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Reviewed work(s):
Source: *Ecological Applications*, Vol. 9, No. 1 (Feb., 1999), pp. 10-16
Published by: Ecological Society of America
Stable URL: http://www.jstor.org/stable/2641163
Accessed: 19/12/2011 15:11

Ecological Applications, 9(1), 1999, pp. 10–16

WOLF–MOOSE INTERACTION ON ISLE ROYALE: THE END OF NATURAL REGULATION?

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Abstract. Long-term population fluctuations of wolves and moose in Isle Royale National Park, Michigan, are used to evaluate a central tenet of the "natural regulation" concept commonly applied by the National Park Service (NPS) in the United States, namely, that wild cervid populations exhibit density dependence which, even in the absence of large predators, will stabilize population growth. This tenet, restated as a hypothesis, is rejected based on moose population response to a chronic wolf decline. In 1980–1996 with wolf numbers down, partly due to introduced disease, moose numbers increased to a historic high level. There was insufficient density dependence in moose reproduction and mortality to stabilize moose numbers. In 1996 moose suffered a crash; 80% died, primarily from starvation. These fluctuations, along with the possibility that the highly inbred wolf population may become extinct, will challenge NPS policy. The long-standing NPS management tradition of nonintervention may not be compatible with the current policy that stresses maintenance of natural ecological processes, such as a predator–prey system.

Key words: Alces alces; Canis lupus; *disease; genetics; Isle Royale, Michigan (USA); limitation; moose; national park; predation; regulation; starvation; wolf.*

For the first half of the 20th century moose (*Alces alces*) inhabited the 544-km^2 Isle Royale in the absence of gray wolves (*Canis lupus*) or other large carnivores (Mech 1966). There are no records of either moose or wolves on Isle Royale prior to 1900. Isolated 40 km offshore by cold waters or ice of Lake Superior, Isle Royale has been successfully colonized by only one-third of the mammalian species from the adjacent mainland. To my knowledge, Isle Royale provides the only ecosystem where moose coexist with wolves in the absence of bears (*Ursus* spp.).

Following initial colonization early in the 1900s moose increased rapidly. The moose population grew to 3000 or more (5.5 moose/km^2) by the early 1930s, then starvation caused a sudden crash in 1934 (Murie 1934, cf. Peterson 1995). By the late 1940s, buoyed by browse regrowth following extensive forest fires in 1936, moose were again abundant, and winter mortality from starvation in winter recurred (Krefting 1951). Wolves colonized Isle Royale in the late 1940s and introduced a new source of mortality for this moose population. Ecological studies of wolf–moose interaction were initiated in 1958 (Mech 1966) and have continued to the present. As understanding of the three-level trophic system at Isle Royale increased over the past four decades, the National Park Service (NPS) developed, at the national level, policies regarding management of natural resources that eventually included a strong emphasis on maintaining natural ecological processes. The influence of the Isle Royale chronology on policy making for national parks can be traced back at least to Leopold et al. (1963).

Natural regulation, the prominent and controversial approach where wildlife populations are allowed to fluctuate without direct human intervention, was adopted in Yellowstone National Park in the late 1960s (Cole 1971). This was an abrupt break with previous NPS management actions in Yellowstone, which had included periodic culling of elk (*Cervus elaphus*) by park staff (Houston 1982). The natural regulation policy applied at Yellowstone was based on the hypothesis that density-dependent reduction in population growth rate for large herbivores would tend to stabilize animal abundance (D. B. Houston, *unpublished manuscript*). Further, large carnivores would not impose a lower ceiling on herbivore density than that dictated by the interaction of food and climate on reproduction and survival (Houston 1982). In other words, major controls on large herbivores are "bottom-up" (Strong 1992), driven by resource abundance as modified by weather, with no significant "top-down" influence from carnivore predation, which simply compensates for other mortality. At Yellowstone the concept of natural regulation was tested by eliminating culling of elk within the park.

By the 1980s NPS policy had evolved to emphasize maintenance of natural ecological processes as a means

Manuscript received 14 April 1997; revised 10 December 1997; accepted 17 December 1997; final version received 15 January 1998. For reprints of this Invited Feature, see footnote 1, p. 1.

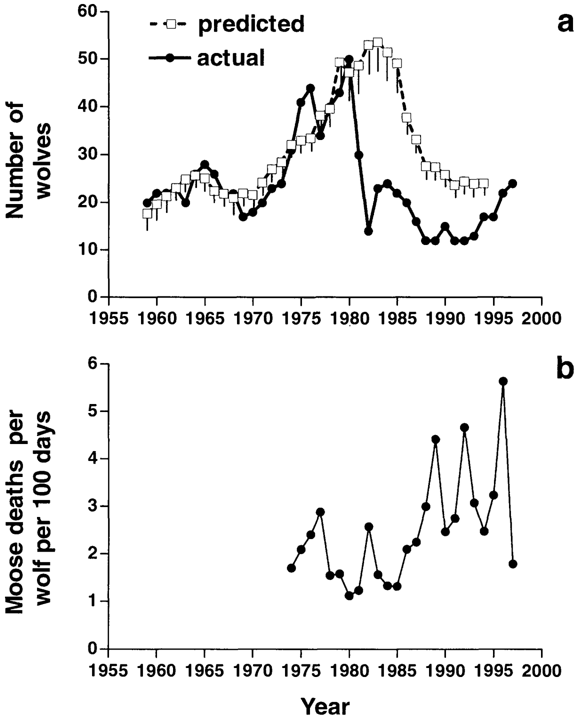

FIG. 1. (a) Wolf population size, predicted and actual, Isle Royale National Park, 1959–1997. Predicted numbers (with tail indicating lower half of 95% confidence interval, assuming no uncertainty in the independent variable) are based on the correlation between the number of wolves and moose ≥10 years old during 1959–1980 (Peterson et al. 1998). Predicted population sizes later than 1994 are not yet available. (b) Moose mortality expressed as number of moose deaths per wolf per 100 d, determined from aerial surveys for 40–50 d in January–February each year.

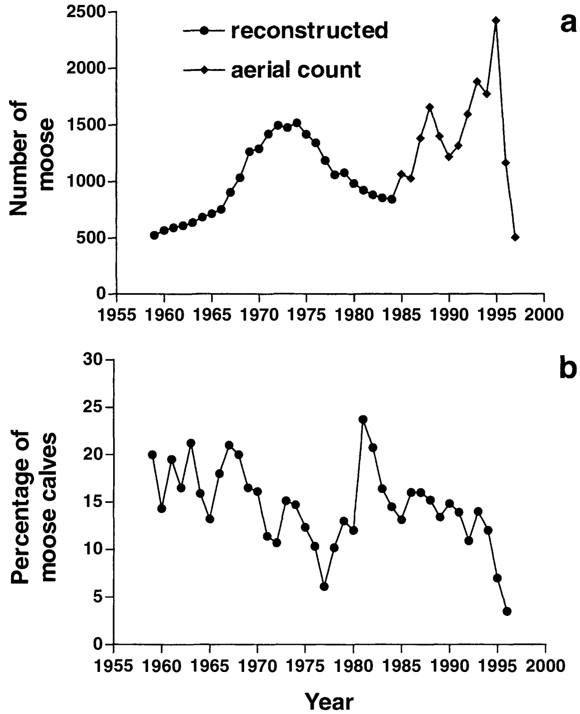

FIG. 2. (a) Estimated moose population size, Isle Royale National Park, 1959–1997, based on reconstruction (1959–1982) and aerial surveys (1983–1996). A 95% confidence interval of 15–25% is associated with each estimate of moose population size. (b) Abundance of moose calves (at ~6 of age) as a proportion of total population size, Isle Royale National Park, 1959–1995 cohorts. These are single best estimates, the mean of all available counts for each cohort, ranging from summer ground counts to aerial counts in autumn or winter.

of managing native wildlife (Risser et al. 1992). The tradition of nonintervention in wildlife dynamics in U.S. national parks is an outgrowth of this policy (Peterson 1995), in contrast to the active ecological maintenance advocated by Leopold et al. (1963). When the notion of natural regulation was first set forth in the late 1960s, wolves had been absent in Yellowstone for >40 yr, and no other national park in the 48 contiguous United States supported gray wolves except Isle Royale. What does the absence or restoration of top carnivores mean for national park ecosystems?

In this paper, I evaluate the central tenet of the natural regulation policy in the context of the ecosystem at Isle Royale. That is, are there density-dependent mechanisms that regulate moose density in the absence of predation by wolves (Peterson 1977)? Second, wolf population fluctuations at Isle Royale are reviewed to illustrate the difficulty of reconciling a noninterventionist management philosophy with maintenance of ecological integrity.

METHODS

Moose population size at Isle Royale was estimated from aerial surveys in winter, 1983–1997 (Peterson 1977), and population reconstruction, 1959–1982 (Fryxell et al. 1988, Page 1988, R. O. Peterson, *unpublished data*). Wolves were also counted from aircraft in winter, and backtracked in snow to locate their kills for 40–50 d in January–March, 1959–1997 (Peterson 1977, Peterson and Page 1988). During 1988–1997, 15 wolves were live-captured to draw blood samples used in studies of genetics and disease, and these wolves were radio-collared and tracked to help characterize survival and reproduction (Lehman et al. 1991, Wayne et al. 1991, Thurber and Peterson 1992, Vucetich et al. 1997, Peterson et al. 1998).

RESULTS

Multiple factors have influenced the dynamics of both wolf and moose populations during 1959–1997. During the 1960s and early 1970s, while wolves remained stable at ~24 individuals (Fig. 1a), moose increased steadily (Fig. 2a) from ~600 (1.1/km^2) to 1500 (2.8/km^2) animals. Coincident with four consecutive winters of above-average snowfall (1969–1972), the moose population stopped growing and then declined rapidly in 1974–1981, as wolves increased to a historic

PLATE 1. Wolf pack in unsuccessful pursuit of a moose at Isle Royale National Park, in a chase that lasted for 2 km. Photo by Rolf O. Peterson.

peak of 50 animals (92/1000 km^2). The wolf population crashed from 50 to 14 individuals in 1980–1982, and moose then increased through 1995 (except in 1989, when there was exceptional mortality from a regional outbreak of winter ticks (*Dermacentor albipictus*) [DelGuidice et al. 1997]). A large die-off of moose from starvation occurred in late winter and spring in 1996, with estimated moose numbers (±95% CI) dropping 80%, from 2412 ± 362 in 1995 to 502 ± 121 in 1997.

The sustained increase in moose numbers from 1985–1995 following the wolf crash was not affected significantly by a density-dependent reduction in reproduction (Fig. 2b), with what reduction there was being too little and too late to stabilize the population. A more influential parameter, moose annual survival, also did not change sufficiently to stabilize moose density, in spite of increased per capita kill rate by wolves (Fig 1b). During the late 1980s and early 1990s wolf numbers were strongly limited by low reproductive success (Peterson et al. 1998), and moose density increased until their numbers exceeded available food. Moose population growth was only stopped by new mortality; the outbreak of winter ticks in 1989 (DelGuidice et al. 1997) and, in 1996, starvation triggered by severe winter weather.

After the wolf population crash of 1980–1982, wolves did not recover their former abundance. They rallied briefly in 1983–1984 (Peterson and Page 1988), declined to their lowest level, 12 animals, by 1988, and then began to increase in the mid-1990s (Peterson et al. 1998).

After the precipitous wolf decline in 1980–1982 annual mortality continued at above-average levels (mean 39%) during 1983–1988, then declined to low levels (mean 14%) in 1989–1996. The population failed to grow quickly because reproduction was low; territorial packs commonly failed to produce any surviving pups, and when packs did reproduce, litter size was usually low (Peterson et al. 1998).

Peterson et al. (1998) reviewed four hypotheses that might explain the continuing decline of wolves on Isle Royale: genetic decay arising from isolation, food shortage, new disease, and demographic stochasticity. There also remains the possibility of factor interaction, simultaneously or in serial fashion. A full explanation must account for high mortality among wolves in the 1980s and low reproductive success in the late 1980s and 1990s.

Genetic studies revealed that Isle Royale wolves are highly inbred, all descendants of a single maternal ancestor. Compared to wolves on the adjacent mainland, they have lost genetic variability (Lehman et al. 1991, Wayne et al. 1991). Inbreeding depression could explain the poor reproduction that has limited wolf population growth, but all other hypotheses must be rejected before we can accept the genetics hypothesis. According to this hypothesis reproductive success should fail to improve in the next generation of breeding wolves appearing in the late 1990s (Peterson et al. 1998).

For Isle Royale wolves, the primary disease of interest in the 1980s was canine parvovirus (CPV), first identified worldwide in 1977. CPV was implicated in the Isle Royale wolf population crash of 1980–1982, and annual mortality of wolves remained high until the disease disappeared in the late 1980s (Peterson et al. 1998).

Around 1990 the wolf decline coincided with a periodic trough in the number of old (≥10 yr) moose which provide most prey biomass. Wolf numbers were significantly related to abundance of old moose both before and after the catastrophic decline in 1980–1982, but after the crash wolf numbers were only about half of the level expected from pre-crash data (Fig. 1a). Thus, while food supply evidently remained influential

TABLE 1. Density of moose (no. animals/km^2) in relation to the number of coexisting predator species other than human hunters. As the number of coexisting predator species increases, moose density typically declines, but there is also considerable variation attributable to site-specific conditions.

Predator species†	Hunted?	Location	Density (no. animals/ km^2)	Source
None	Yes	Southern Finland	0.4	Nygrén (1987)
None	Yes	Rochester, Alberta	0.8	Rolley and Keith (1980)
None	Yes	Southern Sweden	1.5	Cederlund and Markgren (1987)
None	Yes	Elk Island, Alberta	1.5	Cairns and Telfer (1980)
None	Yes	Newfoundland	1.1–2.4	Bergerud and Manuel (1968), Mercer and Manuel (1974), and Fryxell et al. (1988)
GB	Yes	Seward Peninsula, Alaska	0.4	Gasaway et al. (1992)
GW, (BB)	No	Riding Mountain, Manitoba	0.8	Carbyn (1983)
GW	Yes	Hecla Island, Manitoba	1.0	Crichton (1977)
BB	No	Gaspesie, Quebec	2.0	Crête (1989)
GW	No	Isle Royale, Michigan	1.1–4.4	This study
GW, GB	Yes	Aishihik, Yukon	0.1	Larsen (1982)
GW, GB, BB	Yes	Kluane Lake, Yukon	0.1	Larsen (1982)
GW, GB	No	Denali, Alaska	0.2	Singer and Dalle-Molle (1985)
GW, GB, (BB)	Yes	Nelchina Basin, Alaska	0.8–1.2	Gasaway et al. (1992)
GW, GB, (BB)	Yes	Kenai Peninsula, Alaska	0.8–1.4	Bailey (1978), Peterson et al. (1984), Schwartz and Franzmann (1989)

† GW = gray wolf; GB = grizzly bear (*Ursus arctos*); BB = black bear (*Ursus americanus*). Parentheses indicate the presence of a predator species that was rare or did not prey on moose.

after the crash, one or more additional factors limited wolf population growth.

In such a small population, with only three breeding pairs of wolves, demographic stochasticity, including the idiosyncracies of individuals, might overwhelm all other factors. The threat of wolf extinction was reduced suddenly in 1993 when two old female wolves, both with lackluster reproductive histories, each raised four pups (Peterson et al. 1998). Continued monitoring should reveal if this increase represents the initial stages of recovery or simply demographic "noise."

In reviewing the Isle Royale case history, it should be emphasized that moose density on this island is extraordinarily high, an order of magnitude greater than in most mainland areas supporting moose in North America. Haber (1977) and Messier and Crete (1985) proposed a so-called "multiple-equilibrium hypothesis," whereby wolf predation (or predation by two or more species of large carnivores, including wolves, bears, and humans) might regulate moose density at low levels (<0.5 moose/km^2), but that moose could, under some circumstances (e.g., habitat enhancement), "escape" the constraints of predation and increase to a stable upper equilibrium where regulation occurred by density-dependent responses caused by food limitation. Several studies have found little empirical support for this hypothesis (Van Ballenberghe 1987, Gasaway et al. 1992, Van Ballenberghe and Ballard 1994, Hayes 1995, Orians 1997), yet cite evidence that wolf predation is nevertheless a strong limiting factor. Accordingly, Isle Royale probably supports a high-density moose population because moose there have fewer limiting factors; it lacks predation by carnivores other than wolves. Comparably high densities of moose are reached where predation by only bears, or only humans, occurs (Table 1). Adding a second or third species of predator leads to progressively lower densities of moose.

Predator limitation of prey may indirectly influence community structure by reducing herbivory. McLaren and Peterson (1994), using tree rings for Isle Royale balsam fir (*Abies balsamea*) within browsing height of moose, demonstrated that tree growth was facilitated by high wolf numbers, which led to low moose density. Fir growth declined in the 1980s and 1990s as the wolf population faltered at a low level and moose increased. While arguing for the primacy of top-down control in the Isle Royale food chain, McLaren and Peterson (1994) acknowledged that large scale forest disturbance was nevertheless an important bottom-up stochastic influence.

DISCUSSION

The central tenet of natural regulation envisioned by Cole (1971) and D. B. Houston, (*unpublished manuscript*), that moose exhibit intrinsic demographic responses sufficient to stabilize population growth, was not supported by this chronological review of moose fluctuations at Isle Royale. Depressed wolf numbers led to an increase in moose that continued until moose overshot their food supply and crashed from starvation.

In addition to the Isle Royale chronology, a comparison of moose density among geographic areas with different predation regimes suggests that predation is a major limiting factor for this large herbivore. A review of available case studies by Orians (1997) found that where wolves and bears coexist their predation usually limits prey density. Such top-down control of trophic systems can be expected to have profound effects on the structure and function of ecosystems containing large herbivores.

Houston (1982) stressed that the lack of wolf predation for most of this century in most national parks was a significant ecological deficiency. Restoration of large carnivores in parks and other reserves, exemplified by the return of the wolf to Yellowstone (Phillips and Smith 1996), should enhance the value of such areas as ecological research sites, perhaps leading to greater integration of science with national park management in the United States, as called for by Risser et al. (1992). The desired symbiosis between science and management in national parks requires frequent evaluation of scientific hypotheses that explain the dynamics of "the wildlife therein," whose protection was dictated by the U.S. Congress (1916 Organic Act).

The Isle Royale chronology reveals an impressive array of random influences that have led to dramatic fluctuations in wolf and moose populations: winter weather, disease, parasites, and stochastic demography (Peterson 1977, DelGuidice et al. 1997, Peterson et al. 1998). While this review underscores the importance of trophic structure in ecosystem dynamics, a proper appreciation of environmental stochasticity is equally important to ecosystem management (Botkin 1990).

Until the present time, wolves on Isle Royale have been allowed to increase or decline on their own, without direction from scientists or managers, even though wolf extinction remains a possible outcome of nonintervention (Peterson and Krumenaker 1989). The rationale underlying nonintervention has been couched in scientific terms: this park provides a valuable test case to evaluate the significance of genetic deterioration in a small, isolated population under strong natural selection (Peterson et al. 1998).

What should managers do once the genetic question is answered? If the genetic load stemming from isolation is deemed negligible in the short term, then continued nonintervention may be the preferred management alternative for managers and scientists alike. The wolf–moose chronology could continue without disruption. However, if reproductive success in the next generation of wolves continues to falter, suggesting that genetic losses are reducing population viability (Peterson et al. 1998), opinion regarding nonintervention is likely to be mixed and decisions will be difficult. There are two existing NPS policies that may provide guidance (Peterson and Krumenaker 1989):

1) The primary objective . . . will be the protection of natural resources and values . . . with a concern for fundamental ecological processes . . . Managers . . . will try to maintain all the components and processes of naturally evolving park ecosystems (NPS 1988).

2) The NPS will seek to perpetuate the native animal life . . . as part of the natural ecosystems of parks . . . The native animal life is defined as all animal species that as a result of natural processes occur or occurred on lands now designated as a park. Any species that moved onto park lands directly or indirectly as the result of human activties are not considered native (NPS 1988).

According to the first policy directive, wolf predation might be considered a fundamental ecological process that should be maintained, when possible, in national park ecosystems. On the other hand, the dynamic processes of island colonization and extinction might receive priority, come what may for the wolf population. Or, if the probability of natural immigration from the mainland has been decreased by human activities (e.g., the city of Thunder Bay on the adjacent mainland contains 100 000 people), mitigation might include wolf reintroduction, perhaps one that mimics natural colonization.

The second policy might be applicable at Isle Royale where canine parvovirus (CPV) appeared to initiate a long-term decline. The resulting high mortality reduced generation length and thus accelerated the loss of genetic variability. CPV might be viewed as an exotic species, and subsquent intervention during a wolf decline could represent reasonable mitigation. Or, lacking definitive cause-and-effect evidence linking introduced disease to demographic problems more than a decade later, managers could choose to ignore the disease issue.

NPS wildlife management policy does not explicitly address aesthetics in park management, in spite of widespread recognition of such values in wilderness areas (Bennett 1994). The aesthetics of wilderness have been influential in the management of Isle Royale National Park throughout its management history (Little 1980); almost all of Isle Royale was formally designated as Wilderness in 1976. In the context of wilderness values there are important views on both sides of the wolf intervention question. The "hands-off" management tradition remains strong in the National Park Service (Wagner et al. 1995), and one might consider wilderness aesthetics at Isle Royale to be compromised by an intrusive introduction of wolves (yet this action at Yellowstone National Park in 1995 and 1996 was supported by the NPS as mitigation for wolf removals from the park in the 1920s [U.S. Fish and Wildlife Service 1994]). On the other hand, the wolf itself is perceived in modern America as a symbol of wilderness (Allen 1979, Lopez 1979), and there is strong public support for maintaining wolves in the Isle Royale ecosystem (73% of Michigan residents agree and only 10% disagree), even if they had to be reintroduced (Kellert and HBRS 1990). As long as moose inhabit Isle Royale there are compelling reasons, ecological and aesthetic, to maintain wolf predation in this park (Peterson 1995).

The policies of the NPS, at the national level, do not dictate a recipe for park management (Peterson 1995), and there is wide latitude to select appropriate courses of action. In this case of Isle Royale, the value to decision makers of existing long-term ecological data, including the need for continued research, should be self-evident. Nonintervention in the wolf decline finds no obvious basis in the existing management policies of the National Park Service, but it is certainly consistent with the management traditions of this national park. Each park will require thoughtful and informed interpretation of national policy in order to maintain ecological integrity in parks; rote adherence to a simple tradition of hands-off management will not suffice in a world with pervasive human influence (Risser et al. 1992, Peterson 1995). Of course, this raises the difficult question, "what is natural?" (Anderson 1991, Wagner et al. 1995).

The Isle Royale ecosystem provides not only a real-world ecological microcosm, but also a management case history that places stark emphasis on NPS interpretation of its actual mission. Nonintervention as an aesthetic imperative need not preclude other aspects of ecosystem management (Grumbine 1994). In the case of wolf–moose interaction at Isle Royale, there are no management conflicts brought on by neighboring jurisdictions, and the NPS is not handicapped by lack of information on its resources. The question of intervention to maintain the integrity of a prominent wolf population may remain hypothetical, or it may resurface as an urgent agendum for park management (Peterson 1995). In either case, in a public arena, specific ecological goals and thresholds for action should be established and continually examined through time.

Acknowledgments

Recent financial support of this study was provided by the United States National Park Service (Cooperative Agreement No. CA-6310-8001), National Geographic Society, Boone and Crockett Club, and National Science Foundation (DEB-9317401). D. J. Parsons and three anonymous reviewers provided helpful reviews of the manuscript.

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