


Ecological Studies of Wolves on Isle Royale

Wolves

2010-11



A winter landscape featuring a sunset over a calm lake. The sky is filled with dramatic, layered clouds in shades of orange, red, and grey. The water reflects the vibrant colors of the sunset. In the foreground, a moose stands on a snow-covered shore, looking towards the lake. The background shows a dense forest of evergreen trees under a pale, overcast sky.

“We humans fear the beast within the wolf because
we do not understand the beast within ourselves.”

—Gerald Hausman

Ecological Studies of Wolves on Isle Royale

Annual Report 2010–11

by

John A. Vucetich and Rolf O. Peterson

School of Forest Resources and Environmental Science
Michigan Technological University, Houghton, Michigan USA 49931-1295
11 March 2011

During the past year, major support for these studies was received from the National Park Service (Co-op Agreement No. J631005N004/0003), National Science Foundation (DEB-0918247), Dick & Bonnie Robbins, and the Robert Bateman Endowment at the Michigan Tech Fund. Monte Consulting (<http://monte.net/>) and Jeff Holden contributed to outreach efforts. All photographs are by John A. Vucetich or Rolf O. Peterson.

Additional contributions were received from the following organizations and individuals: Louis Arata & Kathryn Lyndes, BP Fabric of America Fund, David Beck & Angela Johnson, Dorthey L. Behrend, Jerry & Jennifer Boeckman, Dominic Bragg & Tracy Dulak, Joseph V. Brazie, Sheri A. Buller, Greg & Janet Capito, Donald C. Close, David R. Conrad, Conserve School, Earl F. Conteh-Morgan, Kevin K. Davis, James E. Deignan, Jennea Denner, Daniel & Karen Dietz, Ronald & Barbara Eckoff, Jessica M. Edberg, Jayson & Sabrina Egeler, Ronald L. Felzer, Fidelity Investments Charitable Fund, Anita J. Friend, C. Michael & K.A. George, Timothy & Natalie Gifford, Edith N. Greene, Violet & Edward Haelterman, Donald & Mary Heaton, John H. Heidtke, Lisa Hofman, Jeffrey Holden & Sandra Noll, Aaron W. Huntington, Robert & Sally Irmiger, Jeanne A. Knowlton, Leslie & Karen Knowlton, Roger & Mary Kolb, H. Robert Krear, David W. Locher, Daniel Luchay & Karen Reardon, Marjorie Luft, James & Jacqueline Mackinnon, Hugh & Georgia Makens, Sarah K. McBeth, Brian E. McLaren, Jeffrey & Susan Morrison, Paul S. Mueller, Richard & Beatrice Ann Murray, David & Michelle Norris, Erik Nyholm, Alex Ong, Michael & Kari Palmer, Janet L. Parker, Emily Perry, Tony & Thelma Peterle, Joseph & Rose Potvin, Allan & Sandra Puplis, Jillian F. Rapes, Robert L. Rich III, David Rolfes & Karen Steffen, Robert & Darcy Rutkowski, John & Linda Schakenbach, Fred & Joyce Scharringhausen, Betty L. Schnaar, Mary D. Seffens, Joan Silaco, Gerald & Lois Skora, The Toledo Zoo, Peter & Kathryn Trussell, Paul & Christa Van Treeck, John & Candice Varco, Linda M. Williams.

We regret that last year we failed to acknowledge Jeff and Sue Morrison and Sharon Smith for their contributions. We thank them for their support.

We gratefully acknowledge the contributions, personal time, and financial assistance of the volunteer members of our research expeditions:

Team IA— Tim Pacey (leader), Jess Edberg, Erik Freeman, Sarah McBeth, Wayne Shannon, Jayson Egeler

Team IB— Rolf Peterson (leader), Dick Murray, Mike Cherry, Earl Conteh-Morgan, Kim Van Treeck, David Locher

Team IIA— Barrett Warming (leader), Ron Eckoff, Sam Warming, Tony Thompson, Erik Freeman, Michael George

Team IIB— Trevor Peterson (leader), Bob Bollinger, Joe Olenik, John Warming, Bob Montgomery, Louise Tomsett

Team IIIA— Ben Betterly (leader), Louis Arata, Velda Hammerbacher, Kathryn Lyndes, Maureen Miller, Rob Rich

Team IIIB— Jeff Holden (leader), David Beck, Angela Johnson, Jeff Morrison, David Norris, Scott Larson

Team IIIC— Tom Rutti (leader), Colleen Brown, David Conrad, Erik Freeman, Anita Friend, Larry Fuerst

Team IVA— Ben Betterly (leader), Jennea Denner, Roger Kolb, Jacqueline MacKinnon, David Rolfes, Kathryn Trussell

Team IVB— Tom Hurst (leader), Lisa Hofman, Aaron Huntington, Emily Perry, Jillian Rapes, Leslie Skora

We regret that last year we failed to acknowledge Michael George's participation on Team III in 2010. We also regret failing to acknowledge Erik Freeman's participation. In spring 2008, Erik was a volunteer on Team II. Erik also joined us for three consecutive teams in 2010.

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.

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Ecological Studies of Wolves on Isle Royale



Wolves may feature in our myths, our history and our dreams, but they have their own future, their own loves, their own dreams to fulfill. -Anthony Miles

Background

Isle Royale 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 fifty-second 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 with the severity of each winter and the bounty of vegetation offered each summer. 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 2010, ground-based fieldwork continued from late April through late October. Rolf Peterson and John Vucetich directed that fieldwork with assistance from Ben Betterly, Scott Larson, Michael Nelson, Scott Kentner, John Webb, 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 Murawski, and Ryan Priest, who all worked in our lab on the mainland. During the course of the year, many park staff and visitors contributed key observations and reports of wolf sightings and moose bones.

In 2011, the annual Winter Study extended from January 12 to February 28. John Vucetich, Rolf Peterson, and pilot Don E. Glaser participated in the entire study, assisted by Leah Vucetich (Michigan Tech), Michael P. Nelson (Michigan State), Fred Anderson (Anderson Communications) and the following personnel from the National Park Service: Mark Romanski, Lara Hutto, Alyssa Becker, Dan Pontbriand, Pete Sweeger, and Levi Brezee. US Forest Service pilots Pat Lowe, Tim Bercher, and Wayne Erickson flew several supply flights to Isle Royale from Ely, Minnesota. During the second week of winter

study, the pump that delivers aviation fuel failed. Joe Bergen and Erin Grivicich, from the National Park Service, came to island and were able to restore partial fuel flow, but a week of field observations was lost for lack of access to fuel.

George Desort filmed and photographed our research activities in February 2011 (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 2011, we conducted the fifty-second annual Winter Study of wolves and moose. Between January 2010 and January 2011, the wolf population declined from 19 to 16. During the past year, approximately 2 pups survived to their first winter, and approximately 5 wolves died. The recruitment rate (11%) is lower than average, and the mortality rate (26%) is near the long-term average. The wolf population presently includes no more than two adult females.

Wolf abundance remains below the long-term average (23 wolves), after declining for several years.

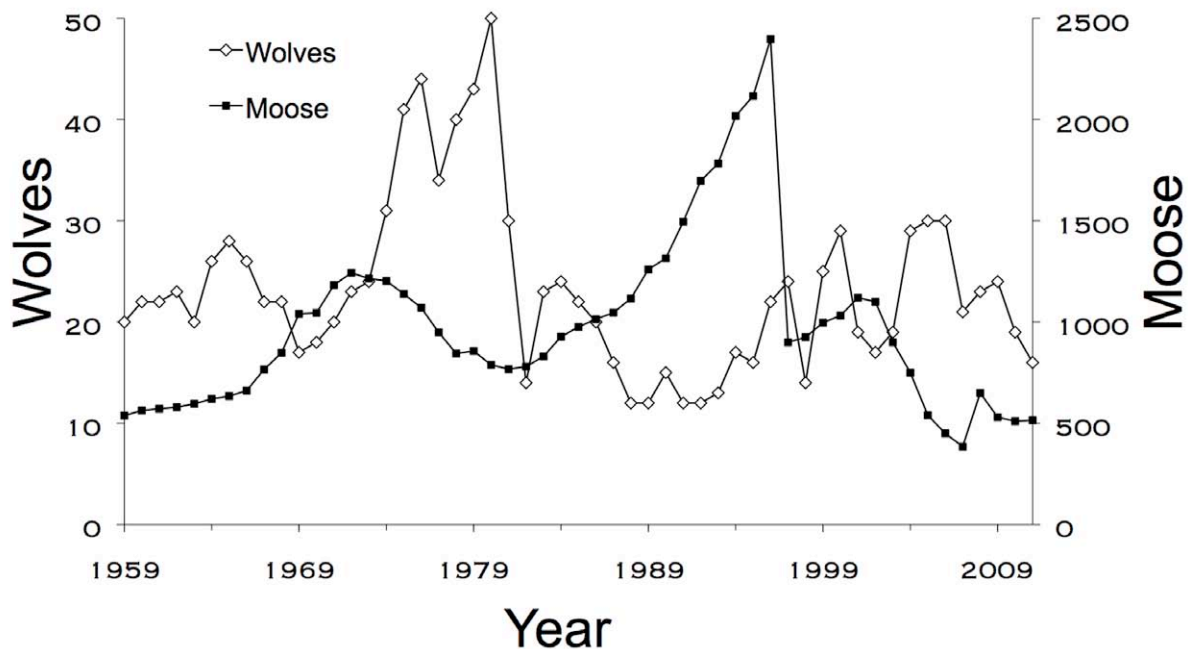


Figure 1. Wolf and moose fluctuations, Isle Royale National Park, 1959-2011. Moose population estimates during 1959–2001 were based on population reconstruction from recoveries of dead moose, whereas estimates from 2002–11 were based on aerial surveys.



Figure 2. All nine wolves of Chippewa Harbor Pack traveling northeast on Lake Whittlesey. Chippewa Harbor Pack seems to have been reinvigorated under the leadership of two new alpha wolves. They maintained a large pack size and relatively high kill rates, and they enlarged the size of their territory.



Figure 3. The last surviving members of Middle Pack. The alpha female who had led the pack for several years died sometime during the past year. And the alpha male (left) died in February 2011.

In late February, the alpha male of Middle Pack was killed by the invading Chippewa Harbor Pack, reducing the population to 15 wolves. These events may result in a reduction to just one reproducing pack, for the first time in four decades.

In February 2011, we estimated moose abundance to be 515, with 90% confidence intervals of [379, 672] (Fig. 1). Moose abundance has remained nearly constant for the past 3 years. For the sixth consecutive year, the moose population remains at approximately half its long-term average (1,000 moose), lower than at any time in the past four decades.

Per capita kill rates, which indicate how well-fed the wolves have been, was 0.56 moose/wolf/month during winter 2011. The monthly mortality rate for moose during winter 2011, which is the proportion of moose that died per month, was relatively high (1.8%). Calves composed 11.9% of the moose

population during winter 2011, which is close to the long-term average. In spring 2010, the intensity of winter ticks that infest moose declined for the third consecutive year. Ticks are now at their lowest level in 9 years.

The moose-to-wolf ratio has been gradually increasing over the past five years from its all time low of 15 in 2006 to 32 in 2011. On Isle Royale, a low moose-to-wolf ratio has been an indication of low kill rates and high predation rates.

The Wolf Population

This year, during the 2011 Winter Study, we counted 16 wolves in the population in mid January, a 16% decline from last year's 19 wolves, and a 33% decline over the past two years (Fig. 1). The number of wolves in each pack was

Chippewa Harbor Pack III (CHP)...	9
Middle Pack II (MP).....	4
Loners.....	3
2011 Total.....	16

Chippewa Harbor Pack was regularly observed to include 9 wolves (Fig. 2). Middle Pack was observed with 4 members on several occasions, but typically observed with 3 wolves (Fig. 3). On February 21st, the alpha male of Middle Pack was killed. His death will likely be followed by the dissolution of Middle Pack. Three wolves that didn't belong to either pack fed regularly from the carcass of a moose that fell through the ice near Beaver Island (Fig. 4).

The population decline from 2009 to 2010 was fueled primarily by elevated mortality rates (Fig. 5). However, the decline of this past year was driven more by low wolf recruitment (Fig. 5), as only two pups could be identified in 2011. Low recruitment was likely the consequence of an old alpha female dying in one pack and a change in leadership for the other pack (see *Pack Narratives*). In the past year, we



Figure 4. This moose died after it fell through the ice on Washington Harbor on January 21st. This carcass provided important observations of lone wolves this winter. Three lone wolves fed from it for several weeks following its death. Although the carcass was located in what had traditionally been Middle Pack territory, they never traveled through this area this year, and consequently never discovered this carcass.

discovered the carcass of only one dead wolf. It was a subordinate male from Middle Pack.

In winter 2011, the wolf population killed at least 11 moose during the 37 days we observed them. They also fed from the carcasses of two other moose that died from other causes. The per capita rate of prey consumption was 0.68 moose per wolf per month. This rate is close to the long-term average, and similar to what would be expected given the ratio of moose to wolves (Fig. 6). We conducted necropsies on 10 moose carcasses. These moose included 6 old cow moose and 4 calves, which is a typical composition. Four of the moose we necropsied suffered from arthritis, none suffered from jaw necrosis, and 6 had relatively high (>70%) fat content in their bone marrow.

In most years, we detect numerous signs of pair bonding and mating in each pack throughout the month of February (e.g., close physical proximity between the alpha pair, estrous blood in the urine of the alpha female, direct observation of copulating wolves). This year we did not observe any signs of pair bonding or mating in Middle Pack, and we did not observe any such signs in Chippewa Harbor Pack until February 26th.

Our most recent analysis of genetic material (extracted from scats collected in winter 2010) indicate that the wolf population included only 4 females in the previous year. Two of those females

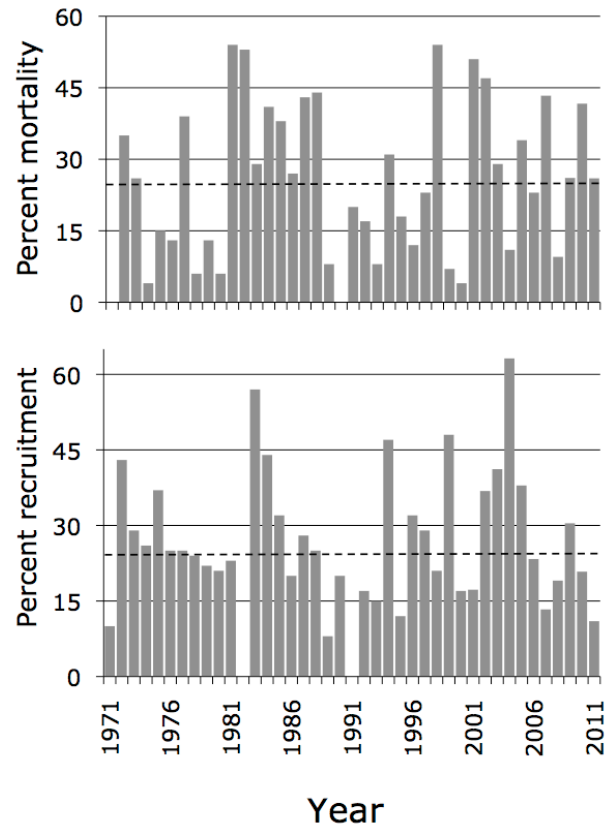


Figure 5. Percent mortality and recruitment for Isle Royale wolves, 1971-2010. The dotted lines mark long-term averages.

had died by January 2011. They were the alpha females of Middle Pack and Chippewa Harbor Pack. At least one of last year's four females survived to January 2011. One or both of this year's pups could be female and sexually mature in February 2012. The limited number of females may be associated with limited signs of mating. Skewed sex ratio is an important threat to the persistence of any small population.

Pack Narratives

In the later half of 2009, two of Isle Royale's four pack went extinct. These extinctions left the wolf population with only two packs, Chippewa Harbor Pack and Middle Pack.

Chippewa Harbor Pack experienced an important change in leadership this past year. They had been led by an alpha male that was born into East Pack in 2003 and an alpha female that was born in Chippewa Harbor Pack in 2005. The alpha male had led since Jan 2006, and the alpha female since 2007. The pelage of both wolves had turned light gray with age. In particular, the alpha female seemed to lack vigor, and lost her

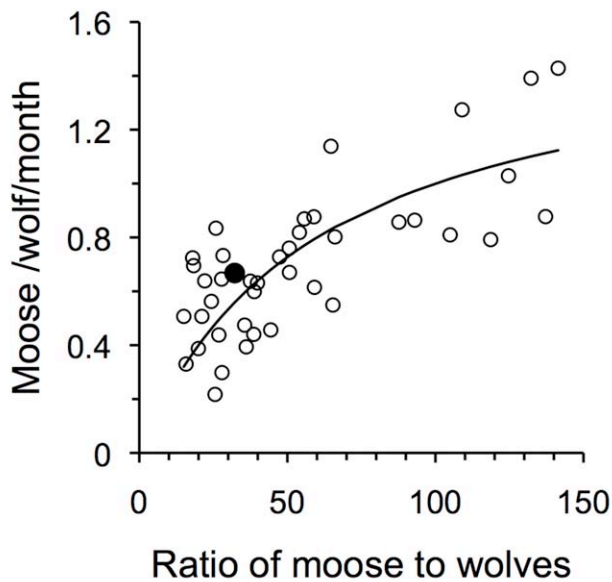


Figure 6. Relationship between ratio of moose-to-wolves and number of moose consumed per wolf per month, 1971-2011. The number of moose consumed is the number killed, plus those scavenged. The filled circle is the observation for 2011.



Figure 7. Upper panel: the alpha male (left) of Chippewa Harbor Pack inspects the alpha female (right). Lower Panel: the alpha male (right) backs-up the alpha female (middle) as she forces a wolf, nicknamed Romeo, into submission. Last year, Romeo attempted to disperse from Chippewa Harbor Pack, his natal pack. As a dispersing wolf, he killed a moose and spent time with a dispersing female from Middle Pack. Except for these photographs the identities of the alpha pair remain unknown. The alpha female could be the young female that had attracted the attention of the last year's alpha male (See the 2010 Annual Report.), or it could be the female that Romeo spent time with last year.

role as alpha to a younger female during the winter of 2010. The older alpha female and the alpha male died sometime during the past year.

During the first six weeks of field observations in 2011, we did not observe any wolf exhibiting dominance over other wolves in the Chippewa Harbor pack. The pack was also very cohesive - all nine wolves were together for 12 of the 15 times that we observed them. On three of these occasions, they were under thick forest cover, and we could have missed wolves that were present. This contrasts from winter 2010 when we observed numerous displays of dominance and several wolves were often missing from the pack. This year's behavior added to our difficulty in identifying the alpha pair of Chippewa Harbor Pack.

One explanation for these observations is that there were no adult females in Chippewa Harbor Pack. Another possibility is that an adult female was present, but normal displays of pair bonding and dominance were limited by inbreeding avoidance, the tendency for close relatives to avoid mating.

On February 19th Chippewa Harbor Pack travelled deep into Middle Pack territory, all the way to the western end of the island. Two days later, while still in Middle Pack territory, they killed the resident alpha male. Afterward we observed signs of pair bonding between two dominant wolves in the pack (Fig. 7). It is possible the apparent alpha female (in Fig. 7) joined Chippewa Harbor Pack after their foray into Middle Pack's territory.

Chippewa Harbor Pack included one or two pups this year, and the only deaths may have been the alpha pair. One of the pups was conspicuously small in size (Fig. 8). Overall, Chippewa Harbor Pack experienced no net change in number of wolves during the past year.

Middle Pack had different experiences during the past year. Between February 2010 and January 2011, they declined from 7 to 4 wolves, and one of the four was with the pack only occasionally. The alpha female (wolf #58) died sometime in the past year. Radiocollared in 2001, she was at least 12 years old when she



Figure 8. Two wolves from Chippewa Harbor pack. The wolf on the right is a nine-month old pup that is extremely small given its age. The wolf on the left is standing over the rear leg of a moose.

died. She is the middle wolf on the image on page 2. This was one of the last times she was ever seen alive. She was the daughter of wolf #93, an immigrant from Canada (see *The Old Gray Guy*). This father-daughter pair produced 20 offspring, including the sibling pair of the short-lived Paduka Pack. Since 2007, she mated

with her son, producing another 7 or 8 offspring. By the end of her long life, this alpha female had only two mates, her father and her son. With the death of wolf #58, no pups were raised in summer 2010.

One of Wolf #93's sons is wolf #152. He began his role as alpha male of Middle Pack in 2007 and continued to lead the pack in winter 2011. Wolf #152 was detected, through telemetry, making extraterritorial excursions during the summer of 2010. One explanation for this behavior is a lack of females to mate with in Middle Pack.

During the winter, Middle Pack spent no time in what had been the southwest portion of their territory (Fig. 9). Although lone wolves traveled through this portion of Isle Royale, we did not detect any territorial behavior by these wolves. At the same time, Chippewa Harbor Pack expanded the extent of their territory (Fig. 9).

On February 21st, Chippewa Harbor Pack killed wolf #152, the alpha male of Middle Pack. He was most likely born in April 2004, making him 6 years old at the time of his death.

Paduka Pack and East Pack went extinct in the later part of 2009. With the death of wolf #152, the survival of Middle Pack is very doubtful. If so, the wolf population will have gone from four packs to one pack in a two year period. It's been four decades since the population comprised just a single pack. The collapse of wolf numbers corresponds to a period when old moose (primary prey of wolves) have finally disappeared - moose that were born in the early 1990s as moose were increasing rapidly.

2011 Wolf Pack Territories and Kill Locations

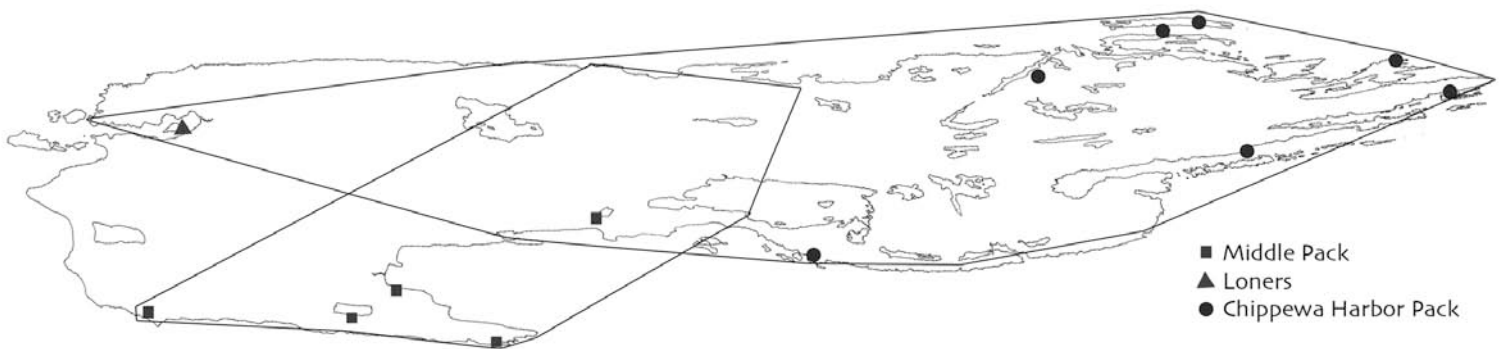


Figure 9. Wolf pack territorial boundaries and moose carcasses found during the Winter Study in 2011. Middle Pack territory is in southwestern Isle Royale. Chippewa Harbor Pack territory is the larger territory.

The Ecology of Arthritis

All mammals senesce, that is, experience a decline in body function with increasing age. But we don't all senesce the same. Some of us are old beyond our years, while others remain youthful as the years roll on. But why? It is a question that has fueled a great deal of research.

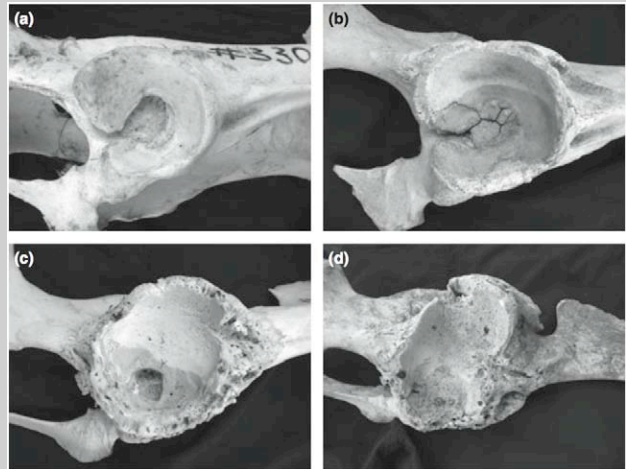
Arthritis is a particularly important form of senescence among humans. The causes of arthritis are complex and not well understood. Genetics and joint injury play a role, but don't tell the whole story. One idea has been that individuals experiencing poor nutrition early in life are more likely to suffer from arthritis later in life. The mechanisms of this idea are not well understood, and evidence to test the idea is also tough to come by.

Recently, the bones of Isle Royale moose have revealed a clue about the causes of arthritis. Each year we conduct necropsies on about 100 different moose. Over the past five decades, we've conducted necropsies on more than 4000 different moose.

One of the most basic observations from all these necropsies is that arthritis is common among Isle Royale moose. More than 40% of the moose that survive to at least 10 years of age eventually become arthritic.

Our next observation involved recognizing that some moose die relatively young with arthritis, and others die quite old without it. Why?

When we find the skeletal remains of a moose in the forest, one of the bones that we give a special effort to find is the metatarsus. The metatarsus is a rear foot bone about 13 inches long. On a moose the metatarsus looks like the



The right hip sockets of moose from Isle Royale, illustrating the progressive bony deterioration associated with osteoarthritis (OA). The upper left panel is a normal hip socket, with an open acetabular fossa (AF), through which a ligament passes through to the head of the femur. Early stages of OA involve the closing of the AF (upper right). OA eventually develops into severe bone deformations and eventually the complete dislocation of the femur (lower panels).

lower leg of a moose, but that is because moose, like other members of the deer family, walk on the tips of their toes. This bone is especially informative. It stops growing after a moose is about 1 year of age, and experiences about half its growth before a moose is born. Metatarsal length is a permanent record of how much a moose grew as a fetus and during its first year of life.



The white arrow points to this moose's metatarsus, which is its rear foot bone. This bull moose was photographed in spring. He has no hair on his shoulders; that was lost to ticks (see Figure 11).

The better nourished a young moose is, the greater the metatarsal length.

We know from measuring the length of a couple thousand metatarsi that nutritional conditions early in life vary tremendously among moose. Some are born in years with much food and easy winters, others are not so fortunate. Some are born to experienced, fit moose; and others are not so fortunate.

What we learned is that moose with the shortest metatarsi (10th percentile and smaller) had twice the odds of dying with arthritis than the largest (90th percentile and greater) moose.

This link between arthritis and early nutritional health may explain the anthropological observation that arthritis became more prevalent in native Americans as their diet became poorer – the result of relying more on corn and agriculture and less on hunting and gathering, especially after Spanish missions began to concentrate native Americans and encourage agriculture. These patterns are also consistent with emerging knowledge, which suggests senescence in older humans is affected by nutrition they experience as young people.

And, we learned more. Nutritional conditions early in life are often similar for an entire cohort of moose. A cohort of moose are all the moose born in the same year. As a result, an entire cohort of moose

may have a similar predisposition to developing arthritis later in life. For example, the moose born between 1969 and 1971 experienced severe winters and much competition for food. Eighty percent of these moose developed arthritis as they reached old age, a decade later. Conversely, only 20% of the moose born between 1949 and 1952 ever developed arthritis. These moose were born when winters were mild and moose density was low.

Wolves are selective predators and rely on moose that are weakened in some way. What we learned is that environmental conditions today affect the prevalence of arthritic moose a decade later, which can affect wolf predation. Long time lags such as this are one of the key reasons why ecological systems are complex and difficult to predict. Arthritis is not merely a physiological phenomena, it can also be an ecological phenomena.

A technical description of these findings can be found in: Peterson RO, JA Vucetich, G Fenton, T Drummer, and C Larsen. 2010. Ecology of Arthritis. Ecology Letters doi: 10.1111/j.1461-0248.2010.01504.x

The Moose Population

The 2011 moose survey began on January 25th and ended on February 25th. The flying conditions were good (calm wind, overcast), and the ground conditions were good while we counted moose on the first 65 plots (i.e., deep snow covered stumps and root tip ups that can distract efforts to observe

moose). However, the loss of snow and development of a thick crust made for very poor counting conditions for the last 36 plots. The survey resulted in an estimated moose abundance of 515. The 80% confidence intervals on this estimate are [421, 613]. Moose density throughout most of Isle Royale was 0.59 moose/km², and there were 2.34 moose/km² in some regions of the east and west ends of Isle Royale

2011 Moose Distribution

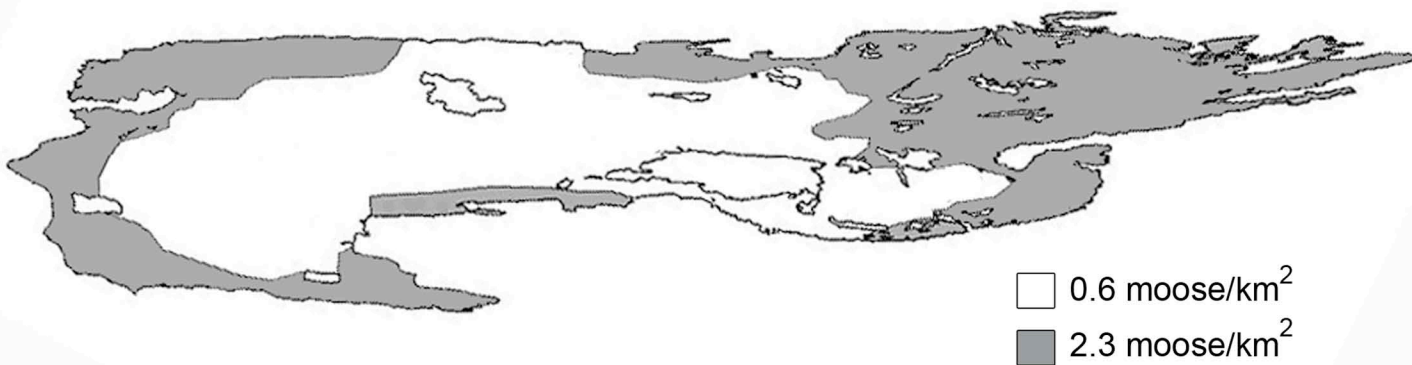


Figure 10. Moose distribution on Isle Royale in 2011 was relatively uniform, as it has been for the past several years. Only two strata were delineated, based on habitat types and results of the aerial counts on 91 plots that comprise 17 percent of the main island area.

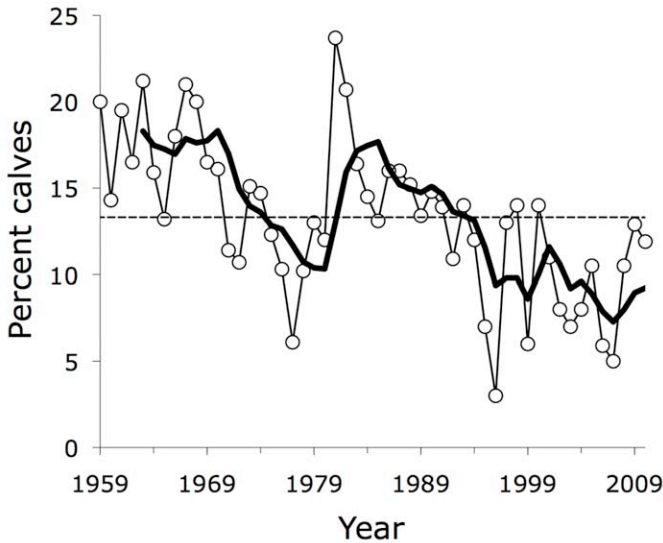


Figure 11. Long-term trends (1959–2010) in the percentage of the total moose population that are 8-month old calves (upper panel). The 50-year average (13.3%) is marked by the light dotted line, and the curved line is a 5-year moving average.

(Fig. 10). Last year, when conditions for counting moose were good, we estimated 510 moose, with an 80% confidence interval of [385, 645]. These and earlier counts suggest that the moose population declined during 2002–06, then stabilized at a low level (Fig. 1).

We calculated this year’s estimate of moose abundance using a sightability factor of 71%.



Figure 13. Rolf Peterson and a fox disagree over who should have the skull of the moose that died at Beaver Island (see Fig. 5).

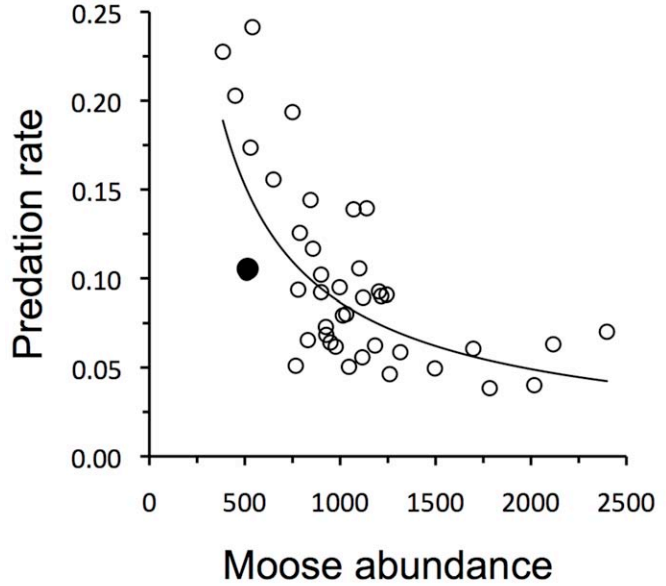


Figure 12. Estimated annual predation rates for Isle Royale moose in relationship to moose abundance, 1974–2010. The filled circle is the observation for 2011. The observations for 2010 and 2011 overlap with each other.

Sightability was estimated by the methods described in the 2010 annual report.

Of the moose that we observed on the census plots and during non-survey flights in 2011, 11.9% (36 of 303) were calves. This is close to the long-

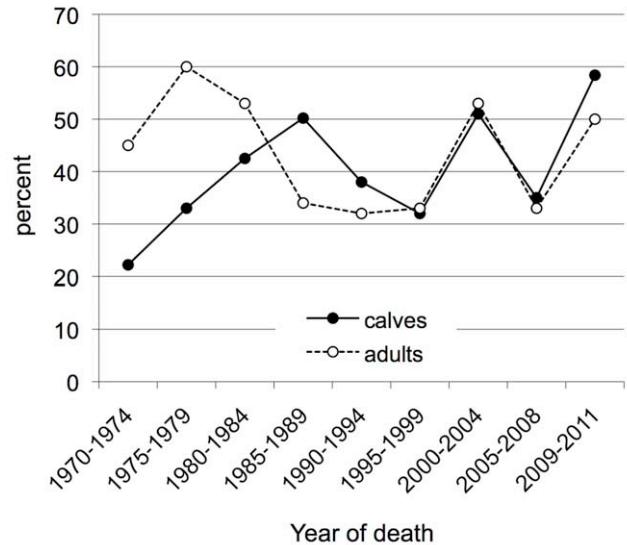


Figure 14. Long-term trends in bone-marrow fat for moose. The line for adults shows the proportion of adults with >70% fat in their bone marrow. The line for calves shows the mean value of percent fat in bone marrow.

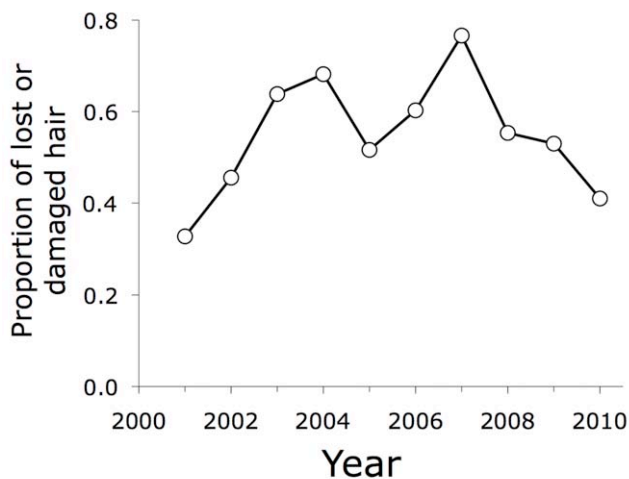


Figure 15. Trends in springtime hairloss for Isle Royale moose, 2001-2010. Each observation is the average hairloss for observed moose. Hairloss is an indicator of the intensity of tick infestation.

term average. However, recruitment during the past two years has been higher than at any time during the past decade (Fig. 11). During the winter of 2011, we observed one set of twins. Last year two sets of twins were observed. These are the first twins to be observed since winter 2005. This year's calves also seemed to have a larger body size than has been typical of recent years. The high rate of reproduction and large body size are attributable to abundant forage and relatively low moose density.

The monthly mortality rate is the percentage of moose population that dies per month from any cause of death (predation, accidents, and starvation). During winter 2011, the monthly mortality rate was relatively high (1.8%).

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. This predation rate (10.5%) is similar to last year's predation rate (10.3%). These two rates are the lowest that have been observed in the the previous 6 years. These predation rates are also lower than expected, given the number of moose (Fig. 12). At this time, lower than expected kill

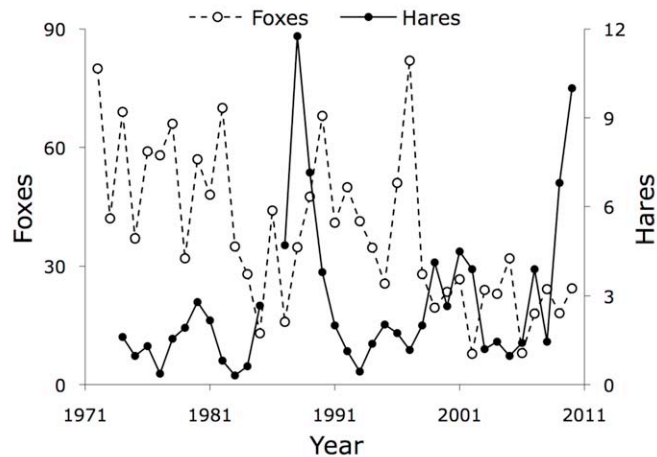


Figure 16. Indices of abundance for red foxes and snowshoe hares on Isle Royale, 1974–present. The hare index is the number of hares seen per 100 km of summer hiking. The fox index is the number of foxes seen from the plane during Winter Study, the sum of the maximum number seen at kills and the number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

rates are necessary for moose abundance to increase.

We conducted necropsies on ten moose (Fig. 13). Relatively few of these moose (3 of 10) showed signs of malnutrition (Fig. 14). Four of the ten necropsied moose had arthritis, which is a typical frequency.

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



Figure 17. The alpha male of Middle Pack feeding from a calf that they killed near Lake Halloran.



Figure 18. Moose are typically solitary creatures. However, in the springtime moose often tolerate each other's presence at springs where the water is rich in sodium. These springs are an important source of sodium, because a moose's diet is otherwise poor in sodium. Sodium is critical for many bodily functions including muscle contraction and neuron firing.

since 2001, when monitoring began. Ticks peaked in 2007, and they have declined since then (Fig. 15).

Other Wildlife

Snowshoe hare observations increased for the second year in a row, reaching the second highest level observed in four decades, while red fox observations in winter continued to be relatively scarce (Fig. 16).

For the fifth consecutive year, aerial counts of beaver using two aircraft in a double count were conducted in October 2010. Observers were Rolf Peterson and NPS staffer Mark Romanski. Pilots were Jim Hummel, from Voyageurs National Park, and Donald Murray, from UpNorth Aerials, flying small, tandem-seat aircraft. During 2006-2009, the total number of active sites observed in the combined efforts of the two teams declined from 112 to 87, but this trend was reversed in 2010 as the

number of active sites observed increased slightly to 93. There is very high turnover in active sites, as rate of abandonment of active sites ranged annually from 55-62%, probably reflecting a small number of beavers per site and high mortality from wolf predation. As the wolf population has declined by half and the number of reproducing packs reduced from four to one or two, we expect conditions for beaver survival to improve somewhat, but a long-term declining trend should be anticipated as forests age and become more dominated by unpalatable coniferous trees.

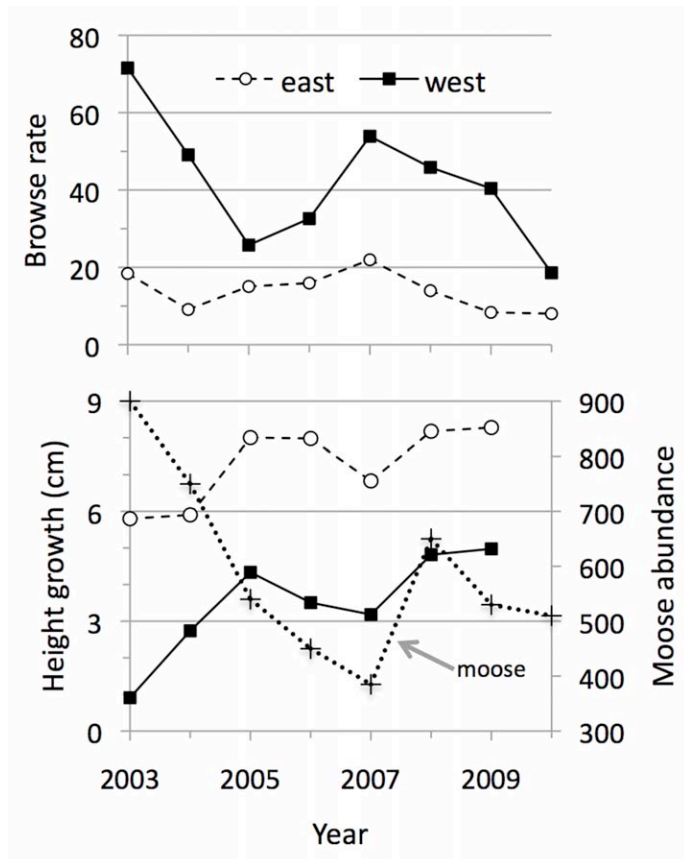


Figure 19. Trends in the browse rate (%) and height growth of balsam fir trees, 2003-2010.

Vegetation

The vegetation on Isle Royale is strongly influenced by the number of moose. Moose abundance has been lower during the past decade than at any point in the previous three decades. This prolonged period of low moose abundance is detectable in the browse rate of balsam fir, which have been declining over the past 7 years, and growth rates of balsam fir, which have been increasing over the same time period (Fig. 19). Balsam fir is an important component of the moose's winter diet. Abundant forage is not only a consequence of low moose abundance, but it also

affects the moose population. Abundant forage contributed to high rates of reproduction for moose and the large calf sizes.

In recent years, we have also increasingly noticed fir trees at the west end of Isle Royale that have grown to heights of two-three meters. The tops of these trees are close to escaping from the teeth of moose. Their escaping into the canopy is critical for the survival of fir trees at the west end of Isle Royale. Only large fir trees that grow into the canopy can produce seeds, which grow into small fir trees, that can be browsed on by moose.

Balsam fir is not the only vegetation to have responded to low moose density. Deciduous shrubs have also been flourishing. Dense shrub growth is difficult to walk through, and we noticed that vegetation slowed backcountry travel more than in past years.

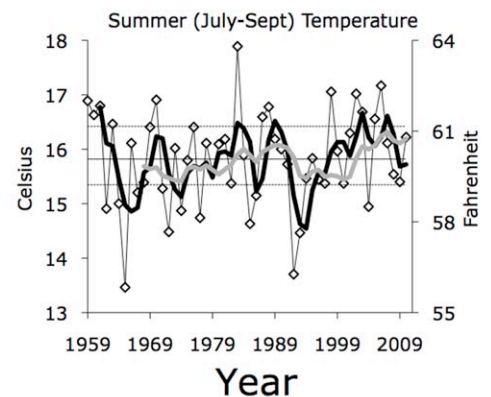
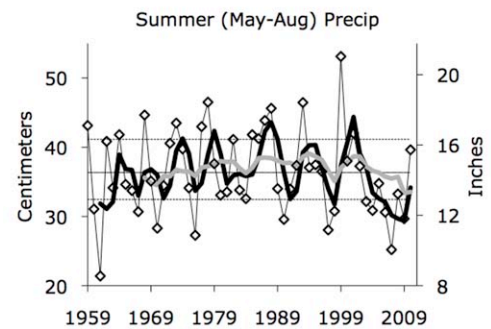
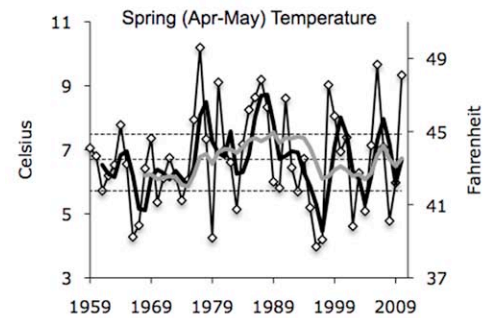
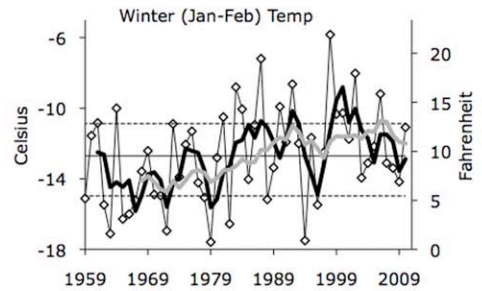
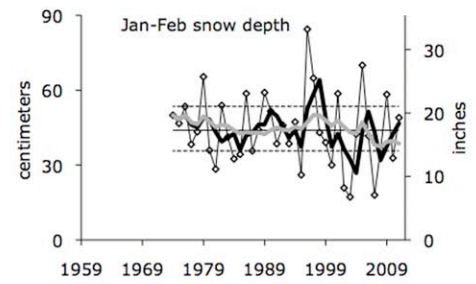


Figure 20. Snow depth (daily) and ambient temperature (hourly) during the 2011 Winter Study on Isle Royale.

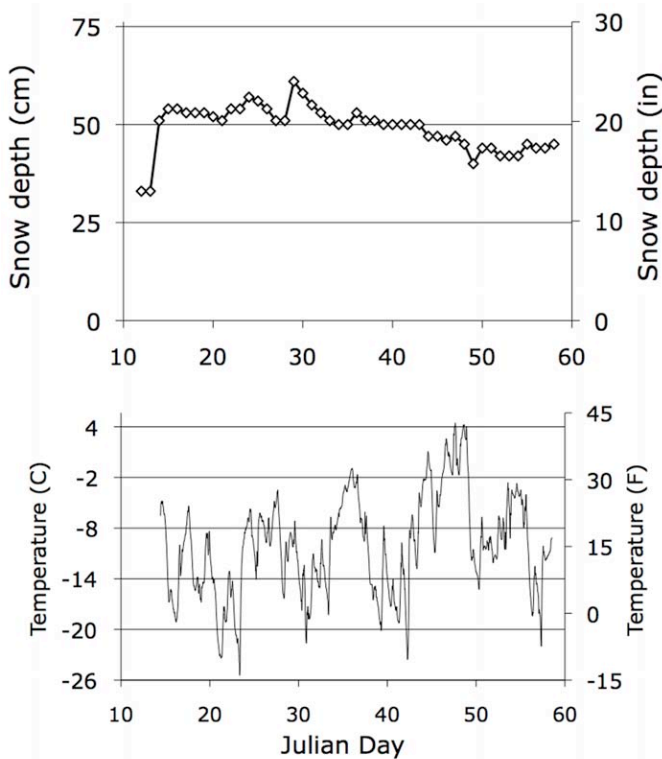


Figure 21. Climate data from Isle Royale (snow depth) and nearby northeastern Minnesota (temperature and precipitation). Climate data is from www.wrcc.dri.edu/spi/divplot1map.html. Solid lines are long-term means and dotted lines mark interquartile ranges. Climate change is highlighted by the 10-year averages (heavy black line), and moose may be affected by a 3-year moving average (heavy gray line).

Weather, Snow, and Ice Conditions

During the 2011 Winter Study, average daily snow depth was 49 cm (Fig. 20), near the 1974–2010 average of 44 cm. In mid-January, snows were deep enough to hinder the movement of moose calves. A warm spell occurred on 16–18 February, and the freezing temperatures that followed resulted in a strong, thick snow crust. This crust severely limited movement of moose to dense conifer stands where snow tends to be shallower. Even though winter temperatures were near the long-term seasonal average, frequent wind prevented the establishment of any ice bridges connecting Isle Royale and the mainland during the winter of 2010–2011.



Figure 22. Wind and snow had a significant impact on the research this winter. Because of bad flying weather, we flew only about half as many hours, compared to a typical year.

The Old Gray Guy

For decades we had thought the wolves of Isle Royale to be isolated and highly inbred, but had also somehow managed to avoid inbreeding depression, the negative consequences of inbreeding. In particular, Isle Royale wolves had rates of survival and recruitment that were similar to other healthy wolf populations. This perspective was important because Isle Royale seemed to some an important exception to the idea that small populations experience an elevated risk of extinction, in part, because of their vulnerability to inbreeding depression.

It was not until 2009 when we discovered the wolf population had long suffered a high incidence of malformed vertebrae (backbone). One third of the skeletons we inspected had a particular kind of malformity known as lumbrosacral transitional vertebrae (LSTV). By contrast, only 1 in 100 wolves suffer from LSTV in healthy populations. Moreover, the incidence of malformities has been steadily increasing over time as the population steadily became more inbred. The incidence of malformity has increased such that we have not detected a normal skeleton in the past fifteen years.

Last year, we discovered another surprise. The origins of this discovery traced to the late 1990s, when we began to

systematically and intensively collect wolf scats. They are a source of DNA, and allow us to learn about the population's genetic history. We stock-piled the samples until we found enough funding to analyze them.

As we analyzed the samples, what caught our attention was wolf #93, who was first detected through his scats in 1997. He carried several alleles that had not previously been observed in the Isle Royale population. These alleles and other genetic patterns indicated that wolf #93 was an immigrant from Ontario, Canada, very likely the first immigrant to Isle Royale since the population was first founded in the late 1940s. Patterns of genetic relatedness also indicated that #93 began reproducing in Middle Pack in 1998.

From field observations made more than a decade ago, we knew that Middle Pack was taken over by a new alpha male sometime between February 1997 and February 1998. We also know that 1997 was one of only two years in the past 15 when an ice bridge connected Isle Royale to the mainland for several weeks. In 1999, during a research flight, we observed the alpha male of Middle Pack defecate on a frozen lake. When the pack left, we landed the plane and collected the scat. The DNA in that scat matched that of wolf #93.

Wolf #93 seemed to be an extraordinary wolf. He was physically larger than other Isle Royale wolves. He exhibited strong territorial behavior that completely displaced West Pack, driving that pack to extinction in 1999. Under his leadership, Middle Pack grew to 10 wolves by 1999, the largest pack size observed on Isle Royale in almost 20 years. We reported all these observations before knowing that the alpha male of Middle Pack was an immigrant.

In addition, and prior to knowing that wolf #93 was an immigrant, we observed the alpha male of Middle Pack turn very light in color, almost white, as he aged. At that time, we dubbed him “The Old Gray Guy.” While turning light colored with age is not uncommon among wolves in general, this had never been observed before on Isle Royale. Before knowing that wolf #93 was an immigrant, we reported two other whitish-colored alpha wolves, and in 2010 we observed a fourth light-colored alpha. We later learned that these wolves were descendants of wolf #93.

With the immigrant’s arrival and the new genetic material he brought with him, the population’s inbreeding coefficient dropped dramatically from 0.81 to 0.09 in just four years (one wolf generation).

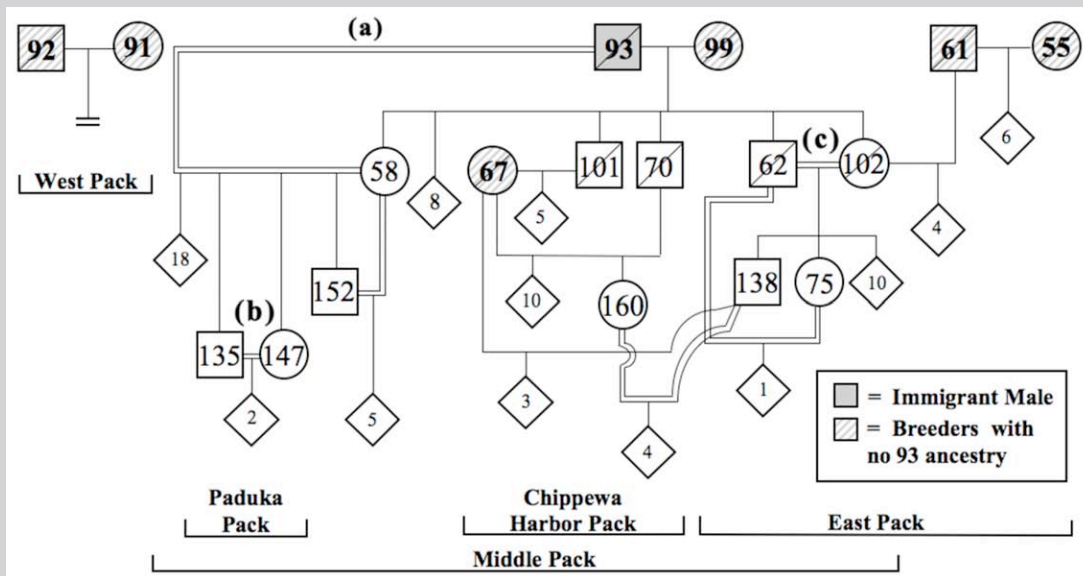
This immigrant event on Isle Royale represents an important opportunity to better understand genetic rescue, which is a potentially important conservation tool that involves

introducing one or more unrelated individuals into an inbred population as a means of mitigating inbreeding depression. However, the effectiveness of genetic rescue is not well understood because the opportunities to closely monitor an isolated population before and after a known immigration event are limited. For this reason, the Isle Royale immigration event represents a special opportunity.

The hallmark of genetic rescue is an increase in a population’s vital rates after immigration. However, the evidence for increased vital rates in the Isle Royale population is equivocal. There was no statistically detectable difference in survival or recruitment after his arrival. However, even important differences can be difficult to detect. Moreover, coincident with the immigrant’s arrival, moose on Isle Royale declined dramatically in response to food shortage, severe winter, and tick outbreaks. A clear response to the immigration event may well have been disguised by lack of food for the wolves. If so, it may be important to recognize that deteriorating ecological conditions can mask the beneficial effects infusing new genetic material. But the story does not end here.

The large gray wolf in the center is wolf #93, an immigrant from Canada. The wolf to his left is his daughter and mate, wolf #58. She died during 2010 and is also the same wolf shown in the image on page 2.





Pedigree of Isle Royale wolves from 1999 to 2009. Circles represent females, squares represent males, and numbers represent wolf identification numbers. Diamonds represent several individuals of both sexes who never reproduced. The numbers in the diamonds are the number of individuals represented by each diamond. Double lines represent matings between closely-related individuals (i.e., full-sibs, parent-offspring, or cousins). Symbols with a diagonal line were known to be deceased by 2008. The double line below wolves 91 and 92 indicates this pair produced no litters. The letters (a), (b) and (c) denote specific breeding events that are described in the text. Since 1999, all Isle Royale wolves are descended from wolves represented by shaded or hatched symbols.

The Old Gray Guy's genetic constitution was so superior to that of native Isle Royale wolves that he soon chose to mate with a wolf that shared half of his genes. That is, he sired 21 offspring with his own daughter (wolf #58; see also event [a] in the pedigree below). Two of the offspring from this parent-offspring mating began breeding with each other (wolves #135 and #147) when they established Paduka Pack in 2007 (event [b]). The inbreeding did not stop there. In 2003, the breeders of East Pack were full sibs (wolves #62 and #102) who had been born to the immigrant and an unrelated, Isle Royale wolf (event [c]). In other words, by 2002, five of the population's six breeders were either the immigrant or an offspring of the immigrant. In the end, wolf #93 was an alpha wolf for 8 years (1998-2006), gave birth to 34 offspring, has 22 grand offspring (and counting).

The Old Gray Guy was successful, but perhaps too successful for the benefit of the population. The dramatic success of the immigrant and his offspring led to quickly rising rates of inbreeding by 2003.

On Isle Royale, the last wolf unrelated to male #93 died in 2007. By 2009, 56% of all the

genes in the Isle Royale wolf population trace back to The Old Gray Guy. He initiated a genomic sweep of the Isle Royale population.

We once thought Isle Royale wolves had avoided inbreeding depression despite being isolated and highly inbred. The discovery of bone malformities in 2009 suggest they hadn't avoided inbreeding depression. And discovery of the Old Gray Guy's identity indicate that the wolves haven't been quite so isolated. We could not hardly have had a less accurate impression. One of the great rewards of long-term research is an opportunity to validate an ancient wisdom, that says: The more we know, the less we understand.

A technical description of these findings can be found in: Adams, JR, LM Vucetich, PW Hedrick, RO Peterson, JA Vucetich. 2011. Genomic sweep and potential genetic rescue during limiting environmental conditions in an isolated wolf population. Proc. R. Soc.

Räikkönen, J., Vucetich, J.A., Peterson, R.O., Nelson, M.P., 2009. Congenital bone deformities and the inbred wolves (Canis lupus) of Isle Royale. Biological Conservation 142(5): 1027-1033.



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