
A Possible Population Response of Moose to Sodium Availability
Author(s): Gary E. Belovsky
Source: *Journal of Mammalogy*, Vol. 62, No. 3 (Aug., 1981), pp. 631-633
Published by: American Society of Mammalogists
Stable URL: http://www.jstor.org/stable/1380412
Accessed: 29-02-2016 14:49 UTC

J. Mamm., 62(3):631–633, 1981

A POSSIBLE POPULATION RESPONSE OF MOOSE TO SODIUM AVAILABILITY

Using the moose sodium requirements set forth by Belovsky and Jordan (1981), population changes of moose at Isle Royale National Park, Michigan, were examined by modelling to assess whether availability of sodium might be responsible for the observed changes. Because aquatic vegetation is the primary source of Na^+ for moose, it is the aquatic plant availability that determines Na^+ availability. Several assumptions were employed in constructing the model: 1) Na^+ limitation has an all-or-none effect that is always fatal, never chronic; 2) calves reached adult size in 1 yr, making Na^+ deficiencies more acute. Nevertheless, the model should present a good approximation of effects of Na^+ deficiency on moose numbers.

The initial moose population was assumed to be 50 in 1904, after moose arrived at Isle Royale at the end of the 19th century by swimming across the intervening 28 km of Lake Superior from Canada (Cooper, 1913*a*; Adams, 1909; Murie, 1934). From a map of Isle Royale and knowledge of beaver pond abundances, 45 km^2 of shallow water suitable for moose aquatic feeding was estimated, of which 32% produced submerged aquatic plants high in Na^+ (Belovsky and Jordan, 1978). Isle Royale exclosures had submerged aquatic production of 129 g/m^2 (Belovsky and Jordan, 1978), comparable to values obtained for Minnesota lakes without moose (Lindeman, 1941). Therefore, 6×10^6 g of Na^+ in aquatic plants (2,950 ppm Na^+) were estimated to be available to moose. Consumption of aquatic plants by beaver (*Castor canadensis*) and muskrat (*Ondatra zibethicus*) was considered minimal because they feed primarily on emergent vegetation on hummocks.

Abundance of Na^+ is reduced by moose consumption and replenished by decomposition. Consumption depends upon Na^+ requirements and numbers of moose. The soil compartment acts as a "sink" for Na^+ until it is freed from organic matter by decomposition and leached back into the aquatic system. Kimmins (1970) suggested that Na^+ has a 10-year lagtime before decomposition makes it mobile in boreal forest soils.

The population model was constructed in the following manner. (1) The population at time *t* was multiplied by the mortality rate, 0.33 per annum (calculated from Jordan et al., 1971), and 358 g Na^+/dead moose were returned to the soil (tissue content: 358 kg × 1 g Na^+/kg). (2) Surviving moose removed 203 g Na^+/moose and returned it to the soil as excrement. If 203 g/moose were not available, moose did not reproduce and the surplus individuals died, returning the Na^+ in their tissues to the soil. (3) If an additional 69 g Na^+/moose (average reproductive requirements based upon fraction of bulls, cows with single calves, and cows with twins in the population, Jordan et al., 1971) was available, moose reproduced. Reproduction was either at a maximum of 0.51 calves/adult/year (Jordan et al., 1971; Simkin, 1965), if 358 g Na^+/calf were available (amount required for body growth to adulthood), or the calf crop was the available Na^+ divided by 358 g Na^+/calf. Irrespective of which calf crop was employed, 358 g Na^+/calf were removed from the Na^+ pool. (4) The next year's Na^+ supply was the amount of Na^+ remaining in the aquatic compartment plus the soil-Na^+ deposited 10 years previously.

Although field population estimates were subject to error (LeResche and Rausch, 1974) and were not made by use of consistent methods, they served as trend counts. By determining whether successive observed and predicted values lead to an increase, decrease, or no change in population size, predicted and observed trends could be compared for agreement (Fig. 1). Thirteen of 14 trends agreed, indicating that observed population changes were consistent with a hypothesis of Na^+ limitation (binomial probability: $P < 0.001$). Other tests for comparing the model with the observed data, such as cross-correlation, were not used because factors other than Na^+ also may have influenced moose numbers.

There has been a general decline in numbers of moose since 1929, although the population has continued to oscillate in a manner consistent with Na^+ limitation, suggesting other factors may have influenced numbers. First, forest plant quality and quantity declined because the forest was in later seral stages resulting from control of forest fires and because moose feeding damaged the forest severely (Snyder and Janke, 1976). Second, a major forest fire in 1936 burned over 30% of the island and destroyed humus, which may have led to more rapid leaching of Na^+ from the soil. This large "pulse" of Na^+ would be lost to the aquatic compartment because it would not be assimilated fast enough before reaching deep water and Lake Superior, areas unsuitable

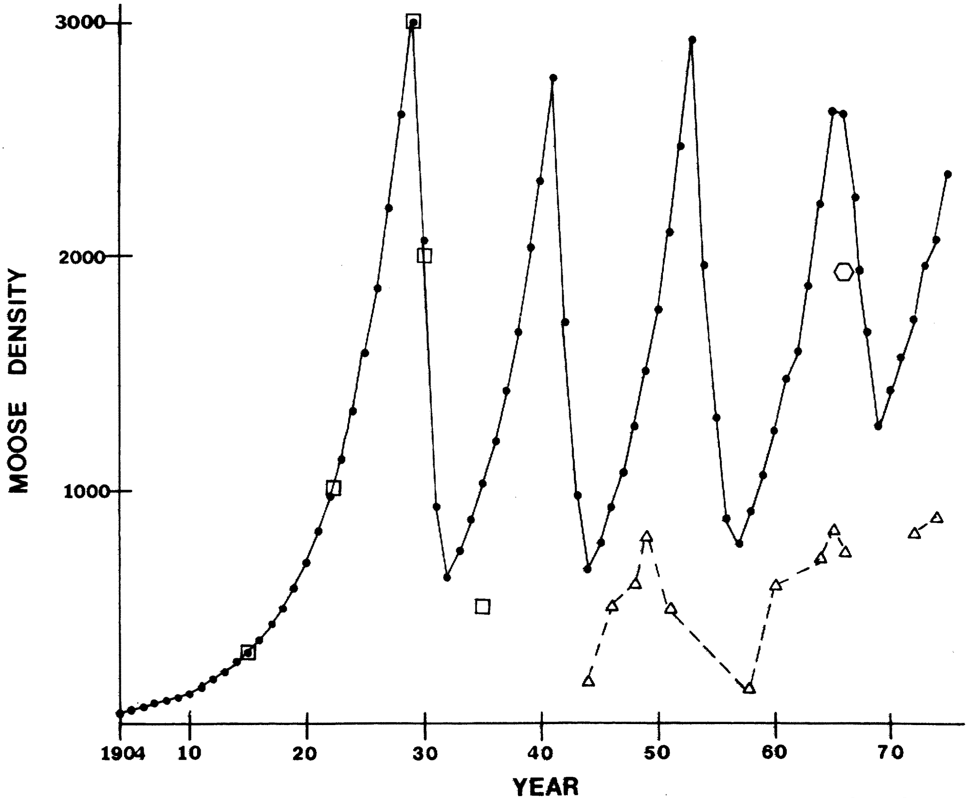

FIG. 1.—A plot of the changes in moose numbers at Isle Royale from 1904 to 1975, based upon a model of moose-Na^+ interactions (solid circle). All other points represent field estimates of the moose population size; open squares indicate subjective estimates (Murie, 1934; Hickie, 1936, ca. 1943), open triangles indicate aerial censuses (Krefting, 1951; Aldous and Krefting, 1946; Mech, 1966; Jordan and Wolfe, pers. comm.; R. Peterson, pers. comm.), and open hexagons were from pellet count estimates (Jordan and Wolfe, pers. comm.).

for moose feeding. Third, moose also may be trampling aquatic areas, increasing Na^+ mobility and losses in the aquatic compartment; ponds during the late 1920's and early 30's became mud holes from trampling (Murie, 1934; Brown, ca. 1935). Fourth, the advent of wolves (*Canis lupus*) since 1947 may have reduced moose numbers by predation (Mech, 1966, 1974).

The most important factor in the decline of moose numbers, however, may be destruction of aquatic plants by moose. During the moose die-off in the late 1920's and early 1930's, there was widespread destruction of aquatic areas; pond lilies (*Nuphar* and *Nymphea* sp.), the most abundant aquatic plants at Isle Royale in the early 1900's (Cooper, 1913*a*, 1913*b*, 1913*c*, 1928) and the highest in Na^+, 10,000 ppm (Botkin et al., 1973), were nearly extirpated (Murie, 1934; Brown, ca. 1935). During the same period, moose killed many trees by removing bark; bark has the highest Na^+ concentration, next to roots, in woody plants (Likens and Bormann, 1970). Again in the late 1940's and early 1950's, removal of bark increased before a die-off and, since 1965, removal of bark has increased in addition to increased use of aquatic plants. A decline in numbers of moose at Isle Royale once again may be approaching: already there is an increase in nonpredatory mortality and in the fraction of prime-aged adults in the diet of wolves (Wolfe, 1977; Peterson and Allen, 1974). Because observed changes in numbers of moose over time at Isle Royale are consistent with the Na^+ deficiency hypothesis, other herbivore population cycles—i.e., microtines, snowshoe hares (*Lepus americanus*), and spruce budworm (*Choristoneura occidentalis*) may result from Na^+ or other mineral deficiencies, as suggested by Hutchinson and Deevey (1949) and Schultz (1964, 1969). Trends in numbers of snowshoe hares and beavers at Isle Royale followed a pattern similar to that observed for moose (Krefting, 1963; Johnson, 1969; Shelton, 1966).

I thank T. W. Schoener, D. B. Botkin, J. B. Slade, and C. R. Taylor for critically reading early drafts of the paper. The work was supported by the Richmond Society, Harvard University, and the Harvard Society of Fellows.

LITERATURE CITED

ADAMS, C. C. 1909. An ecological survey of Isle Royale, Lake Superior. Michigan State Biol. Surv., Bd. Geol. Surv., 468 pp.

ALDOUS, S. E., AND L. W. KREFTING. 1946. The present status of moose on Isle Royale. Trans. N. Amer. Wildl. Conf., 11:296–308.

BELOVSKY, G. E., AND P. A. JORDAN. 1978. The time-energy budget of a moose. Theor. Population Biol., 14:76–104.

———. 1981. Sodium dynamics and adaptations of a moose population. J. Mamm., 62:613–621.

BOTKIN, D. B. ET AL. 1973. Sodium dynamics in a northern forest ecosystem. Proc. Natl. Acad. Sci., 70:2745–2748.

BROWN, C. A. [ca. 1935]. Ferns and flowering plants of Isle Royale, Michigan. Natl. Park Ser., 90 pp.

COOPER, W. S. 1913*a*. The climax forest of Isle Royale, Lake Superior, and its development. I. Contributions from the Hull Botanical Laboratory. Bot. Gaz., 55:1–44.

———. 1913*b*. The climax forest of Isle Royale, Lake Superior, and its development. II. Contributions from the Hull Botanical Laboratory. Bot. Gaz., 55:115–140.

———. 1913*c*. The climax forest of Isle Royale, Lake Superior, and its development. III. Contributions from the Hull Botanical Laboratory. Bot. Gaz., 55:189–235.

———. 1928. Seventeen years of successional change upon Isle Royale, Lake Superior. Ecology, 9:1–5.

HICKIE, P. F. 1936. Isle Royale moose studies. Trans. N. Amer. Wildl. Conf., 1:396–399.

———. [ca. 1943]. Michigan moose. Michigan Dept. Conserv., Game Div., 57 pp.

HUTCHINSON, G. E., AND E. S. DEEVEY. 1949. Ecological studies on populations. Surv. Biol. Progr., 1:325–359.

JOHNSON, W. J. 1969. Food habits of the Isle Royale red fox and population aspects of three of its principal prey species. Unpubl. Ph.D. dissert., Purdue Univ., West Lafayette, 293 pp.

JORDAN, P. A., D. B. BOTKIN, AND M. L. WOLFE. 1971. Biomass dynamics in a moose population. Ecology, 52:147–152.

KIMMINS, J. P. 1970. Cyclic fluctuations in herbivore populations in northern ecosystems: a general hypothesis. Unpubl. Ph.D. dissert., Yale Univ., New Haven, 248 pp.

KREFTING, L. W. 1951. What is the future of the Isle Royale moose herd? Trans. N. Amer. Wildl. Conf., 16:461–470.

———. 1963. The beaver of Isle Royale, Lake Superior. Minnesota Nat., 14:1–11.

LERESCHE, R. E., AND R. A. RAUSCH. 1974. Accuracy and precision of aerial moose censusing. J. Wildl. Mgmt., 38:175–182.

LINDEMAN, R. L. 1941. Seasonal food-cycle dynamics in a senescent lake. Amer. Midland Nat., 26:636–673.

LIKENS, G. E., AND F. H. BORMANN. 1970. Chemical analyses of plant tissues from the Hubbard Brook ecosystem in New Hampshire. Bull. Yale Univ. School Forestry, 79:1–25.

MECH, L. D. 1966. The wolves of Isle Royale. U.S. Natl. Park Fauna, 7:1–120.

———. 1974. A new profile for the wolf. Nat. Hist., 83(4):26–31.

MURIE, A. 1934. The moose of Isle Royale. Misc. Publ., Mus. Zool., Univ. Michigan, 25:1–44.

PETERSON, R. O., AND D. L. ALLEN. 1974. Snow conditions as a parameter in moose-wolf relationships. Le Naturaliste Canadien, 101:481–492.

SCHULTZ, A. M. 1964. The nutrient recovery hypothesis for Arctic microtine cycles. II. Ecosystem variables in relation to Arctic microtine cycles. Pp. 57–68, *in* Grazing in terrestrial and marine environments (D. J. Crisp, ed.). Blackwell Sci. Publ., Oxford, 322 pp.

———. 1969. A study of an ecosystem: the Arctic tundra. Pp. 77–93, *in* The ecosystem concept in natural resource management (G. Van Dyne, ed.). Acad. Press, New York, 383 pp.

SHELTON, P. C. 1966. Ecological studies of beavers, wolves, and moose in Isle Royale National Park, Michigan. Unpubl. Ph.D. dissert., Purdue Univ., West Lafayette, 331 pp.

SIMKIN, D. W. 1965. Reproduction and productivity of moose in northwestern Ontario. J. Wildl. Mgmt., 29:740–750.

SNYDER, J. D., AND R. A. JANKE. 1976. Impact of moose browsing on boreal-type forests of Isle Royale National Park. Amer. Midland Nat., 95:79–92.

WOLFE, M. L. 1977. Mortality patterns in the Isle Royale moose population. Amer. Midland Nat., 97:267–279.

GARY E. BELOVSKY, *School of Natural Resources, The University of Michigan, Ann Arbor, MI, 48109, and Department of Zoology, University of Washington, Seattle, WA, 98195.* *Submitted 23 February 1979. Accepted 1 July 1980.*