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Ecological Studies of Wolves on Isle Royale, 2011-2012

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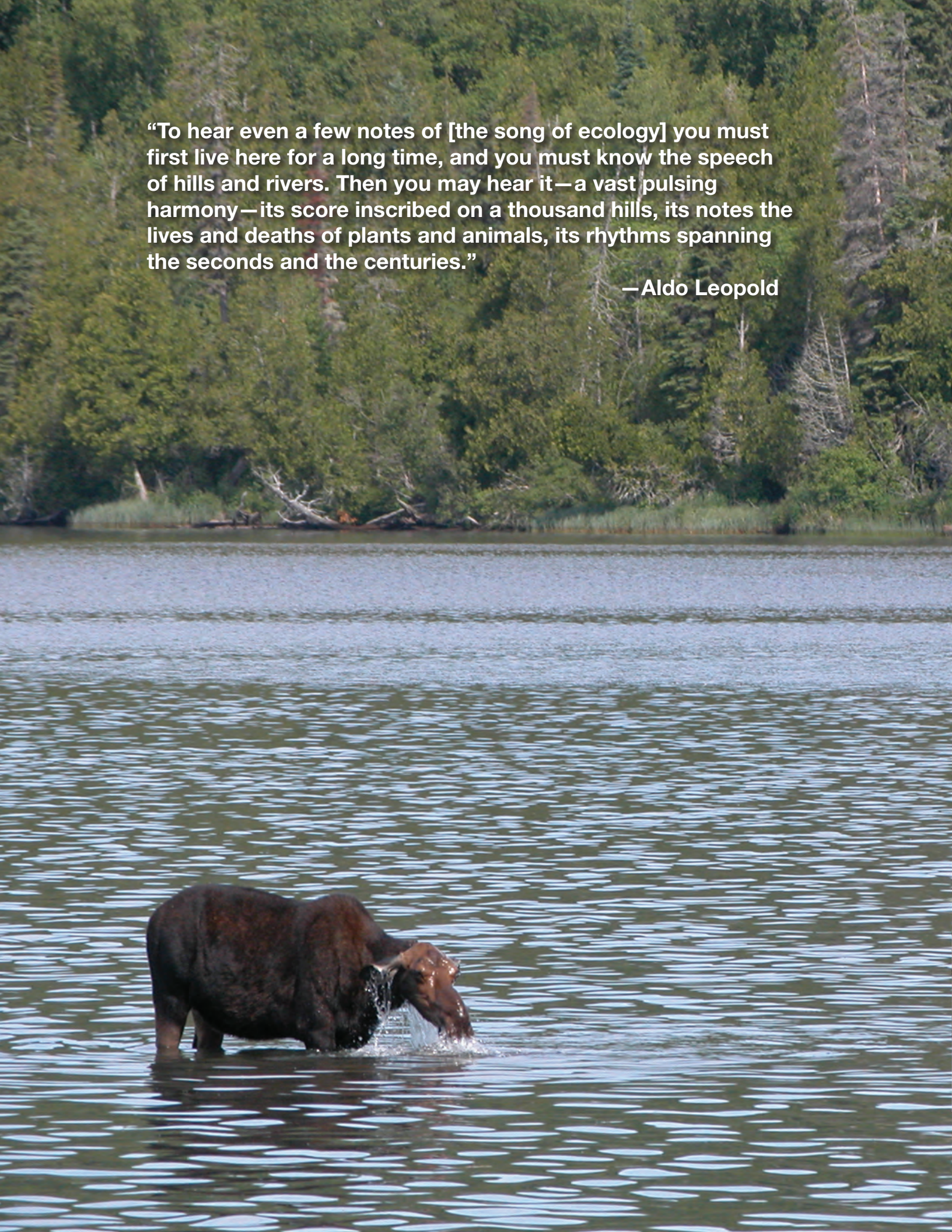
Wolves

2011–12



“To hear even a few notes of [the song of ecology] you must first live here for a long time, and you must know the speech of hills and rivers. Then you may hear it—a vast pulsing harmony—its score inscribed on a thousand hills, its notes the lives and deaths of plants and animals, its rhythms spanning the seconds and the centuries.”

—Aldo Leopold

Ecological Studies of Wolves on Isle Royale

Annual Report 2011–12

by

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To learn more about how you can join one of our research expeditions, visit www.isleroyalewolf.org and click “How you can contribute.” 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Results reported here are preliminary and, in some cases, represent findings of collaborators; please do not cite without consulting the authors.

WOLVES & MOOSE of Isle Royale

www.isleroyalewolf.org

Ecological Studies of Wolves on Isle Royale

I suspect that this curious, impartial sympathy toward all creatures, regardless of their diet, is an attitude of the cultivated mind. It is a measure of a man's civilization. If ever we are to achieve a reasonable concord with the earth on which we live, it will be by our willingness to recognize, tolerate… the living things about us.

–D.L. Allen, founder of the Isle Royale wolf-moose project

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 54th 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 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 2011, ground-based fieldwork continued from late April through mid-October. Rolf Peterson and John Vucetich directed that fieldwork with assistance from Will Lytle, Sean McWay, Zach Merrill, Nick Bennett, Carolyn Peterson, and Leah Vucetich. Leah Vucetich and Marcy Erickson supervised Ben Betterly, Jon Bontrager, Josh Brinks, Michelle Croll, Enrico Ghiberto, Natasha Fetzer, Cathy Hill, Nick Holmes, Scott Larson, Ted Maynard, Chelsea Murawksi, and Ryan Priest, who all worked in our lab on the mainland.

In April 2011 we attempted to radio-collar wolves. That field effort included Bob & Sally Irmiger, Enrico Ghiberto, and from the National Park Service, Cherie Barth, Kevin Castle, Leah Ettema, Kallan Green, Erin Lehnert, Jenny Powers, 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 2012, the annual Winter Study extended from January 20 to March 5. John Vucetich, Rolf Peterson, and pilot Don E. Glaser participated in the entire study, assisted by Dieter Weise, Beth Kolb, and Leah Vucetich (Michigan Tech) and the following personnel from the National Park Service: Erin Grivicich, Rob Bell, Lucas Westcott, Marshall Plumer, Mark Romanski, and Seth DePasqual. US Forest Service pilots Pat Lowe, Tim Bercher, and Scott Miller flew several supply flights to Isle Royale from Ely, Minnesota. George Desort filmed and photographed our research activities in February 2012 (see www.georgedesort.org). 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 early March 2012, we conducted the fifty-fourth annual Winter Study of wolves and moose on Isle Royale. Between January 2011 and January 2012, the wolf population declined from 16 to 9 (Figs. 1 and 2). This is the lowest number of wolves ever observed in the population. During the past year, mortality rates were very high (at least 44%), with at least 7 wolves dying. Recruitment rates were also very low during the past year. More than likely, zero or one pup survived to January. Several

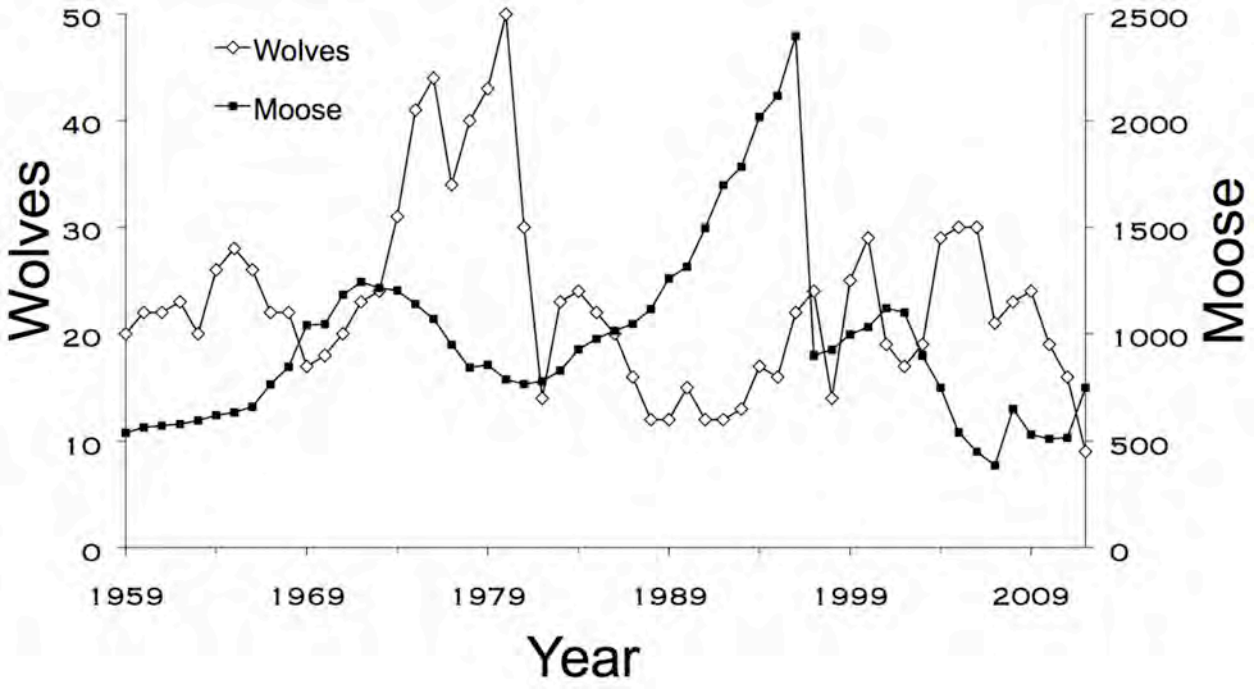


Figure 1. Wolf and moose fluctuations, Isle Royale National Park, 1959-2012. Moose population estimates during 1959–2001 were based on population reconstruction from recoveries of dead moose, whereas estimates from 2002–12 were based on aerial surveys.

Figure 2. Seven of the nine wolves that inhabited Isle Royale in January 2012. The population was comprised of a pair of adult wolves living at the west end of Isle Royale (upper panel), and Chippewa Harbor Pack (lower panel) which was observed with five and sometimes six wolves.

considerations suggest that the sex ratio remains skewed: (i) the wolf population included no more than two adult females in January 2011, (ii) few pups were likely recruited into the population during the past two winters, and (iii) recruitment is the only potential source of new females. While it is possible to estimate sex ratio and recruitment from DNA analysis of already collected fecal samples, funding limitations have precluded such analysis.

In February 2012, we estimated moose abundance to be 750, with 90% confidence intervals of [550, 990] (Fig. 1). This estimate is substantially higher than recent estimates. Moose abundance now appears to have been increasing over the past few years from its lowest recorded level of approximately 400 moose in 2006. Nevertheless, moose abundance remains below its long-term average.

Per capita kill rate, which indicates how well-fed the wolves have been, was low (0.46 moose/wolf/month) during winter 2012. The annual predation rate, which is the proportion of moose (>9 months of age) killed by wolves throughout the year and can be extrapolated from winter kill rate, was 3.3%. This is the lowest value ever observed. Calves comprised 11.4% of the moose population during winter 2011, which is close to the long-term average.

The intensity of winter ticks that infest moose had declined for three consecutive years (2008-2010). However, in spring 2011 tick infestations increased again such that the average moose had lost or damaged hair over approximately 50% of its body.

The moose-to-wolf ratio had been gradually increasing over the past five years from its all-time low of 15 in 2006 to 32 in 2011. In the past year, that ratio increased dramatically to 83, well above the long-term average.

The Wolf Population

In late January 2012, we counted 9 wolves in the population. Wolf abundance was down from last year's count of 16 wolves, and the lowest on Isle Royale since studies began in 1959. Since 2009, the population has declined by 62%, from 24 to 9 wolves

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

Chippewa Harbor Pack III (CHP)... 6
West-end Duo (WD)..... 2
Loners..... 1
2012 Total..... 9

This past year's wolf decline was the result of low recruitment and high mortality (Fig. 3). Our estimate of recruitment is based on behavioral observations and analysis of photographs, methods which provide only an approximate indication of recruitment. Nevertheless, our observations suggest that the population included either zero or one pup, which corresponds to a recruitment rate of either zero or 6%. The mortality rate was 44% or 50%, depending on how many pups survived. For context, mortality and recruitment rates are typically around 25%. This combination of low recruitment and survival that we observed this year is comparable to only one other period in the chronology of Isle Royale wolves – the catastrophic wolf crash of 1980-1982.

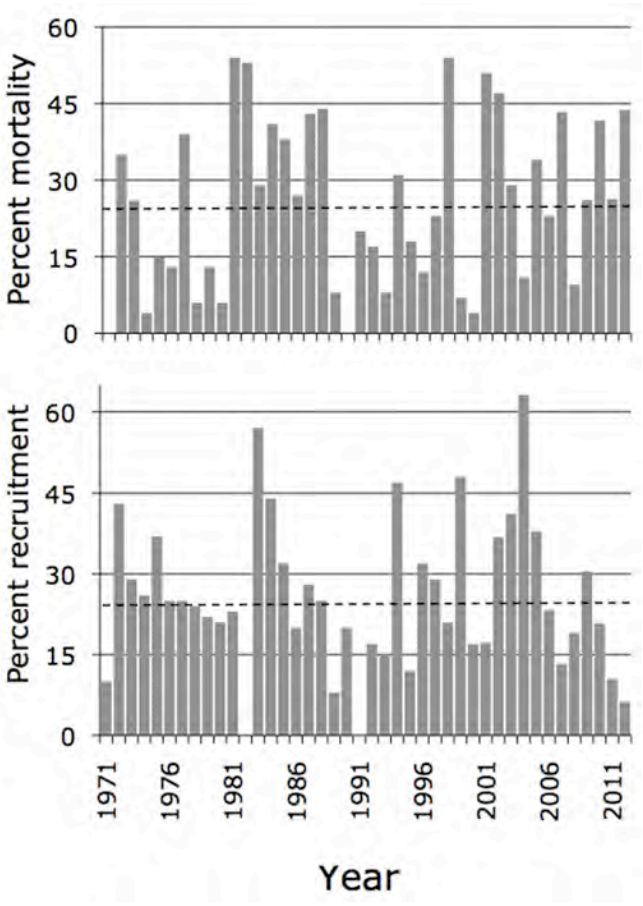


Figure 3. Percent mortality and recruitment for Isle Royale wolves, 1971-present. The dotted lines mark long-term averages.

Of the seven or eight wolves that died in the past year, we recovered the skeletal remains of one. One was the alpha male of Middle Pack, who died in late February 2011 when he was killed by Chippewa Harbor Pack wolves. We also recovered the radio collar of a subordinate adult from Chippewa Harbor Pack from a site southwest of Lake Desor. We also collected the remains of two other wolves that died in 2010-11. One was a carcass of an eight-month old pup that died near Grace Creek, and the other was a skull of a wolf that was found near Sumner Lake. Except for the alpha male, the causes of death for these wolves were unknown.

A wolf we had radio-collared in 2009 also went missing sometime between Fall 2011 and January 2012. We heard a telemetry signal from that collar throughout summer and fall 2011 and then again twice in late January. However, on each occasion in late January we heard the telemetry signal for only approximately 20 seconds, which was not enough time to precisely locate that wolf or make a visual observation. After these occasions, we never heard that telemetry signal. We presume the collar is permanently inoperable. We never saw a wolf wearing an inoperable collar and we never observed sign (e.g., tracks) of a lone wolf that might be this collared wolf. We presume this wolf is dead.

In winter 2012, the wolf population killed at least six moose during the 44 days we observed them (Fig. 4). We were able to estimate per capita kill rate only for Chippewa Harbor Pack. Their kill rate was approximately 0.46 moose per wolf per month. This rate is lower than the long-term average kill rate, and very low given what would be expected for the number of moose per wolf on Isle Royale this year (Fig. 5).

We conducted necropsies on five moose carcasses in winter 2012. Four of these were killed by Chippewa Harbor Pack, and one was killed by the West-end Duo (Fig. 6). Two of the old cows we necropsied suffered from jaw necrosis, and one suffered from arthritis. Two of the four moose had relatively high fat content in their bone marrow.

In March 2011 we reported that the Isle Royale wolf population included no more than two adult females. This was based on the analysis of DNA contained in fecal samples collected in Jan/Feb 2010, and field observations indicating the death of two adult females between Feb 2010 and Feb 2011. Field observations also indicate that at least two pups were

alive in the Chippewa Harbor Pack in mid-October 2011, indicating that at least one female was alive in the spring of 2011.

The sex ratio of the wolf population is unlikely to change much in the upcoming year for two reasons. First, the surviving adult females are not young and will likely die soon. Second, the opportunity for new adult females to be recruited into the population is small, as there was probably only zero to one pup alive in winter 2012 and perhaps only 2 pups that were alive in winter 2011. The sex and survival of these pups is unknown, but one would not expect more than one or two of these to be females.

During winter 2011 and winter 2012 we collected fecal samples containing DNA that can provide information on current sex ratio and whether any pups survived during the past two winters. These samples will be "banked" until funding permits analysis.

The low rates of recruitment and survival that

Figure 4. Two wolves from Chippewa Harbor Pack feed from the carcass of a yearling cow moose, one of only four moose that this pack killed during the entire Winter Study.

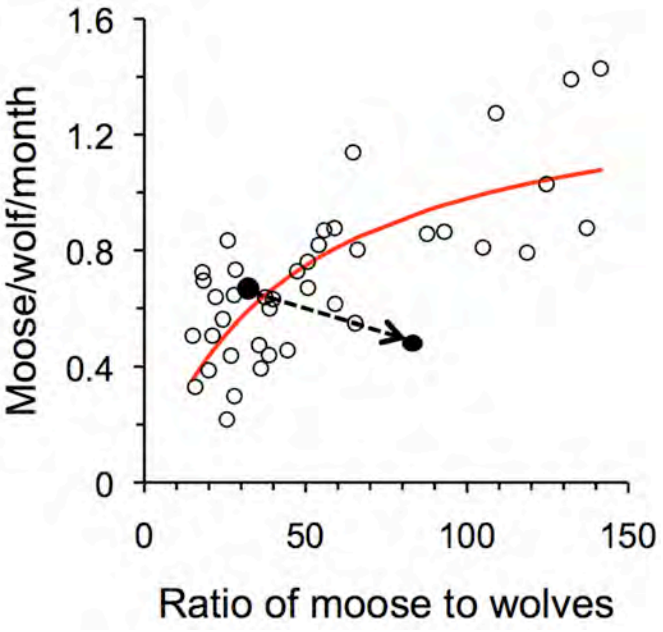


Figure 5. Relationship between ratio of moose-to-wolves and number of moose consumed per wolf per month, 1971-2012. The number of moose consumed is the number killed, plus those scavenged. The filled circles are the observations for 2011 (left) and 2012 (right). The position of these filled circles shows not only how kill rate declined from last year to this year, but also how that decline is not expected, given the ratio of moose-to-wolves.

Figure 6. Rolf Peterson works to remove the pelvis – to inspect it for arthritis – from the frozen carcass of a moose killed by the West-end Duo.

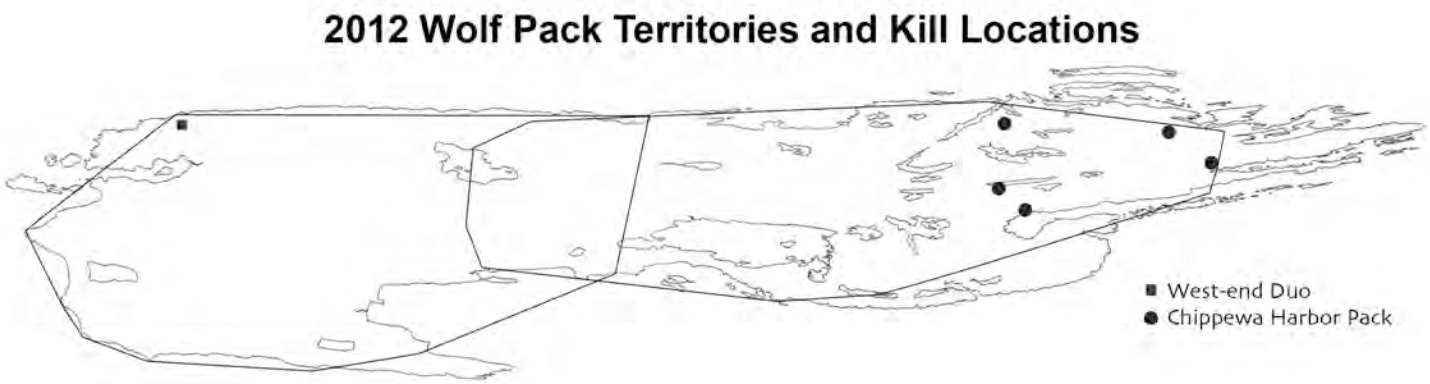


Figure 7. Wolf pack territorial boundaries and moose carcasses found during the Winter Study in 2012. The territory of the West-end Duo is in southwestern Isle Royale. Chippewa Harbor Pack territory is the larger territory to the northeast (right).

have been causing the population to decline in recent years are attributable to some combination of the following factors: genetic deterioration, social structure, skewed sex ratio, disease, and declining food supply:

Genetics/Social structure. – During the past several years, the population declined from four packs to one pack. With only one pack, the opportunities for reproduction are limited. The three packs that disappeared in recent years were founded by closely-related alpha wolves (i.e., full-siblings and parent-offspring) whose offspring were very inbred. The only surviving pack (Chippewa Harbor Pack) was founded by an alpha pair that were more distantly related (see the pedigree presented in the 2010-2011 Annual Report).

Sex ratio. – The number of adult females on Isle Royale in Feb. 2012 is low and will be unknown until there are additional analyses of DNA from scats. Nevertheless, the number of females in the Isle Royale population may be two or fewer. In a typical wolf population, with a balanced sex ratio, only the most fit females would be able to reproduce. However, on Isle Royale, where critically few females are available for reproduction, there is no mechanism to prevent females with low fitness from reproducing.

Disease. – In April 2009, which marked the beginning of the current population decline, 2 of 6 wolves had antibody levels that indicate protection from parvovirus, and 1 of 6 wolves had antibody levels that indicate protection from adenovirus. Live-trapping wolves to collect blood samples, as we have done on a regular basis for the past 25 years, followed by monitoring of survival, will be critical for a better understanding of the impact of disease on the population.

Food supply. – Food supply may also have played a role in the recent wolf decline. That is, in two of the past five years (2010 and 2012), per capita kill rates have been well below their long-term average. During Winter 2010, kill rates were only 60% of the long-term average.

Moreover, food limitation is likely to become increasingly important during the next 5-10 years. Old, vulnerable moose are an important indicator of food availability for Isle Royale wolves, and old, vulnerable moose become rare about ten years after long periods of low calf recruitment. The moose population experienced very low calf recruitment between 2002 and 2008. For these reasons, old, vulnerable moose can be expected to be rare during 2012-2020.

Social structure

In the later half of 2009, two of Isle Royale's four packs went extinct. These extinctions left the wolf population with only two packs, Chippewa Harbor Pack and Middle Pack. Middle Pack disbanded when their alpha male was killed in February 2011. During winter 2012 the wolf population was organized into two groups, Chippewa Harbor Pack and a West-end Duo (Fig. 7).

We observed Chippewa Harbor Pack on more than 20 different days during Winter Study. On most occasions when our observations were not hampered by thick vegetation, five wolves were present in the pack. However, on three occasions (Jan 21st, Feb 4th, and Feb 28th) we observed six wolves. Chippewa Harbor Pack spent most of its time in its traditional core range, between Daisy Farm and Intermediate Lake. They did not spend much time in former East Pack territory, although they did kill one moose near Mount Franklin (eastern-most kill in Fig. 7). Moreover,

Where wolves prefer to be

Spatial homogeneity is the idea that one patch of landscape in an ecosystem is the same as any other. Spatial homogeneity is also implicit in many fundamental ecological theories – theories that reflect many intuitions we have about how nature works. However, we all know the assumption is typically false. A walk through the forest – or a hike across Isle Royale – confirms that the landscape changes considerably over space. In other words, most landscapes are spatially heterogeneous.

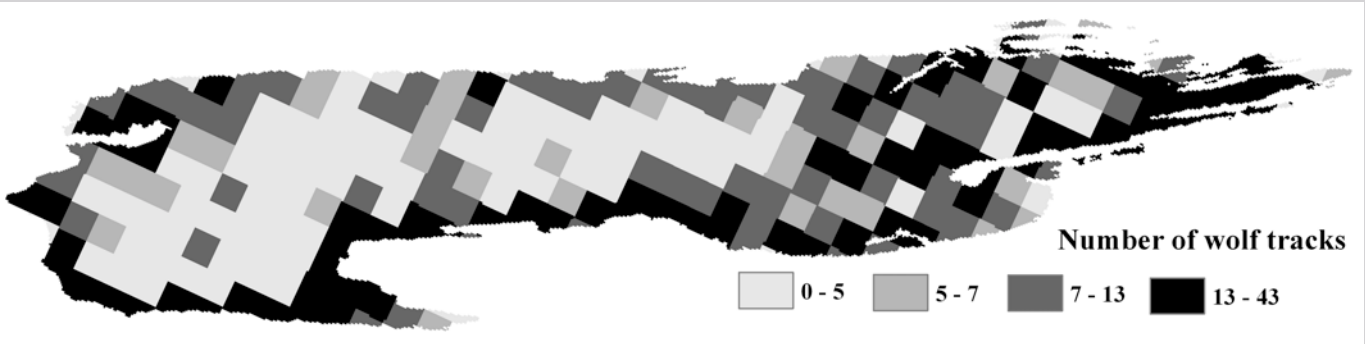
On Isle Royale, spatial heterogeneity is easiest to notice – for a human – in the forest. Inland portions of the west end of Isle Royale, where Pleistocene glaciers dumped thick layers of till, are dominated by hardwoods, especially maple and yellow birch. The middle portion of Isle Royale, which burned in 1936, is dominated by birch and spruce. The eastern portion of Isle Royale, where glaciers scoured the earth to its bedrock, is dominated by transition boreal forest, especially white spruce, balsam fir, and aspen. And Isle Royale's shoreline, whose climate is cooled by Lake Superior, is also dominated by spruce, fir, and aspen.

These are the heterogeneities that a perceptive human can observe. What about wolves? Do they perceive spatial heterogeneity? How are their lives affected by it? Do they prefer to spend more time in some areas than other areas?

Each winter study we record, from fixed-wing aircraft, locations and travel routes (tracks through the snow) of the wolves. We record the locations and routes on 1:274,560 maps that depict each one-square mile sections on Isle Royale. We compiled the travel routes from seven years of observation (1980, 1985, 1990, 1995, 2000, 2005, and 2010) by recording the number of times that wolves traveled through each section. The result is depicted in the graph below, where dark colors indicate more frequent usage by wolves.

If you compare this map to the map of moose density on Isle Royale (see page 11), you will notice some similarities. Wolf use is more common at the east end of Isle Royale and more common along the south shore of Isle Royale. Shoreline habitats not only tend to have more moose, but the snow on shorelines also tends to be windswept. So, during most winter conditions, it is easier for wolves to walk along shorelines than through the forest.

Is it important that use of Isle Royale by wolves and moose is spatially heterogenous? Some sophisticated ecological theories suggest that processes like predation can be greatly complicated by spatial heterogeneity. This map is just one small step we are making in an effort to understand how spatial heterogeneity might be affecting our understanding of predation on Isle Royale.



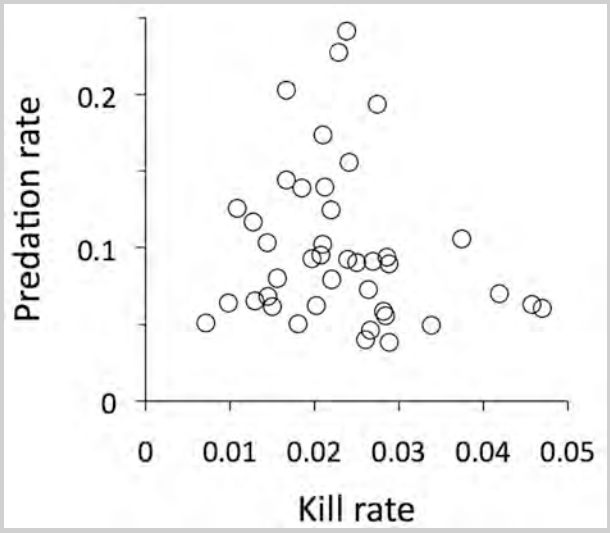
on three occasions, the pack traveled relatively far to the southwest into former Middle Pack territory. Specifically, on two occasions they traveled to Malone Bay and on a third occasion they traveled farther southwest to Hay Bay and Little Todd Harbor.

On four occasions we observed Chippewa Harbor Pack chase adult moose without making a kill. On four other occasions, we observed Chippewa Harbor Pack chase a cow and calf. Those attempts were also unsuccessful, although one calf was wounded and eventually was killed. It is unusual for us

Predation from two perspectives

Kill rate – the frequency at which wolves kill moose – is one of the most important statistics that any predator ecologist could measure. We've been measuring it at Isle Royale for more than 40 years. Kill rate is presumed to be the statistic that connects a population of predator to its prey. At least, that's what long-standing ecological theory seems to have been telling us for almost a century. But the wolves and moose of Isle Royale recently taught us how life is not so simple.

There is another statistic, the predation rate, which is the proportion of moose that are killed annually by predators. It is a more direct indicator of the impact predation has on a prey population. But because it requires that the abundance of wolves and moose be estimated simultaneously, predation rate is more difficult to measure, and consequently it is measured less frequently. But theory and intuition seemed to suggest that kill rate should be a pretty good indicator of predation rate.



The lack of relationship between kill rate (kills per wolf per day) and annual predation rate on Isle Royale, 1971-2011. Kill rate presents the rate at which wolves acquire food, and predation rate represents the proportion of moose (>9 mos. old) that die each year from predation. These two basic predation statistics are unrelated - wolves having a good year is no indication that moose will have a bad year.

But the wolves and moose of Isle Royale had been living a different life than what theory predicted. We gained a chance to better understand this a couple of years ago, when we first realized how to estimate annual predation rate from data we had been collecting at Isle Royale for decades. The main obstacle had been accounting for seasonal differences in predation rate, when we only make direct observations during the winter. Then it occurred to us how the 1300 adult male moose skulls that we'd collected over the decades could help. Of those moose, 6.3% died during the period of antler growth, and 16.5% died with fully grown antlers, and 77.3% died with no antlers. These phases of antler development correspond to specific times of the year – summer, fall, and winter/spring. We used these frequencies and what we observe during the winter as a basis for developing a year-round estimate of predation rate. Simple as it may seem, that approach had eluded us for many years.

What we found in those numbers surprised us. Kill rate and predation rate were completely unrelated (see graph). In retrospect, the theory wasn't wrong. But many ecologists seem to have been glossing over some theoretical details, attracted by the simple story. And simple stories, like sirens on a reef, are often irresistibly attractive. When those theoretical details are taken into account it seemed possible for kill rate and predation rate to be positively related, negatively related, or completely unrelated. Theory didn't eliminate any possibilities. While Isle Royale represented one of these possibilities, it is just one place.

We wondered what life was like for other wolf-dominated ecosystems. We contacted Doug Smith and Mark Hebblewhite, leaders of wolf research in Yellowstone National Park and Banff National Park, respectively. They had each been collecting kill rate data for years, and we showed them how to estimate predation rate from data they'd also been collecting. In Yellowstone, kill rate and predation rate had a slight tendency to be negatively related. And in Banff, the opposite, a slight tendency for a positive relationship. Thus, in three wolf-dominated ecosystems we have observed three different basic ecological relationships. In this way, ecosystems are not so different from people – no matter how important the similarities, there are always important differences.

These observations represent another valuable insight. When wolves kill a moose, it is not so simple as one less moose for the moose population, and one more moose carcass that wolf population will use to increase its rates of survival

and reproduction. A good year for wolves is not necessarily a bad year for moose, and vice versa. But sometimes it is. Nature is diverse in all the different kinds of creatures with which we share the planet. But nature may be no less diverse for the different ways in which they relate to one another.

A technical description of these findings can be found in: *Vucetich JA, M Hebblewhite, DW Smith, RO Peterson. 2011. Predicting prey population dynamics from kill rate, predation rate and predator-prey ratios in three wolf- ungulate systems. Journal of Animal Ecology 80:1236-1245.*

to make so many observations, as most hunting occurs at night. These observations may be a sign of the difficulty Chippewa Harbor Pack had this winter killing moose.

In the 2011 Winter Study we did not observe any signs of mating or courtship in Chippewa Harbor Pack until the last flight of Winter Study (2/26/11). At that time, we speculated the lack of such behavior until so late in the season may have been attributable to the absence of any female from Chippewa Harbor Pack until one dispersed into the pack late in the season. Such an event may have occurred when Chippewa Harbor Pack spent several days traveling through Middle Pack territory in late February 2011. During the 2012 Winter Study we did not observe any signs of courtship or mating whatsoever in Chippewa Harbor Pack. If a female is present, we now wonder whether the alpha pair of Chippewa Harbor Pack are closely related (full siblings) and the lack of courtship behaviors are symptomatic of inbreeding avoidance.

The alpha pair of Chippewa Harbor Pack attained that status shortly before January 2011. When they became alphas, the only pack that could have supplied a relatively unrelated male or female was Middle Pack. Middle Pack declined from 7 to 3 wolves during this period. If that decline was attributable to mortality, it is unlikely that Middle Pack could have been the source of an alpha wolf for Chippewa Harbor Pack. For these reasons, it is possible that the alphas in Chippewa Harbor Pack were both born in Chippewa Harbor Pack and are full siblings. Genetic analysis of existing fecal samples collected in 2011 and 2012 would likely shed insight on this aspect of the wolf population.

In addition to Chippewa Harbor Pack, the other social group of wolves that were observed was a pair of wolves that we began referring to as the West-end Duo. We observed these wolves five times during February. On the first occasion (Feb 2nd), we watched these wolves double-mark a rock at the mouth of the Big Siskiwit River. On the same day, the tracks of these wolves indicated they had come from as far northeast as Spruce Point. Five days later we found tracks of two wolves on Washington Harbor, which led to a freshly-killed moose approximately one mile north of Washington Harbor. Here the pair remained until the kill was largely consumed. A single wolf of unknown origin fed on this kill when the duo was absent.

Subsequently, we observed the pair traveling briskly in a parallel-walk along the south shore of Isle Royale. Here, we observed additional courtship behavior (Fig. 8) and tracks on Mud Lake that were indicative of copulation.

If Chippewa Harbor Pack continues to decline, this pair of wolves may become critical to the future of wolves on Isle Royale. For this reason, it would be valuable to know how these wolves are related to each other (e.g., are they siblings, cousins, or more distantly related?). We collected fecal samples from the single kill-site we recorded for this pair. Analysis of the DNA in those samples will almost certainly answer these questions.

Figure 8. We observed several signs of courtship in the West-end Duo on February 24 and 25th. Here the male sniffs the vulval area of the female while she averts her tail, a prelude to mating.

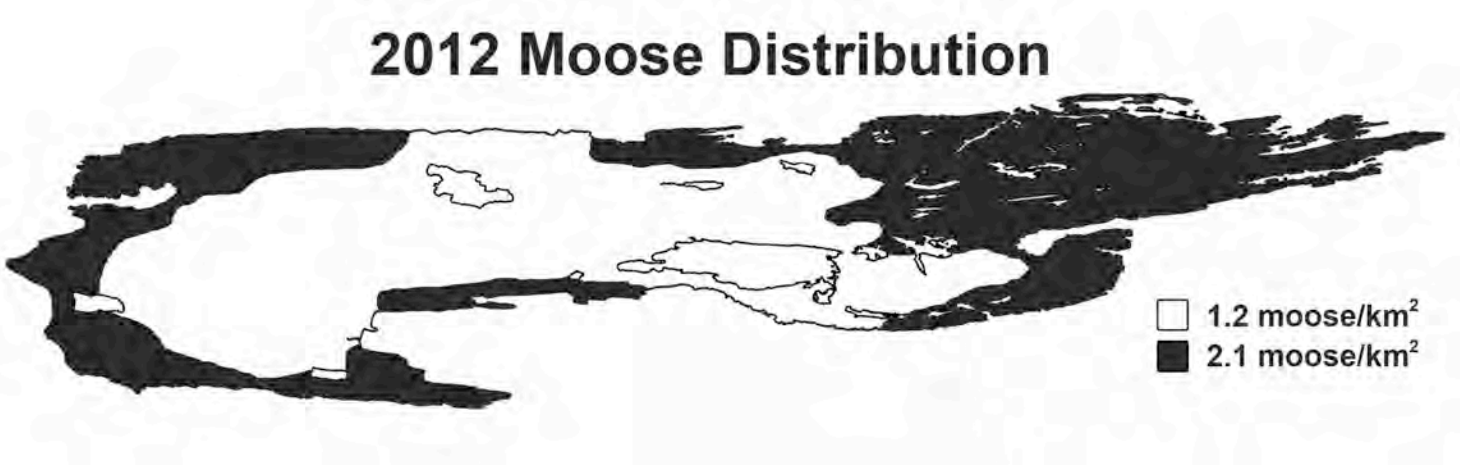


Figure 9. Moose distribution on Isle Royale in 2012 was relatively uniform, as it has been for the past several years. Only two strata were delineated, based on habitat types and results of the aerial counts on 91 plots that comprise 17 percent of the main island area.

The Moose Population

The 2012 moose survey began on January 31st and ended on February 15th. The survey resulted in an estimated abundance of 750 moose. The 90% confidence intervals on this estimate are [550, 990] , and the 80% confidence intervals are [610, 895]. Moose density throughout most of Isle Royale was 1.2 moose/km^2, and there were 2.1 moose/km^2 in some regions of the east and west ends of Isle Royale (Fig. 9). We calculated this year's estimate of moose abundance using a sightability factor of 90%. The flying conditions were good (calm wind, overcast), but snow was not very deep (about 10 cm). Although shallow snow exposed some stumps which distract from seeing moose, the snow was also shallow enough to allow moose easy access to deciduous habitats where they are easiest to see. Last year, we estimated 515 moose, with an 80% confidence interval of [421, 613]. 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 750 moose (Fig. 1). These moose estimates will be refined when the population is statistically "reconstructed" from

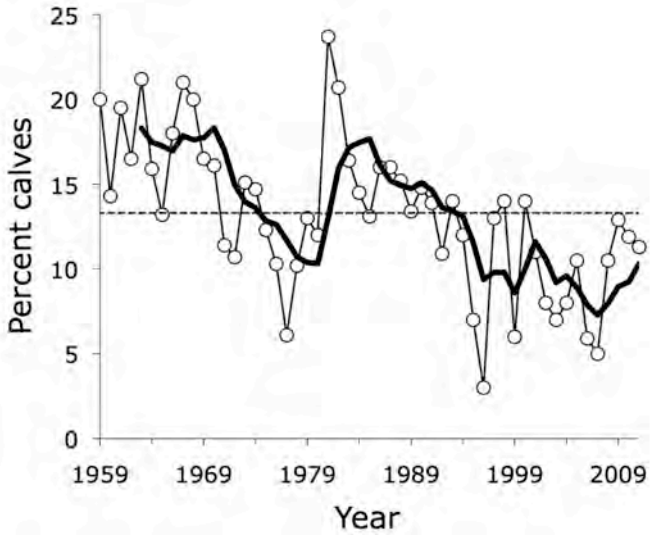


Figure 10. Long-term trends (1959–present) in the percentage of the total moose population that are 8-month old calves (upper panel). The 50-year average (13.3%) is marked by the light dotted line, and the curved line is a 5-year moving average.

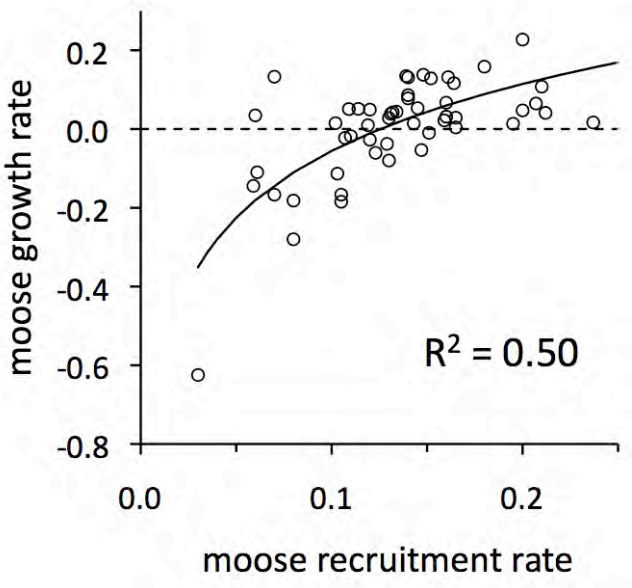


Figure 11. The relationship between moose population growth rate and recruitment rate, 1959-present.

Figure 13. Recent increases in moose abundance are attributable, in part, to recruitment rates returning to normal and forage being relatively abundant.

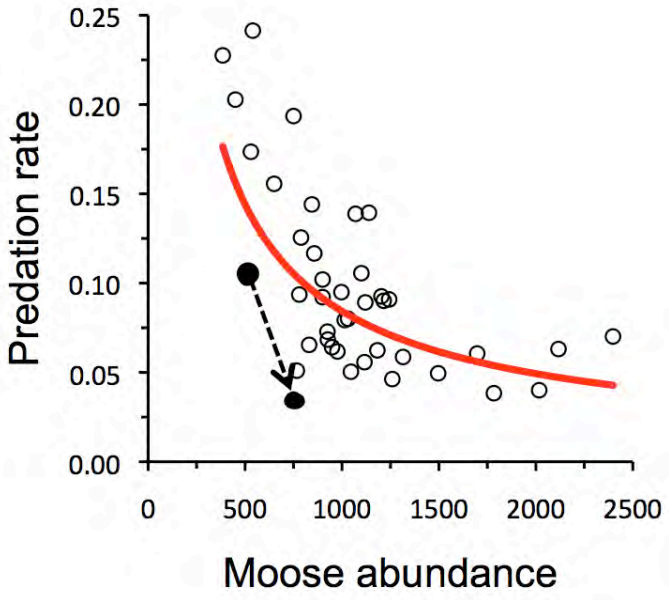


Figure 12. Estimated annual predation rates for Isle Royale moose in relationship to moose abundance, 1974–present. The filled circles are the observations for 2011 (upper) and 2012 (lower). The position of these filled circles shows dramatic change in the past year.

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 and during non-survey flights in 2012, 11.4% (40 of 350) were calves (Fig. 10), close to the long-term average. Recruitment rate is important because it explains about half the variation that we observed in moose population growth rate (Fig. 11). During the winter of 2012, we observed three set of twins. In the last two years, we observed a total of three sets of twins. Prior to this, twins had not been observed since winter 2005.

Calves were most common at the west end of Isle Royale (26 observed, including twins), where predation pressure has for the past year been lower due to the loss of Middle Pack. On the eastern half of the island, only seven calves (no twins) were observed. A similar pattern was evident on census plots -- 14 calves were in territory occupied exclusively by the West-end Duo, one was in territory occupied exclusively by Chippewa Harbor Pack, and two were in the area used by both packs (see Fig. 7).

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 during winter 2012, was 3.3%, the lowest level ever observed on Isle Royale. This predation rate

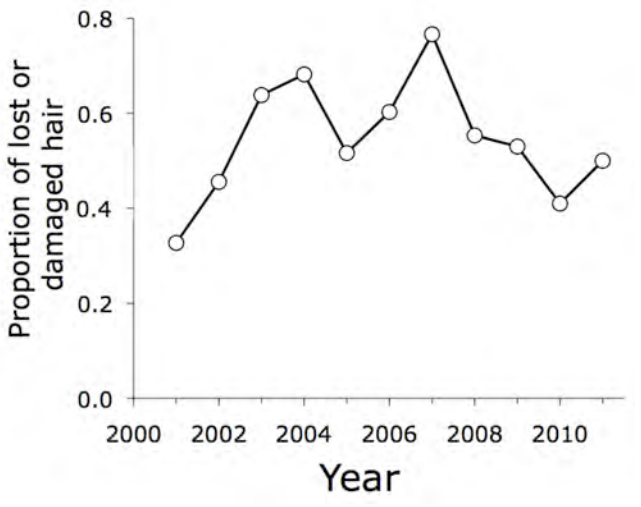


Figure 14. Trends in springtime hairloss for Isle Royale moose, 2001-present. Each observation is the average hairloss for observed moose. Hairloss is an indicator of the intensity of tick infestation.

is also lower than expected, given the number of moose (Fig. 12). Because recruitment rate remains lower than average, lower-than-expected kill rates are necessary for moose abundance to increase.

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, declining until 2010, and began to rise again in spring 2011 (Fig. 14).

Figure 15. Snowshoe hares are at or near the peak of their ten-year cycle on Isle Royale.

Other Wildlife

In 2011 snowshoe hare observations during ground-based field work reached the highest level recorded in the past 40 years (Fig. 15). While there has tended to be a peak in hare numbers at the turn of each decade, there were especially noteworthy peaks in 1988 and 2011. Probably several factors acting together contributed to these high levels. Before each of these exceptional peaks the moose population reached historic low levels at a time when foxes were also relatively scarce. Avian predators have responded to the high hare population -- great-horned owls, usually rare, were frequently heard in 2011, and goshawks were seen in both summer and winter during the past year.

In the winter of 2012 foxes were frequently seen unassociated with moose carcasses, which were very limited in number. A long-term index of fox abundance during winter observations involves foxes both counted at moose carcasses and seen off carcasses. The combined index for 2012 suggested no change in fox density, although foxes seen off carcasses were above average in number.

During the winter of 2011-2012 snowy owls were seen frequently in the lower 48 states, including

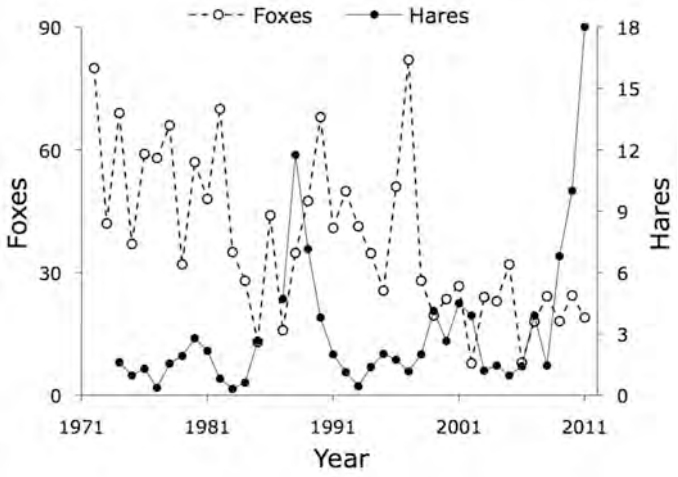


Figure 15. Indices of abundance for red foxes and snowshoe hares on Isle Royale, 1974–present. The hare index is the number of hares seen per 100 km of summer hiking. The fox index is the number of foxes seen from the plane during Winter Study, the sum of the maximum number seen at kills and the number seen otherwise per 100 hr flight time.

Calves might be easier to kill, but there's less to eat

Kill rates are tremendously variable from year to year. That variation has a critical influence on the life of a wolf, because kill rate is an indication of how much food a wolf gets. Kill rate also varies from one wolf population to another. For example, Isle Royale wolves kill moose, on average, only about a third as often as wolves in southern Scandinavia. Håkan Sand, a wolf researcher from Sweden, brought that difference to our attention a few years ago. And we all wondered why.

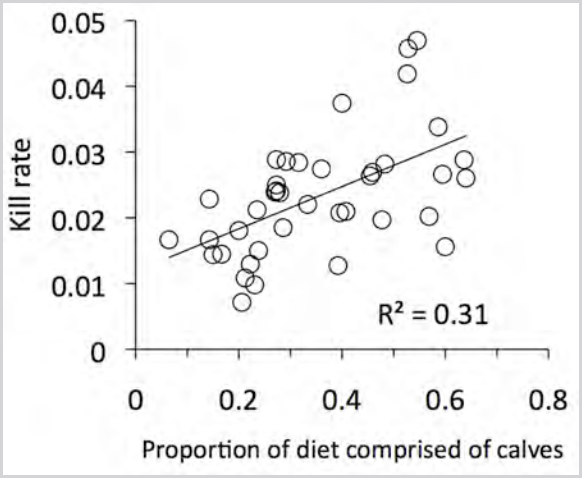
Traditional theory – the same theory alluded to in Sidebar #1 – says that kill rate increases with moose density (number of moose per square kilometer). The idea is simple, if moose are more common, they'll be easier to find, allowing wolves to kill more frequently. But these ideas didn't help us understand anything, because moose density is similar in Isle Royale and southern Scandinavia. We wrestled with the problem for more than a year. We exchanged data with Håkan, and we traded ideas, lots of ideas. Eventually, we began to focus on an idea that had long been considered but had gone largely untested because no one had the data. The idea is that kill rate might depend not only on how many moose are available, but also on the kind of moose that are available. In particular, calves are easier to kill than adult moose and they provide a smaller meal. Maybe kill rates are greater during years when calves represent a larger portion of wolves' diet. So we checked our data.

For Isle Royale wolves, the frequency of calves in their diet fluctuates considerably from year-to-year. In some years, only one in twenty of the moose that wolves kill is a calf; in other years, about half of the moose that wolves kill are calves. And during those years when calves represent a large share of diet, kill rates tend to be twice as great when calves are rare in wolves' diet (see graph).

Scandinavian wolves show the same tendency to kill more frequently when they eat mostly calves. Moreover, Scandinavia and Isle Royale differ greatly in that calves show up far more frequently in the diet of Scandinavian wolves. For these wolves, calves represent 50% to 80% of diet in most years. This difference in the age structure of the diet accounts for much of the difference in kill rates.

And why are calves more common in the diet of Scandinavian wolves? There seem to be several reasons. In southern Scandinavia moose are hunted intensively and the forest is logged industriously. Logging keeps a forest in an artificial state of youth, which favors the nutritional demands of cows raising calves. And, hunting mortality is typically compensated by increased reproduction and calf survival. This finding represents a subtle, but important, influence of how human influences – logging and hunting – can have important indirect effects on the lives of wolves and their prey.

A technical description of these findings can be found in: *Sand H, Vucetich JA, Zimmermann B, Wabakken P, Wikenros C, Pedersen HC, Peterson RO, Liberg O. in press. Assessing the influence of prey-predator ratio, prey age structure and social predation dynamics on wolf kill rates. Oikos*



The relationship between share of wolves' diet that is calves and the kill rate (kills per wolf per day) for Isle Royale, 1971-2011.

one in Hawaii. This was usually attributed to an abundant vole year in the Arctic in 2011, leading to high production and survival of juvenile owls. One was seen on Isle Royale this winter, on 23 February.

Abundant open water provided otters with good access to the entire shoreline of Isle Royale and otter sign was also recorded in many interior lakes. Otter tracks were recorded in 108 square-mile sections, roughly half of the island.

With very few moose carcasses on the landscape, ravens were relatively uncommon. On the other hand, open water allowed several eagles to overwinter at Isle Royale, and one was seen at a wolf-killed moose.

Weather, Climate, and Ice

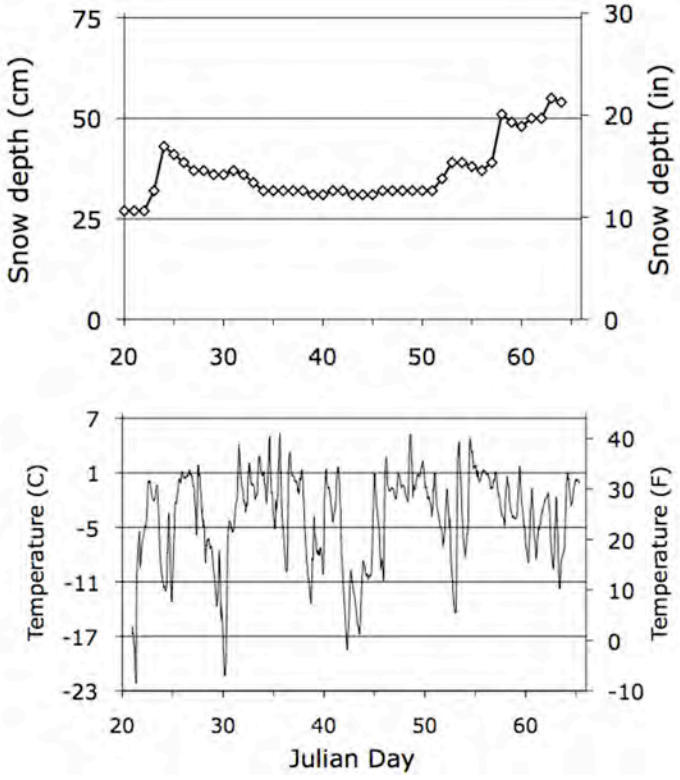


Figure 17. Snow depth (daily) and ambient temperature (30-minute intervals) during the 2012 Winter Study on Isle Royale.

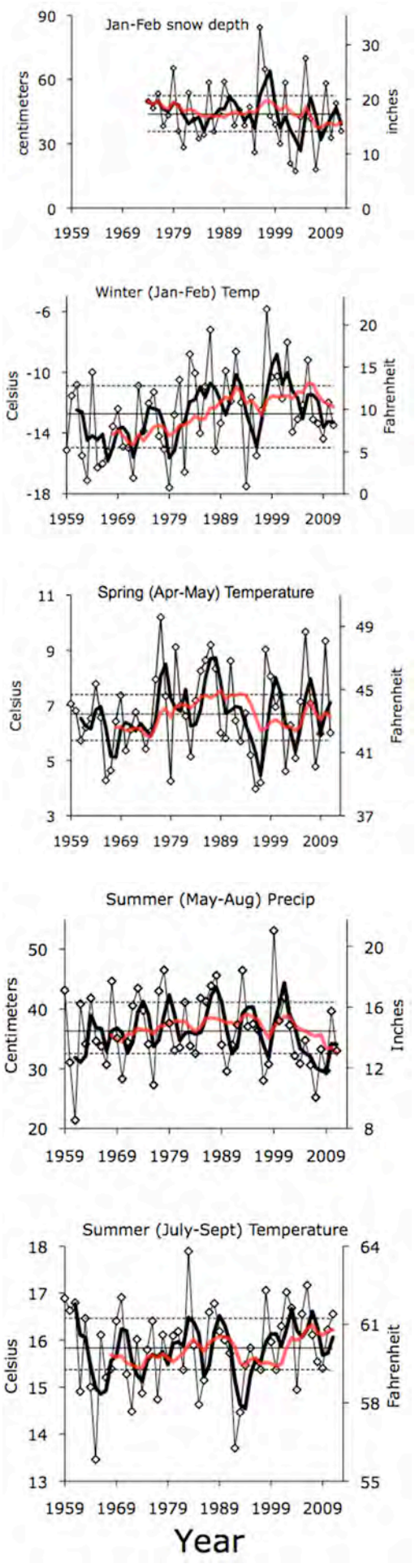


Figure 18. Climate data from Isle Royale (snow depth) and nearby northeastern Minnesota (temperature and precipitation). Climate data is from www.wrcc.dri.edu/spi/divplot1map.html. Solid lines are long-term means and dotted lines mark interquartile ranges. Climate change is highlighted by the 10-year averages (heavy grey [red] line), and moose may be affected by a 3-year moving average (heavy black line).

During the 2012 Winter Study, average daily snow depth was 36 cm (Fig. 17), below the 1974-2011 average of 44 cm. Snow depth was only 30-40 cm for most of the winter study, but frequent snowfall brought snow depth to near-average levels of about 50 cm by the end of February. In early March warm weather quickly reduced the snowpack. Overall, the winter of 2011-2012 was very mild with relatively little snow.

Air temperature was above the long-term level throughout the 2012 Winter Study (Fig. 17). Fortunately for our landing fields, the daily minimum temperature was always below freezing, averaging minus 10 deg C. In the 1970s the average minimum temperature at Isle Royale during Winter Study was fully eight degrees colder, near minus 18 deg C.

During the past five decades average winter temperature has clearly increased several degrees (Fig. 18). The past decade has also seen a tendency for warmer and drier summers (Fig. 18).

During the winter of 2011-2012 warm temperatures and frequent high winds prevented the formation of any ice bridge to the mainland. With each passing decade, ice bridges have formed less frequently (Fig. 19). In the 1960s an ice bridge formed two out of three winters, on average, while in the 2000s ice bridges formed about one year in ten. The declining frequency of ice bridge formation is probably a consequence of anthropogenic climate change, reflecting warmer winters but especially windier conditions. The decline in ice is significant because it reduces the possibility of a wolf immigrating from the mainland, which appears to be necessary for maintaining the genetic health of the Isle Royale wolf population.

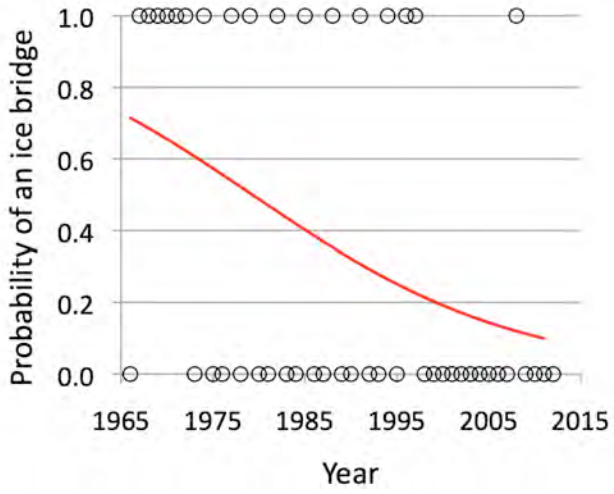
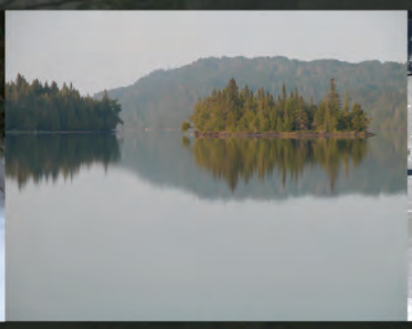


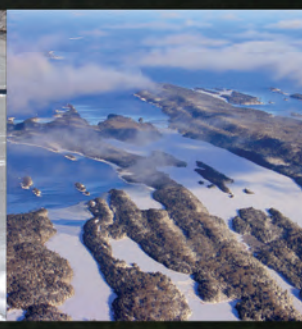
Figure 19. Ice bridge formation, connecting Isle Royale to the mainland, 1965-2012. Each circle represents the present (1) or absence (0) of an ice bridge each winter. The solid curve is the result of logistic regression and indicates how the probability of an ice bridge forming has declined greatly over the past several decades. These data were collected during Winter Study and compiled by Dan Licht (NPS) and Robert Gitzen (U Missouri).

PARTING SHOT

Chippewa Harbor Pack was frequently observed howling during winter 2012, an uncommon behavior during previous years. Wolves typically howl most frequently during the breeding season, and we speculate that increased howling in this pack may result from lack of suitable females.

Ecological Studies of Wolves on Isle Royale 2011–12



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THANK YOU to all who help!