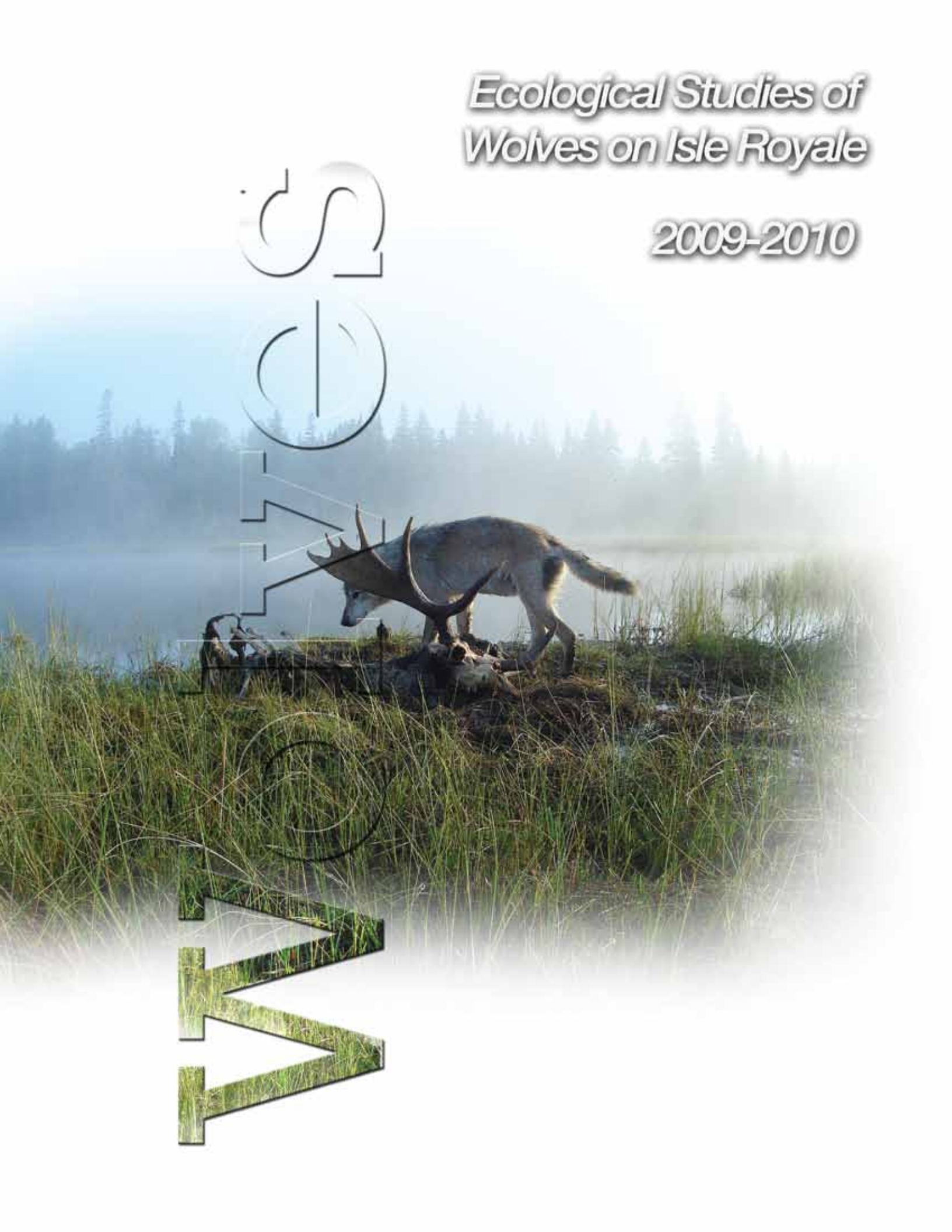
Ecological Studies of Wolves on Isle Royale

2009-2010



Ecological Studies of Wolves on Isle Royale

Annual Report 2009–10

by
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All photographs are by John A. Vucetich, Rolf O. Peterson, or George Desort.

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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!

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Ecological Studies of Wolves on Isle Royale

Without stories, places are desolate.

—Robert Archibald 1995

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, increasing 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 first arrived 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 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 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 2009, ground-based fieldwork continued from late April through late October. Rolf Peterson and John Vucetich directed that fieldwork with assistance from Paul Castle, Rubin Gutstein, Phil Krupczynski, Michael Nelson, Michelle Somers, Joshua Wied, Carolyn Peterson, and Leah Vucetich. Volunteers Tom Hurst, Kevin Hanley, and Keenan McFall reroofed the historic Bangsund cabin summer field headquarters. Jen Adams and Leah Vucetich supervised Marcy Erickson, Ben Betterly, Jon Bontrager, Ben Kamps, Scott Larson, Chelsea Murawksi, Josh Brinks, Ryan Priest, and Brian Southerland, who all worked in our genetics lab. During the course of the year many park staff and visitors contributed key observations and reports of wolf sightings and moose bones.

In 2010 the annual Winter Study extended from January 15 to March 8. John Vucetich, Rolf Peterson, and pilot Don E. Glaser participated in the entire study, assisted by Leah Vucetich (Michigan Tech), Dean Beyer (Michigan Department of Natural Resources) and the following personnel from the National Park Service: Jon Spencer-Hudson, Chris Lawler, Beth Kolb, Dieter Wiese, Paul Brown, and Marshall Plumer. US Forest Service pilots Dean Lee, Pat Lowe, and Tim Bercher flew several supply flights to Isle Royale from Ely, Minnesota.

George Desort filmed and photographed our research activities in February 2010 (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 2010, we conducted the fifty-second annual Winter Study of wolves and moose. Between January 2009 and January 2010, the wolf population declined from 24 to 19. In February 2010, we estimated the moose abundance to be 510, with 90% confidence intervals of [330, 730] (Fig. 1). This estimate is similar to last year's estimate of 530 moose (90% confidence intervals = [375, 705]). Wolf abundance has now declined below the long-term average (23 wolves). For the sixth consecutive year, the moose population remains at approximately half its long-term average (1,000 moose). In 2010 the ratio of moose to wolves remained low at ~27 to 1. The most important change during the past year is the loss of two of the island's four wolf packs.

During 2009, approximately 5 pups survived to their first winter, and approximately 10 wolves died. The recruitment rate (21%) is slightly lower than average, and the mortality rate (42%) is higher than average. The per capita kill rate, which indicates how well-fed the wolves have been, was 0.44 moose/wolf/month during winter 2010. This kill rate represents only 60% of what the wolves kill in a typical year.

The monthly mortality rate for moose during winter 2010, which is the proportion of moose that died per month, was relatively high (1.7%). Calves comprised 12.9% of the moose population during winter 2010, which is close to the long-term average, but the highest recruitment rate observed in the past nine years. In spring 2009, the intensity of winter ticks that infest moose was similar to what it had been the previous year. For the past two years tick infestations were lower than what they had been in the two previous years and close to the average intensity for the past nine years. Most of the moose that the wolves killed were adults that suffered from arthritis, jaw necrosis (periodontitis), or malnutrition.

In 2009 and 2010, *Fortunate Wilderness,* a documentary of the project by George Desort, aired on several PBS stations across the country.

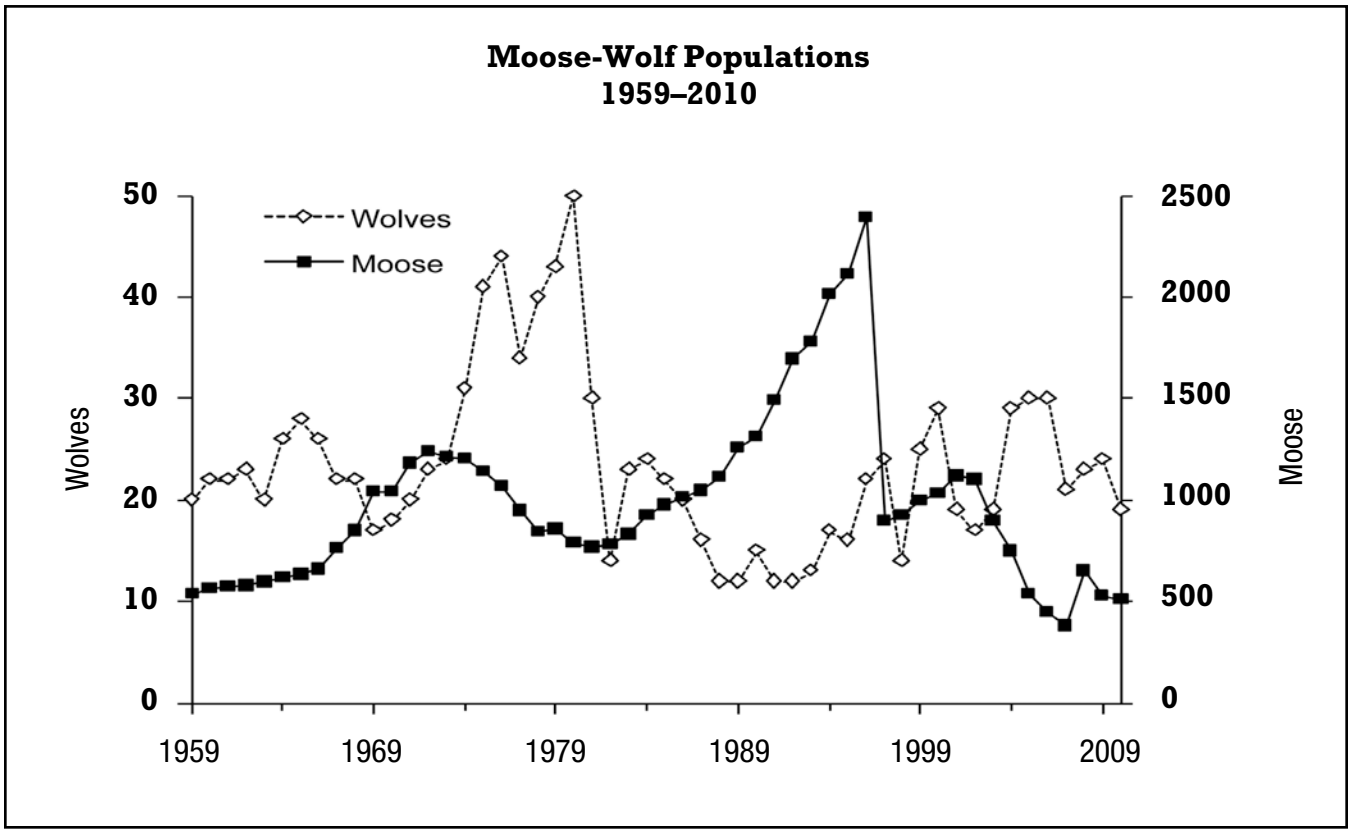

Figure 1. Wolf and moose fluctuations, Isle Royale National Park, 1959–2010. Moose population estimates during 1959–2001 were based on population reconstruction from recoveries of dead moose, whereas estimates from 2002–10 were based on aerial surveys.

The Wolf Population

During the 2010 Winter Study, the wolf population contained 19 individuals, a 21% decline from last year's 24 wolves (Fig. 1). The wolf population contained only two packs, down from last year's four packs. The number of wolves in each pack was

Chippewa Harbor Pack II (CHP)	9
Middle Pack II (MP)	7
Loners	3
2010 Total	**19**

Middle Pack was regularly observed to include 7 wolves (Fig. 2). Chippewa Harbor Pack was observed with 9 members on only one occasion and observed with 8 wolves on several occasions (Fig. 3). One of the lone wolves was radio-collared and was sometimes observed with a partner. He had dispersed from Chippewa Harbor Pack and was occasionally seen with his former pack on kills. On a couple of occasions he was observed with a partner while Chippewa Harbor Pack and Middle Pack included 8 and 7 wolves. We also observed and photographed a lone wolf on Todd Harbor and one on Washington Harbor. Photographs indicate that these wolves were different individuals, and neither was the radio-collared wolf's partner. The lone wolf on Todd Harbor was chased by the Chippewa Harbor Pack (Fig. 4). We also observed the tracks of a lone wolf that performed a raised leg urination on the south side of Washington Harbor. Finally, we observed tracks of two wolves (usually traveling separately), on a regular basis, in the area of Mud Lake, the southwest end of Siskiwit Lake, and Hatchet Lake. On the basis of these observations, we infer the presence of three loners. Genetic screening of wolf scats may result in small adjustments in this year's estimate.

During the past year, recruitment rates were below the long-term average. Specifically, it is likely that 5 wolves born in 2008 survived to their first winter—a recruitment rate of 21%. During the past year, mortality rates were above average—it is likely that 10 wolves from the 2008 population died in the past year, for an annual mortality rate of 42% (Fig. 5).

In the past year, we examined carcasses of two dead wolves. One wolf carcass washed ashore at Raspberry Island, at the northeast end of Isle Royale; it was probably killed by wolves on the ice. On May 3, 2009, we discovered the carcass of East Pack's alpha female. The circumstances of her death are described below.

In spring 2007, we live-captured and radio-collared 6 wolves. By March 2009, 3 of these wolves had died, and one probably dispersed from Isle Royale across an ice bridge in March 2009. The fate of the third is unknown. To aid our effort to observe wolves and estimate kill rates, we set out to live-capture and collar more wolves in spring 2009. Between April 26 and May 10, 2009, we radio-collared 5 wolves: 2 males from Middle Pack, and 3 males from Chippewa Harbor Pack (Table 1).

Figure 2. All seven wolves of Middle Pack walking across Lake Desor. The alpha female is on the right, and the alpha male is on the left.

Figure 3. Chippewa Harbor Pack traveling across Intermediate Lake. The old alpha female is in the foreground looking left toward the alpha male, and the new alpha female is on the alpha male's left side.

Figure 4. On January 30, Chippewa Harbor Pack chased this lone wolf out onto Todd Harbor. The wolf could be the sole surviving member of Paduka Pack. In early March, we observed a similar looking wolf partnered with a smaller (presumably female) wolf.

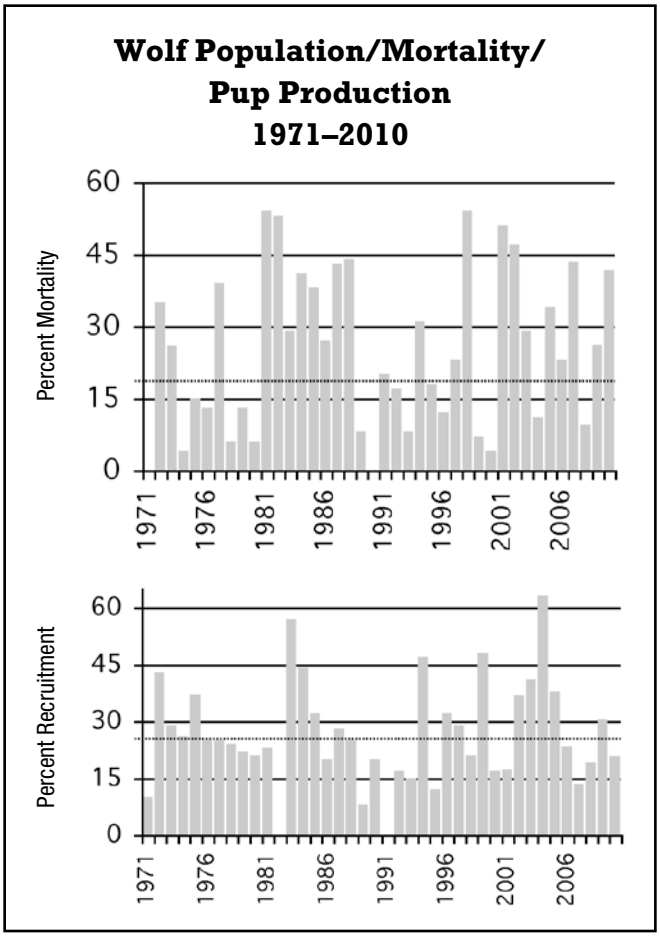

Figure 5. Percent mortality and recruitment for Isle Royale wolves, 1971–2010. The dotted lines mark long-term averages.

Analysis of blood samples collected at the time of handling these wolves suggests that 2 of the 5 wolves had previous exposure to canine parvovirus and 1 of these wolves showed exposure to adenovirus. By comparison, 2 of the 6 wolves collared in spring 2007 had previous exposure to West Nile virus and canine parvovirus. These are the first instances of exposure to canine parvovirus since 1988 and the first ever instances of West Nile virus.

In winter 2010 the wolf population killed at least 11 moose during the 39 days we observed them. For the two packs that we observed consistently enough, the per capita kill rate was 0.44 moose per wolf per month. Although this is significantly lower than the long-term average kill rate, it is not surprising given the reduced size of the moose population. Carcasses were very well utilized (see page 12). We conducted necropsies on 16 moose carcasses. These moose included 15 old adults (7 cows, 6 bulls, 2 unknown sex) and 1 calf. At least 6 of the moose we necropsied suffered from arthritis, at least 11 suffered from jaw necrosis, and 7 had low (<70%) fat content in their bone marrow.

In a typical year, Isle Royale wolves often travel along the shorelines of Lake Superior or inland lakes, where the snow is wind-blown and crusty. However, in 2010 the snow was shallow and heavily crusted until mid-February. Although the crust disappeared under new snow by mid-February, snow depth remained low. Because of these snow conditions the wolves spent much more time than usual traveling over inland routes, and hunting moose farther from shorelines.

In most years, we detect evidence of reproduction in each pack. The most common signs are estrous blood in the urine of the alpha female, direct observation of

Table 1.
Summary of wolves collared in spring 2009 and the results of blood tests for various pathologies.

Sex	Weight (lbs)	Estimated age* (yrs)	Pack membership	Status as of March 2010	Pathology test results **
male	78	≥8	Middle Pack	alpha	antibodies indicate a protection against adenovirus and parvovirus
male	68	2	Middle Pack	subordinate	all test results negative
male	54	yearling	Chippewa Harbor Pack	subordinate	all test results negative
male	83	3 – 5	Chippewa Harbor Pack	dispersing wolf	antibodies indicate a protection against parvovirus
male	65	yearling	Chippewa Harbor Pack	subordinate	all test results negative

* Age estimates are based on tooth wear.
** All tests results were negative, except those noted in the column. Each wolf was tested for West Nile virus, *Blastomyces, Bratislava, Canicola, Grippotyphosa, Hardjo, Ichterohaemorrhagiae, Pomona, Leptospirosis, Ehrlichiosis, Anaplasma phagocytophilum, Rickettsiosis*, canine parvovirus, canine adenovirus, canine distemper, and heartworm.

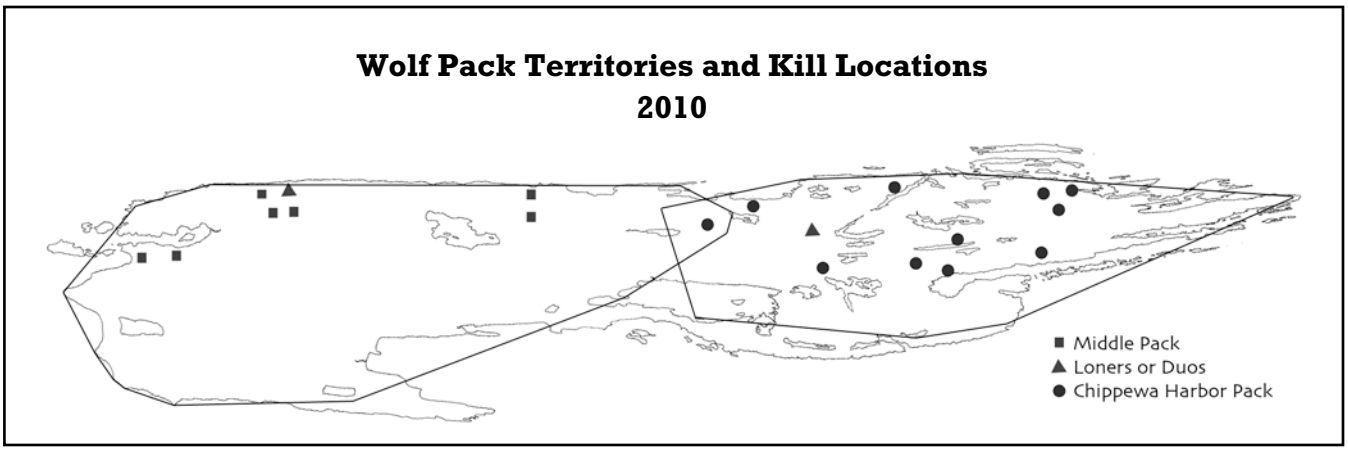

Figure 6. Wolf pack territorial boundaries and moose carcasses found during the Winter Study in 2010.

copulating wolves, or tracks in the snow that are characteristic of copulating wolves. This year we observed, for both packs, tracks in the snow that might be (but not certainly) interpreted as a sign of copulations.

Pack Narratives

The most important changes in the past year for Isle Royale's wolf population were the extinctions of East Pack and Paduka Pack, two of the population's four packs (Fig. 6). East Pack's decline took several years. In 2004–06 they numbered 9 wolves, in 2007 there were 6, and then 5 in 2008. East Pack was formidable competition, even during these early years of decline. They killed the alpha male of Chippewa Harbor Pack in January 2006 and the alpha female in January 2007. Serious trouble for East Pack began in the summer of 2008. None of East Pack's pups survived that summer, and by January 2009, 4 of the 5 adult wolves in East Pack had died, including the pack's alpha and beta males. In January 2009, the pack consisted only of a middle-aged alpha female and a newly recruited alpha male. In late April 2009, the female died in her den while giving birth to 8 pups (Fig. 7). The male was never seen alive after he was photographed on February 23, 2009, but there was a wolf tending the densite where the female died.

The East Pack alpha female was born in East Pack in April 2003. She was alpha female from winter 2006 to April 2009, and during her lifetime she produced three offspring, all with her uncle. While a decline in local

Figure 7. Bob Irmiger, DVM, is conducting a necropsy on the alpha female of East Pack who died in April while giving birth to pups. The pups are shown in the inset. Her death marked the end of East Pack's existence and was attributed to "uterine inertia," meaning the uterus stopped contracting during labor. We are unaware of any reported cases anywhere involving the death of a wolf while giving birth.

Figure 8. Two of the three adult moose that Middle Pack killed this winter involved their waiting for nine or ten days for the moose to die after being wounded by Middle Pack. Their difficulty in killing adult moose may be attributable to the alpha female (left) being injured. We suspect she was injured or suffering in some way because of the poor posture she exhibits in this image.

moose abundance almost certainly contributed to the decline of East Pack, inbreeding depression also likely played a role. In any event, East Pack's extinction is the end of a dynasty—there has been a territorial wolf pack centered on the east end of the island since 1972.

During winter 2010, the only sign of wolves in East Pack's former territory was the occasional foraging run of Chippewa Harbor Pack and a dispersing male from Chippewa Harbor Pack. Much of this former territory went largely unused—a sign of the lack of moose in the area.

Paduka Pack also went extinct in the past year. This pack first formed in winter 2007 when a brother and sister from Middle Pack established a territory on the north side of Isle Royale. In April 2007, they gave birth to two pups that survived through the summer of 2007. In 2008 they seem not to have produced any offspring. By January 2009, Paduka Pack included just the alpha pair and one wolf who was likely a yearling born in 2007. During winter 2009, Paduka Pack suffered from territorial incursions from both Middle Pack and Chippewa Harbor Pack. During the winter of 2010 we never saw evidence of Paduka Pack. Perhaps one of the lone wolves that we observed was a survivor of Paduka Pack.

Middle Pack, one of the two surviving packs, consistently contained 7 wolves in 2010. Two or 3 of these were likely pups, suggesting that 4 or 5 of Middle Pack's wolves died or dispersed in the past year. The alpha female is very old, at least 11 years. We observed her in an image taken on February 6, 2010, showing her walking with an unusual posture, suggesting that she may suffer some pathology or injury (Fig. 8). This apparent injury coincides with a period of time when Middle Pack had wounded a large cow moose but was unable to kill her for nine days.

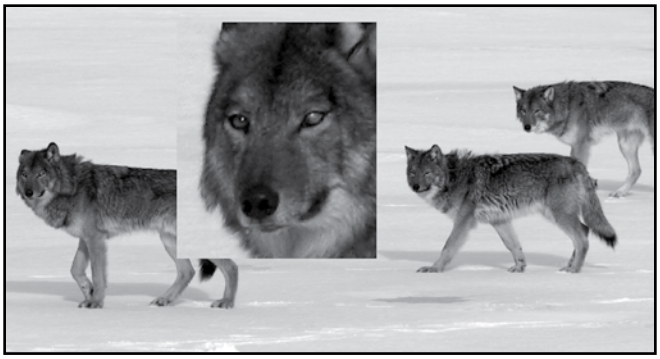

Figure 9. One of the subordinate wolves (left) of Middle Pack seems to suffer from an eye injury or pathology.

We also observed a wolf in Middle Pack with a clouded eye (Fig. 9). Bob Irmiger, veterinarian and long-term associate of the project, suspects this wolf could be suffering from corneal edema, a circumstance where the cornea, which normally dehydrated, has failed to "pump" out water, making it cloudy. Among the many causes of corneal edema are injury (e.g., a moose kick) or infection (e.g., caused by a stick in the eye).

We determined that one of the collared wolves in Middle Pack is the alpha male. The primary evidence for this conclusion is that he led Middle Pack in its effort to chase a loner out of its territory, actively scent-marked on several observations, and mated with the alpha female on March 3.

Chippewa Harbor Pack was 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. They've been leading the pack since East Pack killed the previous alpha pair (Fig. 10). Although Chippewa Harbor Pack was observed with as many as 9 wolves, they were often observed with only 5 to 7 wolves, with the other wolves unaccounted for. That Chippewa Harbor Pack was less cohesive than is typical may have been the result of infrequent kills (less interest to stay with the

Figure 10. During the winter the old alpha female (middle) of Chippewa Harbor Pack lost her position to a new, younger alpha female (left).

pack), low snow depth (making it easier to travel alone or in pairs), and a high proportion of older, subordinate wolves looking for opportunities to disperse.

For the Chippewa Harbor Pack, our observations suggest that 2 pups born in spring 2009 survived to see their first winter. If so, then only 1 wolf in Chippewa Harbor died in the past year.

One of the wolves we collared in April 2009 was initially a member of Chippewa Harbor Pack. However, by January 2010, he had dispersed and lived primarily as a lone wolf. The ambitions of a lone wolf are to learn how to kill moose on its own, find a mate, and establish a territory. Most dispersing wolves die in this effort. During winter 2010, we observed this wolf attack two different cow moose with their calves. One attack resulted in injury to the cow and calf, the other attack likely did not, and neither attack ended in a meal for the wolf. Although we usually observed him resting or traveling alone, he often did so with one other wolf, presumably a female. On February 19, he and another wolf killed a calf moose. They fed from it for one day before Middle Pack discovered the kill site and chased the wolves out of Middle Pack territory. We observed this lone wolf scent mark on one occasion within what had been East Pack territory. We observed this wolf near other members of Chippewa Harbor Pack on three brief occasions. We also observed him feeding from the carcasses of three moose on which Chippewa Harbor Pack had finished feeding. These happenings that surround the life of a lone, dispersing wolf, occur every year. However, it is less common for such details to be observed.

The Moose Population

The 2010 moose survey began on February 2 and ended on February 20. The flying conditions were good (calm wind, overcast), but ground conditions were poor (crusty snow and many patches of bare ground). The survey resulted in an estimated moose abundance of 510. The 90% confidence intervals on this estimate are [375, 705]. Moose density throughout most of Isle Royale was 0.69 moose/km^2, and there were 2.14 moose/km^2 in some regions of the east and west ends of Isle Royale (Fig. 11). Last year, when conditions for counting moose were good, we estimated 530 moose, with a 90% confidence interval of [375, 705]. These and earlier counts suggest that the moose population declined during 2002–06, has since been stable, and may be just beginning to increase (Fig. 1).

We calculated this year's estimate of moose abundance using a sightability factor of 65%. In most years we assume sightability is 75% based on the observed sightability of moose that had been radio-collared in the 1980s. This year we categorized the sightability of each moose as low, medium, or high. Moose with low sightability could be seen for just a brief moment, due to heavy forest cover, as the plane passed overhead. Moose with high sightability were observable for many seconds, typically because they were standing in open terrain with little vegetation to obscure our view. We assumed easy-to-see moose had 90% sightability, medium moose had 70% sightability, and difficult-to-see moose had 50% sightability. This year, we categorized 59 of the 85 moose observed on the plots. The average sightability for these moose was 65%.

Of the moose that we observed on the census plots in 2010, 12.9% (11 of 85) were calves. This is close to the long-term average, but higher than any recruitment

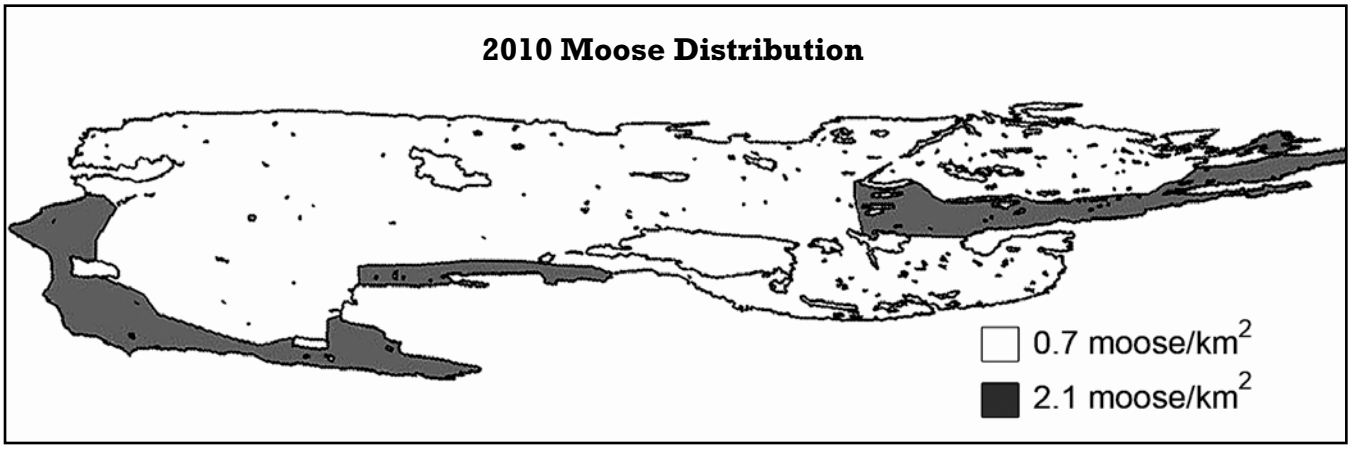

Figure 11. Moose distribution on Isle Royale in 2010 was relatively uniform, as it has been for the past several years. Only two strata were delineated, based on habitat types and results of the aerial counts on 91 plots that comprise 17% of the main island area.

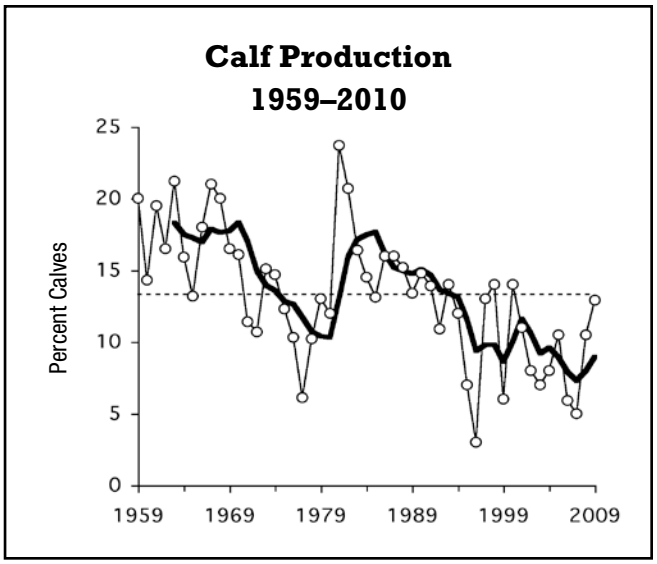

Figure 12. Long-term trends (1959–2009) in percent of the total moose population that are 8-month old calves. The 50-year average (13.3%) is marked by the light dotted line, and the curved line is a 5-year moving average.

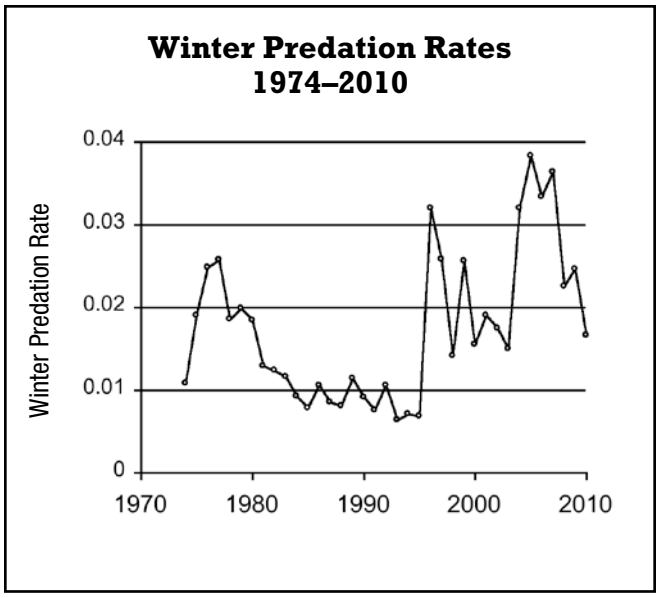

Figure 13. Winter predation rates (proportion of living moose killed per month) for Isle Royale moose, 1974–2010.

rate observed in the past nine years (Fig. 12). During the winter of 2010, we observed two sets of twins, both at the east end of Isle Royale, where East Pack had gone extinct. No sets of twins had been seen in winter since 2005.

The monthly mortality rate (percentage of living moose killed per month) was 1.7% during winter 2010 (Fig. 13). All of these moose died from wolf predation. Although the moose mortality rate is near the long-term average, it is lower than expected given the relatively high ratio of wolves to moose (1 wolf for every 27 moose), and lower than mortality rates documented for the previous six years.

Each spring we estimate the degree to which moose had been impacted by winter ticks (*Dermacentor albipictus*) during the preceding winter (Fig. 14). This is done by photographing moose and estimating how much hair they have lost during the preceding winter (Fig. 15). It is thought that tick abundance has been high since 2001, when monitoring began. Ticks peaked in 2007, declined in 2008, and remained at a similar level in 2009.

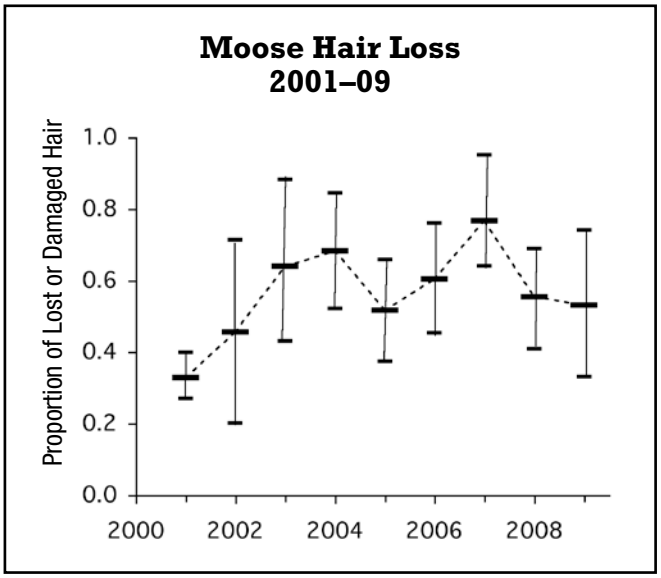

Figure 14. The extent of moose hair loss in spring, caused by winter ticks. Heavy bars are annual averages, and smaller bars mark interquartile ranges.

Figure 15. A bull moose in May with most of its fur lost to infestation by thousands of winter ticks.

Compared to recent years (Fig. 16), a greater proportion of wolf-killed moose showed signs of malnutrition (Fig. 17). Specifically, the fat content of bone marrow was below 70% for 7 of the 15 adult moose that we had necropsied in 2010. The moose that wolves killed also showed a high incidence of periodontitis (i.e., at least 11 of the 16 necropsied moose) (Fig. 18). In a typical winter, about 30% of wolf-killed moose are arthritic. This winter, at least 6 of the 16 necropsied moose were arthritic, and 1 (6%) was a calf. In a most winters, between 24% and 50% of wolf-killed moose are calves.

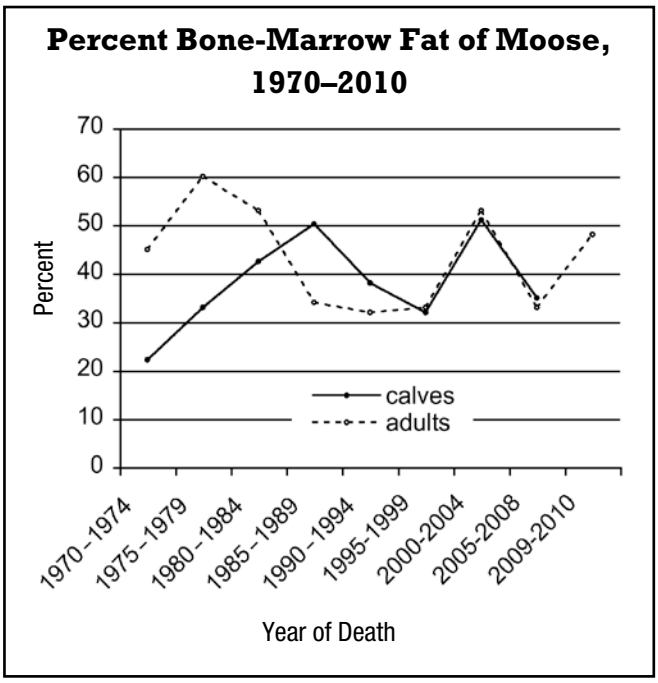

Figure 16. Long-term trends in bone-marrow fat for moose. The line for adults shows the proportion of adults with >70% fat in their bone marrow. The line for calves shows the mean value of percent fat in bone marrow.

Figure 17. The winter diet of moose is reduced to needles and twigs. We recently began efforts to use moose scat to better understand the relationship between diet, nutrition, and pregnancy rates in cow moose.

Figure 18. A normal jaw bone of a moose (below) and one with severe periodontitis (above). Among moose older than nine years of age, 70% die with at least slight jaw necrosis. Moose with jaw necrosis are vulnerable to being malnourished. Because the odor of the bacterial infection is strong, wolves are likely able to smell whether a moose has severe jaw necrosis before they attack it.

Remains to Be Seen

A long-held opinion about wolves maintains they are wasteful gluttons that regularly kill more than they can eat. This misperception is one of several reasons that some people use to rationalize persecuting wolves. The wolf-moose project has been collecting information on carcass utilization for years. Every winter, when we see that wolves have finished feeding on a carcass and have left the area, we hike to that site and conduct a necropsy. As part of the necropsy, we answer a set of questions: How many bones are left? Have the legs, skull, and pelvis been disarticulated from the vertebral column? How many of the bones are still covered in hide? We also have documented a rather precise relationship between this information and the proportion of the carcass that has been consumed. We recorded this information on 293 carcasses killed by wolves in winter between 1995 and 2008. From these observations, we find that wolves typically consume between 91% and 95% of the edible portions of a carcass (i.e., the interquartile range is [0.91, 0.95]). And wolves almost always (90% of the time), consume at least 73% of the edible portions of a carcass (Fig. A).

Nevertheless, it is interesting that wolves don't eat every edible portion of a carcass. Why not? If it is so difficult to kill a moose, why not eat everything available? The question is of interest to more than just wolf biologists. This phenomenon of not eating all that you capture is so important and so wide-spread in the animal kingdom, that scientists refer to it by a special phrase: partial-prey consumption. Partial-prey consumption has been observed and studied in various species of zooplankton, spiders, predaceous mites, insects, shrews, weasels, marsupials, canids, and bears. Even humans exhibit behaviors that are analogous to partial-prey consumption. Think, for example, about the food you leave behind on your dinner plate.

So, why is partial-prey consumption so common? Ecologists have considered two possible explanations. The first possibility is that partial-prey consumption is a simple physiological constraint. That is, an animal doesn't eat all that it's killed because it is full. It cannot digest all that it has captured. An alternative possibility is that partial-prey consumption is an optimal foraging strategy—an intricate, albeit counterintuitive, behavioral adaptation shaped by natural selection. The idea is that when prey are relatively scarce it pays, obviously, to eat all that you kill. However, when prey are relatively easy to catch, it pays to eat only the good parts (or perhaps leave behind the least choice parts). It may take more effort than it is worth to chew and digest the last few bits of low quality scraps that remain after most of the carcass has already been eaten.

These two ideas have been thoroughly tested for only two species, both were species of spider.

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Figure A: Typical remains of a moose after wolves have finished eating it. Organ meat is the first to be eaten. Except in rare cases, all significant pieces of muscles are eaten. Ribs are typically eaten, bones are often partially consumed, and nearly all the hide is commonly eaten. Even the muscles that make up the lining of the stomach are eaten.

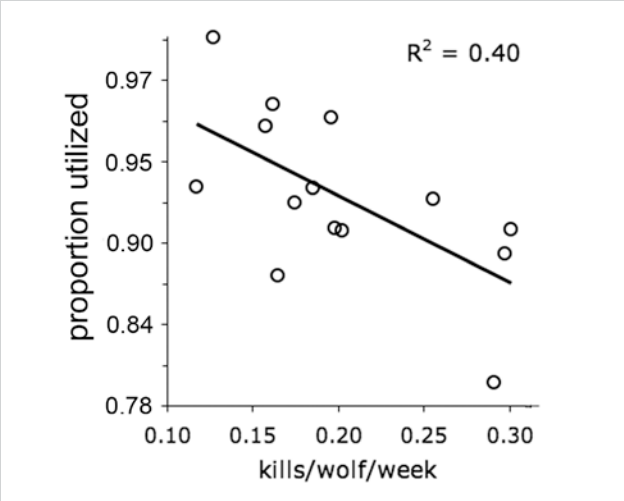

Figure B: Wolves typically eat most of the edible remains of a moose, and tend to utilize a carcass more fully during years when kill rates are lower. Each data point represents a population-wide average for each year between 1974 and 2008. Analogous patterns are observed in a wide range of species, including humans.

Other Wildlife

The National Park Service conducts aerial surveys of known osprey and bald eagle nests each summer. For the past twenty years these species have recovered to relatively low levels after being wiped out by organochlorine pollutants in the Lake Superior watershed in the 1960s. In 2009 NPS staff counted 11 active eagle nests and 4 active osprey nests. The long-term average for active eagle nests is 6 and 4 for osprey.

Snowshoe hare observations in summer increased in 2009 (Fig. 19) and aerial observations the following winter confirmed that local populations reached high levels. Red fox observations in winter continued to be relatively scarce (Fig. 19). Tracks of American marten were regularly seen at the west end of the island, and summertime surveys by NPS personnel have documented marten primarily in the island's west half. This is a recent colonizer of the island that was first documented (since historic extinction a century ago) almost twenty years ago.

For the fourth consecutive year, aerial counts of beaver using two aircraft in a double count were conducted in October 2009. 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. In 2006–08 the results suggested a low but stable population occupying 124–133 sites. In 2009, in spite of increased survey experience, only 92 active sites were estimated. Over the past four years, the total number of active sites found declined steadily from 112 to 87, suggesting a continuing decline. During 2006–09, 16 sites were active in all four years, and a total of 242 sites showed activity in at least one year. The rate of annual abandonment ranged from 55% to 62% over a three-year period, and 36% of the sites with beaver activity in 2009 had no previous history of activity in 2000–08. All these results point to a core population of beavers in a few dozen secure sites, with dispersing animals occupying marginal sites each fall and relatively few surviving. Given the marginal habitats available, wolf predation is likely an important limiting factor as beaver are forced to forage beyond a safe distance from water.

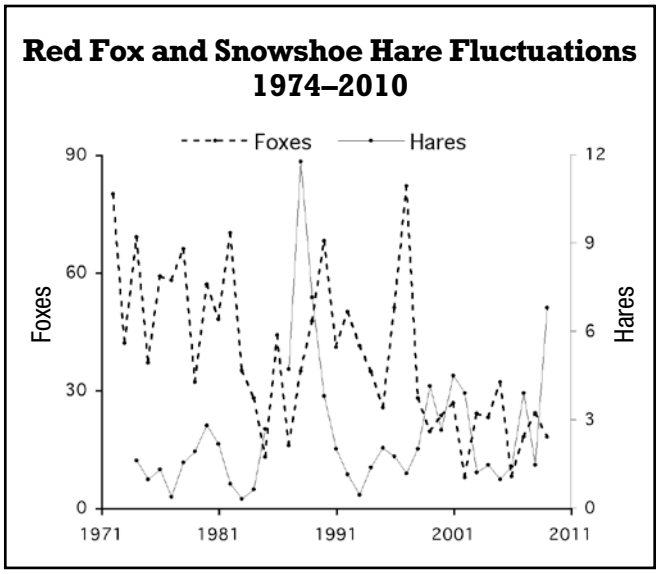

Figure 19. Indices of abundance for red foxes and snowshoe hares on Isle Royale, 1974–present. The hare index is the number of hares seen per 100 km of summer hiking. The fox index is the number of foxes seen from the plane during Winter Study, the sum of the maximum number seen at kills and the number seen otherwise per 100 hours of flight time.

Remains to Be Seen *(Continued from page 12)*

One species seemed to be limited by physiological constraint and the other seemed to be exhibiting an optimal foraging strategy. We set out to test the idea for wolves. A critical test for distinguishing these patterns is to assess whether carcass utilization is greatest when food is most difficult to come by (or when kill rates are the lowest). If so, then there is a good chance the behavior represents an optimal foraging strategy. Sure enough, for Isle Royale wolves, we found carcass utilization to be greatest when kill rates were lowest (Fig. B).

Wolves are not wasteful gluttons; they exhibit a behavior that has been observed in just about every species an ecologist has taken time to observe, and that behavior appears to be an optimal feeding strategy shaped by natural selection. Something similar has even been observed in humans. Specifically, William Rathje, a garbologist from the University of Arizona, has observed that you tend to find more food in the trash of people living in higher-income neighborhoods. So, what is a wasteful glutton?

The technical details of this research are described in manuscript that will soon be submitted for publication in a scientific journal: Vucetich J. A., L. M. Vucetich, R. O. Peterson. *The causes and consequences of partial prey consumption by wolves preying on moose.*

What Moose Teeth Tell us about Air Pollution

For many decades, we have been polluting our air with, among other toxins, mercury and lead. These pollutants eventually fall from the atmosphere and contaminate the Earth's land and water. During the environmental movement of the 1970s, anti-pollution regulations, like the US Clean Air Act of 1970, and the removal of lead from gasoline, first mandated in 1975, were enacted in Canada and the United States. By the early 1980s, the concentrations of lead and mercury in the atmosphere over eastern North America had declined significantly.

However, it remains difficult to assess whether current air pollution regulations have adequately reduced mercury and lead contamination in terrestrial ecosystems. One of the great difficulties is that for most places that can be easily monitored, lead and mercury contamination is heavily influenced, not by region-wide levels of pollution, but by local point sources of pollution, like individual factories.

Isle Royale is an ideal place to observe declines in mercury and lead because there are no local point sources and Lake Superior has a large airshed. That is, about 90% of the mercury that is deposited into Lake Superior comes from more than 200 kilometers away from the shoreline. This means that any decline in mercury would represent declines in pollution over a large region, not just changes in a single point source of pollution.

Although Isle Royale would be an ideal place to monitor mercury and lead pollution, no one monitored these pollutants before or after the enactment of anti-pollution regulations. Nevertheless, the concentrations of mercury and lead in the Isle Royale ecosystem have been recorded each year in the teeth of Isle Royale's moose that we've been collecting for each of the past five decades. Once mercury or lead was deposited from the atmosphere onto vegetation, it was consumed by moose. Then, by

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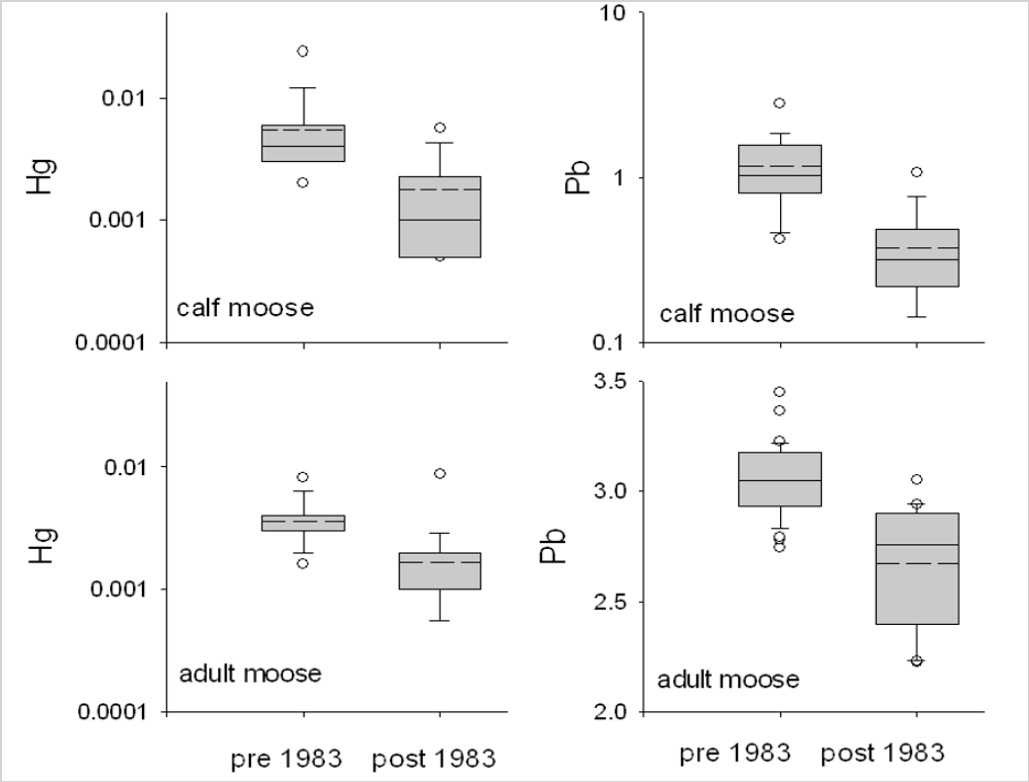


Box plot comparisons of Hg and Pb concentrations in calf and adult moose teeth for two periods of time: 1952–82, and 1983–2002. Units are mg/g dry weight. The boxes are interquartile ranges, the solid line is the median, dashed line is the mean, whiskers are 10th and 90th percentiles, open circles are data outside 10th and 90th percentiles.

Weather, Snow, and Ice Conditions

During the 2010 Winter Study, average daily snow depth was 33 cm (Fig. 20), well below the 1974–2009 average of 44 cm (Fig. 21). In spite of heavy snowfall affecting much of the eastern US, Isle Royale was relatively starved for fresh snow. A late January thaw produced a hard surface crust that supported humans without snowshoes, provided wolves with unlimited mobility, and hampered moose. Wolves were very active in the island's interior, and moose were found primarily in heavy coniferous cover where snow depth was minimal. 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.

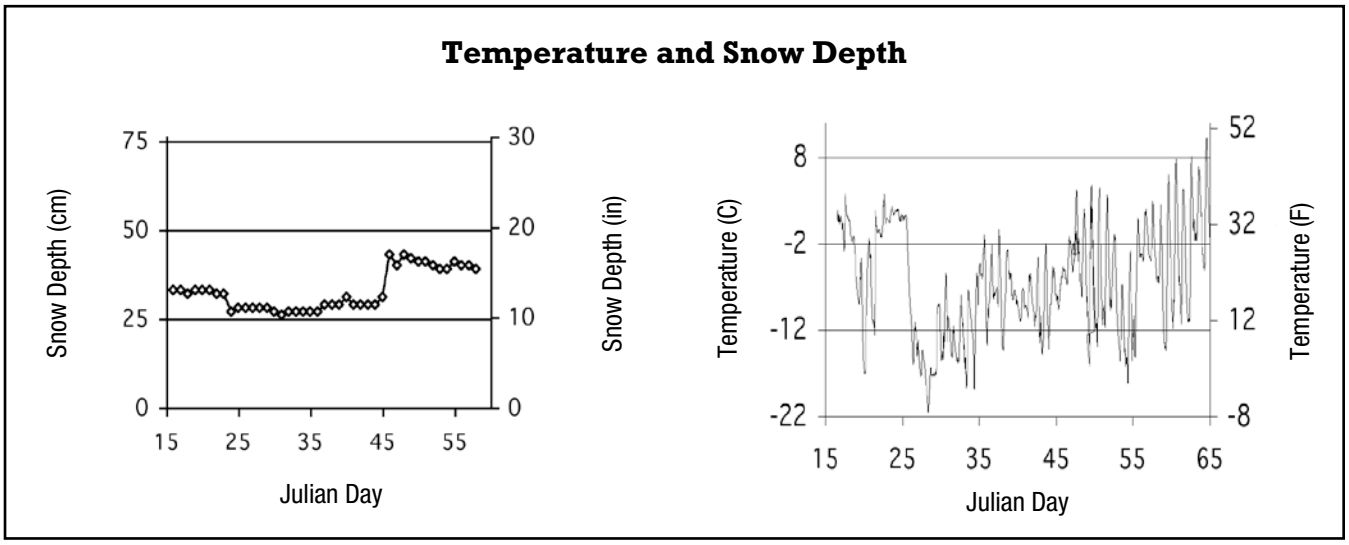


Figure 20. Snow depth (daily) and ambient temperature (hourly) during the 2010 Winter Study on Isle Royale.

What Moose Teeth Tell us *(Continued from page 14)*

a complex set of physiological processes, some of it was incorporated, permanently, into the teeth of moose. There the mercury and lead remained sealed in enamel until we collected and analyzed it.

Through collaboration with Peter Outridge (Geological Survey of Canada) and Rune Eide and Rolf Isrenn (both from University of Bergen, Norway), we measured the concentration of mercury and lead in the teeth of moose for which we knew the year of birth, thus the year when their teeth were formed. The moose we analyzed had lived in different years between 1952 and 2002. What we found is that mercury concentration dropped suddenly by about 65% in the early 1980s and has remained constant for the following two decades. Lead began declining in the early 1980s and continued declining throughout the next two decades. By 2002 lead concentrations in adult moose teeth were 80% lower than they had been prior to the early 1980s.

These declines clearly indicate the value of our current anti-pollution regulations. One of the most important remaining questions is whether these reductions in pollution are sufficient. Science alone cannot answer that question.

Each year for the past five decades, the wolf-moose project has been collecting samples of the skeletal remains of each dead moose we have discovered. In total, we've collected samples from the bones of more than 4,000 different moose. These bones have been valuable for reasons that never could have been imagined when this collection first began.

The technical details of this research are described in Vucetich J.A., P.M. Outridge, R.O. Peterson, R. Eide, and R. Isrennd. 2009. *Mercury, lead and lead isotope ratios in the teeth of moose* (Alces alces) *from Isle Royale, U.S. Upper Midwest, from 1952 to 2002.* Journal of Environmental Monitoring 11:1352–1359. That paper can be downloaded from the "Technical Papers" section of our website.

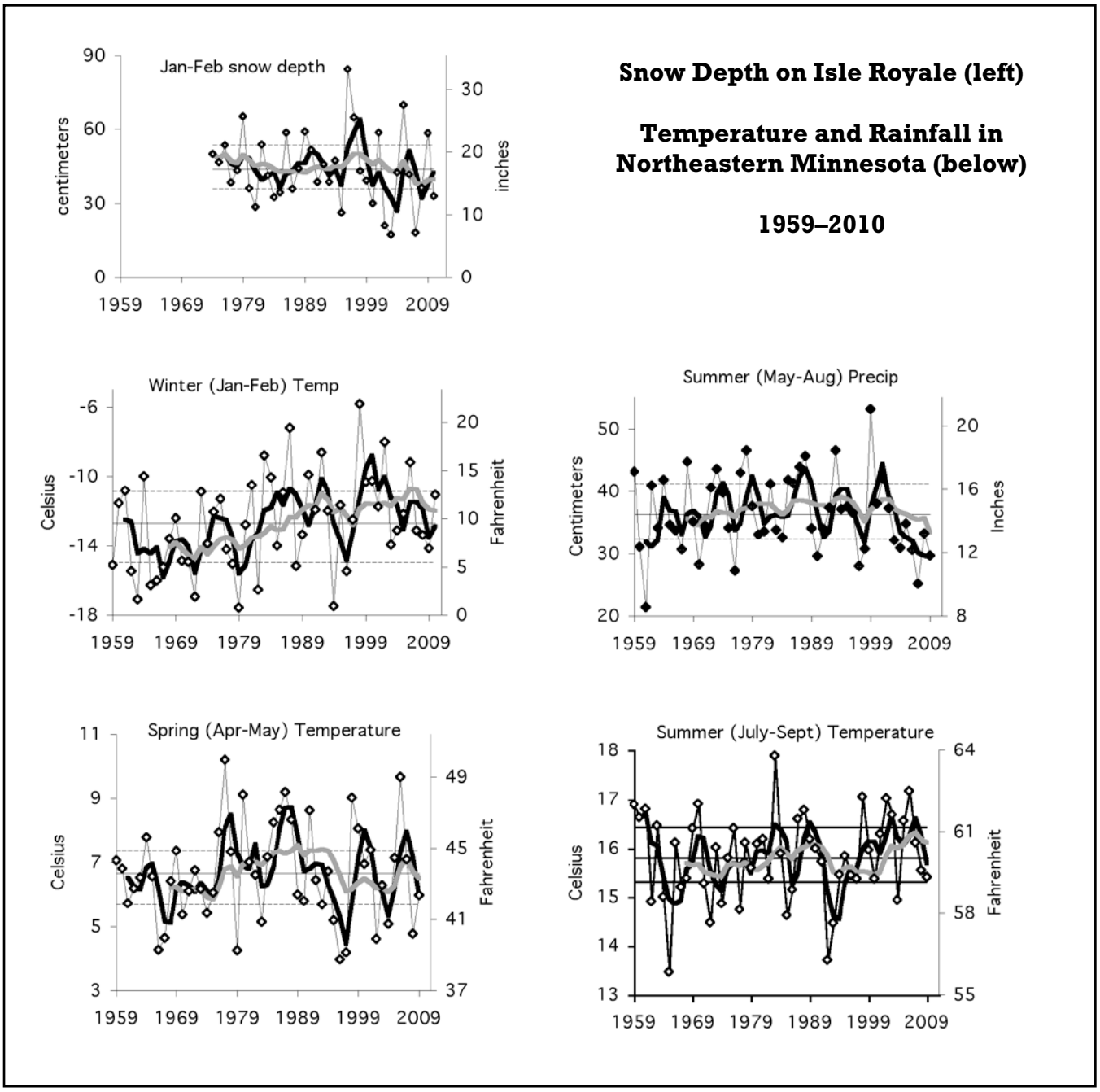
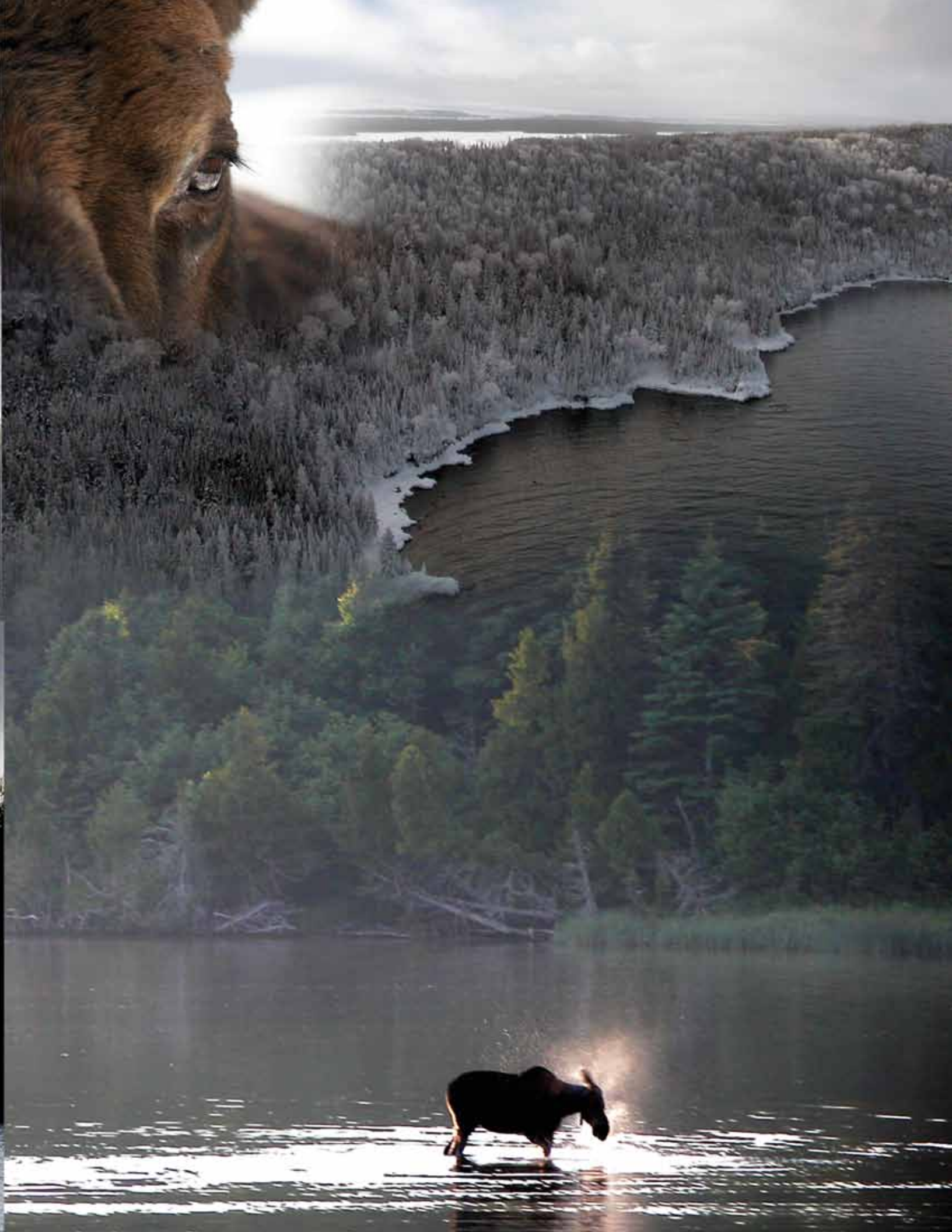


Figure 21. Climate data from Isle Royale (snow depth) and nearby northeastern Minnesota (temperature and precipitation). Climate data is from www.wrcc.dri.edu/spi/divplot1map.html. Solid lines are long-term means and dotted lines mark interquartile ranges. Climate change is highlighted by the 10-year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



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