

## A SUMMARY OF RESEARCH ON MOOSE AND RELATED ECOLOGICAL TOPICS AT ISLE ROYALE, U.S.A.

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**ABSTRACT:** The following summary evolved during the 35th North American Moose Conference, 1999, from a session that reviewed 40 years of moose and related research at Isle Royale National Park, Michigan, USA. The account here covers this history in more complete detail than was possible at the Conference, and includes studies and accounts that pre-date the beginning of the intensive moose-wolf research under Durward Allen, in 1958. A brief description of the key researchers is included. An extensive list of research papers on moose and moose-related studies at Isle Royale is provided. Also appended is a set of time-comparison photos of vegetation changes influenced by moose and beaver, provided by Philip C. Shelton.

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For nearly a century, Isle Royale National Park has been renowned for its moose (*Alces alces*) population and, for the past half century, for the well-documented predation by wolves (*Canis lupus*) on these moose. A steady stream of research findings has drawn worldwide attention to the ecological systems of Isle Royale - primarily to the system dominated by these two large mammals and the forest vegetation.

At the 35th annual North American Moose Conference held in Grand Portage, Minnesota, in 1999, there was a session reviewing 40 years of moose research on Isle Royale and a field trip to the island. From this a consensus arose that a summary of all published studies relating to the moose of Isle Royale should be prepared - hence this paper. Moose studies have included population dynamics, physiological responses to environmental changes, diseases and parasites, foraging habits, and nutritional considerations, along with the impact of moose on vegetation. Other major components are the effects of wolf

predation on moose, as well as how moose affect population dynamics of wolves and other related species including beaver (*Castor canadensis*), snowshoe hare (*Lepus americanus*), red fox (*Vulpes vulpes*), and the extirpated coyote (*Canis latrans*). The many studies cited are accompanied with brief summaries of results and conclusions. Their order of presentation is first according to ecological topic and second according to chronology. Research has been pursued by individuals and by groups, some of the latter having maintained continuity over several decades. Research on moose and related ecological aspects at Isle Royale are ongoing. This compilation is a review of progress over the first century.

### THE ISLAND

Isle Royale, "the island," is actually a 544-km<sup>2</sup> archipelago, dominated by a single large island some 71 km long and 13 km at its widest, with numerous inland lakes - the largest 11-km long - and small offshore islands. Lying 22-25 km off the northwest

shore of Lake Superior, the island is surrounded by deep and cold waters. Jurisdictionally, Isle Royale is part of the state of Michigan, even though it lies closer to Minnesota and closer yet to Ontario, Canada. Official establishment of Isle Royale as a U.S. national park evolved slowly between 1936 and 1946, and subsequently 99% of its area was congressionally designated to be managed as wilderness.

### Geology

Isle Royale is part of the Lake Superior formation, reflecting an ancient history of lava flows interspersed with long periods of sedimentary deposition (Huber 1973, 1975). The deposits are layered, with an upward strike from the center of the lake. Thus, formerly horizontal surfaces are now exposed as gentle slopes to the southeast, and eroded edges of the layers as steep, northwest slopes. The resulting landscape, oriented with the island's long axis, is one of small, parallel ridges and depressions, the latter containing frequent lakes and swamps, often altered by beaver impoundments. The eastern two-thirds of Isle Royale was scraped to bedrock by the most recent glaciation, while over the western third, a layer of till was deposited; hence soils are deeper and better developed on the west end. Overall, the basalt- and sedimentary-derived soils are far more productive than those derived from base granitics of the Canadian Shield that lies somewhat inland from the Lake Superior shore.

### Climate

Temperatures at Isle Royale are more moderate than in mainland regions well back from Lake Superior. In summer, Lake Superior serves to cool the air; while in winter, the lake being mostly open, tends to warm the otherwise cold air off the mainland. Mean annual snow depths (45-82 cm) are somewhat higher than on the mainland

to the west, due to the open-lake effect producing local snowfall. Within the island itself, there is marked local variation in growing season temperatures, which range from a relatively cool, shore-line zone influenced by the cold lake to a considerably warmer zone inland and >50 m higher than the lake. This gradient is one factor contributing to distinct differences among plant communities within surprisingly short distances (Linn 1957, 1962).

### Vegetation

Isle Royale is mainly forested, comprising a wide variety of types within its relatively small area (see Hansen *et al.* 1973, Sheldon 1975, and, for species used by moose, Krefting 1974). Poorly drained lowlands support stands of northern white cedar (*Thuja occidentalis*) and black spruce (*Picea mariana*) or shrub stands of speckled alder (*Alnus incana rugosa*), or simply open grass, particularly within past and present beaver impoundments. Pure stands of sugar maple (*Acer saccharum*) are found primarily in the deeper soils at the western end mostly in areas well removed in distance and elevation from the lake. These grade into yellow birch (*Betula alleghaniensis*) on deeper soils, and elsewhere into the mixed transition forest of white birch (*Betula papyrifera*), quaking aspen (*Populus tremuloides*), balsam fir (*Abies balsamea*), and white spruce (*Picea glauca*), the upland forest-type most common on the island. Young forms of the common trees are preferred by moose as follows: year-round, highly preferred - white birch and quaking aspen; year-round, moderately preferred - yellow birch and sugar maple; winter only, moderately to highly preferred - balsam fir; winter, low preference - northern white cedar; and not used at all, the two species of spruce. The cool, coastal zone close to Lake Superior in elevation and distance tends to be more boreal,

usually dominated by balsam fir - except where moose in many sectors have suppressed fir reproduction for many decades. Small stems of mountain ash (*Sorbus americana*) are highly preferred by moose, but the species is considerably less abundant than those listed above. Even less abundant, but highly palatable, are red oak (*Quercus rubra*), red maple (*Acer rubrum*) and the moderately preferred white pine (*Pinus strobus*). Browsing by moose threatens to extirpate from the island the relatively sparse big-tooth aspen (*Populus grandidentata*), red oak, and possibly balsam poplar (*P. balsamifera*).

Much of the shrub layer is dominated by thimbleberry (*Rubus parviflorus*), a species little used by moose. It reportedly replaced the previously abundant, coniferous shrub, American yew (*Taxus canadensis*), that moose had reduced to mostly ground-level, non-reproducing stubs. Among common shrubs, species preferred by moose include beaked hazel (*Cornus cornuta*), mountain maple (*Acer spicatum*), bush honeysuckle (*Diervilla lonicera*), and green or mountain alder (*Alnus viridis* subsp. *crispa*). Less abundant, but still important forage for moose, are two species of *Prunus*, juneberries (*Amelanchier* spp.), several species of willow (*Salix* spp.), and, in wetter sites, red-osier dogwood (*Cornus stolonifera*).

Important herbs used by moose in summer (particularly when forage supplies are declining) include big-leaf aster (*Aster macrophyllus*), sarsaparilla (*Aralia nudicaulis*), lady fern (*Arithrium felis-femina*), and many others. Aquatic macrophytes important to moose are listed in Aho and Jordan (1979), with a more complete list in Aho (1978). It appears that various species of *Potamogeton* may comprise the bulk of macrophytes taken.

The most up-to-date and detailed listing of the island's flora is that of Slavick and Janke (1987). An early account with valuable notes on history and ecology of the vegetation is that of Brown (1937).

### European Settlement and Commercial Activities

While there was somewhat extensive resource exploitation and recreational development from the mid-1800's through the mid-1900's, little evidence of those activities remain today - simply some interesting historical artifacts. There was widespread, but ultimately unsuccessful, surface mining of copper (Rakestraw 1965). This did include extensive burning of forests in some sectors with long-term implications for moose habitat (see above). Commercial fishing, operated from dozens of relatively primitive stations around the island, was a major industry during the first half of the past century (Cochrane 1987, Sivertson 1992). Logging was very limited, consisting of local cutting for pulp logs during the 1930's, and cutting of timbers for mining activity during the 1800's. A few modest tourist lodges, only one of which is still operating, and a small number of summer cottages on offshore islands all in one sector, were developed before the island became a national park. A good review of history is found in Nute (2000). Sheldon (1975) and Waters (1987: Chap. 16) offer comprehensive summaries of Isle Royale.

### Vertebrate Fauna

The vertebrate biota of Isle Royale is less diverse than in similar habitats on the adjacent mainland except for birds and for fishes in Lake Superior (Mech 1966, Sheldon 1975, Jordan 1982). Of note here is the relatively depauperate mammalian fauna: only moose, timber wolf, red fox, beaver, snowshoe hare, river otter (*Lutra canadensis*), mink (*Mustela vison*), musk-

rat (*Ondatra zibethicus*), a few bat species, and other small mammals are present. Caribou (*Rangifer tarandus*), coyotes, lynx (*Felis lynx*), and possibly marten (*Martes americana*) disappeared during the past century (Mech 1966). Moose have been known only since the early-1900's, and wolves since the late-1940's, but both now exist on the island at densities far above normal for the two species in similar habitats elsewhere. Wolves are the sole predator of moose on the island, and they depend almost exclusively on moose for prey. Coyotes were probably extirpated by wolves soon after the latter became established (Krefting 1969).

#### EARLY ECOLOGICAL STUDIES, INCLUDING ORIGINS OF THE MOOSE POPULATION

The first serious scientific investigation at Isle Royale was a detailed survey of natural history around the turn of the century by C. C. Adams (1909), and provided the first published lists of plant and animal species. A decade later, a distinguished plant ecologist, William Cooper (1913), made a detailed analysis of forest succession in the boreal type at the east end of the island, and then made subsequent comparisons 17 years later (1928). All early plant studies are reviewed by Hansen *et al.* (1973:11).

Adams (1909) did not list moose as present before 1905, but Murie (1934) believed that browsing signs that Adams attributed to caribou were actually from moose. Murie also cited unpublished records of occasional moose sightings some time before the 1880's, and speculated that hunting must have kept the numbers low. More recent reviews (e.g., Mech 1966 and Allen 1979) suggest there were no moose on the island prior to the 1900's. If moose were present earlier, they remained strangely sparse. Also, according to DeVos and Peterson (1951), moose were previously

sparse or absent along the adjacent Minnesota and Ontario shore and only began to increase around the turn of the century. In contrast, moose were clearly present on the island in 1912, by which time they were clearly in the initial stages of a true irruption (Murie 1934). From these records Mech (1966:21) calculated that the population would have originated sometime around 1905 - most likely from a small number of moose swimming from the adjacent mainland. The population reportedly peaked in 1930, by which time, according to Murie (1934), all forage sources were severely depleted; a winter die-off followed in 1934 (Hickie 1936, 1943). In 1936, wildfire, "the 1936 burn," covered some 19% of the island (Hansen *et al.* 1973), and this led to major increases in forage with a resultant increase in moose (Aldous and Krefting 1946). The population began to decline again by the late-1940's. Krefting (1951) further reported that a die-off seemed imminent in the winter of 1948, and his ground observations in 1950 led to him to conclude that a significant drop had occurred.

Recent information raises the possibility that moose may have been taken to the island by humans. W. (Bill) Peterson (1998) was told second-hand, but from an apparently reliable source, that 11-12 moose were transported from northwestern Minnesota to the island around 1905. Peterson, however, has been unable to find any written confirmation of this. At the same time, Hundertmark (1998) analyzed mitochondrial DNA from moose of the Lake Superior region and concluded that moose on Isle Royale appear more closely related to those in northeastern Minnesota than to those in Ontario. However, on further investigation, it appears that the origin of the Ontario DNA samples he examined is uncertain, so the Minnesota specimens may in fact have come from sites closer to the island than did the Ontario specimens. So we do not know

exactly what underlay the sudden irruption of moose in the early-1900's, but it is interesting to note that Bill Peterson's report of a 1905 introduction coincides with Mech's (1966) estimated date of population origin.

### THE RESEARCHERS

A brief compilation of affiliations and chronology of primary researchers should help the reader fit together the lengthy details of moose related research at Isle Royale.

**Adolph Murie** was a classical naturalist working most of his career with the National Park Service; however his report on Isle Royale moose was done for the Museum of Zoology, University of Michigan.

**Paul Hickie** was a biologist with the Michigan Department of Natural Resources, and served as a field assistant to Murie. In the 1930's, the island was partly under the jurisdiction of the Michigan Department of State Parks.

**Shaler Aldous and Laurits Krefting** were with the research branch of the U.S. Fish and Wildlife Service during the period when that agency was responsible for biological research in national parks. Krefting continued his research at Isle Royale until retirement in 1974, collaborating with forest ecologists Henry Hanson and Vilus Kurmis of the Forest Resources Department, University of Minnesota, St. Paul.

**Robert Linn**, though not working directly with moose, was the park naturalist at Isle Royale for several decades after completing his Ph.D. thesis (1957) on the island's spruce-fir, maple-birch forest transition, an important cornerstone for those tracking forest changes related to moose.

**Durward Allen** was acting director of research within the U. S. Fish and Wildlife Service when in 1952 he learned that wolves had appeared on Isle Royale. Having been fascinated with the island for many years,

he made a personal commitment to undertake a major investigation of this predator-prey relationship. This was best done from an academic position, and he joined the faculty at Purdue University. Allen initiated the now famous wolf-moose research in 1958 and continued as its director until 1975. He instituted a tradition of detailed annual reports that has been followed by Rolf Peterson, with an ever-widening distribution to interested parties (Peterson 1999b). Allen (1979) provides a full account of the study's evolution and personnel during his years.

**David Mech**, Allen's first Ph.D. student, 1959-62, focussed on the moose-wolf dynamic, documenting what was then a landmark study (Allen and Mech 1963, Mech 1966). During Mech's tenure, a monitoring protocol was developed that has remained remarkably constant ever since: 6-8 weeks residence on the island during mid-winter, with data collection mainly from a small plane; and ground-based projects in summer, based out of an old fisherman's abandoned cabin. Mech has subsequently become the world's leading expert on wolves, while conducting long-term, ecological studies on this species in northern Minnesota and elsewhere.

**Philip Shelton**, Allen's next Ph.D. (1966) student, 1962-64, focussed on the ecology of beavers, while continuing the monitoring of moose and wolves. In subsequent years, he continued to inventory beaver numbers on the island. Shelton contributed the time-comparisons photos appended below.

**Peter Jordan** was with Allen 1963-66 as a post-doctorate fellow. While continuing the moose-wolf monitoring, he undertook studies of moose-vegetation relationships and started a system of permanent data plots still in use. Since the time with Allen, he has been continuously involved in studies at Isle Royale, first from Yale Uni-

versity, 1966-74, and then from the University of Minnesota, 1974-present.

**Robert Janke**, a plant ecologist at Michigan Tech University, has been examining effects of moose on forest vegetation from the early-1960's to the present and, with A.D. Slavick, has updated the flora of Isle Royale.

**Wendell Johnson** was the fourth of Allen's Isle Royale graduate students, 1966-67. While still collecting the moose-wolf data, his Ph.D. thesis (1969) focussed on small mammals - foxes, snowshoe hares, red squirrels (*Tamiasciurus hudsonicus*), and the deer mouse (*Peromyscus maniculatus*).

**Michael Wolfe** did post-doctoral research with Allen, 1967-70, investigating population dynamics of moose, including age determination from tooth cementum layers, and studying behavior of wolves.

**Rolf Peterson** was Allen's last graduate and post-doctoral student, 1970-75. Upon Allen's retirement in 1975, Peterson moved to Michigan Technological University (Michigan Tech) and assumed responsibility for Allen's project, which he has continued to direct up to the present. He and his students have explored many aspects of wolf and moose biology.

**John Snyder** did his M.S. thesis (1973) with Janke, 1969-70, on the impact of moose on boreal forests of Isle Royale.

**Daniel Botkin**, then on the faculty at Yale, joined Jordan in the ecosystem studies at Isle Royale, 1970-74, which led to an investigation of sodium ecology and physiology in moose. Subsequently, as an environmental writer, Botkin (1990) has reflected on implications of their moose research at Isle Royale.

**Gary Belovsky**, an M.S. student at Yale with Jordan, 1972-74, focused on foraging strategies of moose, including the importance of obtaining sodium. He continued to analyze moose related data for his

Ph.D. at Harvard University (1980).

**John de Waal Malefyt**, an M.S. student (1974) with Bob Janke, investigated relationships between moose, hares, squirrels, and forest types in the early 1970's.

**Joan Edwards**, a University of Michigan Ph.D. student (1978) in botany, 1974-76, studied the adaptive ecology of an important summer food-item of moose, wild sarsaparilla, plus examining feeding and maternal behavior in moose.

**Robert Aho**, an M.S. student (1978) of Jordan's at University of Minnesota, 1976-78, studied the impact of moose-grazing on aquatic-plant communities on the island.

**Dale Miquelle**, an M.S. (1979) student of Jordan's, experimentally tested the tendency of moose to select for a diversity of forage species, 1976-79.

**Dennis McKaig**, an M.S. student (1978) of Linn's at Michigan Tech, reconstructed 19th-century forest communities at Isle Royale from historic records.

**Joe Scheidler**, an M.S. (1979) student with Peterson, analyzed moose mortality patterns during the late 1970's.

**Phil Stephens**, another of Peterson's M.S. students, studied moose behavior and population trends (1981).

**Rhett Faaborg** studied sodium dynamics in a beaver pond, 1980, for his M.S. thesis (1981) with Jordan.

**Ken Risenhoover**, Peterson's Ph.D. (1987) student during 1983-86, divided his time between Isle Royale and Denali National Park, analyzing feeding ecology of moose in winter plus their use of mud licks.

**Tim Ackerman**, using moose radio-collared by Risenhoover, examined reaction of moose to summer heat for his M.S. thesis (1987) with Peterson.

**Rick Page** worked with Peterson during 1985-88, analyzing moose-wolf dynamics for his Ph.D. (1988).

**John Pastor**, a research associate with the Natural Resource Research Institute

(NRRI), Duluth, Minnesota, and Professor at the University of Minnesota, initiated a research project in 1987 to examine interactions between moose-foraging and soil-fertility at Isle Royale. He now also pursues studies of moose in Voyageur's National Park, Minnesota.

**Pamela McInnes**, an M.S. student (1989), University of Minnesota, worked with Pastor and Cohen, 1987-88, to compare vegetation and soil-nutrient differences related to exclusion of moose at Krefting's 1950's exclosures.

**Robert Naiman**, an NRRI co-investigator with Pastor in the initial stages of their work, moved to the University of Washington in 1989.

**Yossef Cohen**, Department of Fisheries and Wildlife, University of Minnesota, has cooperated closely with Pastor during the 1990's, contributing as a theoretical ecologist and ecosystems modeler.

**Ronald Moen**, a Ph.D. student (1995) advised by Pastor and Cohen, and currently a post-doctoral associate with them, developed an explicit spatial model of moose foraging relative to moose nutrition and growth.

**Glenn DelGiudice**, a specialist in ungulate nutritional physiology, has worked with both Peterson and Moen on evaluating condition of moose from biochemical analyses of urine collected from snow.

**Brian McLaren** studied interactions between growth patterns in balsam fir saplings and long-term browsing by moose for his Ph.D. (1996a) with Peterson during 1991-95.

**Mary Hindelang** studied physiology and pathology of bone in moose for her Ph.D. (1996), during 1991-1996.

**Steve Fettig** examined long-term vegetation changes at Jordan's permanent plots, 1992-94, for his M.S. thesis (1995).

**Linda Quarnemark** studied aquatic grazing for her M.S. thesis (1999) at Kent

State University under the advisorship of aquatic ecologist, Sallie Sheldon.

**Scott Sell**, a current Ph.D. student of Jordan's is working, 1997-present, on models that track differences in forest succession attributable to moose, and has done a study on how moose impact dispersal of sugar maple.

**Jeff Dorale** currently, 1998-2000, with Jordan, is updating the aquatic-sodium work of Faaborg for his M.S.

## MOOSE-CENTERED RESEARCH

### Natural History

Murie's (1934) unquantified observations provided new information on moose behavior and ecology for that era and emphasized the apparent imbalance between high moose density and degraded plant communities. Mech (1966) contributed extensive new observations on reactions of moose to attacks by wolves. From her close-up observations, Edwards (1976) concluded that forage-species selections by calves reflect an imitation of selections made by the mother. She also suggested (1983b) that tongue-to-tongue contact between the two facilitates microbial inoculation of the rumen when calves begin to forage. Miquelle (1983b) reported on rates of defecation and urination in summer, and Martin (1989) documented seeing a cow with possible quadruplets.

Risenhoover (1987), working with radio-collared animals, quantified activity patterns in winter, comparing moose populations at Isle Royale with those in Denali National Park, Alaska. Risenhoover (1987) also quantified home range patterns in winter, showing a decrease in area with an increase in snow depth. His most intensive measurements were on feeding rates and forage selection. Ackerman (1987), using some of the same radioed animals, recorded daily activity in relation to daytime temperature in summer.

### Numbers of Moose

Following Murie's (1934) wholly qualitative estimates in 1929-30, 2 quantitative methods - aerial counting and pellet-count indices - have been in use for estimating total number on the island since the 1940's. A third technique, reconstructing dynamics from moose-carcass remains through cohort analysis, was begun in the 1980's by Rolf Peterson (Mich. Tech. Univ., *unpubl.*). For inventory, the moose at Isle Royale offer the great advantage of being essentially a confined population with no measurable immigration or emigration.

Aldous and Krefting (1946) made the first aerial count in winter 1945; flying island-long transects and covering 30% of the island, they estimated the population at 510. Krefting (1951) made a similar count in 1947, and estimated the total as 500. In 1957, an island-wide count was made by Park Service biologist, Jim Cole (1957), who estimated only 240 animals.

Mech (1966:95) made aerial estimates in 1959 and 1960, using a more intensive transect method than previous workers. In 1964, Jordan (*unpubl.*) concluded that counting along transects over forests that often comprise >50% conifer cover was subject to unacceptable observer error. He and statistician Peter Dress of Purdue University devised a stratified-sampling scheme with the unit being small plots that are intensively searched (Jordan and Wolfe 1980, Jordan *et al.* 1993). This approach has been used by the Allen-Peterson research project ever since. Peterson and Page (1993) describe adjustments to counts related to density of forest cover.

Various workers have used pellet-count indexes over the years: 1948-70, by Krefting (1951, 1974) and Hansen *et al.* (1973), in spring on small, non-fixed plots; de Waal Malefyt (1974) used pellet counts in analyzing habitat preferences of moose; and, Jordan has made counts on fixed plots

from 1964 to the the present in the majority of years (Jordan and Wolfe 1980, Jordan *et al.* 1993). Pellet results were tied to aerial results for each winter 1964-79 (Jordan and Wolfe 1980). For years in which pellets were counted, 1980-93, results were compared with Peterson's aerial estimates, and the fit between the two independent approaches was found to be close (Jordan *et al.* 1993).

Trends in total moose between 1959 and 2000, estimated with reasonable reliability, appear to have fluctuated between 700 and 2,400 (1.3-4.4 /km<sup>2</sup>). Numbers of moose increased throughout the 1960's until 1970, then dropped to a low by 1977 and remained relatively low as wolves during the same period were increasing to a peak in 1980 (see below). Subsequently, the wolf population was unexpectedly low from the 1980's until the mid-1990's, and numbers of moose increased up to possibly as high as 2,400; then, during the unusually severe winter of 1996, they suffered a major die-off. Since then, the population has been slowly recovering from a low point of around 500 (Peterson 1999b).

### Population Structure

From the outset of Allen's research project, remains from all wolf-killed moose during the winter study, plus all carcasses found incidentally during other seasons, have been recorded, with relevant specimens, particularly mandibles, being collected. Peterson (1999b) has greatly intensified ground searches during summer over the past 12 years.

Working with mandibles collected from 1959 to 1968, Wolfe (1969) estimated ages from cementum layers. Peterson, with many more years' material, has been reconstructing population structure through time. Also, Peterson *et al.* (1983) compared tooth eruption patterns between Isle Royale moose and two other populations, and Hindelang



and Peterson (1994) evaluated toothwear patterns of Isle Royale moose.

Herd composition counts from the air in fall were made by the Allen-Peterson team from the early-1960's to 1983. Much data on age-sex composition of wolf-killed moose in winter came from carcass recoveries (Allen and Mech 1963, Mech 1966, Peterson 1977, Wolfe 1977, Page 1988). Natality, very difficult to measure directly, has been inferred from ground-based, cow-calf ratios estimated in summer, coupled with fall and winter composition counts from the air. Mech (1966), in estimating predation dynamics, calculated biomass of moose killed and eaten by wolves. Jordan *et al.* (1971) modeled the numeric and biomass dynamics of the population, using age structure from Wolfe's (1969) life table.

### Pathology and Physiology

In addition to nutritional questions (see below), studies of pathology and general physiology of moose started with observations by Mech (1966) and his successors, showing levels of tapeworm cysts in lungs and livers of moose, as well as advanced periodontal disease (Hindelang and MacLean 1997), predisposed moose to predation. Also, arthritic deterioration in leg joints, first pointed out by veterinary student assistant, Erik Stauber, in 1964 appeared strongly related to such vulnerability (Peterson 1977). Extensive work with bone morphology has been pursued by Mary Hindelang (1996), who has been collaborating with medical experts using sophisticated laboratory procedures. Topics include osteoporosis (Peterson 1988; Hindelang and MacLean 1996, 1997; Hindelang *et al.* 1992, 1998; Hindelang and Peterson 2000), tooth wear, and periodontal disease (Hindelang and Peterson 1993, 1994). Peterson *et al.* (1982b) also compared bone morphology and pathologies between moose in Alaska and those on Isle Royale. Bada *et al.*

(1990) examined tooth tissue for accumulation of airborne isotopes of anthropogenic origin.

Records of parasite infestations have been made whenever possible throughout the Allen-Peterson project. Hydatid cysts (*Echinococcus granulosus*) in liver and lungs were believed by Mech (1966) to predispose moose to wolf predation. Mech (1966) reviewed several other parasites found in moose during the early-1960's. Karns and Jordan (1969) believed they had found larvae of the meningeal worm, *Parelaphostrongylus tenuis* or brainworm, that is fatal to moose, in moose pellets from the island. In retrospect, the organism was probably a closely related nematode found in moose, rather than *P. tenuis*, whose normal host is the white-tailed deer (*Odocoileus virginianus*).

In some winters, incidence of winter tick (*Dermacentor albipictus*) on moose has been extremely heavy, and ungulate physiologist, Glen DelGiudice, working with Rolf Peterson and parasitologist Bill Samuel, examined the impact of these parasites on the host population (DelGiudice *et al.* 1997).

Ackerman (1987) examined reaction of moose to summer heat, and he concluded that high temperatures were associated with depressed foraging behavior, decreased foraging time, and increased frequency of behavioral indicators of higher metabolism.

Indices of nutritional condition have included examining size of mandibles and fat levels in bone marrow throughout the Allen-Peterson studies (e.g., Peterson *et al.* 1982a). Also, in recent years, urine deposited in snow has been used to judge whether undernourished animals are catabolizing protein sources for energy (DelGiudice *et al.* 1991, 1997).

### WOLVES AND WOLF PREDATION

Wolves dispersed from the mainland to the island most likely over an ice bridge

some time in the late 1940's, and were first reported by Cole (1952). Since their arrival as much, if not more, ecological study at Isle Royale has been focussed on wolves as on moose. The new moose-wolf relationship offered an opportunity to make a scientific comparison of the prey population and the status of its forage resources before and after establishment of what has developed into a classical predator-prey dynamic. The moose-wolf interaction on Isle Royale, being a "simple," one-predator-one-prey system, might seem to be the ideal case-study for simulation with a simple, interactive model that in turn would offer reliable predictability. Although fluctuations in moose numbers have been far less pronounced than before establishment of wolves, a simple, stable equilibrium - as Mech (1966) had assumed would persist - has not been the case. For one, variations in certain independent factors (i.e., introduced diseases, variable winter severity, multi-generational nutritional effects on prey vulnerability, and internal dynamics of wolf packs) appear responsible for several dramatic changes in numbers of both moose and wolves. Furthermore, variation in wolf and moose numbers is inalterably tied to variations in the food resources of moose, whether such changes are dependent, semi-independent, or entirely independent of the impacts that moose themselves have on the vegetative community.

Opportunity to observe hunting behavior of wolves as they prey on moose has been outstanding at Isle Royale and reported in detail, particularly by Mech (1966, 1975), Peterson (1977), and Stephens and Peterson (1984).

### **Numbers and Social Structure of the Wolf Population**

Mech (1966) carefully documented numbers and pack structure during winters 1959-61, and the process he and Allen established

has continued to the present (Shelton 1966; Jordan *et al.* 1967; Wolfe and Allen 1973; Peterson 1977; Peterson and Page 1983, 1988; Peterson *et al.* 1998). When the wolf population declined to an unusually low level during the 1980's and 90's, focus on that population became intense (Peterson and Krumenaker 1989, Peterson 1995b). Since the wolves appeared in jeopardy of disappearing from the island, Peterson and his colleagues were given permission by the Park Service to trap and radio-collar animals. This led to further understanding of social structure in this population (Thurber and Peterson 1993). It also afforded collection of specimens for genetic analysis of the population (see below).

### **Wolf Dynamics**

Since the onset of the Allen-Peterson project, a central focus has been on predation efficiency in wolves relative to the age and condition of the moose that they take (Mech 1966, 1970; Shelton 1966; Jordan *et al.* 1967; Peterson 1974, 1975, 1977, 1999b; Peterson and Allen 1974; Wolfe 1977; Page 1988). A potential shift in spatial patterns of predation may have been influenced by the social structure of the island's wolves in winter. From the first year of study, 1959, until 1965, the population in winter aggregated primarily as a single pack (Mech 1966). Early in that period, it hunted the full length of the island but, even with increased numbers, by 1963 it had reduced its hunting area to the western half to two-thirds of the island. During 1964, the primary pack numbered 22 on one occasion, the largest aggregation ever recorded there; but by 1965 this had decreased, and was smaller yet in 1966, even though total numbers on the island remained about the same over these years (Jordan *et al.* 1967). Since 1966, winter aggregations have always comprised two or more packs, this being a change that Jordan (1979) suggested may have reflected

loss of a particularly strong alpha male who had engendered strong social cohesion at least during winter. Along with the shift from one large pack to two or more smaller packs, spatial coverage and hence presumably intensity of predation in winter, became more uniformly distributed throughout the island.

Wolf numbers increased steadily from 1975, reaching the unusual peak of 50 in 1980 (Peterson and Page 1988). Numbers then declined to an unprecedented low level that lasted from the mid-1980's into the early-1990's (Peterson *et al.* 1998), as discussed in the next section.

### **Wolf Genetics and Pathology**

The unexplained depression of wolf numbers in the 1980-90's caused great concern that the island's population was in jeopardy of disappearing, leading to an intense search for causes. It became apparent that availability of prey was not a likely cause - at least not for the entire period (Peterson and Krumenaker 1989, Peterson 1995b). An introduced pathogen, canine parvovirus (CPV), was detected and may well have been responsible for part of the abnormally low level (Mech and Goyal 1993), but CPV titers did not persist during the entire span of depressed numbers. Although high adult mortality ceased after 1988, low recruitment in the absence of food shortage suggested that inbreeding or stochastic population events were responsible for the decline (Peterson *et al.* 1998). Given the small number and relative isolation of these wolves, it was suspected that inbreeding depression might be having an adverse population effect. Wayne *et al.* (1991) found heterozygosity in Isle Royale wolves to be 50% lower than among adjacent, mainland animals that are presumably similar to the population from which the island population was founded some 40 years earlier. However, phenotypic evidence of

inbreeding has not been clearly shown. By the late-1990's, increasing numbers indicate the wolf population has been recovering. In any case, the cause of the prolonged depression may never be known for certain. Vucetich *et al.* (1997), using extinction models, showed that inclusion of prey abundance could substantially alter probabilities of time-to-extinction for such a predator.

### **Wolf Management Policy**

With the precipitous decline of wolves from an undetermined cause, the question arose as to how managers should respond in the event the island's population did die out (Peterson and Krumenaker 1989). On the one hand it was argued that being a national park, there should be no manipulation of wildlife; on the other, Peterson (1995b) made a case for restoring wolves, if necessary, in order to maintain predation as an important natural process.

## **WOLF-MOOSE DYNAMICS**

### **Population Regulation**

Mech's (1966) investigation of the natural, moose-wolf interaction at Isle Royale was the most detailed, quantified analysis of a large-mammal predator-prey system reported up to that time, with his monograph detailing numerous wolf-moose encounters. Through carcass recoveries and direct observation, Mech (1966) concluded that vulnerability of moose to killing by wolves in winter was restricted mainly to calves and relatively old or debilitated animals. He thus suggested that healthy animals in their prime years were essentially not vulnerable. This conclusion was better quantified by determination of ages of wolf kills by Wolfe (1977), who counted cementum annulation in teeth from carcasses collected 1959-1969. Mech (1966), combining herd composition data, winter kill rates, carcass information, and wolf-scat analysis with natality rates and moose weights (from

elsewhere), reconstructed the dynamics of numbers and biomass in order to characterize this balance. Similar calculations were derived later by Jordan *et al.* (1967) using a dynamic computer model. Mech (1966), by comparing trends in the moose population before and after wolves appeared, was readily convinced that predation had become a mechanism that regulated this moose population. Parallel observations on impacts of browsing by moose corroborate this conclusion. In posing that, within 13-15 years of the wolves' arrival, equilibrium had developed between predator and prey, Mech (1966) estimated that such a balance should continue indefinitely, albeit with fluctuations. While fluctuations subsequent to Mech's (1966) work have perhaps been greater than anticipated, the only irruptive rise in moose numbers, with an accompanying die-off (Peterson 1999a), was most likely underlain by a depression in wolf numbers that occurred independently of availability of moose prey (Peterson *et al.* 1998). Peterson (1995a, 1999a) has challenged the idea, supported by the National Park Service, that ungulates are self regulating, offering the recent events during the unusual drop in wolf numbers as strong evidence.

Peterson (1977), reporting on moose-wolf dynamics during 1970-74, believed conditions seen in the 1960's were changing, partly related to a steady increase in moose numbers. Peterson (1977) concluded that a combination of higher moose densities and more severe winters had led to increased limitation of food for moose and, in turn, to lower production and survival of calves. Wolf kills began to include an increased portion of calves and younger adults (Peterson 1975), and, during the 1970's, moose declined while wolves increased (Peterson and Page 1983). Peterson (1977) believed that, while moose may show some degree of intrinsic or self regulation, the

effect of predation, especially in the circumstance at Isle Royale, tends to hold numbers in a better balance with their preferred forage than if there was no predation. Eberhardt and Peterson (1999) found that the rate at which wolves kill moose was not easily predicted by moose density, contrary to a classical notion in predator-prey theory. Peterson *et al.* (1984), examining fluctuations in both wolves and moose 1959-83, suggested that time lags underlie a cyclicity of 38 ( $\pm 13$ ) years in moose numbers, conforming with an hypothetical allometric relationship. McLaren and Peterson (1994, 1995) further associated this cycle with growth rates in balsam fir and other trees.

#### **Climate as a Contributing Factor**

The influence of weather, particularly snow accumulation, on the vulnerability of moose to predation was first reported for Isle Royale by Peterson and Allen (1974); they suggested that, as snow deepened, moose became confined to stands of mature conifers where forage was limited. This habitat change led to malnutrition and consequent higher vulnerability to wolves, particularly among calves, but also prime-age animals. Also, calves surviving such winters were subsequently more vulnerable in later years. Mech *et al.* (1987), analyzing snow impacts on both deer in Minnesota and moose on Isle Royale, showed evidence for a significant relationship between accumulation of snow during 1-3 previous winters and rates of twinning, survival of calves, and calf vulnerability. This pattern held for several subsequent years and suggested a prolonged effect from poor winter nutrition in deer. The interpretation was challenged by Messier (1994), who analyzed the same data and concluded the effects could better be explained as functions of wolf and prey densities and competition for forage among the ungulates. This paper

was countered by McRoberts *et al.* (1995), who claimed that Messier's (1994) analyses were flawed, and that the initial conclusions were still valid. More recently, Post *et al.* (1999) claim evidence for a global climate influence, namely that the North Atlantic Oscillation has led to greater snow depths, which in turn have underlain higher predation rates by wolves, lower moose densities, and better growth in small balsam fir trees (McLaren and Peterson 1994).

### OTHER HERBIVORES

Some studies of the other two principal mammalian herbivores on the island, snowshoe hares and beavers, have been independent of moose. However, because food habits of both overlap to a considerable degree with moose, all studies of these animals are relevant to understanding influences on the food resources of moose.

#### Snowshoe Hare

For observations by early workers on hares and their impacts on vegetation, see Hansen *et al.* (1973:36). Jordan (*unpubl.*) has counted hare pellets in small subplots at the permanent, moose-pellet plots, with some of these records extending from the mid-1960's to present. Snowshoe hares on the island have shown a periodic cyclicity, with a frequency of approximately 10 years: 4 peaks, some far more pronounced than others, have appeared, 1964-1999 (Jordan, *unpubl.*). Hansen *et al.* (1973:36) noted 2 peaks of the same periodicity during the 1940's and 1950's. Krefting (1969) found hares to comprise a major portion of prey of coyotes, a predator that disappeared after arrival of wolves; Hansen *et al.* (1973) suggested hares might increase in the absence of coyotes, but that apparently has not been the case. Johnson (1969) examined hare predation by red foxes, a factor, which may have substituted in part for prior predation by coyotes. De Waal Malefyt

(1974) reported the habitat affinities of hares on Isle Royale.

It is a general assumption that hares on the island are potential competitors for forage with moose, since there is considerable overlap in their preferences for deciduous, if not coniferous, winter browse species. They also share a number of summer forbs - though supply of these is not suspected to be limiting to either. Belovsky (1984a), using data from the west end of the island, speculated on the degree of competition between hares and moose based on a mechanistic explanation from foraging theory.

#### Beaver

The most complete study of beavers at Isle Royale is Shelton's (1966), in which island-wide beaver numbers, habitat associations, and potential competition with moose are reported. Shelton (Univ. Virginia, College at Wise, *unpubl.*), followed by Douglas W. Smith (Yellowstone Natl. Park, *unpubl.*) have continued periodic aerial counts of food piles over the entire island as an index of beaver numbers (Peterson 1999b). Shelton and Peterson (1983) described beaver's co-actions with moose and wolves. A critical co-action between beavers and moose stems from the widespread cutting of quaking aspen by beaver. The resultant sprouts are highly preferred by moose in both summer and winter, but, when moose browsing prevents the sprouts from escaping, new generations of mature aspen will fail to develop. This change would reduce long-term capacity for beaver on the island - which, in turn, will impact moose through loss of sites for aquatic feeding (see Appendix). Moen *et al.* (1990) compare effects of moose and beaver on the island's vegetation, while Pastor *et al.* (1987) offer an hypothesis concerning effects of foraging by moose and beaver on the dynamics of soil nitrogen and carbon.

Belovsky (1984c) studied summer foraging of beaver and estimated how they optimize their diet during that season.

A critical contribution of beaver to nutritional resources for moose at Isle Royale is their creation of numerous impoundments where aquatic macrophytes can grow - these plants are a key source of sodium for Isle Royale's moose. At the same time, beavers themselves consume the same macrophytes during the growing season, hence would be competing directly for what may be a limited, critical resource for moose.

#### **FORAGING HABITS, NUTRITIONAL CONSIDERATIONS, AND SODIUM ECOLOGY/ PHYSIOLOGY IN MOOSE**

An extensive set of forage studies for moose of Isle Royale has been accumulated. These are treated here first in terms of what moose eat and how it relates to nutrition, then, in a separate section, how this foraging affects plant communities. There is special focus on one nutrient, sodium (Na), because of the environmental sparseness of this essential mineral and the specific strategies shown by moose in response to this shortage. Also, several complex models of feeding strategies and their ecological and nutritional implications for Isle Royale moose have been developed.

#### **Food Habits**

Murie (1934) and Hickie (1936, 1943) provide one of the first accounts of how severely moose can exhaust their preferred forage species and then turn to less preferred items - reflecting the peak of an irruption after this herbivore had colonized an ideal environment with no predators and a plant community rich in unused, nutritious forage. Murie (1934) and Hickie (1936, 1943) also emphasized the degree to which moose were foraging in ponds. Aldous and Krefting (1946) and Krefting (1951, 1974)

undertook the first quantitative browse studies, using island-wide plots and semi-quantitative measures to describe availability and winter-use of woody species. Of particular interest was the replacement, between the mid 1940's and early-1950's, of quaking aspen by white birch as the most used winter forage in the 1936 burn. In the early-1970's, de Waal Malefy (1974) compared evidence of winter moose browsing with that of hare browsing at scattered locations in the eastern portion of the island.

During the ecosystem studies of Botkin and Jordan 1972-74, Belovsky *et al.* (1973), and Belovsky (1981c) quantified species used by moose in both summer and winter at the island's west end. Also, Ackerman (1987) recorded summer food habits at the west end of the island. At appropriate intervals during summer, 1993-96, Tom Shay and Steve Windels, working with Jordan, recorded (*unpubl.*) use of woody and herbaceous plants in an island-wide subset of the permanent plots used for winter pellets and browse measurements. Miquelle (1979) and Miquelle and Jordan (1979) tested the idea that the set of plant species taken within a span of one to several days reflects partly the tendency of moose to select for a diverse diet. Their study included experimental *ad lib* feeding trials with captive moose in nearby Ontario, using the principal forage species observed being taken at the island study sites. During 1983-86, Risenhoover (1987) recorded species consumed by moose in winter by direct observation, comparing foraging habits on Isle Royale with those of moose at Denali National Park, Alaska.

Edwards (1978) focussed on summer use of wild sarsaparilla but recorded other plants being eaten at the same time. She concluded that cows with calves that spend early summer on small offshore islands, while achieving greater security from predation, forego nutritional benefits realized

by moose that forage along interior ridges of the main island. In these latter areas, warmer temperatures early in the growing season lead to an earlier leaf-out of woody species. Leaf-out on the much cooler offshore islands can be as much as 2 weeks later; in addition, preferred deciduous species are less abundant there, due to a greater presence of mature conifers (Edwards 1983a, 1984). In their studies of soil nutrient-vegetation-moose interactions, Pastor's group has recorded feeding habits in the course of testing hypotheses concerning soil nutrient consequences of moose preference for deciduous species relative to conifers (Moen *et al.* 1990).

#### **Sodium Physiology and Ecology**

At the onset of their ecosystem studies in the early-1970's, Botkin *et al.* (1973) examined concentrations of 6 mineral elements essential to animals - nitrogen, phosphorus, potassium, calcium, magnesium, and Na - in terrestrial vegetation, and found that only Na was at inadequate levels. At the same time, availability of phosphorus was just adequate for animal growth based on nutritional requirements for ruminants. Na was at such low concentrations in all terrestrial forages used by moose in summer and winter that the animals could never ingest enough of these plants to meet their growth and reproduction requirement for this essential nutrient regardless of how physiologically efficient they are in conserving it. At the same time, the population showed no indication of being deficient in Na. It appeared moose met their requirements by feeding on aquatic macrophytes whose Na levels are orders of magnitude higher than in terrestrial plants (see below) (Botkin *et al.* 1973, Jordan *et al.* 1973, Belovsky and Jordan 1981, Jordan 1987). Risenhoover and Peterson (1986, 1987) showed that use of mud licks having relatively high Na levels was greater than found by the group cited

above. Risenhoover and Peterson (1986, 1987) concluded that geophagy is an important source of the Na for moose on the island; Jordan (1987) would, however, argue that the evidence indicates aquatic plants are a more important source for this population; neither of us has conclusive evidence either way. It is interesting that during the 1920's, at least one salt block was put out on the island, and Murie (1934) found its use by moose to be quite heavy.

Botkin *et al.* (1973), Jordan *et al.* (1973) and Aho and Jordan (1979) reported selection of aquatic species taken by moose. Quarnemark (1999) installed underwater exclosures in one shallow lake, and examined species richness and moose grazing in 8 other lakes, 1997-98.

#### **Models of Foraging Dynamics and Moose Nutrition**

Continuing the ecosystem studies of Botkin *et al.* (1973), Belovsky (1978, 1981b,c) and Belovsky and Jordan (1978, 1981) estimated how much foraging time, based on their thermal physiology, moose ought to allocate among habitats; how much effort moose should expend in foraging among woody, herbaceous, and aquatic plants; and factors that determine moose preferences for some individual plant species. These studies included application of optimal foraging theory and provide models developed from linear programming that incorporate constraints on feeding as a function of time, digestive capacity, energy needs, and Na requirements (Belovsky 1978, 1984b, 1986). The models closely predict the foraging behavior actually observed in moose, and they indicate that moose are apparently maximizing daily energy intake, given their foraging constraints and their sex and reproductive status. These results suggested that moose were energetically stressed at Isle Royale during the study period of 1972-74. The models and observations also indi-

cated that no single plant species would be consumed to the exclusion of others, because some fraction of all species eaten meets the animals' criteria for food selection (Belovsky 1981a) and corroborates the findings of Miquelle and Jordan (1979) that moose select for diversity.

Moen (1995) and Moen *et al.* (1997, 1998) developed a spatially explicit model of moose browsing based on their earlier work at Isle Royale. This model includes spatial distributions of available browse bites, and it incorporates detailed aspects of energetics and requirements for growth and reproduction coupled with time and digestive constraints in achieving required intake of forage. Moen's (1995) model has subsequently been expanded to permit nutritional interpretation of N:creatinine ratios in frozen urine collected from snow (Moen and DelGiudice 1997).

#### RESPONSES OF VEGETATION TO MOOSE FORAGING

With Isle Royale's moose irruption attracting national attention in the 1920's, widespread concern arose over the fate of forests and other vegetation on the island. Apparently having never been subject to moose foraging - at least severe foraging - the vegetation here was suddenly subject to a rapid transformation. Of equal, if not greater, interest are the changes in recent years that have occurred subsequent to the natural mortality of mature trees present before moose arrived and are now dying. Normal regeneration of several dominant species has been partly or completely suppressed by moose for >70 years; hence, normal replacement of the forest has been impeded. Among the several species in this circumstance, the very abundant balsam fir has attracted greatest attention.

#### Early Studies - Before and After Moose

Various vegetation records that pre-

ceded the arrival of moose provide a basis for comparing trends measured under the impacts of moose since the 1920's (see Appendix). Records include systematic notes on dominant vegetation at section corners by U.S. government land surveyors in the 1840's (Ives 1847, Janke *et al.* 1978). Both Adams (1909) and Cooper (1913) documented plant communities at sites that would be relatively easy to relocate today for pre- and post-moose comparisons. Murie's (1934) observations in 1929-30 were essentially of the initial impact of moose. Murie (1934:39) contrasted Adams' (1909) and Cooper's (1913) description of the widespread abundance of American yew or ground hemlock, finding that "...today nothing remains of this spreading shrub except the dead branches and a few leaves near the roots." Qualitatively, Murie (1934:40) emphasized the impact of moose on reproduction of fir, quaking aspen, white birch, and mountain ash, as: "...thousands of the smaller trees have been broken over by the moose." Murie (1934) predicted that, if moose numbers were not controlled, the animals would destroy the vegetation and then die out themselves from disease and starvation.

Aldous and Krefting (1946) found balsam fir reproduction hedged more extensively in 1945 than had been reported for 1929-30 by Murie (1934). The former authors claimed that distribution of quaking aspen would be significantly reduced, given the rate at which its reproduction was being browsed, even in dense, extensive stands in the 1936 burn. Aldous and Krefting (1946) also noted widespread suppression of white birch and mountain ash reproduction, along with hedging of several deciduous shrub species. Again, from visits in 1948 and 1950, Krefting (1951) concluded that suppression of many species continued, and that balsam fir would become a much lower component in future forests than in forests



of the past.

### Potential Impacts on Plants and Changes in Forest Succession

Janke *et al.* (1978) and McKaig (1978) compared current forest vegetation with records from a century earlier (Ives 1847) as an approach to estimating the effect of browsing by moose during the interim. To compare continued impacts of moose on vegetation, Janke (1976) and Snyder and Janke (1976) reconstructed histories of the boreal forest at the east end of the island on 4 offshore islands with differing densities of moose, on 1 far island with no moose, and on the main island. Janke (1976) and Snyder and Janke (1976) found substantial differences in age structure of forest stands. They noted that a reduction in density of balsam fir and mountain ash and an increase in white spruce were positively related to the level of moose.

In the 1970's, Edwards (1978, 1985) focused on potential effects of summer grazing by moose on a clonal herb, wild sarsaparilla. Intense cropping - 33% of vegetative shoots and 63% of flowering shoots - occurred; and foraging intensity was positively related to plant density. Growth and reproduction were negatively impacted by foraging the preceding year, so Edwards (1983c) further speculated that the spatial distribution of plants was partly influenced by foraging of moose. Miquelle (1983a) measured the extent of summer regrowth of leaves and shoots in woody plants that had been browsed earlier in the season by moose.

Brandner *et al.* (1990) analyzed relationships between browsing intensity and density of both moose and fir. The strongest association was an inverse relation between fir density and browsing by moose.

Jordan's permanent plot system includes some plots on which detailed systematic vegetative descriptions were first recorded

in the 1960's. Fettig (1995) repeated a subset of these at the west end of the island, primarily in forests dominated by yellow birch. He showed that balsam fir and white birch, dying naturally, were not being replaced, because saplings of these species, while present, were completely suppressed by moose. In the shrub layer, only spruce had increased, while white and yellow birch, sugar and mountain maple, and mountain ash had all decreased.

### The Use of Exclosures

In 1949-50, Krefting (1974) directed construction of four 15 × 15 m (225 m<sup>2</sup>), moose exclosures at widely scattered locations and summarized before-and-after vegetation measurements up to 1966. Striking effects resulted from moose exclusion: re-emergence of American yew, and escape of hedged tree saplings into normal, mature form in balsam fir, quaking aspen, white birch, mountain ash, pin cherry, and mountain maple. Risenhoover and Maass (1987) repeated Krefting's measurements inside and outside the 4 exclosures in 1982 to compare changes expected with normal forest succession vs. those related to browsing by moose. Overstory shading inside exclosures in spruce-birch-fir forests had reduced stem density relative to the adjacent, unprotected vegetation, where stems of palatable species had been suppressed. Comparisons of the birch-aspen stands at exclosures within the 1936 burn showed only slight differences, if any. This no doubt reflects that post-burn vegetation, covering nearly one-fifth of the island when moose numbers were relatively low, grew beyond the reach of moose before suppression could occur.

McInnes *et al.* (1992) used the same exclosures in the mid-1980's to explore effects of 35 years' protection, and found further differences in species composition and forest structure, the most pronounced

contrast being at the exclosure with the oldest forest stand of the 4. Other aspects of that study are discussed below under effects of moose browsing on soil nutrients. An exclosure of similar size was constructed at the west end of the island in 1979, and plants inside and outside have been measured by Jordan (*unpubl.*), who is attempting to determine not only effects on trees and shrubs, but also on herbaceous cover and species diversity. This study will also consider ecosystem impacts, including the apparent sharp reduction in vulnerability to natural fire associated with persistent heavy browsing. McLaren (1996a, b) and McLaren and Janke (1996) earlier described another relationship between forest canopy disturbance, by insect kill and wind damage to trees, and regeneration of balsam fir and its subsequent browsing by moose.

#### Impacts on Aquatic Communities

In the late-1920's, Murie (1934) found that moose were causing major degradation of ponds on the island from their grazing and trampling, and expressed concern over impacts on the fish communities. Murie (1934) also noted the absence of pondweeds on lake bottoms where moose had been feeding, and presumed grazing had depleted them. Two species, white pond lilies (*Castalia* [*Nymphaea*] *odorata*) and yellow pond lilies (*Nymphaea Americana*, [*Nuphar variegatum*]), listed as common 24 years earlier by Adams (1909) and 19 years earlier by Cooper (1913), were now "practically gone; only an occasional plant is seen;" Murie (1934) comments that this formerly abundant source of summer food had become greatly depleted.

Murie's (1934) concern for the demise of submerged aquatics took on additional ecological importance, considering the subsequent discovery that this plant community has unique nutritional significance to moose

as their prime source of Na. Aho (1978) and Aho and Jordan (1979), using exclosure comparisons within 2 drainages at the west end of the island, determined that 60-95% of annual production was being removed by moose in these heavily used beaver ponds. In addition, Aho (1978), using aerial photos and on-site sampling, inventoried aquatic forage over the entire island. Quarnemark (1999), using underwater exclosures in deeper waters, found that grazing by moose significantly reduced both plant biomass and species richness.

#### MOOSE AND ECOSYSTEM DYNAMICS

Faaborg (1981) experimentally analyzed Na flux within a well-used beaver pond and the surrounding small watershed. Small cylinders enclosing pond water were imbedded in the pond bottom and planted with the prevalent macrophyte, *Potamogeton alpinus*; these plants were then subjected to a variety of treatments. Faaborg (1981) reported that the plants obtain Na from the upper few cm of substrate, and do so more effectively from the normal pond substrate than from substituted forest soil. He also found that the plants concentrate Na >1000-fold above the level present in pond water, and that they experience better growth when Na in the water is increased. The last point suggests that Na is an essential element for such macrophytes, a possibility that apparently has not been addressed by limnologists or plant physiologists.

Pastor *et al.* (1987, 1988) began ecosystem-based research at Isle Royale in the mid-1980's, emphasizing how the fact that moose select hardwoods and avoid conifers affects not only composition of plant communities but also nutrient cycles and overall primary productivity. Pastor and Naiman (1992) suggested that differences in rate of soil decomposition of leaves and needles from various species of plants closely par-

allels ruminal digestion rates of those same plant tissues in moose. Mechanisms by which moose might affect ecosystems were tested in 3 of the Krefling exclosures. Availability of soil nutrients and microbial activity, including exchangeable cations, total carbon (C) and nitrogen (N), N-mineralization rates, and microbial respiration rates were uniformly higher inside exclosures than outside (McInnes 1989, McInnes *et al.* 1992). These differences were most significant where intensity of browsing outside was highest. N-mineralization, a key indicator of nutrient availability to plants, was lower where spruce litter was dominant; and spruce was observed to be replacing other species in areas long heavily browsed by moose. Moose pellets alone mineralized less N and more C than soil alone, but pellets combined with soil stimulated N- and C-mineralization more than the sum of the 2 separately (Pastor *et al.* 1993). However, this did not appear to be sufficient to offset the depression in N- and C-mineralization in soil associated with increased spruce.

Studies were made on the effects of moose herbivory on ecosystem processes at a landscape scale, using 2 sites near the east end of Isle Royale. Availability of soil N decreased rapidly as annual consumption of browse by moose increased to  $>2$  g/m<sup>2</sup>. With greater browse consumption, N availability was uniformly low and constant among years (Pastor *et al.* 1998). Oscillatory patterns on the landscape in N availability, browse availability, and browse consumption suggest that the interactions of moose with the forest ecosystem cause the development of both local patches of vegetation and associated nitrogen-cycling rates, as well as the development of higher-order patterns of vegetation across the landscape (Pastor *et al.* 1997).

## CONCLUSIONS AND THE FUTURE

It is apparent from the extensive and varied record of studies related to moose at Isle Royale that the island has become one of the world's most notable sites for ecological research, particularly where large mammals and forest vegetation are among the dominant biota (Botkin 1990). There appears to be a continuing momentum of scientific initiatives and creativity in the search for clearer understanding of the biological dynamics of this community. For one, Mech (1996) makes the case for further study of wolves. The future of research at Isle Royale offers ever-increasing promise. The great value of even more decades of continued long-term, consistent measurements, so critical to appreciating temporal variations in natural systems, appears certain to be combined with ever-expanding scientific creativity.

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#### APPENDIX: MOOSE, WOLVES, AND BEAVER

Shelton and Peterson (1983), in summarizing the study of beaver on Isle Royale, showed the role of that animal in shaping forests and forest soil drainage, a role which has direct implications for habitat quality for moose (Pastor and Naiman 1992). Beaver, like moose, experienced wide population fluctuations during the 20th Century. Unlike moose, there is evidence of beaver presence on the island during the 18th and 19th Centuries, but the population in 1900 was absent or very low. Fires during the late 19th Century and in 1936 created abundant birch and aspen forests that supported large population increases in beavers beginning at least in the 1920's and continuing into the 1950's. Studies in the 1940's indicated rapid cutting of aspen and birch stands, and a decline in beavers due to food shortage was predicted (Krefting 1963). A significant decline did occur in the mid-1950's, but it probably resulted from tularemia (which swept through the region in the 1950's) rather than from food depletion. Studies begun in the early 1960's (Shelton 1966) revealed a healthy, recovering beaver population of at least 125 colonies with food caches counted by aerial survey in 1962. The population increased to a maximum of 286 colonies with food caches in 1974 (Shelton and Peterson 1983).

As wolves increased during the late-1970's, the beaver population declined, reaching a low of 83 colonies in 1980, the year of maximum wolf numbers. Beavers increased during the period of low wolf numbers in the 1980's, reaching about 200 colonies by 1986, then declined slowly

through the 1990's to about 100 colonies in 1998, as forests reverted to spruce or spruce-fir, and heavy moose browsing prevented regeneration of birch and aspen. Throughout the period, the numerous beaver ponds have continued to provide important aquatic food and nutrient sources for moose (Belovsky and Jordan 1978). However, beaver cutting sped conversion of birch-aspen stands to spruce-fir by removing canopy trees, while moose browsing effectively eliminated recovery of aspen and birch after beaver cutting. A very important modeling exercise was the result of this history (Moen *et al.* 1990, Pastor and Naiman 1992) - a history which led to the description of a positive degenerative cycle for the Isle Royale moose population and its habitat (Pastor and Cohen 1997; Pastor *et al.* 1993, 1998); here we show it as a sequence of "photo-stations" developed by Phil Shelton (University of Virginia, Clinch Valley College, Wise, VA).

**Set A.**

**1962 May 15.** Cow moose and stump on Greenstone Ridge, southwest of Hatchet Lake Trail Junction, in the 1936 burned area. Aspen and birch with scattered spruce occupy thicker soils not eroded after the fire. Bare rock and thin soils with heavily browsed shrubs, mostly juneberry (*Amelanchier*), in the foreground result from intense soil erosion following the fire.



**1999 May 20.** Aspen, birch, and spruce have grown dramatically, while most low shrubs have been eliminated or are heavily suppressed by moose browsing. Recovery of the small tree on left and around the stump has occurred since 1996. The bare rock and stump are scarcely changed. (The moose moved).

## Set B.



**1974 Oct 12.** This area is in the 1936 burn south of Moskey Basin. Young aspens escaped from moose browsing, and many smaller aspens and juneberry were browsed by moose.



**1986 Oct 19.** Escaped aspens and spruce in background are thriving. The shrub layer has been severely depleted by moose browsing.



**1999 May 19.** Small shrubs have been almost completely removed. Proliferation of lichens has occurred on rocks-conversion from moose habitat to caribou habitat. Absence of grass in this photo is a function of the early season.

**Set C.**



**1990 Oct 24.** Aspen saplings have been lightly browsed by moose; up the Chickenbone Trail about 100 m from Daisy Farm. Windthrown spruce appears at right.



**1999 May 19.** The aspen saplings survived the moose peak in 1996, but show severe browsing effects.

**Set D.**



**1962 May 18.** Porter Island from Merritt Lane, probably burned in late 19th Century. Beaver-cut birch logs appear with fir reproduction.

**Set D. (Continued)**



**1974 Oct 12.** Fir reproduction is rapidly growing, especially where released from competition when beavers cut overstory birch.



**1989 May 26.** Fir forest is developing rapidly; decadence of birch is evident on skyline.



**1994 Oct 18.** Continued rapid growth of firs and decadence of birch.

**Set E.**



**1963 May 29.** Beaver pond in 1936 burn south of Moskey Basin. Note white pine at left, good view of distant horizon, alder along pond margin and bare rock in right foreground.



**1974 Oct 9.** White pine is browsed between the minimum snow line and maximum reach of moose; spruce is evident on far side of pond, beavers have cut some alders, and lichens are beginning to grow on the rock.



**1986 Oct 19.** Increased size of pine and spruce cause the distant horizon to be obscured. Beavers have removed all alders, and the lichen cover has increased.



**Set E. (continued)**



**1990 Oct 20.** Continued growth of pine and spruce with a new white pine at the right of the beaver lodge (light snow cover).



**1999 May 19.** Continued growth of conifers and thick lichen cover on rocks.

**Set F.**



**1962 Nov 11.** Second beaver pond in 1936 burn south of Moskey Basin. Note floating bog mat in pond, raised by beaver flooding, lodge and large food cache at right, canal to cutting area on far side of pond, small spruce on far side of pond, and birch cut from slope in foreground.

**Set F. (continued)**



**1974 Oct 3.** Pond temporarily abandoned. Spruce on far side have increased size; birch and alders have regenerated on the slope in the foreground.



**1988 Sept 29.** Continued growth of spruce. Spruce appear on the slope in the foreground among birches that survived beaver cutting and moose browsing. Lichens are conspicuous on rocks.



**1990 Oct 16.** Continued growth of spruce and birch.

**Set F. (continued)**



**1999 May 19.** Continued growth of spruce and birch cause the distant horizon to be almost obscured.