Proc. Nat. Acad. Sci. USA
Vol. 70, No. 10, pp. 2745-2748, October 1973

Sodium Dynamics in a Northern Ecosystem*

(moose/wolves/plants)

D. B. BOTKIN†, P. A. JORDAN†, A. S. DOMINSKI†, H. S. LOWENDORF†, AND G. E. HUTCHINSON‡

†School of Forestry and Environmental Studies, and ‡Department of Biology, Yale University, New Haven, Connecticut 06520

Contributed by G. E. Hutchinson, June 11, 1973

ABSTRACT **Analyses of terrestrial sources of sodium and estimates of the sodium requirement of moose (*Alces alces*) on Isle Royale, Lake Superior, suggest that availability of the element controls the moose population. The terrestrial vegetation is very poor in the element, but, as elsewhere, submerged and floating leaved water-plants are relatively rich. Consumption of such plants in summer would provide an adequate source, if the animal can store the element. The fairly high sodium contents of freshwater vegetation have been little appreciated. In general, sodium concentration in water-plants, unlike that of potassium, is not correlated with chloride but the latter is ordinarily in excess of the sodium, so that uptake of the latter implies an equivalent supply of NaCl.**

For mammals, sodium is a major constituent, comprising about 0.1% of their live body weight. In contrast, few terrestrial green plants are known to require sodium, and such plants need only trace amounts (1, 2). Except for halophytes, terrestrial green plants do not concentrate sodium; therefore one might expect that herbivores in regions of low soil sodium or far removed from marine aerosols might be limited by an inability to maintain a positive sodium balance. Only a few reports, however, have dealt with this important possibility (3–7).

In Isle Royale National Park, Lake Superior, a north temperate wilderness essentially undisturbed by man, wolves (*Canis lupus*) and moose (*Alces alces*) exist in apparent equilibrium, although both are relatively new to the island. The moose were first observed there about 65 years ago and the wolves about 25 years ago (8). Before the appearance of the wolves, the forage demands of this population exceeded the productive capacity of available vegetation, and mortality in the moose was widespread (9, 10).

Studies are being made of the flow of minerals and energy through the soil–vegetation–moose–wolf system at Isle Royale. Analyses have been made by atomic absorption spectrophotometry by use of special techniques to avoid contamination (11); values compare favorably with estimated standards (Dominski, A. S. & Lowendorf, H. S., unpublished). The data obtained indicate that the required amounts of sodium are not easily available to moose. Four other elements of key nutritional importance, N, K, Ca, and Mg, appear to be present in adequate concentrations in the vegetation eaten by moose, though the availability of phosphorus may be marginal. This study apparently provides the most complete inventory of sodium reported for a single ecosystem, including terrestrial and aquatic components in the same watershed (Table 1).

The estimated 1000–1200 population (prepartum) of moose (Jordan, P. A. & Wolfe, M. L., unpublished) within the 550-km² wilderness archipelago of Isle Royale is one of the most dense populations of moose known. The animals are productive and show no gross symptoms of sodium deficiency. For domestic ruminants, it is recommended that sodium comprise 0.1% or more (dry weight) of intake (12–14). Moose have a diet consisting of browse—current leaves and twigs of woody plants with occasional bark—taken year round and supplemented by some herbaceous plants in spring and some aquatic plants in mid-summer (15). Browse, comprising about 90% of annual intake by moose, has an average sodium concentration of 10 ppm at Isle Royale, 1% of the level recommended for livestock.

An estimate of the annual sodium requirement for the Isle Royale moose population was made by adding the amount of sodium associated with all new tissues grown during the year to that needed to balance all urine and feces losses. Data were derived from previous calculations of secondary production (16) and from sodium values given here; this rough calculation indicates the population requires 243 kg/year. Preliminary measurements of the annual production of available browse (just those species eaten by moose) in representative forests indicate this food source, at 10 ppm, contains 170 kg of sodium. This represents 70% of the population's need, but it is not all available because the bulk of all browse far exceeds the consumptive capacity of the moose population. While the moose have a marked impact on forest vegetation at Isle Royale, preliminary measurements (Belovsky, G. E., Jordan, P. A. & Botkin, D. B., unpublished) indicate they remove but 10–20% of annual browse production; this would provide but 7–14% of their estimated annual sodium requirement. The small but unknown portion of herbaceous plants added to the annual diet would not alter the sodium intake appreciably because concentrations in these plants are similar to those in woody plants.

The moose use natural mud licks on the island. However, long-term observations suggest that only some animals use the licks regularly. Furthermore, sodium concentrations in the mud and water at licks, averaging 24 ppm, are not so much greater than in terrestrial plants that one would assume these animals are being attracted by sodium.

During 8 weeks or so in summer, moose of this region feed extensively on aquatic macrophytes (17, 18). A series of analyses made on the common plants of the area (Table 1) show the sodium content of submerged and floating aquatics to be

* Isle Royale material contributed by the first four authors; additional information and interpretation contributed by G. E. Hutchinson.

TABLE 1. *Isle Royale sodium concentration (ppm)*

Material	Mean	SD	*n*	Mean	SD	*n*
	Leaves			Twigs		
A. Terrestrial woody plants						
Abies balsamea[a]	2.8	3.1	26			
Acer spicatum[b]	9.3	6.3	22	8.7	10.7	31
Alnus rugosa	13.7	15.7	5	28.1	35.5	2
Betula alleghaniensis[b]	19.5	4.5	5	24.0	20.3	5
Betula papyrifera[b]	15.8	17.1	31	10.7	9.8	45
Corylus cornuta[b]	4.4	6.2	8	9.1	3.9	7
Populus tremuloides[b]	7.0	4.9	14	6.4	5.2	20
Myrica gale	28.1	35.5	2	10.5	—	1
Sorbus americana[b]	7.5	4.6	35	5.6	4.9	49

Material	Mean	SD	*n*
	Leaves		
B. Aquatic vegetation			
1. Typically emergent or rooted along shore			
Calamagrostis canadensis	2	—	1
Calla palustris	1713	—	1
Carex aquatilis[c]	378	459	2
Carex rostrata[c]	246	290	4
Carex scabrata[c]	222	—	1
Carex sp.[c]	714	—	1
Eleocharis smallii	1440	—	1
Iris versicolor	28	13	3
Juncus gerardii	44	—	1
Menyanthes trifoliata	892	—	2
Polygonum sp.	575	63	2
Potentilla palustris	300	51	2
2. Typically submerged or floating			
Callitriche sp.	3532	2392	2
Chara sp.[c]	1023	717	5
Equisetum fluviatile[c]	1574	—	1
Myriophyllum tenellum	4750	—	1
Nuphar sp.	9375	—	1
Potamogeton gramineus[c]	6202	2536	6
Potamogeton richardsonii[c]	7227	—	1
Utricularia vulgaris[c]	8048	785	3

Material	Mean	SD	*n*
	Leaves		
C. Moose tissues			
Bone[d]	2983	1329	10
Liver[d]	712	—	1
Muscle[d]	791	—	1
Skin & Hair[d]	1573	—	1
Winter feces (from snow)[e]	112	15.1	5
Winter feces (in rectum)[e]	1013	—	1
Summer feces[f]	89	56.9	23
D. Substrate and water			
Rain[g]	0.2	0.4	7
Surface water[h]	1.6	1.4	15
Alluvium	9.4	3.6	3
Pond bottom, mainly inorganic	41.8	26.5	7
Pond bottom, mainly organic	302	335	4
Pond bottom, inorganic & organic	136	222	11
Mud lick H_2O	24.0	17.7	9
Mud lick soil	24.0	10.1	4

[a] Sample includes leaves and twigs; this species is taken extensively by the moose only in winter. [b] Important summer and winter food for moose. [c] Observed to be taken by moose at Isle Royale. [d] Live-weight basis; all tissues from one adult male autopsied in winter. [e] Dry-weight basis. [f] Dry-weight basis; collected within 24 hr, no precipitation intervening. [g] Six of seven were equivalent to that of glass-distilled water, one value was 1.1 ppm, which we suspect was due to contamination. [h] Collected from ponds, harbors, and streams.

about 500-fold and of emergent aquatics and hygrophytes about 50-fold greater than the terrestrial plants of the region. Enrichment of sodium in freshwater angiosperms is apparent in the analyses published by various workers (19–22) using modern techniques; none of these investigators appears to have realized the interest of their finding. The analyses from Isle Royale, however, are particularly startling because, while the mean sodium content of fully aquatic species is normal for freshwater vegetation, the content of the terrestrial plants is extremely low; Bowen (23) gives a mean of 0.12%, which suggests that more usually the enrichment in water plants is by a factor of five rather than 500.

The considerable body of data published by Riemer and Toth (19) for the water plants of New Jersey and their habitats

permit some statistical analysis. There is no indication of any significant correlation between the sodium and either the potassium or chloride contents of the plants, nor are the sodium contents significantly related to the sodium concentrations of the ambient water. The most important determinant of the sodium content of a plant appears to be its taxonomic identity. *Cabomba caroliniana* is always rich in the element, while the closely allied *Brasenia schreberi* is always much poorer. Similarly, different species of *Myriophyllum* appear to have characteristic sodium contents. Since the chlorine content of aquatic angiosperms is nearly always in stoichiometric excess of the sodium, any animal depending on water plants for the latter element would ordinarily obtain a more than sufficient amount of chloride. Parenthetically it may be noted that the chlorine contents both in Riemer and Toth's water plants and in the long series of terrestrial plants studied by Robinson, Steinkoenig, and Miller (24) are significantly correlated with the potassium contents.

Measurements of production of aquatic macrophytes at Isle Royale are inadequate. If net annual production is taken as 0.5% of the annual incoming radiation, or half the value reasonably expected for agricultural crops or forests (25), aquatic production would be 5×10^5 kg/km^2-year, essentially all of which is available to moose. The average concentration in the Isle Royale aquatics is 546 ppm dry weight for the hygrophytes and emergent species and 5216 ppm dry weight for the submerged and floating leaved species. Members of the former group tend to predominate, a fact that may reflect selective influence of moose. The lowest reasonable minimum estimate of the sodium content might be taken as 500 ppm. The total area of shallow water in which aquatic plants grow at Isle Royale was roughly estimated from maps as 30 km^2. Since the production given above as 5×10^5 kg/km^2-year may be an overestimate, the area colonized is here taken as 10 km^2 giving an annual production of 5×10^6 kg. This will contain, at a concentration of 500 ppm, 2500 kg of sodium, some 10-times the calculated requirement of the moose herd.

Organic matter in the pond bottoms contains much more sodium than does the water with which it is in contact, or for that matter the mud-lick soil or the ordinary alluvial soil of the area. This is in line with findings in other lakes (26, 27) that so-called exchangeable sodium is associated with the brown organic coloring matter that can be extracted from sediments by ammonium acetate; other common cations are not so associated. It is suggested that such sediments serve as a major reservoir of sodium that can be taken up and concentrated even in a system where sodium is very low. It is, however, noteworthy that *Utricularia*, which almost certainly gets all its minerals from the ambient water, has the second highest sodium concentration of the water plants of Table 1. Assuming 10% dry matter and a sodium content in the water of 1.8 ppm, the concentration factor must be around 500.

Field observations of moose feeding indicate the animals consume primarily submerged plants (17) which, as a group, have higher than average sodium concentrations. While their annual requirement can thus be met, moose would require a mechanism for retaining sodium during 10 months, since the period of aquatic feeding is but 2 months. Storage of sodium is not generally discussed by mammalian physiologists. It may be accomplished by ion shifts within the rumen–saliva system or by storage and withdrawal in bone. Preliminary data of the Na^+/K^+ ratios in rumen fluid from Isle Royale moose indicate that these moose probably substitute potassium for sodium in parotid secretion, a response found in sheep during sodium deprivation (28).

We thank members of the staff of Isle Royale National Park, particularly H. P. Beattie, Superintendant, and F. M. Deckert, District Ranger, for assistance in field work. We are grateful for suggestions provided by Gary E. Belovsky and H. C. Skinner. This investigation was supported by the National Science Foundation Grant GB 29566.

1. Black, C. A. (1968) *Soil Plant Relationships* (John Wiley & Sons, New York).
2. Brownell, P. F. & Crossland, C. J. (1972) "The requirement for sodium as a micronutrient by species having the C_4 dicarboxylic photosynthetic pathway," *Plant Physiol.* **49**, 794–797.
3. Hutchinson, G. E. & Deevey, E. S. (1949) "Ecological studies on populations," *Surv. Biol. Progr.* **1**, 325–359.
4. Denton, D. A., Goding, J. R., Sabina, J. R. & Wright, R. D. (1961) in *Salinity Problems in the Arid Zones, Proc. Teheran Symp.* (UNESCO, Paris), pp. 193–198.
5. Aumann, G. D. & Emlen, J. T. (1965) "Relation of population density to sodium availability and sodium selection by microtine rodents," *Nature* **208**, 198–199.
6. Scoggins, B. A., Blair-West, J. R., Coghlan, J. P., Denton, E. A., Myers, K., Nelson, J. F., Orchard, E. & Wright, R. D. (1972) "Physiological and morphological responses of mammals to changes in their sodium status," in *Mem. Soc. Endocrinol.* **18**, 577–600.
7. Wier, J. S. (1972) "Spatial distribution of elephants in an African national park in relation to environmental sodium," *Oikos* **23**, 1–13.
8. Mech, L. D. (1966) *The Wolves of Isle Royale, U.S. Nat. Park Fauna* 7. 210 pp.
9. Murie, A. (1934) "The moose of Isle Royale," *Univ. Mich. Mus. Zool. Misc. Publ.* **25**, 1–44.
10. Krefting, L. W. (1951) "What is the future of the Isle Royale moose herd?" *Trans. N. Amer. Wildl. Conf.* **16**, 461–470.
11. Likens, G. E. & Bormann, F. H. (1970) "Chemical analysis of plant tissues from the Hubbard Brook ecosystem in New Hampshire," *Yale Univ. Sch. Forest. Bull.* **79**, 1–25.
12. Hafez, E. S. E. & Dyer, I. A. (1969) *Animal Growth and Nutrition* (Lea and Febiger, Philadelphia).
13. National Research Council, Subcommittee on Beef Cattle Nutrition (1970) "Nutritional requirements of beef cattle," *Nat. Acad. Sci.* (Washington, D.C.), rev. 4th ed.
14. National Research Council, Subcommittee on Sheep Nutrition (1968) "Nutrient requirements of sheep," *Nat. Acad. Sci.* (Washington, D.C.), Pub. 1963, rev. 4th ed.
15. Peterson, R. L. (1955) *North American Moose* (Univ. of Toronto Press, Toronto).
16. Jordan, P. A., Botkin, D. B. & Wolfe, M. L. (1971) "Biomass dynamics in a moose population," *Ecology* **52**, 147–152.
17. DeVos, A. (1958) "Summer observations on moose in Ontario," *J. Mammal.* **39**, 128–139.
18. Cobus, M. W. (1972) *Moose* (Alces alces) *and campers in Sibley Provincial Park: A study of wildlife aesthetics*, M.S. thesis (unpubl.) Univ. Guelph.
19. Riemer, D. N. & Toth, S. J. (1968) "A survey of the chemical composition of aquatic plants in New Jersey," *New Jersey Agr. Exp. Stat. Bul.* **820**, 14 pp.
20. Boyd, C. (1970) "Chemical analyses of some vascular aquatic plants," *Arch. Hydrobiol.* **67**, 78–85.
21. Lawrence, J. M. (1971) Final report on OWRR Project B-010-ALA. *Dynamics of Chemical and Physical Characteristics of Water, Bottom Muds, and Aquatic Life in a Large Impoundment on a River* (Auburn University Agricultural Experiment Station).
22. Lancaster, R. J., Coup, M. R. & Hughes, J. W. (1971) "Toxicity of arsenic present in lake weed," *N. Z. Vet. J.* **19**, 141–145.
23. Bowen, H. J. M. (1966) *Trace Elements in Biochemistry* (Academic Press, London and New York).

24. Robinson, W. O., Steinkoenig, L. A. & Miller, G. F. (1917) The relation of some of the rarer elements in soils and plants, *U.S. Dept. Agr. Bull. 600.*

25. Helmers, H. (1964) "An evaluation of the photosynthetic efficiency of forests," *Quart. Rev. Biol.* **39**, 249-259.

26. Cowgill, U. M. & Hutchinson, G. E. (1966) "A general account of the basin and the chemistry and mineralogy of the sediment cores," in *The History of Laguna di Petenxil. Mem. Conn. Acad. Arts Sci. Lett.* **17**, 7-61.

27. Cowgill, U. M. & Hutchinson, G. E. (1970) "Chemistry and mineralogy of the sediments," in *Ianula: An Account of the History and Development of the Lago di Monterosi, Latium, Italy. Trans. Amer. Phil. Soc.* **60**, pt. 4, 37-101.

28. Denton, D. A. (1957) "The study of sheep with permanent unilateral parotid fistulae," *Quart. J. Exp. Physiol.* **42**, 72-95.