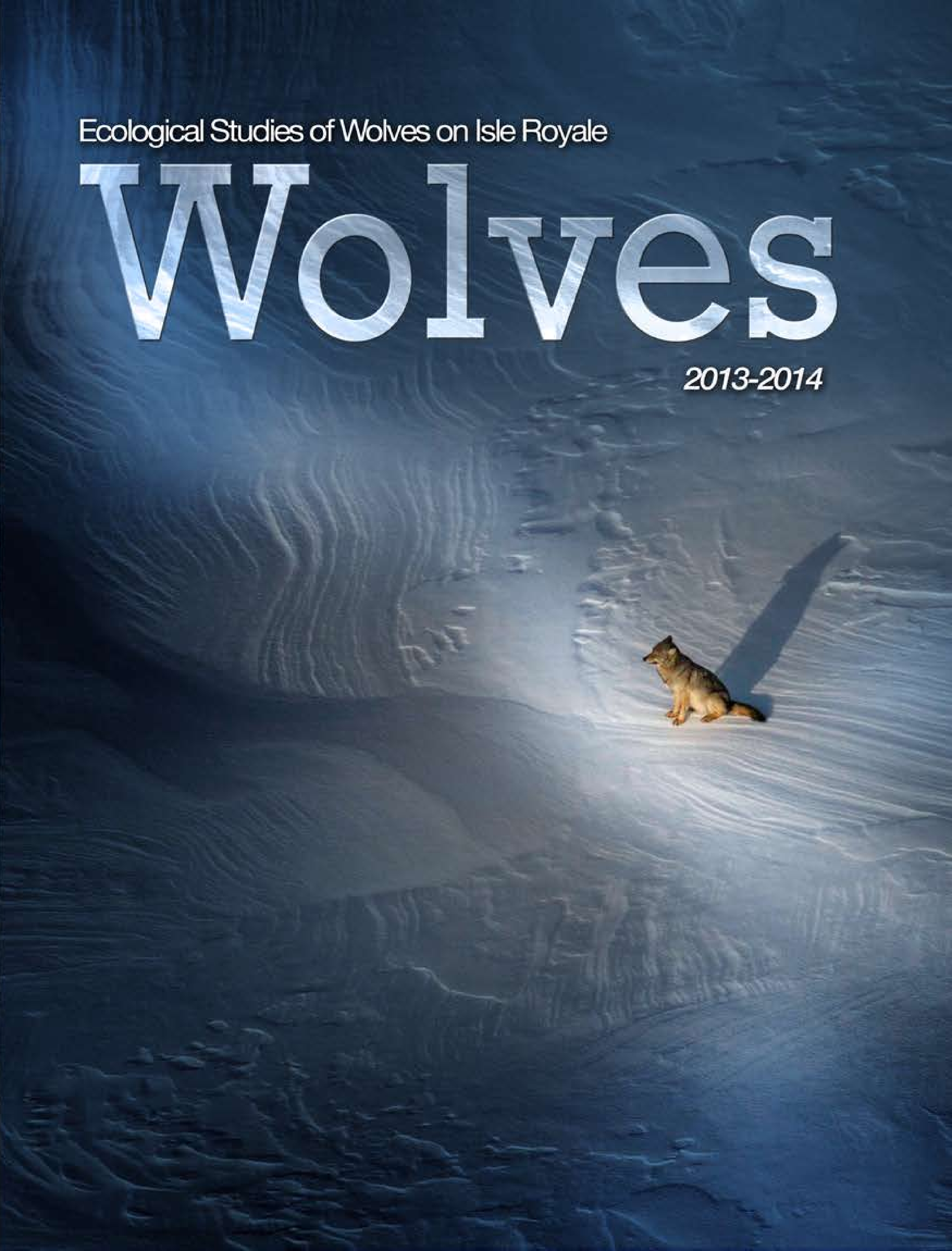
Ecological Studies of Wolves on Isle Royale

Wolves

2013-2014



Ecological Studies of Wolves on Isle Royale

Annual Report 2013–14

by

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Team IIC – Barrett Warming (leader), Dominic Bragg, Tracy Dulak, Thomas Grajauskas, Cathy More, John Warming.

Team IIIA – Joe Olenik (leader), Erik Freeman, Jimmy Funkhouser, Cody McGregor, David Dzubinski.
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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!

Results reported here are preliminary and, in some cases, represent findings of collaborators; please do not cite without consulting the authors.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 U.S. National Park Service or the U.S. National Science Foundation.

WOLVES & MOOSE of Isle Royale

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Ecological Studies of Wolves on Isle Royale

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 comprises between 18 and 27 wolves, 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 56th 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 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. The lives of Isle Royale moose would never be the same. Researchers began annual observations of wolves and moose on Isle Royale in 1958.

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 mere wanderings of wolves and moose to or from the island. Nature is difficult to understand because it usually includes interactions among so many species. It helps to observe where ecological relationships are relatively simple. On Isle Royale, wolves are the only predator of moose, and moose are essentially the only food for wolves. To understand nature it also helps to observe an ecosystem where human impact is limited. On Isle Royale, people do not hunt wolves or moose, or cut the forest.

The original (and current) 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 had been that knowledge about wolves would replace hateful myths and form the basis for a wiser relationship with wolves.

After five decades, the Isle Royale wolf-moose project continues. Today, wolves also 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 2013, we conducted ground-based fieldwork from late April through mid-October. Rolf Peterson and John Vucetich directed that fieldwork with assistance from Tes Jackson, Kari Grebe, Joe Ackerman, Micah Leinbach, Carolyn Peterson, and Leah Vucetich. Leah Vucetich also led a number of people working in our lab, especially John Henderson, Grace Parikh, Joshua Isaac, and Jon Bontrager.

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

In 2014, the annual Winter Study extended from January 14 to March 3. John Vucetich, Rolf Peterson, and pilot Don E. Glaser participated in the entire study, assisted by Leah Vucetich and Ky & Lisa Koitzsch. Ky and Lisa's efforts focused on collecting urine (yellow snow) and pellet samples to assess nutritional condition of moose. Bob Glaser and Lucas Westcott provided ground transportation. U.S. Forest Service (USFS) pilots Pat Loe and Scott Miller flew supply flights to Isle Royale from Ely, Minnesota. Several National Park Service employees also attended a portion of Winter Study; they are Ted Gostomski, Seth DePasqual, Greg Bickings, and Rob Bell. A special thanks to Adam Hanson of Voyageurs National Park, who travelled to Isle Royale this winter to repair the NPS snowmobile that had been inoperative for the first three weeks of the winter field season.

Summary

From mid-January to early March 2014, we conducted the fifty-sixth annual Winter Study of wolves and moose on Isle Royale. Between January 2013 and January 2014, the wolf population increased from 8 to 9 (Fig. 1). Despite that modest increase, mean wolf abundance has been lower for the past three years than any other three-year period since observations first began. The population was organized into two social groups, West Pack and the Chippewa Harbor Group. West Pack produced two, and likely three, pups that survived throughout the winter. The Chippewa Harbor Group failed to reproduce in either of the past two years and we do not expect them to reproduce this year.

Per capita kill rate, which indicates the wolf population's capacity to kill moose, was 0.46 moose/

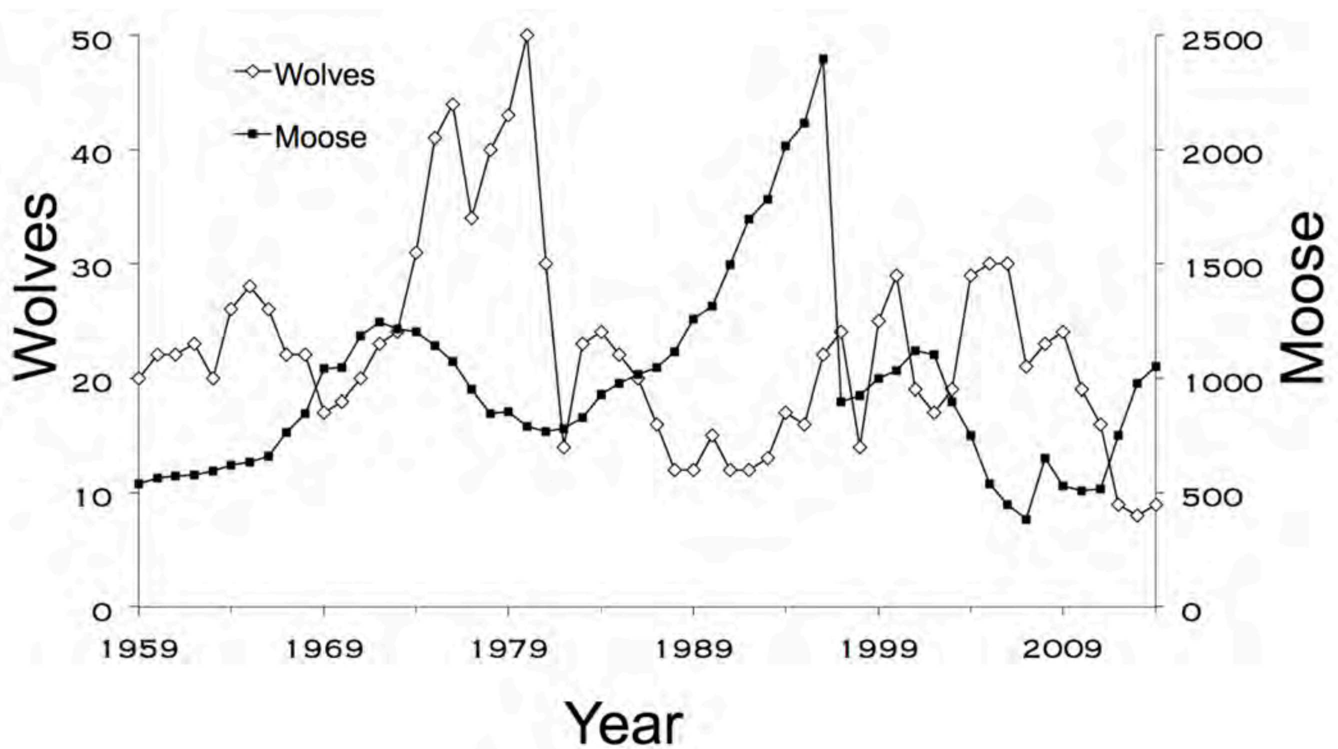


Figure 1. Wolf and moose fluctuations, Isle Royale National Park, 1959-2014. Moose population estimates during 1959–2001 were based on population reconstruction from recoveries of dead moose, whereas estimates from 2002–14 were based on aerial surveys.

Figure 2. The nine wolves in this year's population on Isle Royale are pictured. These wolves are the West Pack (top) and the Chippewa Harbor Group (lower left). A lone wolf, nicknamed Isabelle (lower right), was observed once during the winter on Isle Royale (January 21st). She left the island, crossing an ice bridge sometime in late January or early February. She was found dead on the mainland near Grand Portage, Minnesota in early February.

wolf/month during winter 2014. The kill rate has been especially low for the past three years, given the high ratio of moose to wolves on the island. The estimated annual predation rate, which is the proportion of moose (>9 months of age) killed by wolves, was 2.4%. The three lowest rates of predation on record occurred during the three most recent years.

Over the past three years, moose abundance has doubled. In February 2014, we estimated moose abundance to be 1050, with 90% confidence intervals of [650, 1540] (Fig. 1). Calves comprised 12% of the moose population during winter 2014, which is near the long-term average.

In the past year, we also discovered multi-year patterns indicating how inbreeding depression has been adversely impacting the demography and ecosystem functioning of wolves on Isle Royale.

The Wolf Population

On 1 February 2014, we counted nine wolves in the population, compared to last year's count of eight wolves. Last year the population was comprised of a group of three wolves that have now become the West Pack, the three wolves belonging to the Chippewa Harbor Group, and two loners. One of these loners died sometime during the past year and the other loner died during the 2014 winter field season. The wolf population was comprised of two groups (Fig. 2):

Chippewa Harbor Group...............3
West Pack.................................6
2014 Total...............................9

The two wolves that died during the past year, represent a 25% mortality rate, which is near the long-term average. Recruitment rate is the percent of the population that are pups who survived to see their first winter. The production of three pups in a population of just eight wolves yields a large recruitment rate (38%). However, the number of surviving pups is small given that the population is organized into two social groups. One of the two groups of wolves has not reproduced in either of the past two years. Record low wolf abundance for the past three years has been driven, in part, by low recruitment.

In the 2011-12 Annual Report we reported that behavioral observations indicated that one or zero pups had been present. Genetic analyses conducted since that time indicate that zero pups had been present that year, meaning zero recruitment was recorded for cohorts in both 2011 and 2012. This update is reflected in Figure 3.

The age structure of a population can be useful for understanding various processes occurring within that population. We estimate age structure for wolves by analyzing DNA extracted from dozens of fecal samples collected each year from trails and sites where wolves have killed moose. The first year in which each wolf's DNA profile (at microsatellite loci) is detected is an estimate of the year in which that wolf was born, and the last year in which any individual's profile is detected is an estimate of that wolf's year of death. The details are given in Marucco et al. 2011 (Conserv. Genet. 13, 1611-1622). From those estimates of years of birth and death, we estimate the population's age structure for any given year. For most of the past decade the proportion of young wolves has steadily declined, prime-aged individuals have steadily increased, and older wolves have remained low (Fig. 4). Being comprised of so many prime-aged individuals has likely contributed to the low-to-average mortality rates observed over the past two years. In the next two years, if recruitment is much below average, as it has been for six of the past eight years (Fig. 3), an increasing portion of the population will likely be older wolves that are characterized by higher rates of mortality.

Genetic analyses conducted within the past year also offer insight about why the Chippewa Harbor Group has failed to reproduce during either of the past two years. Late in 2011, just 2-3 months prior to the 2012 mating season, the alpha male of Chippewa Harbor Pack drowned in a flooded mine shaft along with two other wolves. The alpha pair of Chippewa Harbor Pack had successfully produced many pups in previous years and they likely would have continued to do so, possibly preventing much of the recent decline in Isle Royale's wolf population (from 16 wolves in 2011 to eight in 2013). The mine shaft event – an artifact of 19-century copper mining – appears to

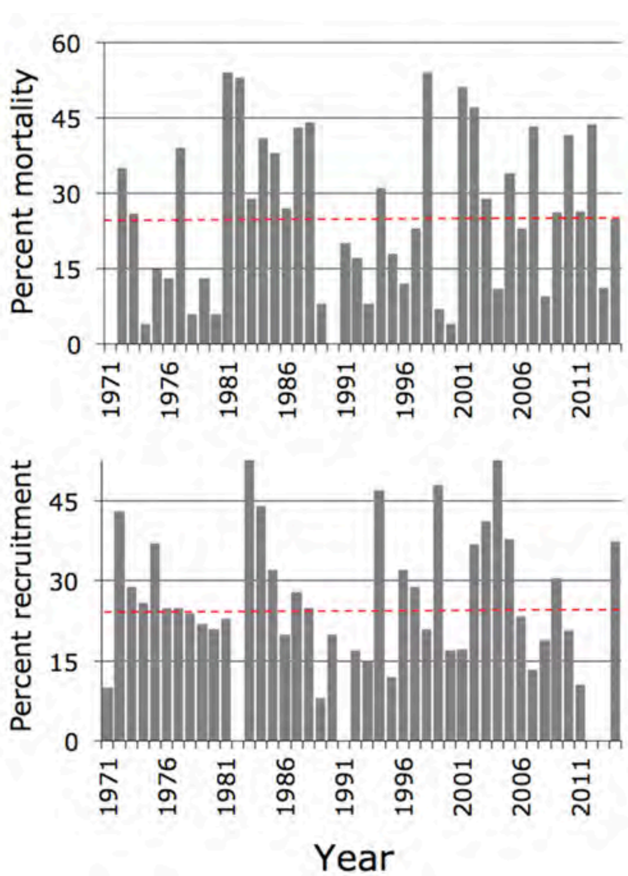


Figure 3. Percent mortality and recruitment for Isle Royale wolves, 1971-present. The dotted lines mark long-term averages.

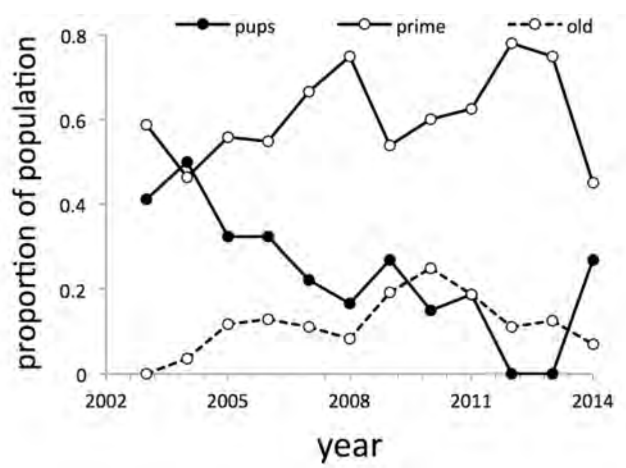


Figure 4. Age structure of the wolf population during the winter from 2003 to the present. Prime-aged wolves are yearlings and wolves that are up to and including 4.75 years of age. (Wolves are born in late April.) The proportion of prime-aged wolves could be underestimated for the years 2012, 2013, and 2014, because there is one adult of unknown age in 2012 and 2013, and two adults of unknown age in 2014. Subsequent genetic analysis will likely resolve those uncertainties.

Figure 5. On 1 March 2014, the elderly one-eyed matriarch of the former Chippewa Harbor Pack stands in dominant display over her adult daughter, with her adult son viewing the action. The old female lost her mate in late 2011 when he drowned in a historic mine shaft, and there are no available mates for any of these three wolves that aren't closely related. The daughter and son in this group are more closely related than brother-sister because of a heritage of extreme inbreeding among their ancestors. There is good reason to believe that the matriarch's bad eye is a congenital deformity associated with inbreeding.

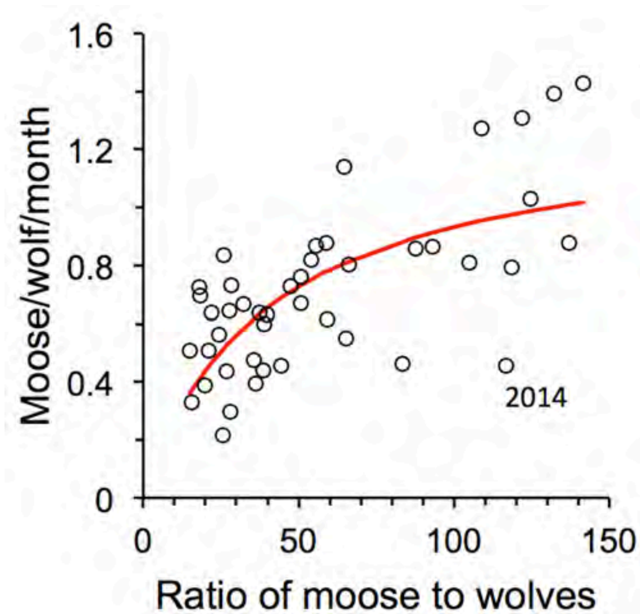


Figure 6. Relationship between ratio of moose-to-wolves and number of moose consumed per wolf per month, 1971-2014.

have been more important than previously appreciated.

We did not detect any signs of courtship or mating among the Chippewa Harbor Group during this year's winter field season. The Chippewa Harbor Group is comprised of an alpha female, one son, and one daughter. That alpha female is old and will turn nine years of age in April 2014. Her two offspring are middle-aged, probably four or five years old. If those two younger wolves were to reproduce their offspring would be particularly inbred (see below). If the Chippewa Harbor wolves do not reproduce in 2014, it will be the third year in a row with no recruitment in this pack.

We observed West Pack for a 44-day period. During that time they killed four moose. We observed the Chippewa Harbor Group throughout a 45-day period. During that time they killed and fed from two moose. In early February, two of the wolves (we suspect the two offspring) left the kill site and traveled southwest along the north shore of Isle Royale to Little Todd Harbor (Fig. 5). Both wolves scent-marked frequently. At Little Todd Harbor they detected the tracks of West Pack from a few days earlier, and the pair then headed inland and eventually, after approximately 4 days, they ended up back at the

2014 Wolf Territories and Kill Locations

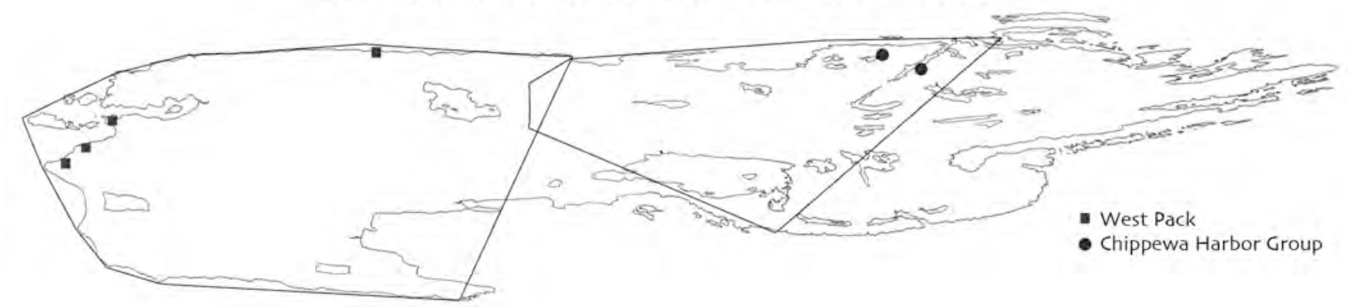


Figure 7. Symbols mark the location of wolf-killed moose. The polygons mark the territorial boundaries for each group of wolves.

kill site. The third wolf of the Chippewa Harbor Group (presumably the older alpha female) did not participate in that territorial excursion and remained at the kill site.

The rate at which we observed each pack kill moose corresponds to a population-wide average (weighted for differences in pack size) rate of 0.46 moose per wolf per month. In general, the rate at which wolves kill moose is influenced by the number of moose per wolf on the island (Fig. 6). The kill rate observed this year was the lowest ever observed, given the number of moose per wolf on the island. In the past kill rates as low as 0.46 moose per wolf per month have been associated with population decline in the upcoming year.

We conducted necropsies on carcasses belonging to two of the six moose that wolves killed during the 2014 winter field season (Fig. 7). Both moose were old females with osteoporosis, and one had a bone infection in one mandible.

Inbreeding

We have analyzed the DNA in more than a thousand fecal samples from wolves collected over the past 15 years. Doing so has allowed us to construct a pedigree ("family tree") of the Isle Royale wolves for the period 1999-2013. From that pedigree we can monitor the rate of inbreeding in the population. This effort represents an on-going collaboration with Phil Hedrick of Arizona State University and Jennifer Adams of Idaho State University. An important discovery from that analysis is that per capita kill rate has tended to decline as the mean rate of inbreeding in the population increased (Fig. 8A).

Wolf recruitment rate has also tended to decline as the mean rate of inbreeding in the population increased (Fig. 8B). Throughout the period during which estimates of inbreeding are available, fluctuations in recruitment from year-to-year account for about 78% of the fluctuations in abundance. That is, declining wolf abundance in recent years is largely attributable to declining recruitment.

Those statistical patterns are also reflected in a fascinating chronology of events. These events began in 1997 when a wolf immigrated to Isle Royale from the Canadian mainland. That wolf, the Old Grey Guy, and his descendants exhibited superior fitness and vigor compared to the native Isle Royale wolves. By about 2010, the immigrant's descendants had come to comprise a large portion of the population. In technical terms, the Old Grey Guy's ancestry had risen to 0.59, meaning roughly that 59% of the genes in the Isle Royale population traced back to the Old Grey Guy. The remarkable degree to which his lineage outcompeted the native Isle Royale lineage contributes to what is at least a extremely high standard of evidence that Isle Royale wolves had been, prior to the immigrant's arrival, suffering from inbreeding depression.

Outcompeting the native lineage in such a dramatic manner was, it turns out, accompanied by inbreeding among the immigrant's lineage. In particular, nine descendants of the Old Grey Guy, all living after 2008, had high inbreeding coefficients (f = 0.375), as they were the result of two consecutive generations of inbreeding between first order relatives (sibling-sibling or parent-offspring). Each of these wolves lived short lives and only one reproduced - in this case a single pup during its life. Their deaths, between 2009 and 2011, also contributed to the decline in wolf abundance between 2008 and 2013. Their short, unproductive lives appear to mark the waning benefits of the genetic rescue event that occurred with the immigrant's arrival in 1997. This decline may also have been exacerbated by canine parvovirus, which reappeared in 2007 for the first time in 17 years. (These findings are reported in a recent paper published in Conservation Genetics and in another article that has been submitted for publication in a peer-reviewed journal.)

For additional context, if the two younger wolves alive today in the Chippewa Harbor Group were to produce offspring, the inbreeding coefficient of those pups would be 0.328, which is not that different from those nine wolves with short, unproductive lives (i.e., 0.375). One can, for example, compare that level of inbreeding with the x-axis of Figure 8.

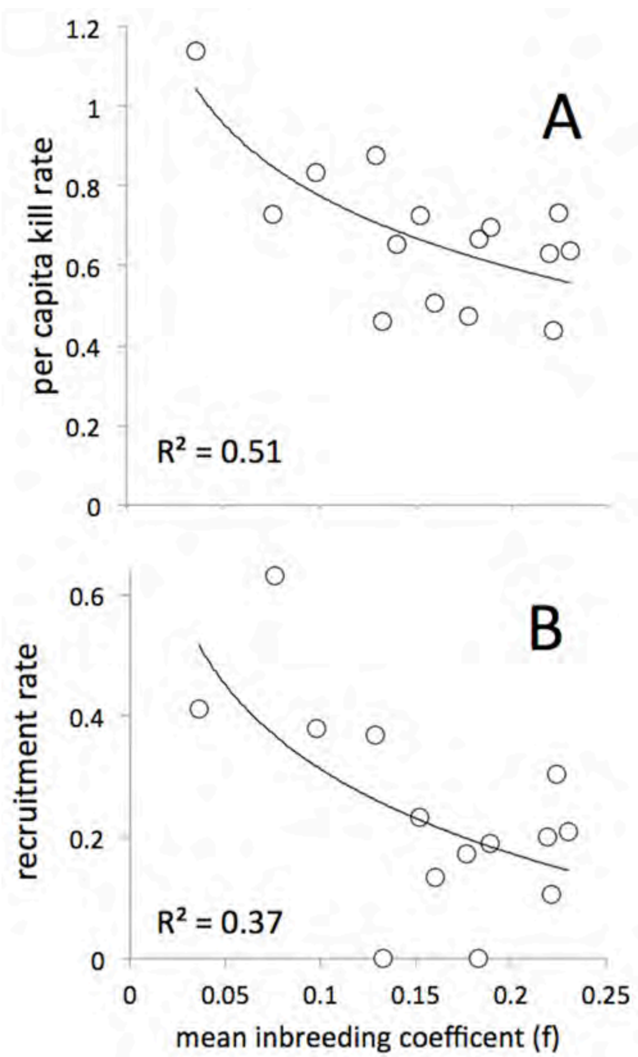


Figure 8. The influence of inbreeding on recruitment rate and per capita kill rate for the period, 1999-2013, the period for which we have estimated the mean inbreeding coefficient in the Isle Royale wolf population.

Undetected gene flow in the past

A great deal of scientific knowledge indicates that small, isolated populations exhibit high rates of inbreeding and consequently lose genetic variation, which is generally vital to a population's fitness. The health of such populations requires what geneticists refer to as gene flow, which involves the infusion of new genetic variation into the population from time to time. That infusion involves the periodic immigration of individuals into the otherwise isolated population.

For decades it had been assumed that the Isle Royale population was completely isolated from the mainland population of wolves. We set that belief aside in 2011 when we discovered that the Old Grey Guy had immigrated in 1997 from the mainland. New considerations suggest that the Old Grey Guy's arrival was not an isolated event in the history of Isle Royale wolves.

Prior to 1997, the Isle Royale wolf population had lost approximately 32% of its original heterozygosity (a measure of genetic diversity) due to inbreeding since the time it had been founded in the late 1940s. However, if the population had been completely isolated for all those decades, one would expect it to have lost approximately 82% of its original heterozygosity.

In principle, it is possible that the slower-than-expected loss is attributable to inbreeding avoidance. However, recent research has demonstrated that inbreeding avoidance among Isle Royale wolves is modest (Geffin et al. 2011, Molecular Ecol, 20, 5348-5358). It is also possible, in principle, that the slower-than-expected loss of genetic diversity is attributable to a genetic process known as "selection against homozygotes." Research on other wolf populations and inspection of the Isle Royale wolf pedigree indicates that those processes are also very unlikely to explain the slower-than-expected loss of genetic diversity.

The only remaining possible explanation for the slower-than-expected loss in genetic diversity is that wolves have periodically immigrated to Isle Royale on ice bridges that had once been common. In particular, theory suggests that retaining the diversity that the population had would require the population to have received on the order of approximately two migrants every three generations (12-15 years).

That circumstance prompted us to review field notes from the past four decades for the possibility that undetected gene flow had taken place in the past. That review revealed several plausible gene flow events. First, 7-8 wolves, including four that were black, arrived over an ice bridge in 1967, and the next winter three of the black wolves were believed still present in two different packs. One of these black wolves persisted in the single pack that comprised the population in 1969-1970, and he became the alpha male in 1971 and 1972. Other field observations indicate that two pups had been recruited into this pack in 1971 and another four in 1972. Because no black pups were observed, the black wolf was presumed, at the time, not to be the father. Contemporary understanding for the inheritance of coat color in wolves, however, indicates that gray offspring would not necessarily be unexpected. About two generations later, in the summer of 1980, a National Park Service employee photographed a wolf pup that may have been black. That photograph was preserved in the Park's archives. After it is retrieved and inspected we are likely to know more about this event.

These field observations of black wolves are noteworthy because the arrival of Old Grey Guy would not have been detected were it not for genetic techniques that were unavailable to us prior to the late 1990s. That is, because of his gray appearance, his arrival would have been undetectable from field observations alone. Furthermore, black wolves are uncommon in the Great Lakes region, representing approximately 3% of the population. The rarity of black wolves and the detection of four and possibly five black wolves in the four decades of observation prior to 1998 suggests the plausibility of additional undetected gene flow involving gray-colored wolves. The new immigrant pack arriving in 1967, for example, may have restarted the population relative to genetic integrity, almost two decades after the initial founding of the population.

In 1977 we observed a pack of wolves chase a pack mate across an ice bridge halfway to the mainland. During three years (1996-1998) following a period when ice bridges had been present in 1994, 1996, and 1997, a lone animal that appeared to be a coyote was observed on Isle Royale.

The current population of fox is thought to have been established on Isle Royale sometime about the year 1924 by foxes that would have crossed an ice bridge. The current population of coyotes is thought to have been established on Isle Royale sometime during the first half of the 20th century by coyotes that would have crossed an ice bridge. *The Wolves of Isle Royale* (1966) by L. D. Mech recounts several instances that likely involved individual wolves crossing ice bridges during the first half of the 20th century. (The coyote population was driven to extinction shortly after a wolf population was established in the late 1940s.)

In 2008, the previous time a bridge formed, two radio collared wolves disappeared shortly after the bridge had formed. In late January 2014 an Isle Royale wolf walked across an ice bridge and was found dead near Grand Portage, Minnesota.

Collectively, these observations indicate how readily a wolf (or any canid for that matter) can cross an ice bridge if it is present. Traveling at a typical speed, a wolf could cross an ice bridge in three to six hours.

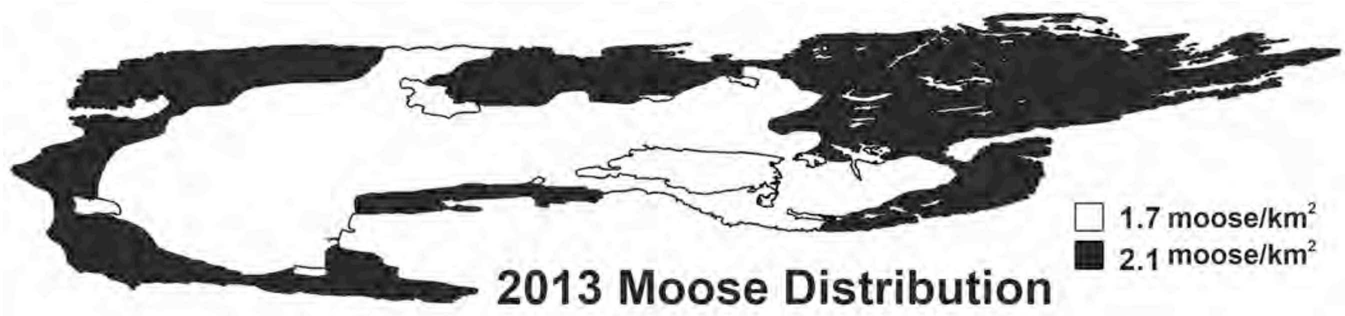
The available evidence suggests the Isle Royale wolf population had experienced periodic gene flow throughout much of its history. The concern is that gene flow is much less likely now because ice bridges form far less frequently now, due to anthropogenic climate change.

Figure 9. The alpha male of West Pack in 1972 was a black wolf and an immigrant from the mainland.

The Moose Population

The 2014 moose survey began on February 1st and ended on February 27th. The survey resulted in an estimated abundance of 1050 moose. The 80% confidence intervals on this

Figure 10. Moose distribution on Isle Royale in 2014 was relatively uniform, as it has been for the past several years. Only two strata were delineated, based on habitat types and results of the aerial counts on 91 plots that comprise 17 percent of the main island area.



estimate are [770, 1350], and the 90% confidence intervals are [650, 1540]. Moose density throughout Isle Royale was 2.1 moose/km^2 at the east and west ends of Isle Royale and 1.7 moose/km^2 in the middle portion of Isle Royale (Fig. 10). Flying conditions for the count were good (i.e., not too windy). The snow was deeper than is typical. As a result most moose spent time under thick vegetation, where the snow is less deep, but the moose are very difficult to detect. Using the techniques described in the 2009-10 Annual Report, we calculated this year's estimate of moose abundance using a sightability factor of 62%. Last year, we estimated 975 moose, with an 80% confidence interval of [750, 1230]. These and earlier counts suggest that the moose population declined during 2002–07, from approximately 1100 moose to approximately 400 moose; and then began increasing to its current level of about 1050 moose (Fig. 1). These moose estimates 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.

Of the moose that we observed on the census plots in 2014, 12% (of 119) were calves. This rate of recruitment is near the long-term average.

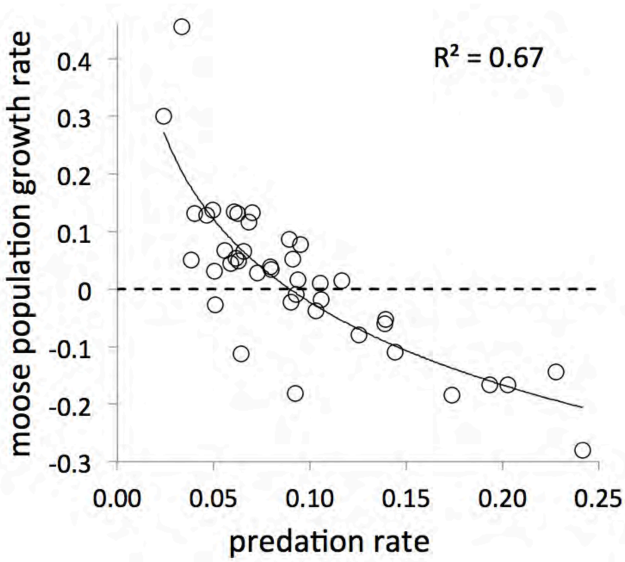


Figure 11. The influence of predation rate on growth rate of the moose population for the period, 1971-2013. The growth rate for 2011 (0.46) is likely an overestimate, the result of unusual counting conditions in winter 2011 and 2012. Nevertheless, the relationship between predation rate and growth rate is not significantly influenced by the inclusion or omission of that observation.

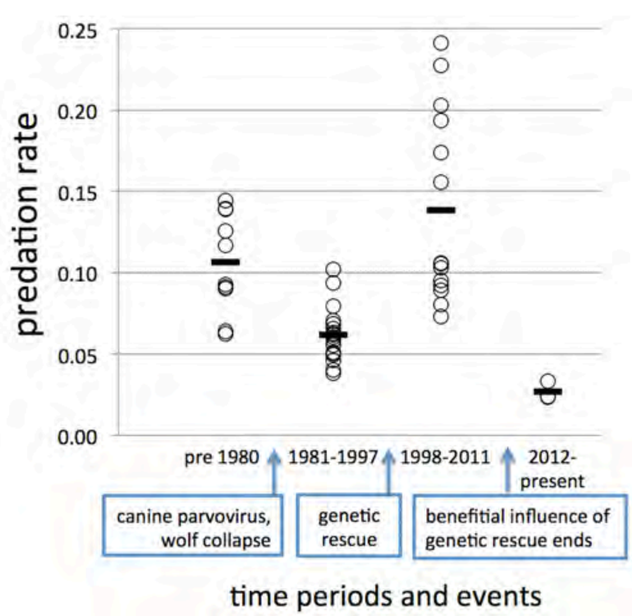


Figure 12. Predation rate during each of several time periods throughout the history of observing predation dynamics on Isle Royale. Boxes with arrows indicate the events triggering shifts from one time period to the next (see text for details).

Recruitment rate is important because it explains about half the variation that we observed in moose population growth rate (see Fig. 11 of the 2012-2013 Annual Report).

The moose population has not been limited by wolf predation for the past three years (see below). Vegetation is also still plentiful (see below). Consequently, the primary limiting factor for the moose population has been winter severity. Moreover, the past two winters have been severe, each in their own way. In particular, spring 2013 arrived late, and the winter of 2013-14 was characterized by unusually deep snow.

This winter we observed only one set of twins, fewer than we have observed in recent years. We also observed ten moose that still had antlers, including two as late as February 16th. See the 2012-13 Annual Report for an interpretation of the significance of those observations.

Each spring we estimate the degree to which moose had been impacted by winter ticks (*Dermacentor albipictus*) during the preceding winter. This is done by photographing moose and estimating how much hair they have lost during the preceding winter. It is thought that tick abundance has been high since 2001, when monitoring began. Ticks peaked in 2007 and then declined until 2010. For the past two years, tick abundance has been near the long-term average.

The effect of wolf predation on moose

Predation rate is the estimated proportion of moose (>9 months old) that are killed annually by wolves. Predation rate indicates the strength of predation pressure on the moose population and the degree to which wolves are performing their ecological function. For the period during which estimates of predation rate exist (1971-2014), predation rate has been the strongest predictor of growth rate for the moose population (Fig. 11).

The manner in which predation rate has varied over time is also important (Fig. 12). Prior to 1980 the average predation rate had been 10.7% (±0.1%, SE) and had a significant influence on moose abundance.

In the early 1980s, the wolf population crashed by 80% due to the synergistic effects of food stress and a disease (canine parvovirus) that was very likely introduced by humans. During that time, the population also suffered increasingly from inbreeding depression (The evidence for this claim is associated with the genetic consequences of the Old Grey Guy). Wolf abundance remained low for

Figure 13. Balsam fir represents a primary source of food for Isle Royale moose during the winter. Image by George Desort.

Figure 14. For decades fir trees in the western portion of Isle Royale have been severely browsed by moose. The browsing is intense enough to have severely altered the shape of most trees. Many fir trees that are only a meter tall are also more than forty years old.

more than a decade and mean predation rate dropped to 6.2% (±0.4%). With that reduction in predation, the density of moose increased dramatically from 1.5 to 5 moose/km^2 over the period 1981-1995 (Fig. 1). The result was severe overbrowsing of the forest.

In the late 1990s two events triggered another sustained shift in predation dynamics. In 1996 a severe winter interacted with food stress and about 80% of the moose population died from starvation. In 1997 a wolf immigrated to Isle Royale, resulting in a genetic rescue of the wolf population. With those events, mean predation rate increased to 13.8% (±1.6), moose abundance declined to its lowest level (Fig. 1), and balsam fir responded with increased growth (see below).

As the beneficial effects of genetic rescue ended (see pages 7-8) and as wolf abundance has declined in the past few years, predation rate has dropped to the lowest level ever observed. For the past three years (2012-2014), mean predation rate has been 2.7% (±0.3). During this period moose abundance has doubled. That increase will likely have a significant impact on the vegetation of Isle Royale.

The effect of moose on balsam fir

Balsam fir trees are a foundation that support wolf-moose dynamics on Isle Royale. Fir is a dominant source of food for moose during the winter (Fig. 13). Fir are common in two areas of Isle Royale, the eastern portion (~25% of the island's area) and most habitats throughout the remainder of the island that are within approximately one to two kilometers of the Lake Superior shoreline (~25% of Isle Royale's area, hereafter the "western" portion). That spatial distribution sets the stage for where most wolf-moose dynamics occur on the island. Moose density is typically three to six times greater in these regions of Isle Royale where fir are common, compared to regions where they are rare or absent. Wolves spend most of their time in these regions where moose are more abundant (see the sidebar, *Where Wolves Prefer To Be*, in the 2011-12 Annual Report).

Life for balsam fir trees varies considerably across the Isle Royale landscape. In the eastern portion, fir is present in every size class from seedling to canopy tree. While browsing pressure by moose varies considerably over time, it is not high enough to suppress the growth of fir trees in any significant manner in most years in this eastern region.

Life on the west side is different. On the west side, where fir are common, they exist either as senescent canopy trees, established roughly a century ago before moose became abundant, or they have for decades been shorter than about 1.5 meters. In those regions, fir has been prevented from growing into the canopy by a century of moose browsing, and many short firs have a morphology reflecting decades of severe browsing (Fig. 14). These differences between

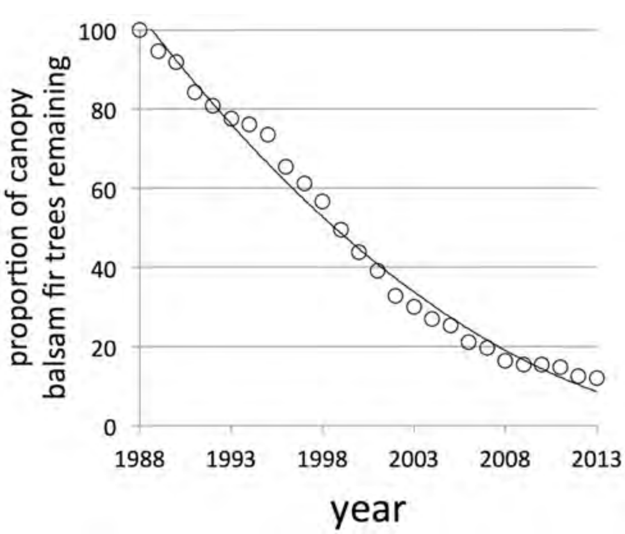


Figure 15. Proportion of canopy balsam fir trees that were tagged in 1988 and are still alive during each year. These dying canopy trees have not been replaced by younger fir trees due to intense moose herbivory.

Figure 16. Moose abundance increased dramatically during the mid 1990s when wolf predation was unable to limit the increase in their abundance. Moose then severely depleted their food supply, browsing many trees so severely that they died. Wolf predation had been impaired in those years by inbreeding depression which was as likely exacerbated by a disease that was likely introduced by humans.

Figure 17. Temporal trends in the rate at which moose browse balsam fir trees in relationship to the density of moose for the period, 2003-2013. Browse rate is the proportion of trees from the east end of Isle Royale, between 0.5 and 3.0 meters tall, that were terminally browsed.

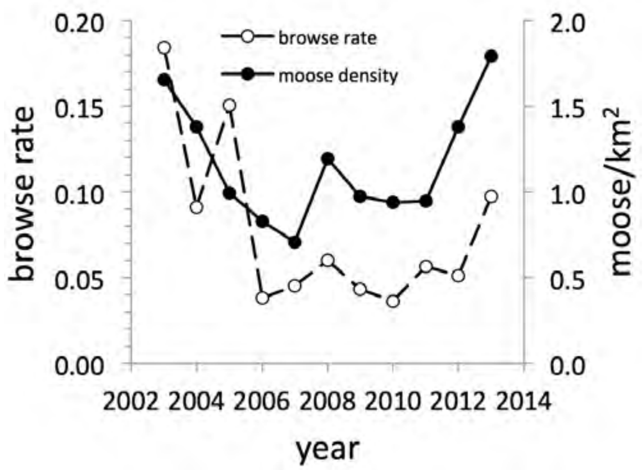
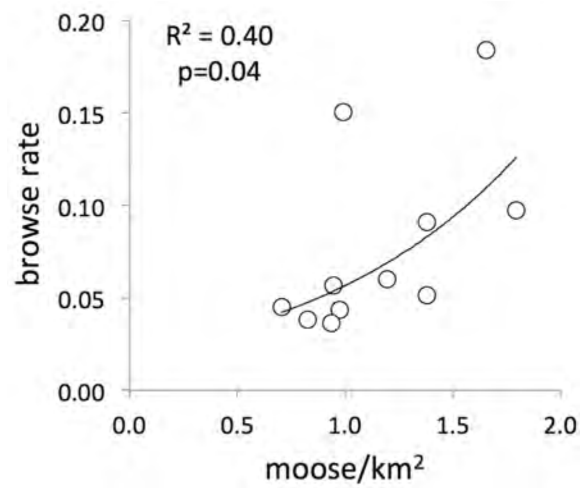


Figure 18. The relationship between moose density and browse rate. Data are the same as that depicted in Figure 17.



the eastern and western portions of Isle Royale are likely a result of differences in soil quality which is a consequence of glacial history.

Large canopy trees are the only source of seeds to regenerate balsam fir. Because of their age, canopy trees in the western region have been rapidly dying and will soon be functionally absent (Fig. 15). Some short balsam firs might have grown into the canopy in the late 1980s and early 1990s were it not for the dramatic increase in moose abundance during those years (Fig. 1). That increase in moose abundance resulted from the loss of wolves during those years, which was caused in part by a human-introduced disease, whose effect was likely exacerbated by inbreeding depression.

During the mid 1990s intensive moose browsing killed many fir trees. On one survey plot in 1996, moose browsing killed 17% of the fir trees. They also broke the vertical stems of trees whose tops were out of reach, reducing their height by as much as a meter (Fig. 16). The indirect impact of that reduced wolf abundance on balsam fir trees was first reported in a 1994 *Science* article – the first trophic cascade to be documented in a large terrestrial ecosystem.

The most severe winter on record in this region occurred in 1995-96. The moose population collapsed that year, and a year later a wolf immigrated from the mainland. With that infusion of new genes, inbreeding depression was mitigated for almost two decades. Those two events contributed to a protracted period of extremely low moose abundance (2005-2011, Fig. 1).

Shortly after moose abundance declined, so too did the rate at which they browsed on fir trees (Figs. 17, 18). As a result, fir trees on the western portion of Isle Royale began growing at a rate not previously observed (Fig. 19). By 2014, many firs in the western region were reaching a height at which they will soon grow out of the reach of moose herbivory, grow into the canopy, and begin to produce seeds that would result in the next generation of fir trees.

This potential growth into the canopy is an event that has not occurred in more than a century in the western region of Isle Royale. However its occurrence will likely depend on whether and how quickly wolf predation is restored (Fig. 12). In the most recent three-year period during which predation has been impaired (Fig. 11), moose abundance approximately doubled (Fig. 1). Unless the next five winters are especially harsh moose abundance is likely to increase to a level that would result in a significant risk of causing significant and long-lasting harm to Isle Royale's forest.

If enough short fir trees do not escape into the canopy in the near future, the likely eventual result will be a virtual absence of fir trees from most of Isle Royale, excepting the eastern portion of the island. That loss would not be mitigated by the subsequent restoration of predation.

Other Wildlife

The impairment of wolf predation is also the likely explanation for the dramatic rise in the abundance of beaver colonies observed in recent years. Between 2010 and 2012, the same period of time during which wolf predation dropped to low levels (Fig. 12), the number of beaver colonies increased by 69% (Fig. 20).

Ravens and wolves are also known to have a strong connection. Raven abundance has been on the decline for the past 17 years, the period for which data are available (Fig. 20). Throughout that period the decline in raven abundance is significantly

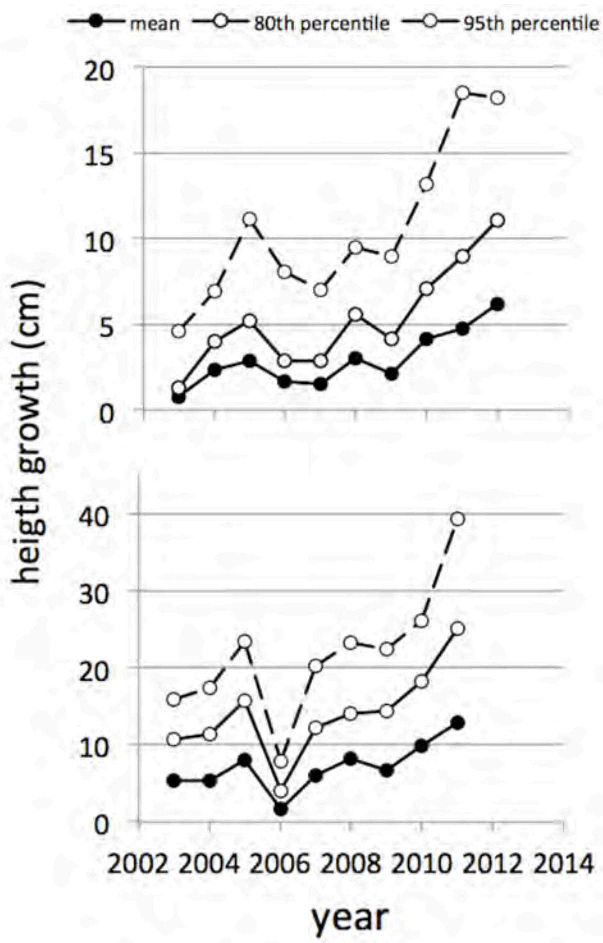


Figure 19. Temporal trends in the height growth of balsam fir trees for the western (upper panel) and eastern (lower panel) portions of Isle Royale. The increase in height growth is a result of declining moose abundance. If moose density and browse rates continue to increase, these increases in height growth are unlikely to continue. The sharp decline in growth for 2006 is likely the influence of drought.

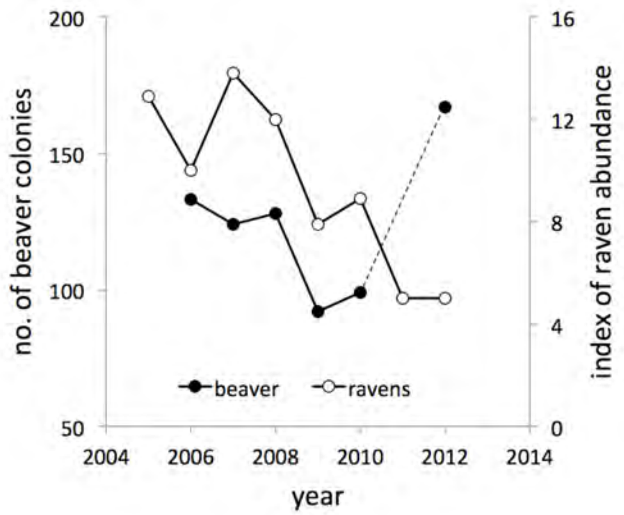


Figure 20. The number of beaver colonies increased by 70% between 2010 and 2012, which corresponds to the period of time when wolf predation had become severely impaired. An index of raven abundance measured during the summer time exhibited a long-term decline in ravens. Raven data were taken from a 2013 NPS report prepared by A. Egan and T. Gostomski. The beaver data were collected by M. Romanski (NPS) and Rolf Peterson.

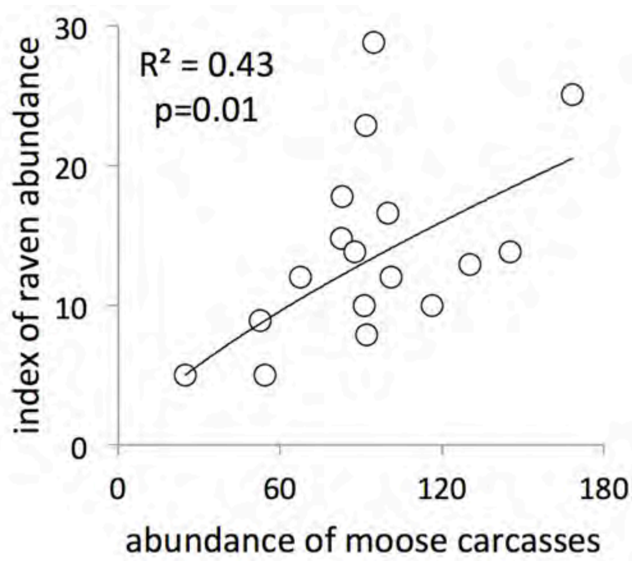


Figure 21. The decline in raven abundance is significantly correlated with the number of moose carcasses that are provided by wolves each year, which is calculated as the predation rate times the number of moose.

correlated with the declining number of carcasses that wolves provide (Fig. 21). Further research may be required to better understand the explanation for those correlations.

Snowshoe hares were extraordinarily abundant during summer 2013, for the second consecutive year. Foxes have exhibited a long term decline over the past 15 years.

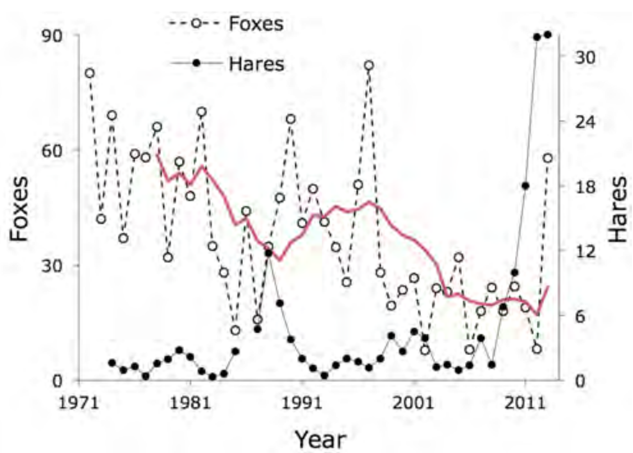


Figure 22. Indices of abundance for red foxes and snowshoe hares on Isle Royale, 1974–present. The hare index is the number of hares seen per 100 km of summer hiking. The fox index is the number seen from the plane during Winter Study. More specifically, the sum of the maximum number seen at kills and the number seen otherwise per every 100 hours of flight time. The declining (red) line is a 7-year moving average for the index of fox abundance.

Weather, Climate, and Ice

Winter weather in 2014 was distinctly cold and windy. Winter snow cover probably began in early December on Isle Royale, and we found snow depths up to 60 cm when we arrived on Isle Royale in mid-January (Fig. 24). Lacking any thawing temperatures, snow was consistently soft without crusts through the entire Winter Study. Snow depth increased through the Winter Study, peaking at 100cm in late February. Snow reduced mobility for both moose and wolves for most of the winter study in 2014.

Temperatures were notably cold during the winter study in 2014, with daily low temperature usually less than -20 degrees C (Fig. 23). Maximum temperature reached 0 degrees C just twice, and only briefly, but not enough to form surface crusts on the snow.

During the 2014 winter study we observed an ice bridge on two separate occasions, totaling 17 days. This ice connection was just the second in 17 years. For context, ice bridges formed during 7 of 10 years during the 1960s (Fig. 23). Anthropogenic climate change is the cause of the declining frequency of ice bridges.

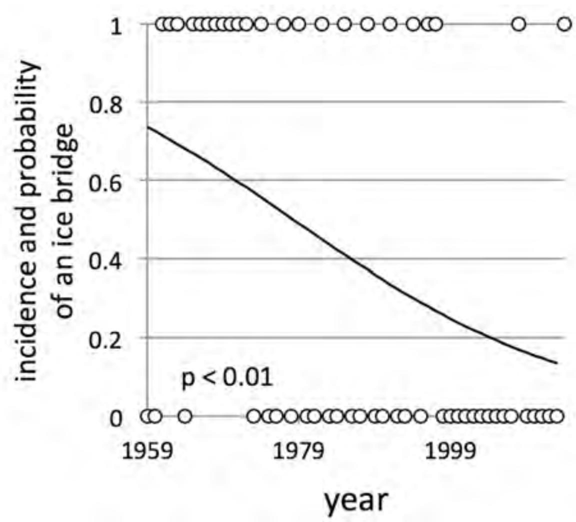


Figure 23. Incidence and probability of an ice bridge forming between Isle Royale and the mainland for the period 1959-2014. This year's ice bridge has not changed the overall tendency for ice bridges to be far less frequent over time.

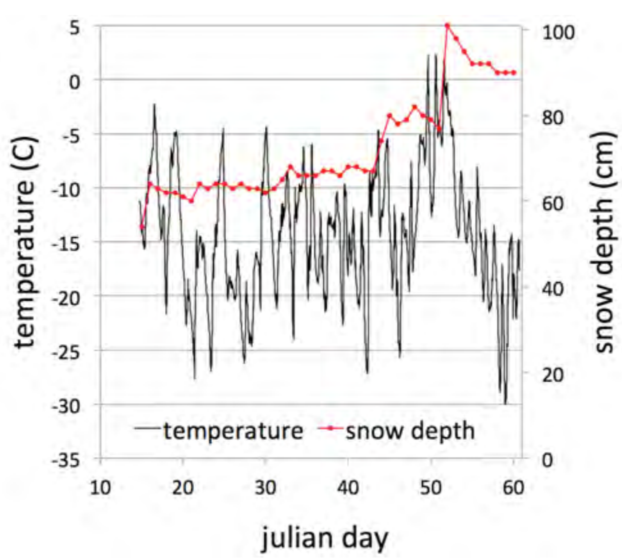


Figure 24. Snow depth (daily) and ambient temperature (30 minute intervals) during the 2014 Winter Study on Isle Royale.

Wild Wolves We Have Known

is a new collection of essays published by the International Wolf Center and written by wolf biologists from around the world. The essays celebrate the value of individual wolves. The collection includes an essay by Rolf Peterson about the Old Grey Guy. The collection is also introduced with an essay by John Vucetich. Here is an excerpt (reprinted with permission):

"*Understanding the life of a wolf – how it is the same and how it is different than ours – helps us understand ourselves and our humanity. The most remarkable lesson to learn from stories of individual wolves is also the simplest: The most important similarity between you and a wolf is that you both experience a life. That lesson is so simple and easy to overlook it merits being repeated – wolves are experiencers of life. Life breathes and respires. It is created, transformed, and recreated. Life is complicated, interconnected, and contingent beyond our imagination. It is material, energy, and experience flowing across landscapes, over time, and through the hierarchy of life – genes, organisms, populations, and ecosystems. Understanding that hierarchy of life is critical for understanding our relationship with nature…*

Too often, we create circumstances where we feel we must kill individuals of one species to protect some aspect of ecosystem health... Do two wrongs really make it right? The solution involves greater respect for life at each level in the great hierarchy. And the solution almost certainly involves better understanding the lives of individual organisms.

This book is an opportunity to develop such an understanding, in this case for wolves. Understanding the life of an organism from its perspective should generate not so much respect, but empathy. Empathy is vivid, knowledge-based imagination about another's circumstances, situation, or perspective. Empathy tends to generate care, sociopaths excluded...

The similarities we share with wolves are considerable. Many arise from a central nervous system that we inherited from a common ancestor that lived some 40 to 60 million years ago, during the early days of mammalian evolution. Other similarities rise from the adaptations associated with living intensely social lives.

The idea of anthropomorphism, which literally means "turn into a human," raises another concern. Wolves are certainly not human, and we possess capabilities that they do not. But it is an entirely separate concern to ask, Is a wolf a person? The etymological root of person is a Greek word that means "mask," referring to the mask an actor would wear on stage. A person is an actor in the world. And so Shakespeare wrote, "All the world's a stage, and all the men and women merely players." Possessing [the traits that wolves do] – sensory consciousness, memory, dreams, intentions, personality, emotions – certainly qualifies as being an actor in the world, as the experiencer of a life. It is perfectly right to treat our dogs as people. Native Americans were certain that wolves and many other creatures were people.

The essays in this book present us with two basic opportunities. After hearing the stories of a few individual wolves, you will be only a tiny step away from realizing that every wolf that has ever lived has a story to tell. When you see a wolf track, hear a wolf howl, or if you are lucky enough to catch a glimpse of a wolf as it slips over the hill or into the forest's shadow – you will know that wolf has a story. You just won't know the details of that story. Wolves are like all the people we brush past in our own lives; people whose names we never learn. They all have a story. With some knowledge we can imagine those stories, and they are true. Some are tragic and others triumphant. We just don't know who is living which life. With that realization, you will be only a step away from realizing that all mammals experience lives – elk, deer mice, leopard seals… Imagine, if you can, the life of a leopard seal. Each has a story to tell and a life with which to empathize. It is true of all vertebrates – all creatures, in fact. If you think, for example, it is impossible to empathize with the life of a plant, then you might pick up (after reading this book) a copy of Shel Silverstein's The Giving Tree. If you think it is impossible to empathize with individuals and ecosystems at the same time, you might consider Aldo Leopold's Thinking Like a Mountain."

The essays in *Wild Wolves We Have Known* are interesting for serving, in part, the same purpose that motivates a great deal of research conducted on wolves. They represent different ways of coming to understand how we ought to relate to the natural world around us.

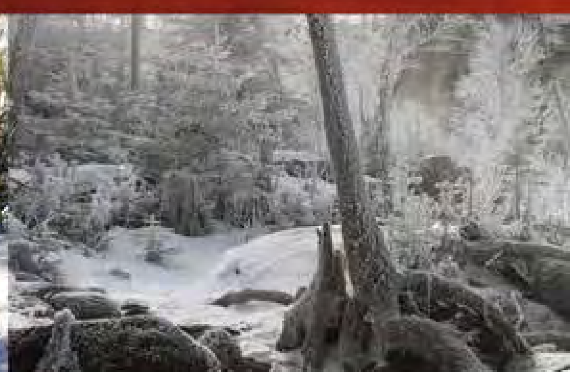
"[There are some areas] in which the top of every tree is broken off, and there is little else to eat except bark. No poplar reproduction was noted. The winter moose food is practically gone from the island."

- Adolph Murie's description of the impact of moose on Isle Royale in the absence of wolves in 1930

". . . The one outstanding thing was the frightful conditions of the range. Throughout this section one cannot find a juniper, or Douglas fir that has not been browsed to the reaching limit. Many trees are dead from this. There is no reproduction. Willows are browsed and battered. The sagebrush has been hammered down. . . . The soil has been packed by countless game trails and is badly cut up. Truly this range looks worse than anything I have seen on the Kaibab."

- George M. Wright's description of the impact of elk on Yellowstone National Park in the absence of wolves in 1932





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