Ecological Studies of Wolves on Isle Royale 2003–2004
"The most beautiful experience we can have is the mysterious. It is the fundamental emotion which stands at the cradle of true art and true science. Whoever does not know it and can no longer wonder, no longer marvel, is as good as dead, his eyes are dimmed."

— Albert Einstein, 1934
Ecological Studies of Wolves on Isle Royale

Annual Report 2003-2004*

by

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and

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31 March 2004

*During the past year, major support of these studies was received from the National Park Service (Co-op Agreement No. CA-6310-9-8001), National Science Foundation (DEB-9903671), the Earthwatch Institute, and the Robert Bateman endowment at the Michigan Tech Fund.

Additional contributions were received from the following organizations and individuals: Ronald & Karen Armstrong, Charles & Elizabeth Boyle, Gregory Capito, Allen & Joan Carrier, Alison J. Clarke, Ronald & Barbara Eckoff, James & Yvonne Eyer, Wanda Ann Foster, Edith N. Greene, Violet & Edward Haelterman, Douglas & Marie Hanson, John & Irene Heidtke, Chris & Audrey Henningson, Mary Hindelang & Mark Silver, Shirley A. Holmes, Horace & Mary Jackson, Melvin & Sharlene Jacobson, David & Diane Judd, Dr. H. Robert Krear, Richard & Carol Lappi, Sandra Mae Larson, Frances R. LeClair, Paul & Gloria Marcus, L. David Mech, James & Jane Moeller, Chandrasekaran Nagaswami, Michael & Kari Palmer, Janet L. Parker, Rolf & Carolyn Peterson, Gerald & Lynn Rossow, Mary D. Seffens, Daniel & Mary Beth Shannon, Joan Silaco, Billie E. Smith, Thomas & Karen Snyder, Viola Spiegel, Nancy Gibson Sternal, Glenn K. Strid, Michael F. Strother, William & Cynthia Veresh, John W. Weisel, Dorothy Zeller.

There were several gifts in memory of Ruth J. S. Peterson. Unless otherwise noted, photographs are by Rolf O. Peterson.

Important contributions and personal time and financial assistance from the following Earthwatch volunteers are gratefully acknowledged:

Team 1: Peter Dally, Clay Ecklund, Emily Fawver, and Tim Pacey (leader).

Team 2: Michael Clark, Ron Eckoff, Jeff Holden, Drew Marold, Craig Ralston, and Jeff Plakke (leader).

Team 3: Maureen Barrett, Courtney Dewart, Mark Dewart, Becky Erickson, Nathan Hambel, Eddie Leventer, Elizabeth Murphy, Rick Noble, Nina Smith, Miranda Struck, Paul Sugg, Lynda Thompson, Eunice Blavascunas (leader), Cindy Carter (leader), and Jason Duetsch (leader).

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.

Cover photo: (Top) Individual hairs shed from an Isle Royale wolf, magnified 770 times with scanning electron microscope after sputter-coating with gold and palladium (contributed by John W. Weisel and Chandrasakaran Nagaswami.) (Bottom) Chippew Harbor Pack wolves in 2004. Other cover photos by John and Leah Vucetich and Rolf Peterson.

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Ecological Studies of Wolves on Isle Royale

"Underlying the beauty of the spectacle there is meaning and significance. It is the elusiveness of that meaning that haunts us, that sends us again and again into the natural world, where the key to the riddle is hidden."

—Rachel Carson

Summary

During 2003-2004, the wolf population surged from 19 to 29 individuals, while moose declined from an estimated 900 to 750 (fig. 1). During the year, the wolf population exhibited high survival (89 percent), and all three territorial packs each raised at least four pups. Both the Chippewa Harbor Pack and the Middle Pack pushed their territories to the northeast, effectively squeezing the East Pack into an even smaller space. The moose population declined for the second year in a row, to an estimated 750 animals. Poor moose calf survival in 2002 and 2003 seems to explain the population decline, and predation loss was high in winter 2004 for both calves and adults. Winter ticks have been implicated in recent years of high mortality and poor reproduction for Isle Royale moose. The moose population faltered during a period of unusually high heat and drought (1998-2002) in North America that has been linked to human-caused global warming. Increased vulnerability of moose to predation may explain the moose decline and the resurgence of the wolf population.

Personnel and Logistics

In summer 2003, Rolf Peterson and John Vucetich directed ground-based field work, aided by Jason Duetsch, Nathan Hambel, Carolyn Peterson, Leah M. Vucetich, and John Weisel (on sabbatical from University of Pennsylvania Medical School). Fieldwork continued from April 26 through October 18. In 2004 the annual winter study extended from January 12 to February 27. Rolf Peterson, John Vucetich, and pilot Don E. Glaser participated in the entire study, assisted in the field by Keren Tischler, Leah M. Vucetich, and the following personnel and volunteers from Isle Royale National Park—Eunice Blavascunas, Larry Kangas, Chris Lawler, Andy Miller, Trevor Peterson, and Marshall Plumer. During the winter study, U.S. Forest Service pilots Wayne Erickson and Dean Lee flew several supply flights to Isle Royale from Minnesota.
The Wolf Population

During the 2004 winter study, a total of 29 different wolves was counted, compared to 19 in 2003. This is equal to the largest annual increase ever recorded at Isle Royale, and it was surprising because the wolves had consistently numbered 17-19 in the previous three years when there was evidence of food shortage and territorial skirmishes (fig. 2). The social organization of the wolf population continued to be dominated by three territorial packs:

- East Pack III ...................................................... 6
- Chippewa Harbor Pack ...................................... 10
- Middle Pack II .................................................. 12
- Singles .................................................................. 1
**Total 2004 ................................................. 29**

After the dispersal of one wolf from the Middle Pack, the three packs maintained their numbers consistently at 6, 10, and 11 wolves until breeding activity caused some splintering in late February. Four wolves in the 2004 population were radio-collared. Two female wolves, alpha 410 (fig. 3) and her daughter 1060, were live-captured and radio-collared in early May 2003, and a radio-collar on alpha male 670 (installed in 2001) in the East Pack continued to transmit in 2004. The radio-collar on alpha female 1072 in the Middle Pack (also dating from 2001) failed in late summer 2003, although when binoculars were used from aircraft she was recognizable as the only collared wolf in this pack (fig. 4).

We anticipated that inter-pack conflict might be high in 2004, but we recorded only one prominent trespass by the Middle Pack into Chippewa Harbor territory. There were apparently no direct confrontations between packs, and no wolf deaths were recorded during the winter study. Single wolves, dispersed from their natal packs, are most likely to be caught and killed by other packs, and the high cohesiveness of the packs in 2004 meant that few single wolves were present on the island.

The Chippewa Harbor Pack has been pushing into East Pack territory for several years, and in 2004 the expansion of Chippewa territory was slight (fig. 5). Both packs scent-marked the NPS docks at the Daisy Farm and Birch Isle campgrounds, and these structures seemed to demarcate the agreed-upon border between these packs (fig. 6). Nevertheless, the Chippewa Harbor Pack

![Moose-Wolf Populations 1959–2004](image-url)

Figure 1. Wolf and moose fluctuations, Isle Royale National Park, 1959-2004. Moose population estimates during 1959-1993 were based on population reconstruction from recoveries of dead moose, whereas estimates from 1994-2004 were based on aerial surveys.
often spent entire days prominently bedded on open ice near the edge of its territory, while the East Pack seemed interested in avoiding its neighbors.

Mating activity was observed among the alpha pairs in all three packs. Female 410, the alpha female in the Chippewa Harbor Pack, was seen mating with the uncollared alpha male four times (on February 16, 19, 21, and 22, see figs. 7 and 8), while the alpha pairs in Middle Pack and East Pack also mated on February 22. The presence of sexually mature subordinate wolves caused visible conflicts within the Middle Pack and the Chippewa Harbor Pack. In the latter case, immediately after mating, alpha female 410 ran down and “punished” her daughter, female 1060, and the next day female 1060 dispersed, picked up a partner, and localized in a far corner of the pack territory where we found tracks suggesting mating on February 26 (fig. 9).

Snow was relatively soft and of near average depth for most of the winter study in 2004, and wolves hunted primarily along the lakeshores where they could most easily travel (fig. 10). Kill rates for the three packs ranged from 2.5 to 3.4 moose per wolf per 100 days, above the long-term average of about 2.0.

In 2003-2004, annual mortality in the wolf population was only 11 percent (2 out of 19), lower than average and much lower than in the previous three years (fig. 11). One of the two deaths occurred in February 2003 when the Middle Pack killed a single trespassing male, and the other wolf that died was a physically small, subordinate wolf seen in the East Pack in 2003. In 2004, there were nine wolves at least one year of age in the Chippewa Harbor and Middle packs, so there should be many

Figure 2. The Middle Pack rules about two-thirds of Isle Royale, but moose are sparsely distributed throughout their entire territory. Photo by J.A. Vucetich.

Figure 3. Founding member of the Chippewa Harbor Pack, aging female 410 sports a scarred nose and a missing canine tooth.
Figure 4. The alpha pair of the Middle Pack includes collared female 1072 (left) and a very light-colored alpha male (center). Photo by J.A. Vucetich.

2004 Wolf Population Organization and Kills

Figure 5. Wolf pack movements and moose carcasses (almost all fresh wolf-kills) during the winter study in 2004. Scent-marking was observed by all three of the packs.

Figure 6. East Pack runs from its border with Chippewa Harbor Pack at the Birch Isle dock (left), while the Chippewa Harbor Pack visits its border at the Daisy Farm dock (right).
Figure 7. Chippewa Harbor alpha pair mating on 22 February. They remained tied for 15 minutes.

Figure 8. Middle Pack alpha male rests his head on female 1072 on 22 February, a few hours after they were observed mating.

Figure 9. This dispersing male partnered with subordinate female 1060 from the Chippewa Harbor Pack. Tracks suggested they mated in a part of her pack’s territory as far as possible from her mother, who had repeatedly “punished” 1060 during the breeding season.
dispersing wolves looking for vacancies in the next year.

A substantial increase in the wolf population in 2004 was not predicted, given the seeming stagnation in their numbers in the past three years. We suspect that the increase is partly random fluctuation and partly a response to increased moose vulnerability because of the indirect effects of warmer climate. About 40 percent of the past annual variation in wolf population growth rate is attributable to the abundance of moose more than nine years of age. At least 30 percent of the past variation is unexplained, arising from chance fluctuations in survival and reproduction, which tend to be higher with smaller population sizes. There is little reason to think that the number of old moose will increase much before 2007-2008, based on relative cohort strength following the 1996 die-off of moose. However, warm weather and a resulting increase in prevalence of winter ticks on moose may be increasing moose vulnerability to predation (fig. 11).

Figure 10. In a snowstorm, a Middle Pack wolf rests near the frozen carcass of a moose that died of starvation on Houghton Point in January. Photo by J.A. Vucetich

Figure 11. Wolf population size (top) is explained by patterns of mortality (middle) and reproduction (bottom).
Figure 12. Moose distribution on Isle Royale followed its usual pattern in midwinter. Three strata of moose density were delineated. Also shown are the 91 plots where moose were counted from aircraft.

The Moose Population

During February 2004, the moose population was estimated at about 750 animals (with 90 percent confidence intervals of 863 [upper] and 645 [lower] moose), or 1.4 moose/km² (fig. 12). This compares to an estimated 900 moose in 2003 and 1,100 in 2002. Calves constituted 7 percent of the 134 moose counted on census plots, considerably below the long-term average of 13 percent for Isle Royale moose (fig. 13).

The effects of winter ticks may be the primary indirect influence of climate on wolf-moose interaction. In spring 2003, there was an increased prevalence of hair loss in moose caused by winter tick infestation (fig. 14). This ectoparasite (Dermacentor albipictus) weakens moose in winter and spring by withdrawing blood, so much so that in severe cases, a moose may have to replace its entire blood supply within a few weeks at a time when it is in the worst physical condition of the year. Tick infestation also leads to reduced forage intake, as moose may groom instead of feed. Winter ticks thrive in years that follow warm springs, and an unusually warm autumn preceded a widespread mortality event for moose in North America in spring 2002 (fig. 15). Apparently, warm weather in either spring or fall may lead to growth of winter tick populations. Beginning with the El Nino event in 1998, there was a five-year period of notable drought and warm weather which has been linked to anthropogenic global warming (see Hoerling and Kumar 2003 in Science 299:691-694). Following several years with unusual warm periods at various times of the year, it appears that the tick population has continued at high density, as hair loss was noticeable in moose as soon as we began aerial observations in January 2004.

Figure 13. Moose calf abundance (at approximately six months of age) on Isle Royale, as a proportion of the total population. These are best estimates, a weighted mean of aerial counts in fall and/or winter.
During the 2004 winter study, snow depth increased rapidly to the long-term average level of about 60 cm, resulting in moose movement to coniferous habitats, where snow depth is least and physical protection from wolves is maximized. Moose continue to be heavily concentrated in areas of balsam fir regrowth at the east end of the island (see fig. 12).

The aerial moose census in 2004 was flown during 31 January–15 February. On 91 plots, which average 1.15 km² in area, we counted 134 moose, compared to 132 moose in 2003. Although the number of moose on plots was similar in 2003 and 2004, moose distribution was distinctly more stratified in 2004. The resulting estimate for 2004 was 750 moose, suggesting a decline from the 2003 estimate of 900. Two improvements in analysis of census results were implemented. Results were stratified post-census using a modeling approach to minimize variance, and a more appropriate statistical distribution (negative binomial instead of normal) was used to calculate density and confidence intervals for each stratum (fig. 12).

In winter 2004, we recorded moose mortality across the island for 44 days, based on snow-tracking and telemetry locations for packs. Thirty-five fresh moose carcasses were located during this time, including three moose that fell or were chased off cliffs and three moose that apparently died of malnutrition. The measured mortality rate during winter 2004 was 80 moose per 100 days, almost twice the level seen in 2003 (fig. 16). If this rate prevailed for four months, a conservative estimate, it would be almost double the estimated recruitment rate.

Moose were increasingly restricted by snow as it accumulated in January, as is normal for Isle Royale in midwinter. Bone marrow fat content for calves killed by wolves averaged 40 percent, and 40 percent of the adult moose that died of all causes had bone marrow fat equal to or exceeding 70 percent. These reflect a nutritional plane for moose somewhat lower than the average recorded in the previous four years (fig. 17).

**Figure 14.** The prevalence of hair loss from moose in spring increased during 2001-2003, when we systematically recorded hair loss patterns in May and early June.

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Forage for moose in winter is particularly scarce in old forests at the west end of Isle Royale, where moose are often observed feeding on arboreal lichens. Graduate student Keren Tischler is using analysis of stable isotopes of carbon and nitrogen to evaluate the significance of lichens and other forage.

Forest Vegetation

Our studies of forest vegetation have concentrated on balsam fir, as this is the key winter forage in the meager winter diet of moose (fig. 18). Balsam fir is found primarily at the two ends of Isle Royale and is generally absent in the middle of the island, which was burned over in 1936 and 1948. At the west end of the island, fir regeneration in the predominantly old forests is heavily hedged by moose foraging, so that no trees are growing up to replace the century-old trees in the canopy (fig. 19). In contrast, at the east end, where forests were heavily disturbed by fires set by...
In the beginning
Cow moose about to give birth seclude themselves, often in the same location each year, so that the newborn calf bonds only with its mother. At Isle Royale, many cow moose seek shorelines and developed areas when giving birth, as both provide some security from hunting wolves. On May 24, 2003, a moose gave birth just 20 meters from the NPS shelters on the bank of Washington Creek, where Candy Peterson and I, along with John Weisel, were camped. In the dark hours before sunrise, we heard strange vocalizations from the cow during labor, then the first conversation of the cow and her newborn bull calf. After sunrise, as the calf was first able to nurse, the cow began a long process of coaxing the calf to cross the creek. During the next 6 hours the calf built up enough courage to jump in and swim through ice-cold water to follow its mother. From field notes:

"About 0345, on a moonless night with temperatures near freezing, a cow moose crossed the creek and began uttering a regular series of very low-pitched, guttural noises, drawn-out groans lasting one to two seconds, two to three times per minute. Candy called it ‘Darth Vader breathing’. Sometimes the exhalation would end with the rubbery flapping of her nose as she shook her head. By standing in the shelter I could see a cow moose, on her feet at the water’s edge. Spring peepers made their deafening calls, a white-throated sparrow gave a too-early song, and a courting woodcock, himself an occupant of the alder flat next to the creek, carried on with his persistent ‘peenting.’

"For 15 minutes, beginning at 0400, the groans became less frequent and more erratic, but at 0415, rather abruptly, the cow began to grunt regularly, about once per second, in a call commonly used to communicate with a calf. Simultaneously, we heard the soft, very high-pitched bleating of a newborn calf, one of the most endearing noises of the animal world. The grunting of the cow seemed almost frantic for about a minute, but then her calls slowed down while the calf’s continued. At 0430 we heard three more long, drawn-out groans from the cow, separated by long intervals.

"At 0730, the sun was up, but there was no warmth at the north-facing birthsite deep in the valley bottom. The cow stood at the edge of the creek, the same place she had given birth three hours before, and at her side was a very small male calf, standing on shaking, wobbly legs. ‘It’ll never make it; it’s too small,’ I told Candy, hoping I was wrong. The cow frequently licked the calf’s face and, occasionally, the shoulders. The calf followed its mother as she slowly walked to and fro along the creek bank, and several times the calf tried unsuccessfully to reach its mother’s udder and nurse. After bedding down for a half hour, the calf rose and tried to nurse, again without success. At 0900, after several soft grunts and briefly licking its calf, the cow walked into the creek and crossed to the other side, about 15 meters away, where it fed voraciously on newly sprouted grass.

"The calf then took an hour-long nap, after which the mother began to re-cross the creek, toward the calf, calling about every two seconds, until standing in mid-creek. The calf edged over to the bank of the creek, where there was a 30-cm drop to the water. Still
The National Park Service conducts aerial and ground surveys of osprey and bald eagle nests each summer. Production of young was relatively poor in 2003, perhaps because of the late winter (lakes and harbors were still frozen at the end of April). The number of active eagle nests dropped from 11 to 8, although two new nests constructed in 2003 were not discovered until the intensive aerial surveys in winter 2004. The total number of young eagles fledged dropped from 11 in 2002 to 5 in 2003. The number of osprey nests declined from 7 to 6, with 7 young fledged, as in 2002.

Snowshoe hare observations declined during the summer of 2003 to a level lower than most of the past decade, consistent with a cyclical decline following a peak at the turn of each decade (figs. 22 & 23). Observations of red fox, a major hare predator, continue to be relatively infrequent in winter (fig. 24).

Prospectors in the 19th century, fir regeneration is vigorous, and fir is rapidly increasing in the forest canopy and understory. For the island as a whole, the trend in fir production and use by moose is relatively constant (figs. 20 and 21). Moose, however, are heavily concentrated at the east end of the island, taking advantage of the abundant fir in winter.

**Other Wildlife**

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**Figure 20.** Island-wide changes in production and use of balsam fir have been slight during 1998-2002, but there are opposing trends seen at the two ends of the island.

**Figure 21.** John Vucetich measures the history of growth on a young balsam fir tree at the east end of Isle Royale.

**Figure 22.** Noting their eternal vigilance, Durward Allen (who initiated the wolf-moose study in 1958) termed the snowshoe hare “professional prey.”
wobbly on its legs but urged on by its mother, the calf teetered on the brink. When it finally took the important step, it fell headfirst into the cold water. Coming up spluttering and bleating frantically, the calf seemed to swim a little in the deep water along the edge, but its clear panic brought mom quickly to its side. She nudged the calf up onto the shallow edge of the bank, about three meters downstream from its plunge. Here the calf shook itself, and the cow continued to hover until the calf was safely back up on the grassy bank near the birthsite. Then she alone crossed to the other side of the creek, where she used her teeth to bark alder branches, and soon the calf bedded down. There was still no warmth from the sun, and my own feet felt frozen—I couldn’t imagine how the calf could rewarm after its icy introduction to water. As the cow walked out of sight, I wondered if she would ever come back.

“It was almost 1100 when the cow returned and crossed the creek, her loud grunts waking the calf and bringing it to its feet. The cow licked the calf’s hindquarters, and there was much mutual sniffing and nuzzling of faces, then the calf walked under its mother’s belly and finally nursed successfully for about 30 seconds. Then the cow walked off and again crossed to the other side of the creek. The calf bedded down for 90 minutes as the sun at last started to warm its still-wet coat.

“The calf was sleeping when the cow next returned. After a minute-long nursing bout, the cow again left and crossed the creek and called her calf to follow. The calf stood on the creek bank again, where three hours before he had nearly met disaster, and he seemed quite torn between following his mother’s directives to cross the water or staying in the only safe place it knew. He would lower his front quarters briefly toward the water, then lose courage and back up, moving nervously about but always facing the creek and his mother, on the other side.

“Three times in the next half-hour the cow came back across the creek toward the hesitant calf, where they nose-greeted each other but no nursing occurred. The ambivalent calf became increasingly agitated, and even we felt the tension. Finally, the cow led the calf away from the water, into the alders adjacent to the birthsite, as if to reinforce the instincts of the calf to follow. When the cow turned and led the calf back to the creek, the calf again halted at the edge, but at a place where the bank was not so high. The cow turned in the middle of the deep water and faced the calf, then approached the calf while remaining in deep water. The cow called softly as it nuzzled and licked the calf’s face, and the calf now entered the water with head held high and legs already in swimming mode. It swam right to its mother on the other side, and high-stepped confidently through the shallow water, following its mother downstream.”

It was striking how fearless the newborn calf was. While it clearly wanted to follow its mother, it was perfectly content to lie quietly by itself on the bank of the creek. As it watched, an otter swam by, briefly glancing up at the curious calf. A courting pair of mergansers flushed from the creek and flew off, and the calf calmly watched. Within a few short days, with training from its mother, it would learn quickly to be wary of strange noises, other animals, and especially anything to do with wolves.

... and the end.

The moose rut was in full swing on the calm morning of September 29, 2003, the first night of hard frost. Candy and I had seen and heard several courting pairs of moose the day before, so it wasn’t surprising to hear the plaintive moaning of a cow moose at 4:00 am, considerably before sunrise. What was unusual about this cow was the length and volume of her calls, which ended in a most unfeminine, gravelly tone. Some of her wails lasted a full five seconds, drowning out the rhythmic grunting of an accompanying bull moose. I later told a hiker that it sounded like “someone was
**Figure 23.** Relative abundance of red foxes from aircraft observations in winter, 1972-2004. Grey bar is the number of foxes seen away from moose carcasses/100 hours, while the black bar is the number of foxes seen on carcasses.

**Figure 24.** Relative snowshoe hare density reaches a peak around the beginning of each new decade, both at Isle Royale and on the mainland in Minnesota. Counts were made at Isle Royale during all hikes in May through August, while hares were counted in Minnesota on routes used to count drumming ruffed grouse in spring (Minnesota Department of Natural Resources, with thanks to William E. Berg).

### Weather, Snow, and Ice Conditions

Wintertime temperature, snow depth, and extent of shoreline ice were at near-normal levels in 2004, in contrast to the well-established winter warming pattern of the late 1990s (fig. 25). Ice on Lake Superior reached its greatest extent in late January, but after high winds and thawing temperatures in late February the lake was almost ice-free. We were not aware of a solid ice bridge to the island from the Ontario shore at any time during the winter of 2003-2004.

While winter weather is usually of interest to ungulate biologists in North America, moose are also affected by summer weather. Weather during the summer growing season may particularly affect moose because this large mammal doesn’t sweat and, at Isle Royale, it is found near the southern limit of its distribution in North America. The extent to which moose may benefit from the lush summer growth of green plants depends critically on the prevailing temperature. The effects may be delayed,

### Recent publications

sawing off her leg,” not realizing that I would soon be doing just that.

After sunrise I didn’t want to break the morning stillness with motor noise, so I rowed across Rock Harbor from our field camp to Daisy Farm Campground, where three seasoned visitors had watched as a bull had courted the gravelly-voiced cow in front of their three-sided NPS shelter. The action was over by the time I arrived, and the cow stood quietly, almost invisible in a dense stand of alders. She was inactive all day, relocating only once to a small stand of shrubs in the middle of the campground. She was described as “skinny, like a cow moose in spring,” and her ribs were clearly visible.

In late afternoon, campers reported the cow moose was down, unable to get up. I arrived at 5:00 pm and found the cow lying on her side, breathing heavily and rapidly, about 30 times per minute. She occasionally struggled to rise but could only flail the ground with her hooves. We left her alone, uncertain of the outcome, but after we found that the radio-signal from the East Pack alpha male wolf was only a few hundred yards away, we decided to spend the night in the campground. At sunrise on September 30, the cow moose was dead, but the wolf had already left.

I mobilized the campers at Daisy Farm, a dozen in all, to help drag the dead moose out of the campground so that the wolves and scavengers could perform their customary service as agents of disposal. Several campers remained to help with the necropsy, a very revealing experience for us all. But our efforts were postponed for a full hour when the courting bull returned to his female of choice and found her strangely unresponsive. Unable to completely assess her condition with one inspection, he returned with his full antler display and showy walk three more times before finally giving up the quest.

The unusual voice of this cow moose was understandable once we examined her lungs. About two-thirds of her entire lung volume was a semi-solid mass, which did not have the light and airy feel of functional lungs. When I cut open a few of her alveoli, the small air sacs where gas exchange occurs, I found that they were all filled with a yellowish-green, yogurt-like material, a tell-tale sign of pneumonia. Interestingly, in an experiment with captive moose in Alberta, biologist Bill Samuel reported that moose that survived a heavy tick infestation sometimes died of pneumonia the following autumn, when the stress of the rutting season challenged their fragile constitution.

The cow moose was indeed extremely thin, and all the fat reserves of her body were exhausted. Yet she had ovulated, and from the reports of campers and the behavior of the local bull she appeared to have mated.

Our final check, for bone marrow, involved sawing through her leg, and this led to the discovery that the lower bones in all four legs were laden with strangely-shaped osteophytes, growths of new bone that were symmetrical on the right and left legs. We had found no previous moose at Isle Royale with such a bone condition, and we are still polling experts for possible diagnoses.

— By Rolf O. Peterson
however, with resulting mortality (from ticks or shortage of fat) not apparent until the following winter. As spring and fall weather may determine density of winter ticks, the effects of weather on moose (and therefore wolves) are potentially quite complex.

Aside from the obvious impact of deep snow in winter, which reduces moose mobility and foraging, and the effects of ticks that are driven by weather, there is also a direct effect of weather on growth of forage. Analysis of past growth of balsam fir forage (from dendrochronology, or measurement of tree rings) in relation to winter weather indicates that fir growth is reduced following severe winters, probably because of delayed onset of stem growth resulting from cold springtime weather.

**Snow Depth, Temperature, and Wind Speed on Isle Royale**

**Winter 2004**

![Graph showing snow depth, temperature, and wind speed](image)

**Figure 25.** Snow depth (daily), ambient temperature (hourly), and wind speed with barometric pressure (every 10 minutes, measured at Rock of Ages lighthouse) during the 2004 winter study on Isle Royale.