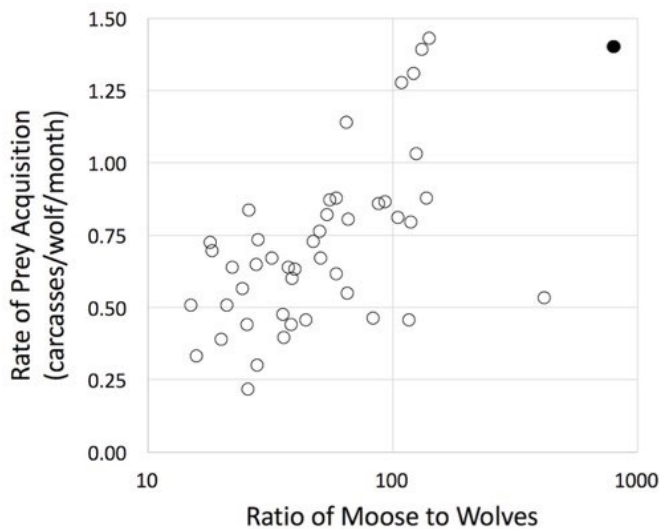
Figure 4. Relationship between the ratio of moose-to-wolves and the number of moose consumed per wolf per month on Isle Royale, 1971-2017. Black data point corresponds to 2017.

Figure 5. Relationship between the ratio of moose-to-wolves and predation rate on Isle Royale, 1971-2017. Predation rate is the proportion of the moose population killed by wolves on an annual basis. Black data point corresponds to 2017.

3rd (our last survey flight), then the acquisition rate would be 1.4 carcasses per wolf per month, among the highest observed on Isle Royale (Fig. 4). While there is important uncertainty about that precise estimate for the rate of prey acquisition, it is most likely that the last two wolves in this population are reasonably well-fed.

The impact of a wolf population on a moose population is indicated by the predation rate, which is the proportion of moose killed by wolves. This statistic is equal to the kill rate times the ratio of wolves to moose and then extrapolated throughout the year (according to methods describe in Vucetich et al. 2011; Journal of Animal Ecology 80, 1236-1245). When the ratio of wolves to moose is very low, as is now that case (i.e., 2:1600), then the predation rate is determined almost entirely by the ratio, rather than the kill rate. Even with a relatively high rate of prey acquisition by the remaining two

wolves, predation rate – expressed as a percentage of moose – would be less than a quarter of one percent. In a typical year the predation rate would be about ten percent (Fig. 5).

The two wolves that likely remain on Isle Royale in 2016, believed to be a male-female pair, are probably the two adults identified by fecal DNA collected on 5 March 2015. They both originated in the Chippewa Harbor Pack, born to the same mother. The female is also the daughter of the male, so any

Figure 6. On 23 February, 2017, the male persistently tried to court the female. She aggressively rejected the male, and a mating between these two wolves, the only wolves left on the island, seemed very unlikely.
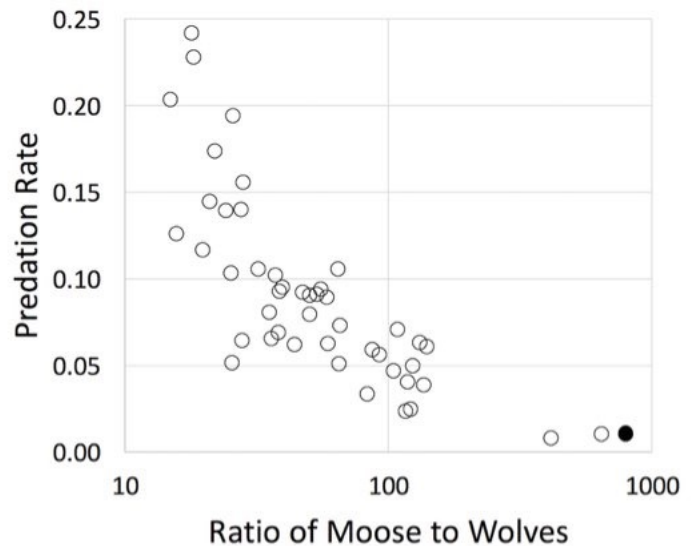
offspring from this pair would be extremely inbred and probably non-viable (Fig. 6). There have been no ice connections between Isle Royale and the mainland since 2015, so there has been no wolf immigration and no mortality in the past two years. The Chippewa Harbor Pack has not produced any viable pups since the alpha male died, along with two pack mates, in a historic mine shaft in December 2011. Under present circumstances reproduction is not expected.

In 2015 the National Park Service (NPS) began work on a multi-year process to consider how the NPS will respond to the decline in wolf predation at Isle Royale. On December 16th, 2016 the NPS released a draft environmental impact statement (EIS), which indicated that the NPS's preferred alternative action is to bring 20 to 30 wolves to Isle Royale over a three-year period that might begin in 2018 or 2019. A final decision by the NPS is expected to be announced toward the end of 2017.

The Moose Population

The 2017 moose survey began on January 30th and ended on February 16th. The survey resulted in an estimated abundance of 1600 moose. The 80% confidence intervals on this estimate are [1240, 1996], and the 90% confidence intervals are [1077, 2238]. Moose density was lowest (1.4 moose/km^2) in the middle portion of the island and greatest (5.4 moose/km^2) on the east end and along the shoreline of the west end of Isle Royale (Fig. 7).

Counting conditions before February 8th were exceptionally poor due to a strong snow crust that formed after several days of above-freezing temperature. During that portion of the moose survey we had two survey aircraft available, which allowed us to perform a double count. That double count allowed for a direct estimate of sightability. The estimated sightability during the early portion of the survey was 36%.

Between February 4th and 7th, 25 cm (10 inches) of snow fell, which greatly improved counting conditions to what could be described as slightly worse than average conditions. During this portion of the moose survey, we had only one aircraft available and we estimated sightability according to techniques described in the 2009-10 Annual Report. The overall average sightability for this year's moose count was 59%. The estimated abundance of moose will be refined when the population is statistically "reconstructed" from remains of dead moose, but this is possible only after most of the moose present in a given year have died.

Last winter the moose census was not completed and consequently taken to be less reliable. More important than comparing this year's estimate of abundance to last year's estimate of abundance is to make note of the multiyear trend. For the past six
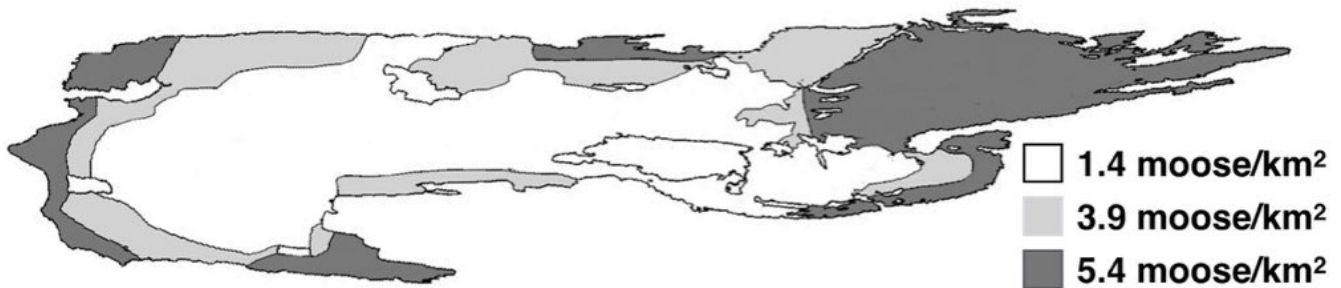
2017 Moose Distribution

☐ 1.4 moose/km^2
▨ 3.9 moose/km^2
■ 5.4 moose/km^2

Figure 7. During the 2017 Winter Study moose distribution was greatest near shorelines of Lake Superior, a typical midwinter pattern.

Figure 8. Most moose on Isle Royale in 2017 were young, born since the wolf population collapse ca. 2012. Being young, they are in good health and have a high potential to reproduce in the future. This "teen-age" bull still had antlers and was accompanied by two other similarly-antlered bulls in mid-February near Windigo (photo by Lynette Potvin).
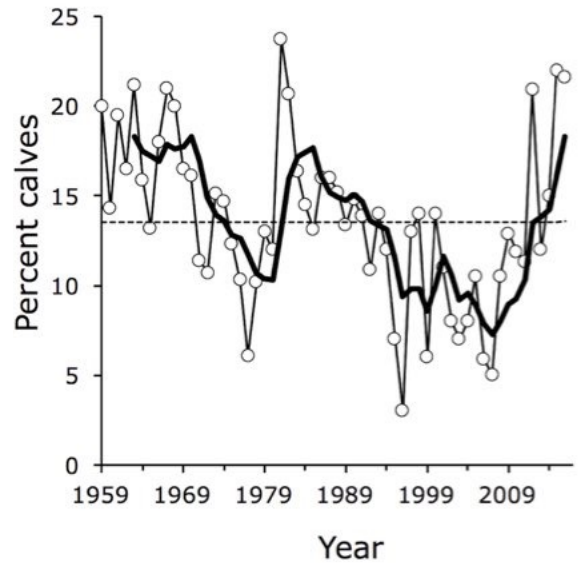

Figure 9. Long-term trends (1959–present) in the percentage of the total moose population that are 8-month old calves. The 50-year average (13.4%) is marked by the dotted line, and the curved line is a 5-year moving average.

years, the moose population has been growing at an average rate of 21.6% per year, and young animals now predominate (Fig. 8). This growth rate is consistent with the convergence of three circumstances: high rates of recruitment into the moose population, low rates of mortality due to wolf predation, and an abundance of forage. In particular, the percent of the moose population that are calves has been, on average, 18% for each of the past five years (Fig. 9). And the estimated proportion of moose killed by wolves has been, on average, 0.018/yr for each of the past four years (Fig. 5). If recent growth rates persist for the next 3-4 years, the population will double in size.

Isle Royale Vegetation

A primary concern as wolf predation dwindled was that a moose population uncontrolled by predation might do irreparable harm to the vegetation community which supports moose (Fig. 10). While this is a large and complicated topic, we can glean some interesting insights by examining recent interactions between moose and vegetation, both terrestrial and aquatic.

The important context is that during 2004-2009 wolf predation was the most intensive ever documented at Isle Royale, when wolves were killing 15-20% of the moose each year. That resurgence in predation followed the genetic renewal that began in 1997 when one male immigrant arrived and became a breeding male. There are two remarkable developments among plants, both on land and in the water, which may be attributed to strong top-down limitation of moose density by wolf predation - a trophic cascade, in this case preceded by

Figure 10. The moose population has been growing without check by wolf predation since 2012, raising concerns about the impacts of foraging moose.

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genetic rescue caused by the arrival of a single, immigrant wolf.

Moose and watershield

Beginning in 2007, the surface of several ponds were taken over by a native aquatic plant called

Figure 11. Lake Ojibway was virtually overtaken by watershield after 2006, when moose density reached its lowest level. In 2016 this plant cover was dramatically reduced and moose foraging was intensive. This is an aerial view in 2012 from NPS imagery, when watershed covered the entire shallow littoral zone.

watershield (Brasenia schreberi), a plant rooted in the pond bottom but with floating leaves and flowers (Fig. 11). All parts of the plant are highly favored food for moose and beaver, and the plant g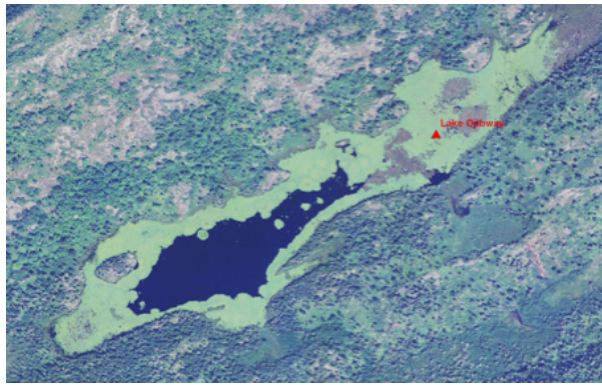ained an edge when both herbivore species were reduced by intensive wolf predation in 2004-2009. Working in 2011-2012, Ph.D. student Brenda Bergman found that watershield came to dominate five beaver-impounded lakes in the eastern portion of Isle Royale, and her work with experimental exclosures indicated that moose were the dominant aquatic herbivore compared to beaver (see Bergman and Bump. 2015. Freshwater Biology 60:1635-1646).

Each of the five ponds affected exhibited unique but unmistaken declines in watershield as moose population size increased three-fold since 2011 (Fig. 12). In Lake Ojibway (impounded by beavers for the past 60 years), watershield remained dominant until

Figure 12. (Left) Watershield covered most of this beaver pond near Moskey Basin in 2011 when beaver moved back in after a long absence and seemed to survive primarily on aquatic plants. (Right) By 2016, watershield had been virtually absent in this pond for three years and beavers had disappeared, perhaps outcompeted for food by moose.
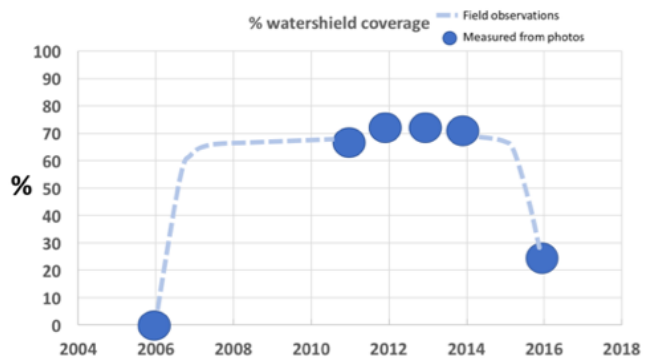

Figure 13. Percent of Lake Ojibway covered by watershield, 2006-2016. No aerial photos are available in 2007-2010 and 2015, but in those years ground photos and field observations indicated coverage similar to 2011-2014.

Figure 14. (Left) For decades balsam fir was unable to regenerate at the west end of Isle Royale because of intensive moose foraging. (Right) During the mid-2000s moose density was low and many short fir began to grow beyond the height of one meter.

2016, when surface coverage was reduced from 70% of the lake surface to just 25% (Fig. 13).

Moose and balsam fir

Balsam fir is the primary food for moose on Isle Royale in winter. When the original land survey was completed in 1848, before moose were present. balsam fir was the dominant tree on Isle Royale. This tree species declined following fires in the 19th century which set back forest succession, and in the 20th century more fires, spruce budworm, and finally

Figure 15. Balsam fir regeneration at the west end of Isle Royale has been the focus of several studies since 1990. Here winter volunteer Lisa Koitzsch collects data on current annual fir growth (photo by Ky Koitzsch.).

moose browsing all reduced balsam fir again. Status of the species on the two ends of Isle Royale is dramatically different, with fir relatively stable on the east end but steadily diminishing on the west end, where it has been in a century-long decline following colonization by moose (Fig. 14). The deep soils on the west end are associated with a greater presence of yellow birch and maple, and fir is unable to regenerate adequately as new sprouts are heavily browsed in winter by moose. The only tree species that grows unimpeded by moose on the west end is spruce, and forest stands are reverting to a moose-spruce savannah dominated by scattered spruce and invasive grasses. Over one-third of west-end forest stands are already converted or show evidence of "breaking up" (see Rotter MC and AJ Reburtus. 2015. Botany 93:75-90).

All the more remarkable, then, is recent evidence that stunted balsam fir stems, browsed for decades and less than one meter tall, had started to grow in the past decade prior to 2012 when the moose population began to increase rapidly (Fig. 15). These short fir trees, some established as seedlings as long as 40-50 years ago, now represent the final cohort of short fir that could grow into seed-bearing trees of the future. This is the species' last chance because the parent trees are reaching maximum life-spans and most have died and fallen over in the past 25 years. As the moose population is presently growing rapidly,
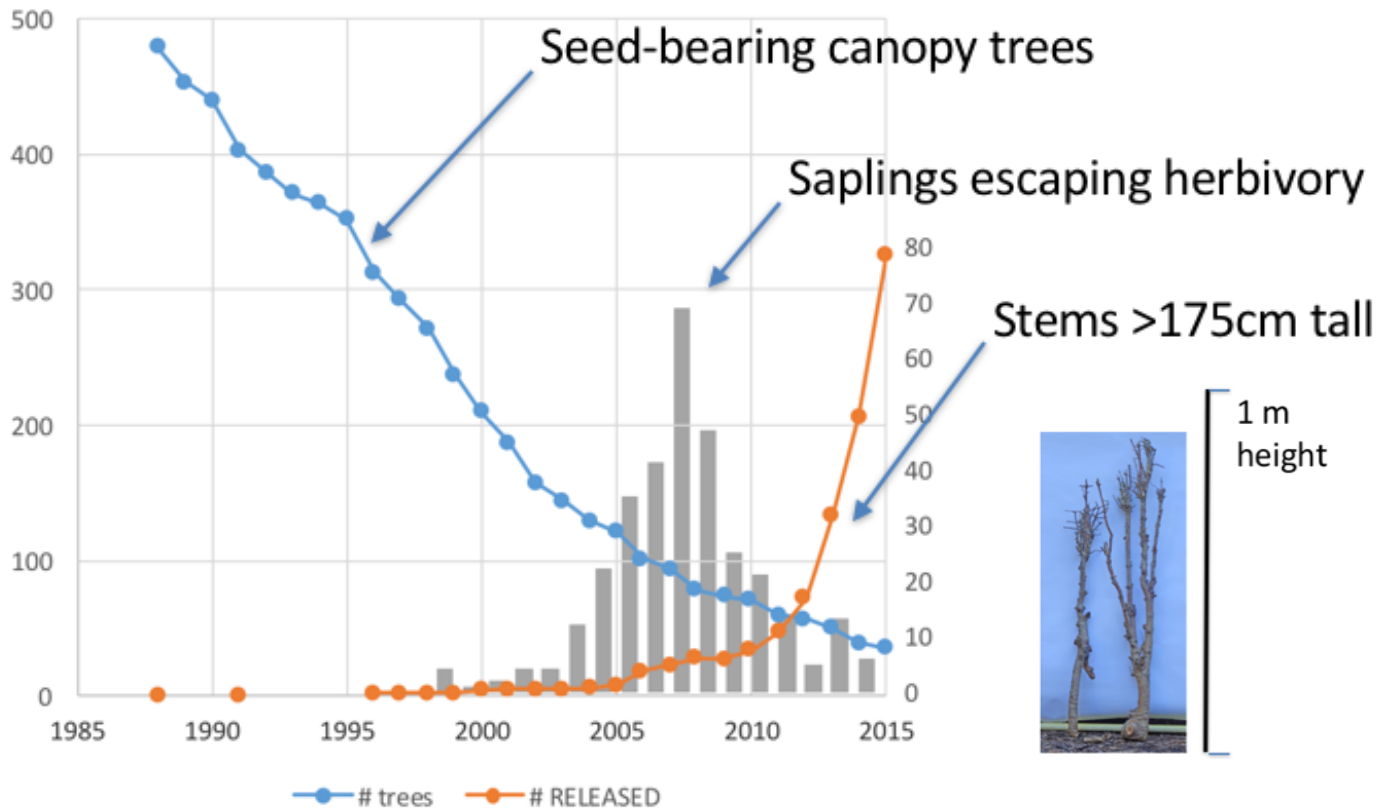
Figure 16. Balsam fir saplings and trees are the primary source of winter forage for moose on Isle Royale. Since 1988, survival of a population of tagged balsam fir trees on the west end of the island has been monitored ("Seed-bearing canopy trees", enumerated on Y-axis). As these trees in the forest canopy reached maximum age and died, they were not replaced by sapling trees because moose browsing was so intense that no stems escaped total suppression. Stem architecture of these saplings (inset photo) reflected high browsing damage. Around 2005, with moose density reduced, some saplings began to grow ("Saplings escaping herbivory", X-axis label), and after 2010 these trees increasingly became apparent ("Stems >175cm tall", X-axis label). These saplings need another 5-10 years before they will reach a height of 3-4 m, where they will be able to survive the impacts of browsing moose and continue growing into seed-producing trees.

there is a race on with an uncertain outcome - will sufficient short fir escape moose browsing and grow into reproducing trees (Fig. 16), or will they suffer the common fate of west-end fir regeneration in the past century — dying without reproducing?

Other Wildlife

During winter 2017 tracks of marten were observed at Windigo and several other nearby locations. Since 1991 marten sign has been observed every year but three, while sign was completely absent during 1959-1990. In the past year, no indicators of presence were recorded for the other two small mustelid residents of Isle Royale, the short-tailed weasel and the American mink.

Interactions between snowshoe hares and their predators have fascinated ecologists for many decades, and research in other locations has revealed a complex picture of how predation, weather and food supply interact to produce roughly decadal fluctuations in hare numbers, at least when lynx are present. Predator populations then typically peak and decline in rough synchrony with their prey. In any single location, such as Isle Royale, there are factors that modulate this pattern. For Isle Royale, given only imperfect indicators of abundance for snowshoe hares and red foxes, a primary predator species, we can only speculate about factors that influence the hare density (Fig. 17). The exceptional peak in hare numbers in 2012-2013 followed a decades-long
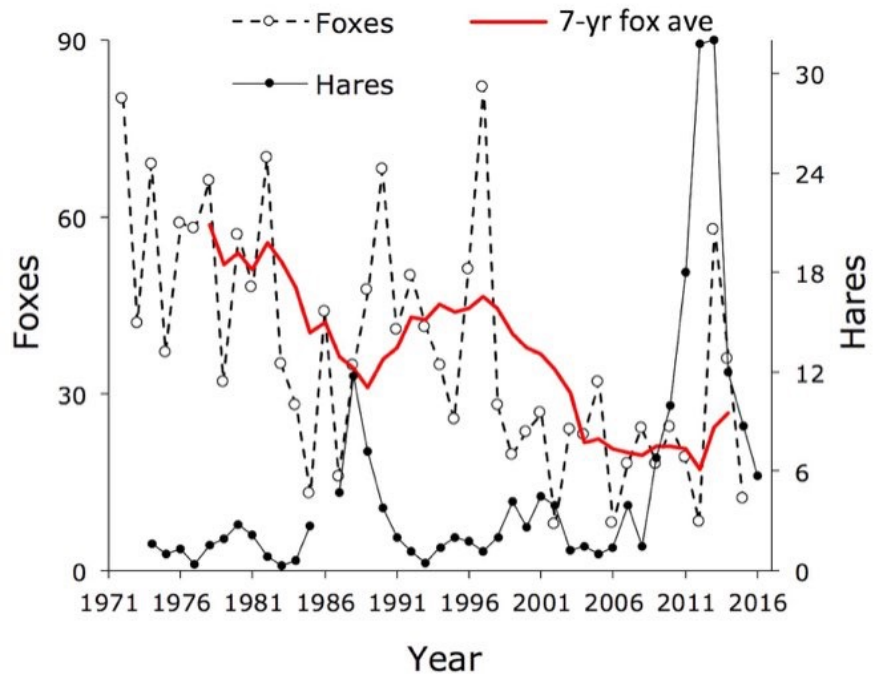
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Figure 17. Indices of abundance for red foxes and snowshoe hares on Isle Royale, 1974-present. The hare index is the number of hares observed per 100 km of summer hiking. The fox index is the number of foxes seen from the survey aircraft during Winter Study, the sum of the maximum number seen at kills plus the number seen otherwise per 100 hours flight time. The red line is a moving average, highlighting a longer term trend in fox abundance.
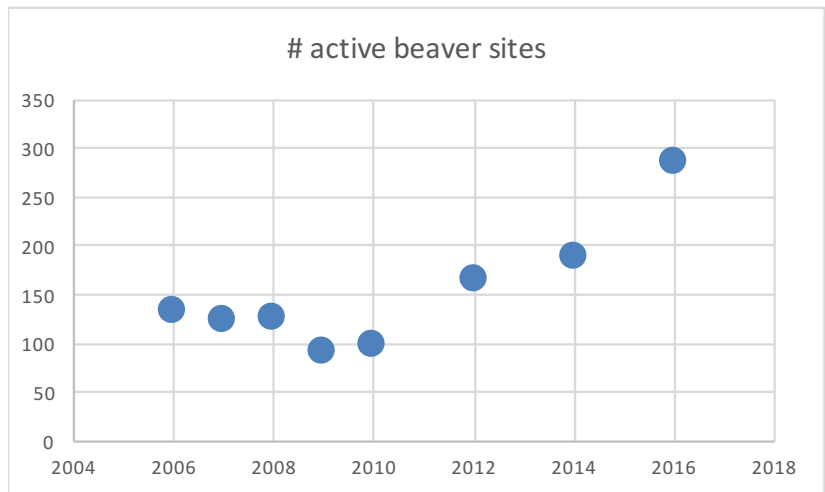

Figure 18. The number of active beaver colonies has been estimated during aerial surveys at least every other year since 1974. During 2006-2010 there were around 100 active sites and intensive wolf predation was probably the primary limiting factor. After the wolf population collapsed in 2012, the beaver population has consistently increased.

decline in the fox index, a multi-year period of low moose abundance (moose may compete with hares for food in winter), and a period of mild winter weather. We could also note that great-horned owls, the other primary predator of hares, seemed to have been relatively abundant during the recent surge in hare numbers, with multiple pairs nesting in the Rock Harbor channel alone.

Active beaver colonies have been counted on Isle Royale about every other year for about four decades. In October 2016 observer Rolf Peterson and pilot Don Murray (with float-equipped survey aircraft) conducted this count. They found that the beaver population has continued to increase, a pattern initiated when the wolf population collapsed in 2010-2012. There were almost 300 active beaver sites in 2016, a three-fold increase in the past half-decade (Fig. 18).

In 2016 one successful nesting of trumpeter swans was recorded on Isle Royale, producing three cygnets. This followed three years when non-nesting swans were observed in several locations on Isle Royale. This species was almost extirpated in the continental United Stated by unregulated hunting more than a century ago, but it was restored in Minnesota in the 1980s and 1990s using eggs that were flown from Alaska by the Minnesota Department of Natural Resources. The Minnesota population was estimated to be 3,600 swans in 2008 and over 17,000 in 2015 (Minnesota Conservation Volunteer 80:8-21, 2017). It is likely that some of these birds have now dispersed to Isle Royale, where the birds probably disappeared in the 19th century.

Weather, Climate, and Ice

Winter arrived as expected by early December 2016, but major thaws occurred at least three times before the winter study ended in early March 2017. During the Winter Study snow depth was below average and temperatures were unusually warm (Fig. 19). Snow depth decreased dramatically during the thaws, and ice layers were established in the snow profile. A hard surface crust 7 cm thick, supporting 2,300 g/m2 (SE = 600 g/m2) was established in late January,

supported traveling wolves and occasionally moose. This overlay a 3-cm crust just 10 cm off the ground, from the December thaw, which supported >70,000 g/cm2 including moose. Moose responded to these hard layers in the snowpack by moving into thick coniferous cover, where they remained for the entire winter study period.

Consistent with a generally warm winter and high winds over Lake Superior, there were no ice bridges to the mainland and very little ice in the bays of Lake Superior. Ice bridges have formed in only three years since 1997, and it is this decline in connectivity to the mainland that has resulted in genetic decay for the wolf population.
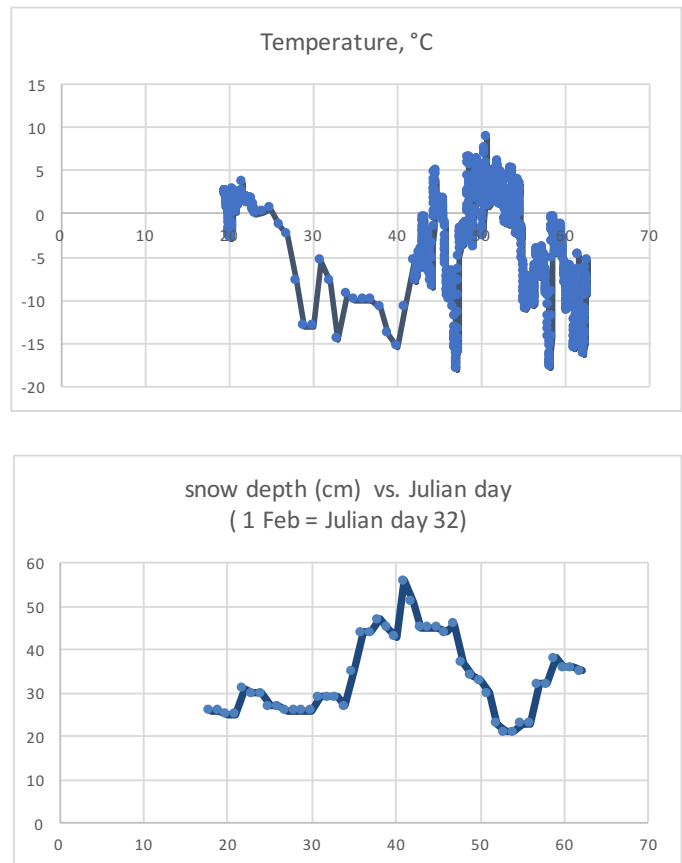

Figure 19 Ambient temperature (30-minute intervals, except daily in 27 January - 6 February, top graph) and snow depth (daily, bottom graph) during the 2017 Winter Study on Isle Royale.

"…our greatest national heritage is nature itself, with all its complexity and its abundance of life…"

— Wright GM, JS Dixon, BH Thompson.
Fauna of the national parks of the U.S. 1933

Available from