

Ecological Studies of Wolves on Isle Royale

Wolves

2012-2013





“The interrelationships of predation are exceedingly complex and variable, and how much they will ever be understood is problematical.”

—Paul L. Errington (1936)



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Annual Report 2012–13

by

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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Results reported here are preliminary and, in some cases, represent findings of collaborators; please do not cite without consulting the authors.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.



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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 55th 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, unable to leave. 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. So 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 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 2012, ground-based fieldwork continued from late April through mid-October. Rolf Peterson and John Vucetich directed that fieldwork with assistance from Ellie Cosgrove, Ryan Oleynik, David Rolfes, Ethan Toczko, Carolyn Peterson, and Leah Vucetich. Leah Vucetich also led a number of people working in our lab, especially Marcy Erickson, Megan Baker, Natasha Fetzer, Nora Heikkinen, Scott Larson, Theodore Maynard, Jake Moran, and Kyle Yarusso.

In April 2012 we attempted to radio-collar wolves. That field effort included Bob & Sally Irmiger, Leah Vucetich and, from the National Park Service, Kevin Castle, Jenny Powers, Rob Bell, Caitlin Clarke, and Mark Romanski. During the course of the year, many park staff and visitors contributed key observations and reports of wolf sightings and moose bones.

In 2013, the annual Winter Study extended from January 17 to February 24. John Vucetich, Rolf Peterson, and pilot Don E. Glaser participated in the entire study, assisted by Ky and Lisa Koitzsch. Ky and Lisa's efforts focused on collecting urine (yellow snow) and pellet samples to assess nutritional condition of moose. Bob Glaser, Mark Romanski, and Rob Bell provided ground transportation and helped

with logistical matters on the mainland. US Forest Service pilots Tim Bercher and Scott Miller flew supply flights to Isle Royale from Ely, Minnesota. A daily account of Winter Study's events and activities are recorded in Notes from the Field, which is available at the project's website (www.isleroyalewolf.org).

Summary

From mid-January to late February 2013, we conducted the fifty-fifth annual Winter Study of wolves and moose on Isle Royale. Between January 2012 and January 2013, the wolf population declined from 9 to 8 (Fig. 1), the lowest number of wolves ever observed in the population. During the past year, mortality rates were low (11%), with just one wolf dying. There was no evidence of any reproduction during the past year. This is the first year in the project's history that we have been unable to document reproduction. Analysis of DNA extracted from wolf scat collected in January and February 2012, and the pattern of mortality during the past year, indicate that the population is comprised of between three and five females. The lack of reproduction is not due to a shortage of females.

For the past two years, the moose population has

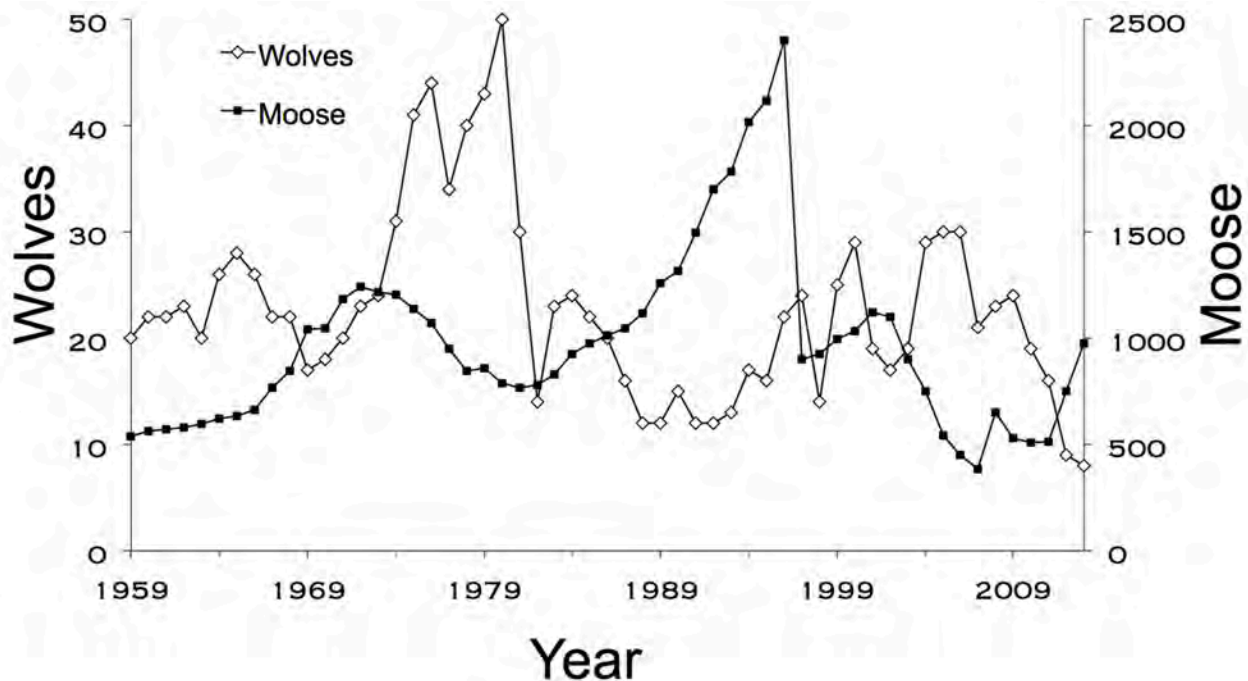


Figure 1. Wolf and moose fluctuations, Isle Royale National Park, 1959-2013. Moose population estimates during 1959–2001 were based on population reconstruction from recoveries of dead moose, whereas estimates from 2002–13 were based on aerial surveys.



Figure 2. Seven of the eight wolves in this year's population on Isle Royale. These wolves are the West-end Trio (upper left), which is comprised of last year's west-end duo, plus a male that dispersed from Chippewa Harbor Pack. The Chippewa Harbor Trio (below), which are remnants of Chippewa Harbor Pack, and a lone female wolf (lower left) who also dispersed from Chippewa Harbor Pack.



grown considerably. In February 2013, we estimated moose abundance to be 975, with 90% confidence intervals of [725, 1220] (Fig. 1). Moose abundance has increased from its lowest recorded level of approximately 400 moose in 2006 to a level that is near the long-term average.

Per capita kill rate, which indicates how well-fed the wolves have been, was 1.3 moose/wolf/month during winter 2013, approximately three times the rate observed in the previous year. The annual predation rate, which is the proportion of moose (>9 months of age) killed by wolves throughout the year, extrapolated from winter kill rate, was 2.4%. This is the lowest value ever observed. Calves comprised 21% of the moose population during winter 2013,

which is one of the highest rates of recruitment ever observed in this population.

The intensity of winter ticks that infest moose had declined for three consecutive years (2008-2010). For the past two years, however, tick infestations increased. In Spring 2012, levels of infestation were near their long-term average, when indexed by the amount of hair loss that moose suffer.

The moose-to-wolf ratio gradually increased from its all-time low of 15 in 2006 to 32 in 2011. Since that time, the ratio has risen dramatically to 122, well above the long-term average.

The Wolf Population

In late January 2013, we counted 8 wolves in the population. Wolf abundance was down from last year's count of 9 wolves, reaching the lowest on Isle Royale since studies began in 1959. Since 2009, the population has declined by 66%, from 24 to 8 wolves

(Fig. 1). The wolves were organized into two groups and two lone wolves (Fig. 2):

Chippewa Harbor Trio (CHP).....	3
West-end Trio (WT).....	3
Loners.....	2
2013 Total.....	8

This past year’s wolf decline was the result of high survival and apparently zero reproduction (Fig. 3). With only one wolf thought to have died during the past year, the mortality rate was 11%. For context, mortality and recruitment rates are typically around 25%. Several factors likely account for the low mortality. First, per capita kill rate, which represents the supply of food for wolves, was among the highest we have ever observed (see below). Second, the wolf population is comprised of relatively young individuals. In particular, analysis of DNA extracted from fecal samples indicate that most individuals in the population are four years of age or younger.

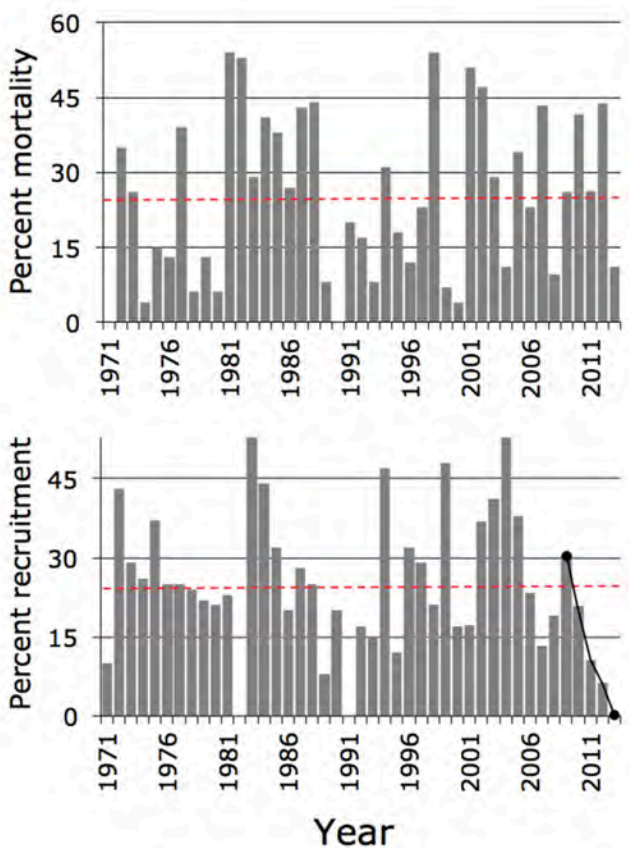


Figure 3. Percent mortality and recruitment for Isle Royale wolves, 1971-present. The dotted lines mark long-term averages. The black line in the lower panel highlights a five-year decline in recruitment.

This young age distribution is, in part, the result of many older individuals dying between January 2011 and January 2012, when the mortality rate was 0.44. In June 2012, we discovered another source of mortality from that prior period of time, 2011-2012. That is, we discovered that three of the seven wolves that died that year had drowned in a mine pit. This particular mine pit is a steep and deep hole, about 200 ft² in size and filled with water up to within about 10 feet of the earth’s surface. This mine pit, a remnant of historic mining in the 19th century, is one of many in the wilderness area of the island.

The extraordinary observation this past year is the apparent lack of reproduction. In only two other previous years did the winter population appear to include no pups. One of those years (1981) was associated with the first time that humans unintentionally introduced canine parvovirus to the population.

In 2013 we observed three wolves living at the west end of Isle Royale. They were the West-end Duo and a wolf that has been nicknamed Pip. We now refer to these wolves as the West-end Trio. Pip is a collared male that was born in Chippewa Harbor Pack in 2008. None of those three wolves was a pup. We also observed three wolves in Chippewa Harbor Pack. Their behavior and appearance all suggest they were adults. Because this pack appears not to have reproduced in the past year, we now refer to them as the Chippewa Harbor Trio. Genetic analysis of fecal samples collected from that group of wolves may be able to confirm that each of those wolves had been alive in previous years. At this moment, there is no funding available to conduct such analyses. Of the two lone wolves that we observed, one is a collared female that was born in Chippewa Harbor Pack in 2009. The other lone wolf is of unidentified sex and almost certainly a dispersing wolf from Chippewa Harbor Pack that we observed in the territory of the West-end Trio. One would not expect that wolf to be a pup.

Recruitment rate is the percent of the population that are pups who survived to see their first winter. While zero recruitment is rare, occurring about once every twenty years in this population; we also failed to detect any sign that pups had even been born this past year. This is the first year since 1971 that we did not detect pups at any point in the summer.

We also failed to detect signs of courtship or mating in Chippewa Harbor Pack last winter (February-March of 2012). Each possible male-female pairing in that pack likely represents a parent-

Figure 4. Two wolves from the West-end Trio feeding from the carcass of a moose that they scavenged.



offspring or a brother-sister combination. Matings between such close relatives have been observed on many occasions on Isle Royale. However, most mammals including most wolf populations avoid mating with such close relatives. It is possible that lack of courtship and mating is a manifestation of inbreeding avoidance. By contrast, we detected signs of courtship and mating in the West-end Duo in late winter (February-March 2012), but we did not detect sign that any pups had been born to those two wolves.

During this winter season (February 2013), we observed signs of courtship in the West-end Trio, but no signs of mating. In particular, on several occasions, we observed this pair of wolves walking parallel to each other and the male sniffing the genitalia of the female. We did not observe signs of courtship or mating in Chippewa Harbor Pack this winter. However, we were unable to observe this pack on enough occasions this winter to draw even speculative conclusions about their reproductive behaviors.

Kill Rates

In winter 2013, we observed the West-end Trio throughout a 31-day period. During that time they killed two moose and fed from the carcasses of two other moose that we suspect they had not killed, but only scavenged (Fig. 4). These statistics correspond to a per capita “kill rate” of approximately 1.3 moose per wolf per month. This rate is among the highest that we have ever observed (Fig. 5). The presence of so many moose and so few wolves may mean that a larger portion of moose are dying of starvation or old age before wolves have a chance to kill them, allowing wolves to scavenge a larger portion of the food they consume. We were unable to estimate kill rate for the Chippewa Harbor Pack due to a lack of radio-collared wolves, which improves observation rate, and persistently poor weather that prevented us from flying over their territory often enough to find them.

We conducted necropsies on three moose

carcasses in winter 2013. Two of these were killed by the west end trio, and one was killed by the Chippewa Harbor Pack (Fig. 6). All three moose suffered from severe arthritis.

Causes of wolf population decline

In the 2012 Annual Report, we explained how low rates of recruitment and survival that have been

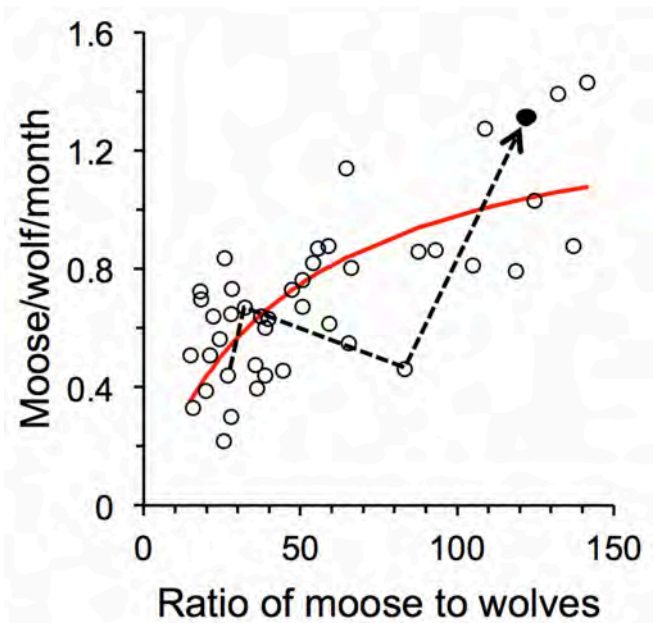


Figure 5. Relationship between ratio of moose-to-wolves and number of moose consumed per wolf per month, 1971-2013. The number of moose consumed is the number killed, plus those scavenged. The filled circle is the observation for 2013. The dotted arrow traces the past several years, showing how the kill rate and ratio of moose-to-wolves has increased dramatically over the past several years.

2013 Wolf Territories and Kill Locations



Figure 6. Wolf pack territorial boundaries and moose carcasses found during the Winter Study in 2013. We did not observe the Chippewa Harbor Trio frequently enough to find all of the moose carcasses from which they fed. This year's estimate of kill rate is based on observations from the West-end Trio.

causing the population to decline in recent years is likely attributable to some combination of the following factors: genetic deterioration, skewed sex ratio, disease, and declining food supply. At present, it seems that skewed sex ratio and food supply are not limiting factors.

Food supply. - The influence of food supply is complicated and depends on a number of countervailing processes. First, the abundance of old moose is an important indicator of food availability for Isle Royale wolves. Because the moose population experienced very low calf recruitment between 2002 and 2008, we expect old moose to be less common between about 2012 and 2020.

Second, wolves can also prosper when calves are abundant, as was the case this winter. We did not observe the wolves to kill any calves. This is noteworthy, because wolves routinely kill calves, except when calves are quite rare.

Third, per capita kill rate is another important indicator of food supply. Low rates of prey consumption in two of the past three years (2010 and 2012) very well may have played a role in declining wolf abundance during those years. However, kill rate was very high this winter (Fig. 5). High kill rates are likely the result of a high number of moose per wolf (Fig. 5), probably enabled by the large number of calves in the population (see below).

Other important insights about how wolf demography is affected by food supply is described in *Wolf DNA reveals complicated demography* (page 8).

Sex Ratio. - Genetic analyses from Feb 2010 and field observation from Feb 2011, suggested that the wolf

population may have been comprised of no more than two adult females in Feb 2011. Funding limitation prevented us from analyzing genetic samples from Jan/Feb 2011 or Jan/Feb 2012 until just recently. From those analyses, completed in Jan 2013, we learned that four or five of the nine wolves in the February 2012 population were females. With only one wolf having died in the past year, the population is no longer limited by the number of females.

Genetics. - Considerable evidence suggests that the Isle Royale wolf population is highly inbred and has been impacted by genetic deterioration. First, the population was founded in the late 1940s about 15 wolf generations ago. Analyses of mitochondrial DNA and the Y chromosome suggests that the population was originally founded by only one female and two males (Adams et al. 2011, Proc. R. Soc.). In most years, the population included 3 pairs of reproducing wolves. A demographic model of effective population size (N_e) suggest that N_e has been ~ 3.8 (Peterson et al. 1998, J Mamm).

Second, considerable genetic deterioration likely occurred in the early 1980s when the population declined by 80%, due in large part to canine parvovirus. Abundance did not return to typical levels until the early 1990s. Prior to 1980, wolf abundance was tied tightly to the abundance of old moose; but after 1980 wolf abundance became unrelated to abundance of old moose (Vucetich and Peterson 2004, Oikos). Additionally, mean wolf abundance has been much lower given the number of old moose after 1980, compared to the time prior to 1980. Inbreeding depression seems a plausible explanation for these differences before and after 1980.

Wolf DNA reveals complicated demography

One of the basic goals of ecology is to explain how and why population fluctuations occur. One way to study these fluctuations is to break them down into three basic, annual demographic processes: adult survival, juvenile survival, and recruitment. Adult survival rate is proportion of adults surviving from one year to the next, juvenile survival rate is the proportion of one-year old animals that survived to become two years old, and recruitment rate is the proportion of the population that is comprised of one-year old animals. (A wolf's birthday occurs in late April. But on Isle Royale we observe wolves in winter, when the youngest wolves are about 9 months old. So, for example, we consider recruitment rate to be the number of 9-month old animals in the population during winter.)

Since 1999, we have been analyzing the DNA of Isle Royale wolves extracted from fecal samples. From these analyses, we identify each individual wolf in the population, each year, from their unique genotypes. We estimate the year during which each wolf is recruited by observing the year when its genotype first appeared. We estimate the year of death for each wolf from the year when a wolf's genotype no longer appears in the population. From those patterns and some sophisticated statistical techniques, we estimated rates of survival and recruitment. These estimates are significantly more accurate than those derived from aerial observations alone.

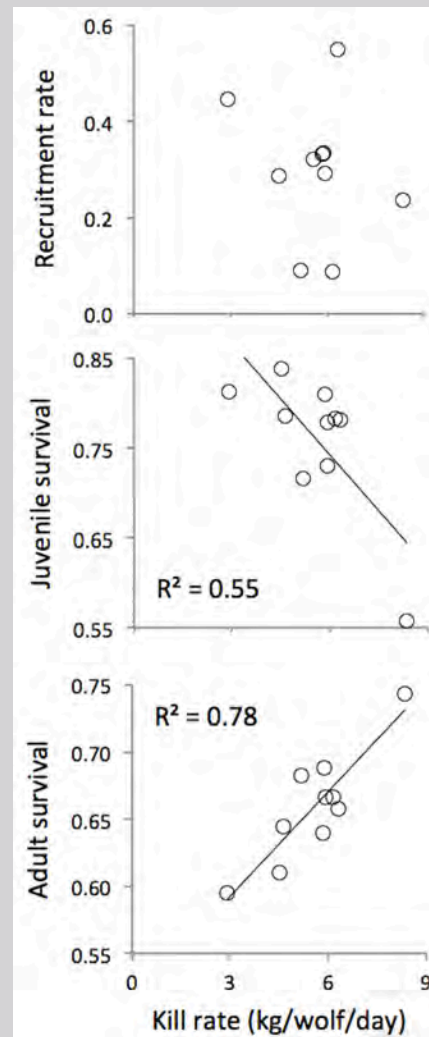
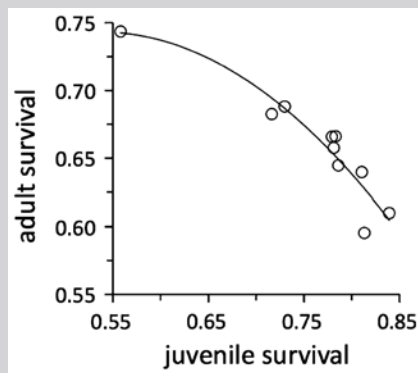
This analysis revealed some interesting patterns. First, juvenile survival tended to be higher than adult survival. This contrasts with many animal populations, where adults tend to have higher survival. Second, juvenile and adult survival were inversely correlated over time. That is, years during which adults had relatively high rates of survival tended to be years when juvenile wolves had relatively low rates of survival (see graph, lower left).

We know from previous research that kill rate (an indication of how much food wolves get each year) explains only a small portion (~20%) of the variation in population fluctuations from year-to-year (Vucetich & Peterson 2004, *Oikos*). Consequently, we were surprised to find that adult survival was strongly correlated with kill rate (see graph, lower right). However, juvenile survival is inversely related to food supply (see graph, middle right), and recruitment is

unrelated to food supply ($p=0.56$, upper right graph).

We do not understand the mechanisms giving rise to these patterns. One vague speculation is that these patterns reflect some complicated interaction between food availability, timing of dispersal (a risky time in a wolf's life), and the how parents' investment in the welfare of their offspring depends on the age of the offspring (pups versus yearlings). Another possibility is that the disconnect between recruitment and kill rate is an unexpected consequence of inbreeding depression. Continued observation and consideration will likely lead to better understanding. Whatever the explanation, these demographic patterns are certainly more complex than we had expected.

This analysis is a collaboration with Francesca Marucco (Turin University, Italy) and Jennifer Adams (Idaho State University). A technical description of these findings can be found in: Marucco F, Vucetich LM, Peterson RO, Adams JR, Vucetich JA. 2012. *Evaluating the efficacy of non-invasive genetic methods and estimating wolf survival during a ten-year period. Conservation Genetics* 13(6):1611-1622.



Third, the incidence of congenital deformities in the vertebral column of Isle Royale wolf population has also been high and on the rise throughout the past several decades (Raikonen et al. 2009, Biol. Cons). We have not collected a normal specimen since 1994.

Fourth, in 1997 a male wolf immigrated from Ontario to Isle Royale by walking across an ice bridge. Inbreeding coefficients plummeted in the years immediately following his arrival, but then began to rise quickly again as the immigrant repeatedly reproduced. Within 2.5 generations of his arrival, he was related to every individual in the population and his ancestry constituted 56 per cent of the population. The superior performance of this immigrant and his lineage, compared to the performance of native Isle Royale wolves, is strong evidence for inbreeding depression in the Isle Royale wolf population.

The immigrant arrived at a time when the moose-to-wolf ratio dropped suddenly. The moose decline was unrelated to wolf predation. Had the immigrant not arrived when he did, the Isle Royale wolf population would likely have declined to dangerously low numbers during that period of low moose-to-wolf ratio. Instead, the genetic input from the immigrant seemed to breathe new life into the population, allowing the population to thrive for over a decade.

Disease. – In April 2009, which marked the beginning of the current population decline, 2 of 6 wolves had antibody levels that indicated exposure to parvovirus, and 1 of 6 wolves had antibody levels that indicate exposure to adenovirus. Under normal circumstances,

neither parvovirus nor adenovirus are expected to impair healthy adult wolves. However, with severe inbreeding, it is possible that the population is vulnerable to such diseases.

The Moose Population

The 2013 moose survey began on January 27th and ended on February 16th. The survey resulted in an estimated abundance of 975 moose. The 80% confidence intervals on this estimate are [750, 1230], and the 90% confidence intervals are [825, 1140]. Moose density throughout Isle Royale was 1.8 moose/km² (Fig. 9). We calculated this year's estimate of moose abundance using a sightability factor of 95%. The flying conditions were excellent (calm wind, overcast). Snow cover was sufficient to cover stumps which distract from seeing moose, but shallow enough to allow moose easy access to deciduous habitats where they are easiest to see. Last year, we estimated 750 moose, with an 80% confidence interval of [610, 895]. 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 975 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.

Figure 8. This winter we observed more twins that recorded in any previous winter study. High twinning rate is a response to improved foraging conditions and low predation rate.

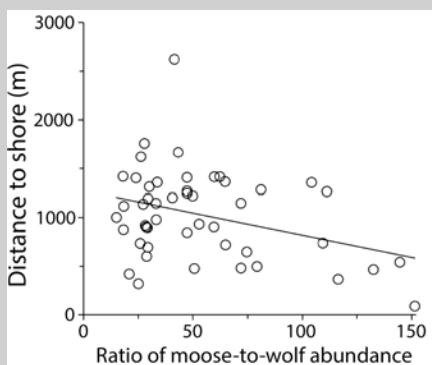


Where the moose are

To a human, Isle Royale might seem like one large, uniformly monotonous forest. But to a moose, Isle Royale is a pretty varied place. One of the most important patterns in habitat on Isle Royale is the tendency for forests near the shoreline of Lake Superior to have more balsam fir and cedar, which moose depend on for forage in the winter. But shorelines are also important travel corridors for wolves during winter (see sidebar in the 2011-2012 Annual Report). Consequently, shoreline habitats are more dangerous, but provide for better foraging; and interior habitats are safer, but provide less food. Each winter, each moose has to decide what kind of life it wants.

When a moose dies on Isle Royale, there is about a 37% chance that we will eventually find its remains. When we do, we record the precise location of that death. Over the years, we have recorded thousands of locations. Each location is a clue about the kind of habitat moose prefer. A few years ago we began a collaboration with a team of scholars from Michigan State University, aiming to put those clues together to see what we might learn.

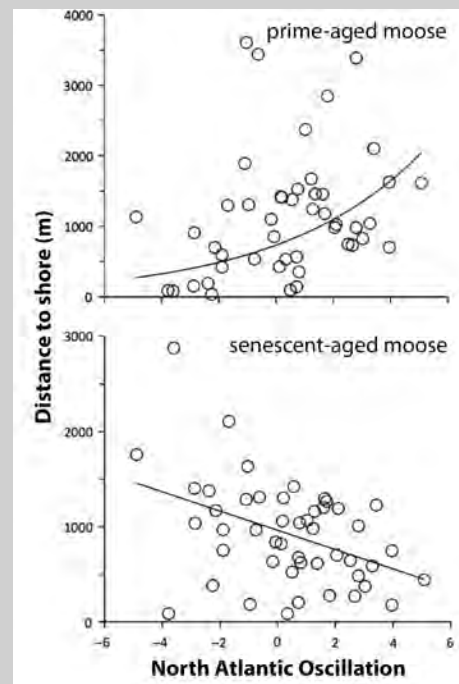
In the graph below, each circle represents observations from a different year. Observations farther to the right represent years of lower predation risk (indexed by the ratio of moose to wolves), and observations to the left represent years with greater predation risk. The vertical position of each



observation is the average of the distances between shoreline and location where each moose died that year. The pattern is pretty scattered, but there is a tendency, a statistically significant trend, for moose to die further from shore (safer habitats with less food) during years when predation risk is greater. That is, in years when predation risk is greatest, more moose tend to spend more time in safer habitats, even though it means less food. Apparently not being killed by a wolf is more important than having high quality foraging opportunities.

Predation risk was not the only factor to influence the kind of habitat that moose prefer. Winter severity also influences what moose consider to be good habitat. To further complicate matters, not all moose choose identical habitats during a severe winter.

The graphs below show what we found. In those graphs, observations farther to the right represent milder winters (indexed by a large-scale weather pattern known as the [North Atlantic Oscillation](#)), and observations to the left represent severe winters. Again, the pattern is noisy, but there is a statistically significant tendency for older moose, who tend to be vulnerable to predation, to die farther from shore (where it is safer) during severe winters, the kind of winter where escaping from predation can be more difficult. Prime-aged moose did the opposite.



Predation, habitat, climatic influences, and life history dynamics, like those that occur as an individual ages from prime- to senescent-aged - these are four major paradigms in evolutionary ecology. This work shows how nature is the result of complex interactions among all of those processes. Despite accounting for all that complexity, the noise in these graphs indicate how much more remains unexplained.

A technical description of these findings can be found in: Montgomery, RA, JA Vucetich, RO Peterson, GJ Roloff, KF Millenbah. 2012. The influence of winter severity, predation, and senescence on moose habitat use. *Journal of Animal Ecology* doi: 10.1111/1365-2656.12000.

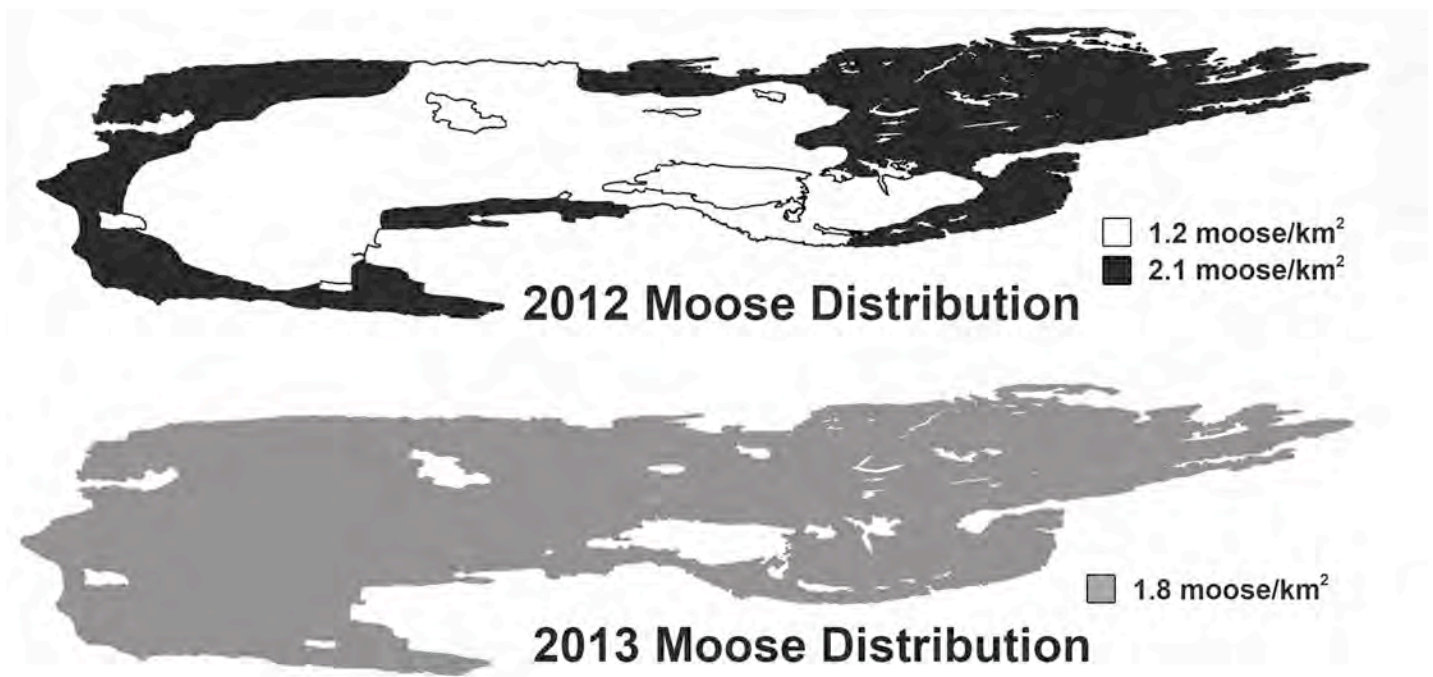


Figure 9. Moose were distributed somewhat unevenly on Isle Royale in 2012 (upper panel). However, as moose abundance increased in 2013, the distribution of moose became more homogenous (lower panel). In particular, low density areas saw more moose in 2013.

The distribution of moose was also different this year, compared to other years. In most years, the east and west ends of Isle Royale exhibit a greater density of moose than does the middle portion of Isle Royale. During last winter, for example, moose density was 1.2 moose/km² in the middle portion of

Isle Royale and 2.1 moose/km² at the east and west ends of Isle Royale. This winter, however, the density was 1.8 moose/km² throughout the entire island, and moose were more uniformly distributed (Fig. 9).

Of the moose that we observed on the census plots in 2013, 21% (37 of 177) were calves (Fig. 10).

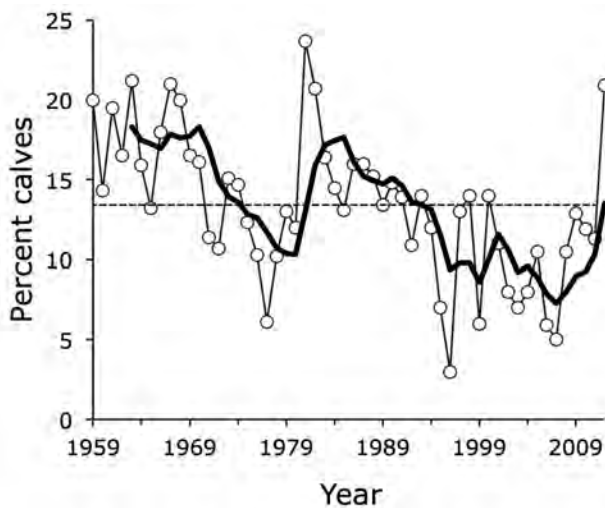


Figure 10. Long-term trends (1959–present) in the percentage of the total moose population that are 8-month old calves. The 50-year average (13.4%) is marked by the light dotted line, and the curved line is a 5-year moving average.

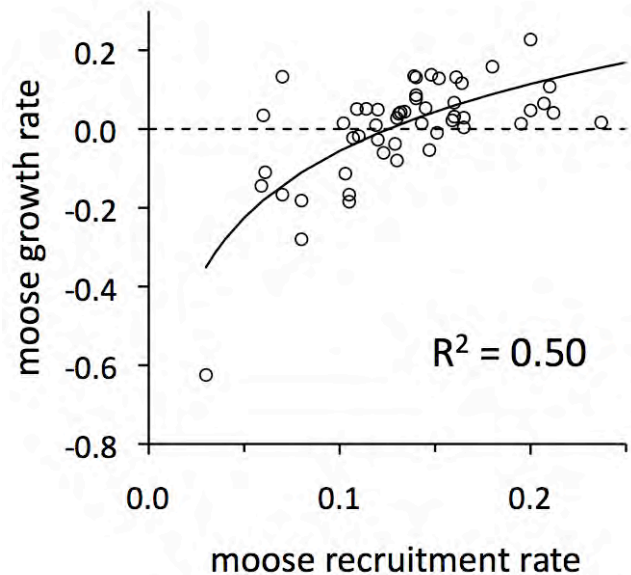


Figure 11. The relationship between moose population growth rate and recruitment rate, 1959–present.

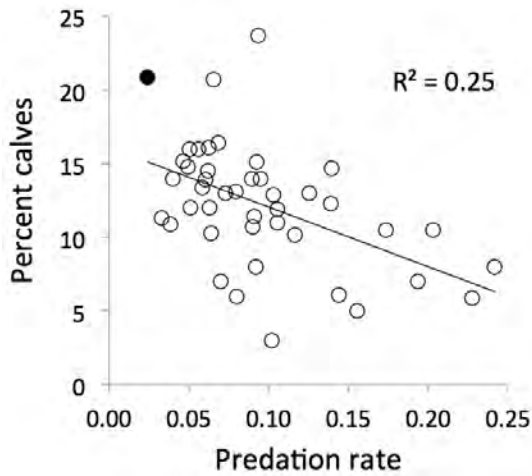


Figure 12. Estimated annual predation rates for Isle Royale moose in relationship to calf recruitment, 1974–present. The filled circle is this year’s observation.

This is one of the highest rates of recruitment that we have ever observed. Recruitment rate is important because it explains about half the variation that we observed in moose population growth rate (Fig. 11).

An important reason for very high calf recruitment is this winter’s very low predation rate. The explanation for this pattern is that wolves, if given a choice, prefer to kill calves, compared to prime-aged

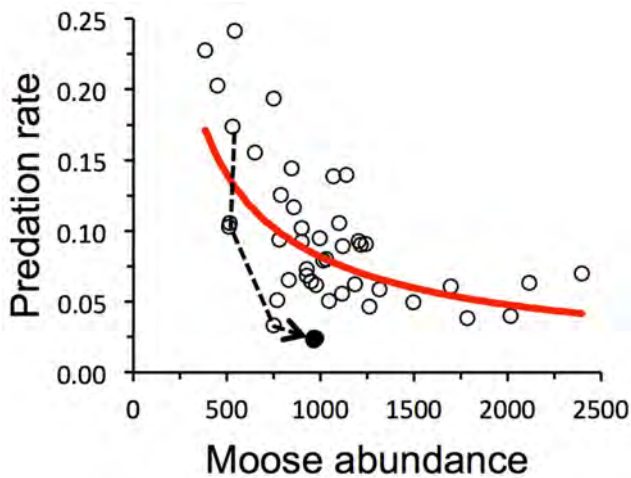


Figure 13. Estimated annual predation rates for Isle Royale moose in relationship to moose abundance, 1974–present. The filled circle is this year’s observation. The dotted arrow traces the past several years, showing how predation rate has declined dramatically as moose abundance has increased.



Figure 14. Fox abundance remains low on Isle Royale, even though snowshoe hares are at an all time high. Foxes depend on carcasses that wolves provide. These carcasses have steadily declined in recent years.

adults. During summer, wolves’ diet is mostly comprised of calves. Consequently, when predation rates are low, more calves tend to survive to see their first winter. This is a pattern we have observed over the past four decades (Fig. 12).

The number of twins that we observe each winter has also increased in recent years. Between winter 2006 and 2009 we observed no twins. We observed three sets of twins in winters 2010 and 2011, combined. We observed three sets of twins in winter 2012. This winter we observed ten sets of twins. That is the most ever observed in fifty-five years of observation.

More than in any year in the past decade, we observed bull moose that still had their antlers in late January. Most moose lose their antlers in late December. However, yearling moose often keep their antlers until late January. This year’s occurrence of antlers is attributable to many calves having been born in spring 2011.

The annual predation rate is the percentage of the moose population (>9 months old) killed during the year by wolves. Annual predation rate can be estimated by multiplying the daily kill rate observed during winter by the ratio of wolves to moose, and then multiplying that quantity by 0.50 to account for the tendency for wolves to kill fewer moose (>9 months old) during the remainder of the year. Annual predation rate, estimated from kill rate observed each winter 2012, has plummeted during

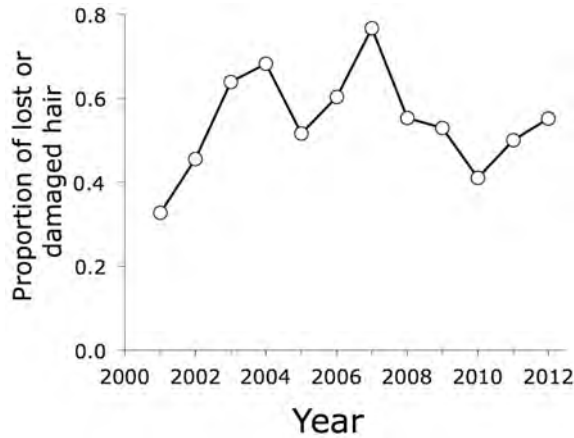


Figure 15. Trends in springtime hair loss for Isle Royale moose, 2001-present. Each observation is the average hair loss for observed moose. Hair loss is an indicator of the intensity of tick infestation.

the past four years (vertical axis of Fig. 13). In 2009 predation rate was 17.4%. Last year predation rate was 3.3%, which had up to that point been the lowest level ever observed on Isle Royale. In 2013 predation rate declined further, to 2.4%. During this period of declining predation rate, moose abundance has been steadily increasing (Fig. 13).

Each spring we estimate the degree to which moose had been impacted by winter ticks



Figure 17. In 2012 snowshoe hares reached the highest level ever documented at Isle Royale. This juvenile, with many ticks (probably *Haemaphysalis leporispalustris*) in its ears, seemed physiologically stressed but survived the day.

(*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 ticks have been on the rise. In winter 2012 the average moose had lost or damaged hair over 55% of its body (Fig. 15).

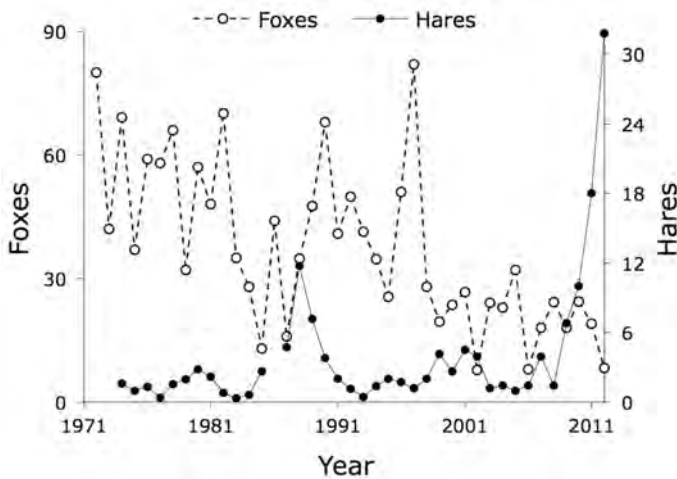


Figure 16. Indices of abundance for red foxes and snowshoe hares on Isle Royale, 1974–present. The hare index is the number of hares seen per 100 km of summer hiking. The fox index is the number of foxes seen from the plane during Winter Study, the sum of the maximum number seen at kills and the number seen otherwise per 100 hr flight time.

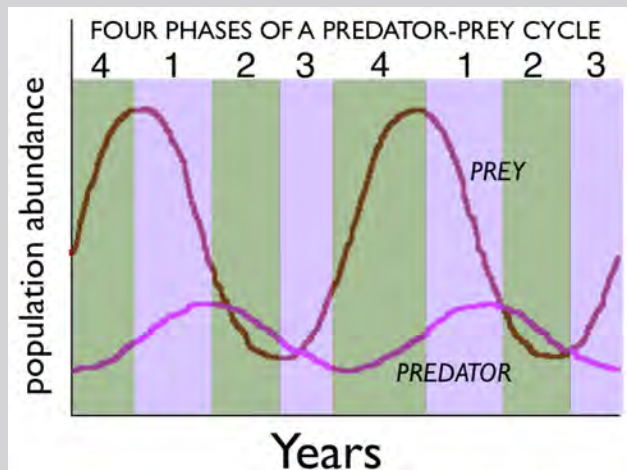
Other Wildlife

There have been a number in intriguing changes in populations of other species of wildlife on Isle Royale that may be ripple effects of the sudden drop in the wolf population in the past two years. We will briefly review possible direct and indirect responses to wolf decline in beaver, red fox, snowshoe hare, and raven.

Beaver are an important alternate prey for wolves, but beaver habitat has declined as forests aged over the past half century, and long foraging distances are associated with a high risk of wolf predation. After slowly declining in 2006-2009 from 133 to 92 sites, there was a small increase in the number of active beaver sites in 2010, to 99. There has generally been high annual turnover in occupancy of individual sites, with wolf predation the likely cause of mortality for beaver. Park Biological Technician, Mark Romanski flew a single-observer survey in 2012, and estimated an increase of about 69% in the number of active sites since 2010. Beaver survival has probably increased significantly as the wolf population declined to an all-

The Anatomy of Population Fluctuations

All populations fluctuate in abundance over time. They do so in a variety of ways and for a variety of reasons. There is a remarkable ecological theory, which has been with us for nearly a century. This theory is a set of mathematical equations, known as the Lotka-Volterra equations, and they suggest that predation causes populations to fluctuate in a special way, that is, to cycle. According to those equations, a cycle can be divided into four phases.



First, prey decline because predators are abundant and predation rates are high (Phase 1). When prey are rare it becomes more difficult for predators to maintain high kill rates, so the predators decline (Phase 2). As predators decline so do predation rates, allowing prey to increase (Phase 3). As prey increase so do kill rates, which allow predators to increase (Phase 4). At this point the cycle begins again with Phase 1. Notice, how these phases of the population cycle are largely governed by kill rate and predation rate. Kill rate is an indication of how much food each predator gets. More food translates into higher rates of survival and reproduction and increased abundance. Predation rate is the proportion of the prey that are killed by predators and represents the impact that predation has on the prey population.

Well that is the theory. Knowing whether or how this theory is a good explanation for what we see in nature is quite a different matter. Making such an evaluation requires observing, over long periods of time, fluctuations in predator

and prey abundance and fluctuations in kill rates and predation rate. This is exactly what we have been doing on Isle Royale for decades.

In recent years, Isle Royale has exhibited patterns with a remarkable match to the theory. In particular, predation rate had declined dramatically in recent years (Fig. 12), which has allowed moose to increase (Fig. 1). Also, as moose have been increasing, so too has the kill rate (Fig. 5). The high kill rate should allow the wolf population to increase from its low abundance.

The theory is understood to be a simplification of nature. And researchers understand that many other processes can cause deviations from this theoretical pattern. Disease, parasites, fluctuations in weather can all lead to deviations in this pattern. In some cases the deviations can be considerable. Of particular concern is the prospect that severe inbreeding depression might prevent an increase in Isle Royale wolves.

Nevertheless, what we've observed in the past few years is a remarkable affirmation of the mechanisms believed to drive predator-prey dynamics. Such a clear affirmation is distinctive. These mechanisms also explain why predators do not, except under rare circumstances, drive prey to extinction; how predator populations can, under normal circumstances recover from low abundance; and how other factors (in this case, inbreeding depression) are expected to alter these basic patterns.

And, there is more insight to be had. Throughout the past few years, as wolves declined and moose increased, the ratio of moose to wolves has increased dramatically, from fewer than 30 to more than 121. Correspondingly, the kill rate has almost tripled during during the same period of time (Fig. 5). Last year, two world-renowned ecologists, Lev Ginzburg and Roger Arditi, published *How Species Interact: Altering the Standard View on Trophic Ecology* (Oxford, 2012). They summarized 25 years of research explaining how the ratio of predator-to-prey is fundamental for understanding fluctuations in kill rate, and in turn fluctuations in population abundance of all species. Observations from the wolves and moose of Isle Royale played a prominent role in the development of their ideas.

time low level.

Indirect effects of the wolf reduction may be responsible for a dramatic change in snowshoe hare density. Across Isle Royale, snowshoe hare density has tended to peak every ten years, approximately at the passage of each decade (Fig. 16). In 2011 our snowshoe hare index hit an all-time high, exceeding the exceptionally high level in 1988 which was observed on both Isle Royale and the Minnesota mainland. Anticipating a crash in this cyclic species, in 2012 we were surprised to see our hare index climb even further, with an 80% increase over 2011. We speculate that the major predator of hares, the red fox, has declined because of the shortage of moose carcasses provided by wolves, allowing hare numbers to grow to an unprecedented level.

The breeding bird survey conducted annually by the National Park Service since the mid-1990s has documented a gradual decline in raven numbers since 1996, but the two lowest years were 2011 and 2012, which correspond to the two years with an

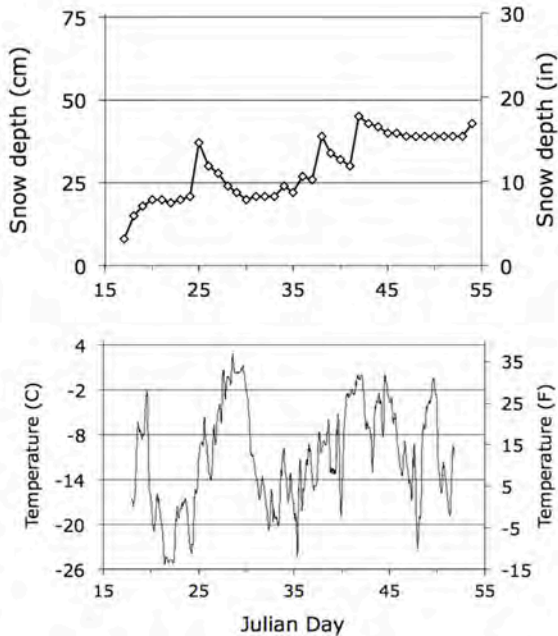
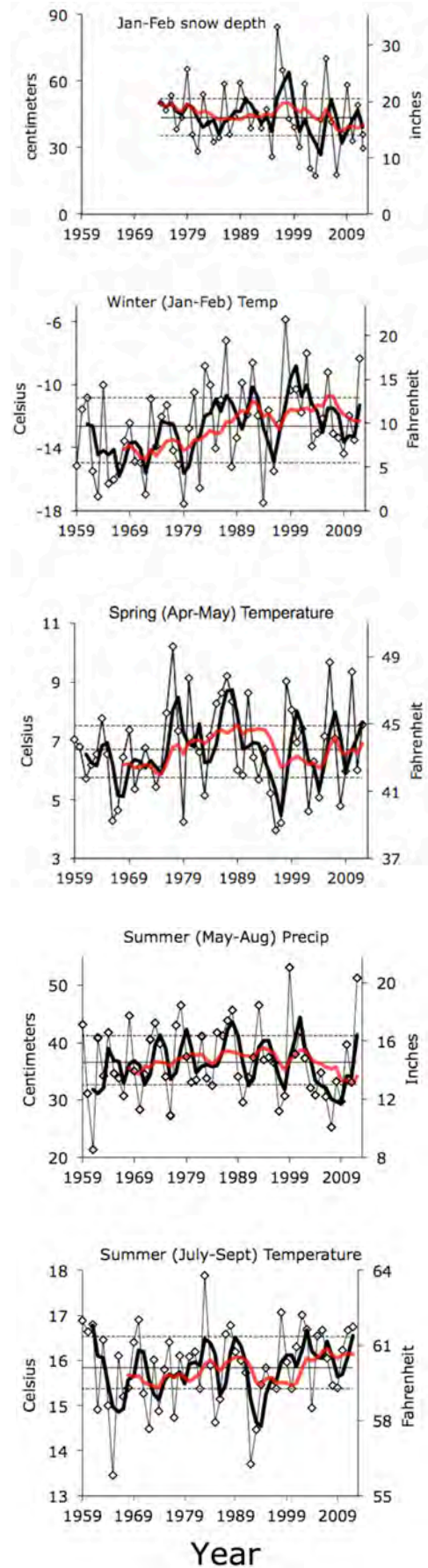


Figure 18. Snow depth (daily) and ambient temperature (30-minute intervals) during the 2013 Winter Study on Isle Royale.

Figure 19. Climate data from Isle Royale (snow depth) and nearby northeastern Minnesota (temperature and precipitation). Climate data is from www.wrcc.dri.edu/spi/divplot1map.html. Solid lines are long-term means and dotted lines mark interquartile ranges. Climate change is highlighted by the 10-year averages (heavy grey [red] line), and moose may be affected by a 3-year moving average (heavy black line).



exceptionally low number of moose carcasses during winter.

River otters continued to exist well-distributed through inland and shoreline areas of Isle Royale. In winter 2013 we documented river otter sign in 51 of the roughly 210 mapped square-mile sections of the island. This was much less than in 2012, but commensurate with reduced flying effort in 2013.

Of the rare small mustelids (ermine, marten, and mink) resident on Isle Royale, we observed sign in winter only for marten, in two locations at the west end of the island.

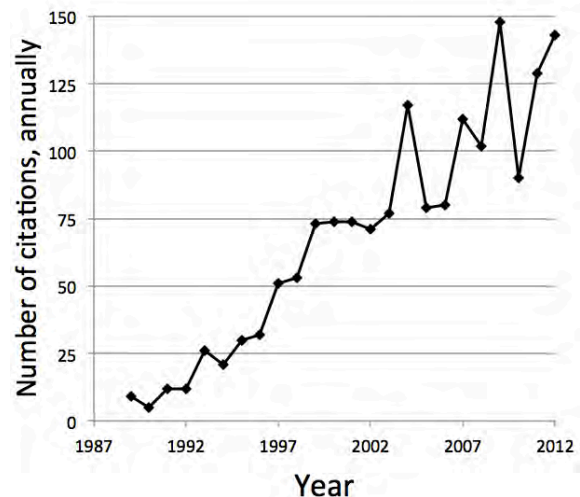
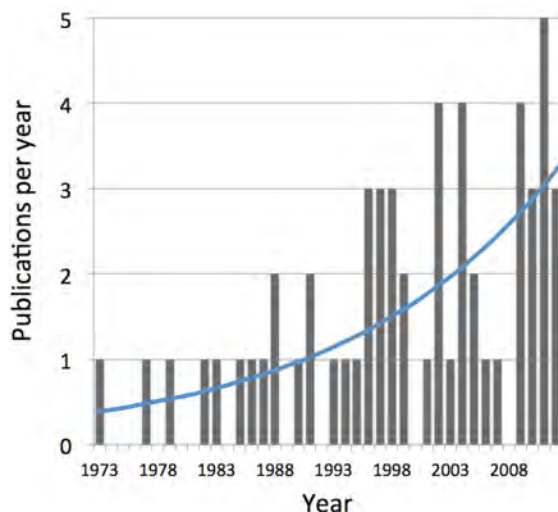
Aerial nest surveys for bald eagles and osprey by the National Park Service in 2012 revealed 9 eagle nests fledging 12 young and 4 osprey nests fledging 1 young. Two previously unknown eagle nests were documented during winter survey flights in 2013.

Weather, Climate, and Ice

During the 2013 Winter Study, average daily snow depth was 30 cm (Fig. 18), below the 1974-2012 average of 44 cm. Snows were especially shallow during the early portion of the winter study. Winter temperatures were colder than in many recent years, but near long-term averages. Spring and summer temperatures in 2012 were both warmer than average, and summer precipitation was much greater than average (Fig. 19).

The temperature of Lake Superior was much warmer than average for much of the winter (www.coastwatch.glse.noaa.gov). These warm temperatures and frequent high winds prevented the formation of an ice bridge at any point in the winter. Cold air temperatures and warm lake temperatures also produced many days this winter with lake-effect snow clouds.

LAST THOUGHT “What is the value of continuing to study in the same place decade after decade? What more could one possibly learn?” This rhetorical question is often the basis for criticizing long-term research, including the Isle Royale wolf-moose project. Knowledge gained from long-term research should not be taken for granted. Unless guided properly, long-term research can arrive at a point of diminishing returns. An important way to assess the growth of knowledge and its value is to chart the number of scientific publications per year and the number of times each year that other scientists cite those publications in their own work. The graphs below represent these statistics for the Isle Royale wolf-moose project. Each decade has produced more knowledge than the decade before - this is a trend that has been maintained for the past five and a half decades. So long as wolves persist on Isle Royale, and so long as there is adequate research funding, we expect that trend to continue. For additional context, many scientists conduct research in Isle Royale National Park. They also have a long record of producing considerable knowledge on a wide range of topics, including fisheries ecology, ecotoxicology, botany, and geology. In that context, of all the Isle Royale scientific publications that are tracked by the Web of Science, 41% are from the wolf-moose project. Of all the citations to that research, 44% are from the wolf-moose project.







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