SODIUM AS A CRITICAL NUTRIENT FOR THE MOOSE OF ISLE ROYALE

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Abstract: We have been tracing the flow and storage of minerals within the soil-vegetation-moose-wolf system at Isle Royale, Michigan, and have found that neither the sources of sodium for moose nor the animals' means for conserving this element are readily apparent. Browse, which comprises 85% or more of their diet, has an average concentration of 10 ppm (0.001%) sodium: it is recommended that diets of domestic reminants include 0.05% to 0.25% sodium. Our data indicate that moose on low-sodium intake are highly efficient in preventing sodium loss through urine but may lose up to 350 mg/day through feces. Our calculated annual sodium budget for a moose, based on data from Isle Royale, indicates that browse supplies but 6% of the annual requirement. Mud licks are used year-round by at least some moose, but water and soil from these licks, averaging 24 ppm sodium, do not appear capable of supplying total requirements. From June through August, moose feed on aquatic plants. Emergent aquatics average some 50 times more sodium, and submerged and floating aquatic macrophytes some 500 times more than found in terrestrial vegetation. We estimate that aquatics supply 88% of these animals' annual sodium. If moose depend so on aquatics, then they must store the element to offset negative balance during the 9

to 10 months that aquatics are not available. We are exploring two possible mechanisms: mineralized storage in hard tissue and substitution of potassium for sodium in saliva, hence in rumen fluid. Preliminary evidence indicates the latter strategy is employed.

The Isle Royale population is now apparently more limited by nutrition than by predation. While these moose have demonstrated behaviourally a drive for some special nutrient factor which we believe is sodium, we have not yet determined whether sodium is a limiting factor. However, current heavy grazing in aquatic habitats, as it threatens to reduce aquatic productivity, will also reduce the primary source of sodium for moose.

For mammals, sodium is an essential macronutrient comprising approximately 0.1% of live body weight (0.3% dry wt). Among terrestrial green plants, however, few are known to require sodium, and in those that do, the need is for but trace amounts. Thus, except for halophytes, terrestrial green plants do not tend to concentrate sodium (Black 1968). In regions lying far from the influence of marine aerosols and having a climate that leaches sodium from the soil, as in mid-continental boreal forests, there should be little sodium available for herbivores. In these regions, including the majority of the goegraphical distribution of moose, one might expect that mammalian herbivores could be limited or excluded due to low availability of sodium. Despite the intriguing implications, ecologists and physiologists have not directed much attention to this possibility: there exist but a few published reports of which the following are a good representation: Hutchinson and Deevey (1949), Denton et al. (1961), Aumann and Emlen (1965), Scoggins et al. (1970), and Wier (1972).

We have been tracing the flow of energy and matter in the soil-vegetation-moose-wolf trophic chain at Isle Royale National Park, Michigan. Our study is described briefly elsewhere along with some background on the study area (Belovsky et al., this volume). Early in our study of nutrient levels, we discovered that sodium concentration in the woody plants eaten by moose is very low -- so low that we doubted the animals could meet their minimum requirements from browse alone. It appeared that to survive in this habitat, moose need specialized feeding strategies and unusual physiological adaptations for finding, storing, and conserving sodium.

To establish whether a population is actually limited by insufficient sodium, one might use the following criteria. Assume the population is at that equilibrium level which results from interactions of all environmental factors other than sodium. If the animals at this density cannot obtain enough of the mineral to maintain the vigor and reproduction efficiency characteristic of their equilibrium state, then sodium is limiting. Were moose at Isle Royale suffering a sodium shortage, one might expect the animals to show deficiency symptoms: "..poor growth, rough coat and general unthriftiness, as well as poor reproduction.." (Smith, Jones and Hunt 1972:1008). Lactational reduction and loss of weight and appetite are cited as symptoms in dairy cows by Cuthbertson (1969). None of these symptoms has been recorded at Isle Royale during the past 14 years' study (from 1959 by Purdue investigators and from 1971 by our group). On the other hand, we doubt that sodium deficiency in a free-living moose population could be detected through deficiency symptoms. Rather, what one might see are population changes such as lower reproduction, poorer survival, or declining numbers, none of which could be causally attributed to a specific agent. In general, it may not be practical when analyzing free-living populations to depend on deficiency symptoms as criteria of mineral shortage. We attempt to show here that other types of observations can be employed successfully for this analysis.

If sodium availability is low in relation to physiological demands, animals may exhibit special feeding strategies. This assumes that sodium is locally concentrated and that these concentrated sources are recognizable and usable by the animals. If limited in extent, the sources may influence spacing within the population and may lead to competition for access.

In our initial work on the sodium question, we are looking at both the adaptations in moose and at the evidence that sodium is becoming increasingly critical to the Isle Royale population. Without benefit of captive animals, extensive collections, or the ability to manipulate populations and their food supplies, we are reconstructing the sodium picture from natural history observations and from our extensive measurements of sodium concentrations in the ecosystem. Two publications are currently planned (Botkin et al. 1973 and Jordan et al. in prep A).

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METHODS

In the survey of sodium levels, fresh materials -- leaves, stems, urine, feces, soil, water and snow -- were collected using special precautions to prevent contamination with sodium from external sources, particularly from our hands. We also collected fresh tissues and digestive-tract contents from one male moose necropsied in February 1972. Sampling intensity and format varied. Browse values are from material collected during a systematic pilot study in 1971 at the west end of the island (Jordan et al. in prep. B); other materials reported here were collected under bias-free conditions, but not with systematic randomization. We are currently analysing vegetation and soil specimens from a systematic survey covering the whole of Isle Royale. All plant, soil, and digestive-tract material was oven dried. Materials not to be dried were stored frozen. Analysis for sodium was by atomic-absorption spectrophotometry, a technique which provides good accuracy down to 1 ppm. Laboratory procedures and equipment used were specially modified

Table 1. Sodium Values in Various Components of the Isle Royale Ecosystem (ppm).

A. Terrestrial Woody Plants

	LEAVES			TWIGS		
MATERIAL	MEAN	S. D.	N.	MEAN	S.D.	N.
Abies balsamea[a]	2.8	3.1	26			
Acer spicatum[b]	9.3	6.3	22	8.7	10.7	31
Alnus rucosa	13.7	15.7	5	28.1	35.5	2
Betula alleghaniensis[b]	19.5	4.5	5	24.0	20.3	5
Betula papvrifera	15.8	17.1	31	10.7	9.8	45
Corylus cornuta[b]	4.4	6.2	8	9.1	3.9	7
Populus tremuloidies	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

B. Aquatic Vegetation

1. Typically emergent or rooted along shore.

	MEAN	S.D.	N.
Calamagrostis canadensis	2	---	1
Calla palostris	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

Table 1. (continued)

2. Typically submerged or floating

MATERIAL	MEAN	S.D.	N.
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	---	3
Utricularia vulgaris[c]	8048	785	3
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

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a) Sample includes leaves and twigs; this species is taken extensively by the moose only in winter.

Table 1. (continued)

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 hours, no precipitation intervening.

g) 6 of 7 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, harbours and streams.

to avoid external contamination. Details of the method and the testing of standards, which demonstrated the reliability of our techniques, are described elsewhere (Lowendorf and Dominski ms.).

Methods for collecting other data, such as numbers of moose, feeding rates, seasonal food habits, and production of browse will be described in separate reports.

RESULTS AND DISCUSSION

Sodium Levels in Sources Available to Moose

Sodium values for several woody species browsed by moose, including those which comprise much of their annual forage, are shown in Table 1. Summer browse comprises primarily the leaves of certain deciduous species, while winter browse includes the stems (mainly but not exclusively current-growth) of deciduous species plus, in conifers, foliage and stems of whatever age stems are foliated. Bark removed from the bole of tree-sized plants is technically browse, but we treat it separately in this discussion. From our determination of food habits in moose and from our species sodium values, we estimate the average sodium concentration in browse to be about 10 ppm (dry-wt) in all seasons.

It is recommended for the feeding of livestock that sodium constitute from 0.05% to 0.15% of the diet (NRC Subcomm. Beef

Cattle 1970, and Sheep 1968, Hafez and Dyer 1969), and in lactating cows as much as 0.25% (Cuthbertson 1969). Moose are primarily browsers, their annual diet consisting of some 85% to 90% woody plants. If browse was their only food, their sodium intake would be two orders of magnitude lower (10 ppm = 0.001%) than the levels recommended for livestock. We do not imply that livestock recommendations apply directly to moose, but it seems unlikely this wild ruminant survives with a sodium intake 100 times less than what is recommended for good health in domestic ruminants. It is more likely that moose are finding additional sources of sodium. Our calculations, described below (Table 2), indicate that browse provides only 6% of the minimum annual sodium requirement for moose at Isle Royale.

In spring the moose include some forbs in their diet, and in mid-summer as much as one-quarter of their intake is aquatic plants. Moose in some circumstances eat bark from trees of up to pole size as well as from the upper limbs of any size Populus felled by beavers. Barking is most prevalent in spring (Murie 1934). Moose during winter probably eat small quantities of arborous lichens which occur on conifers. Finally, some moose at Isle Royale regularly drink at sites we call "mud licks", and some have been observed to eat soil at these sites.

Forbs were found to have sodium concentrations similar to browse, so we discount their being sought as a source of sodium. Bark has not been analyzed by us, but Likens and Bormann (1970), analyzing woody species from a site in New Hampshire that is climatically similar to Isle Royale, found sodium in trunk bark to be 3 to 4 times higher than in leaves. Four species examined by them occur at Isle Royale and are important as browse; these did not include Populus tremuloides, our most commonly barked species. Bark eating by our moose, particularly on Populus and Alnus rugosa, is on the increase, but its extent would not indicate bark is presently an important source of sodium in trees: roots, according to Likens and Bormann (op cit), have the highest sodium levels of all tissues in the plant -- up to 13 times that in leaves. We are now examining roots of upturned trees, the incidence of which is unusually high on wind-swept Isle Royale, for signs of moose browsing. We will also analyze samples of roots available to moose. Lichens have not yet been analyzed by us; however, even were they higher in sodium than browse, it is doubtful they would be an important source to the moose because of their relatively low availability.

For a period of approximately 60 to 90 days in mid-summer, aquatic vegetation comprises some 25% (dry-wt) of the intake by moose in our study area (Belovsky et al. in prep.). The sodium concentration in aquatic plants, when compared with terrestrial plants of the same drainage, was some 50 times greater in emergent species and some 500 times greater in submerged and floating species (Table 1). These findings are corroborated by the few measurements of sodium in aquatic macrophytes reported for elsewhere in North America (Riemer and Toth 1968, Boyd 1970, Lawrence 1971). None of these reports, however, documents or suggests that so great a difference can exist between concentrations in terrestrial and aquatic plants within the same drainage. The physiological implication of aquatic plants concentrating sodium is not understood. We believe that the moose of Isle Royale, and probably moose wherever aquatics are eaten, depend in large part upon this source to meet their annual requirement for sodium.

We have encountered several actively used mud licks; these are visited regularly by moose, most frequently in summer. We observe moose to be strongly motivated to drink at the licks, based on their unusual persistence and boldness in approaching while humans are present. At the licks, the animals appear to select carefully among puddles of muddy water and to consume what seem to be large amounts of water. The licks we have examined appear to be small springs trampled into a muddy condition by the animals. On one occasion we saw calves eating soil from an eroded bank above a lick where their cow was drinking: the bank appeared to have had considerable soil removed from it in the past. Calves show little interest in the muddy water which is sought by adults; if a calf does drink at a lick it most likely takes water from a nearby stream.

Limited evidence indicates that heaviest use of licks occurs where aquatics are not locally available. Overall, we have not found enough mud licks around the island to conclude that all moose make frequent use of them. One lick was observed in use during mid-winter. Were winter usage common, however, we should certainly have been aware of it. Researchers from Purdue University spend some 7 weeks on the island each winter making aerial surveys over the snow. If moose are frequenting localized licks, the fact would be easily identified from track patterns seen by the aerial observers.

It should be noted that sodium retention decreases as water intake increases, because with more water to expel, the kidney becomes less efficient in conserving ions. Thus a moose with a large sodium deficit is unlikely to overcome it simply by drinking enough of that mud-lick water which has only 25-50 ppm sodium, even if the animal can handle the volume of water. In order to meet a deficit of 232 g/yr, minus the 13 g obtained from terrestrial forage (Table 2), a moose would have to acquire 0.6g/day of sodium which, from water with 24 ppm, would require 24 l/day. This water would be additional to that taken in with forage -- in winter 5 to 7 l/day and in summer 22+ l/day. Most water intake will be disposed through the kidney, so sodium conservation, particularly in summer, would be correspondingly limited. Thus mud-lick water alone would not appear to be adequate.

Sodium in Moose

Sodium concentrations in bone, liver, muscle, and integument from the adult male autopsied in winter (Table 1) fall within the wide range of those reported for mammals in general (Spector 1956, Table 55). Rumen content was 2065 ppm (dry wt). Fecal pellets collected from the rectum area of the intestine had 1013 ppm sodium, while five recently deposited pellet groups collected from the snow in the same period and vicinity showed an average of 112 ppm. We judge that pellets being dropped on snow would have lost little sodium before freezing: air temperatures during that period were never above -7°C and usually were well below. Consequently we used the lower value for calculating fecal sodium losses. The much higher value in the one rectal sample remains unexplained. While sodium is taken up by the intestinal tract, it seems unreasonable that its concentration can be reduced by an order of magnitude as the well-formed pellet passes along the last few centimeters of the tract.

We observed a moose urinate in the snow and we immediately collected all frozen material showing yellow coloration. The urine had not penetrated down as far as the ground. The diluted specimen had a sodium concentration of 0.33 ppm, while a control sample of snow had 0.13 ppm. We arbitrarily assigned a dilution of five-fold, which indicates urine sodium was 1.1 ppm. The single sample does not permit a precise estimate, but it does suggest that conservation of sodium by the moose kidney during negative sodium balance in winter is highly efficient. We have not found such low values reported elsewhere. Total sodium in the complete urine deposit was 0.8 mg.

Annual Sodium Budget

To estimate whether moose at Isle Royale are close to or actually faced with a negative sodium balance, we approximated a sodium budget for an individual moose (Table 2). Our subject moose is a hypothetical adult-equivalent animal assigned a weight, 358 kg, but not an age, sex, or reproductive condition. If this moose is to avoid a negative balance, long-term sodium outflow cannot exceed inputs. We calculated the budget on an annual basis, but we also discuss how a balance is maintained from one season of the year to another. Data for this budget are from rates of feeding and defecation measured at Isle Royale, from our sodium measurements in forage, water, feces, urine, and digestive-tract contents, and from previous estimates of biomass and growth in the population (Jordan, Botkin and Wolfe 1971). Where necessary, input was supplemented from literature sources. This first approximation of a budget will be improved as data from current studies are added.

Table 2. Estimated Annual Sodium Budget for a Hypothetical Adult Moose Based on Data from Isle Royale.

	Sodium (g)
Input	
Food	
Terrestrials	13
Aquatics	199
Others	
Water from Licks	20
Total	232
Requirements	
Replacements	
Summer Feces	10
Non-summer Feces	96
Urine	19
New Tissues	107
Total	232
Balance	0

Sodium demand is of two types; that lost in excrement, to be replaced on a regular basis, and that required for growth of new tissues. Our evidence shows that excremental losses are mainly through feces, and, with fecal sodium level relatively constant through the year (Table 1), outflow of the element is closely proportional to the passage of undigested food. New tissues include those annually replaced, such as hair, epithelium, and antlers, and those accumulated as body growth. Sodium in growth includes that accumulated within fetuses, amniotic fluid, and milk. Amount of growth assigned to the hypothetical individual is equal to the sum of all growth in the population divided by the number of adult equivalents: the latter is determined by dividing the population biomass (Jordan et al. op cit) by the weight of the adult equivalent. Since this budget estimates only an average need, minimum requirements for some classes such as the lactating cow are underestimated.

Intake of sodium in forage assumes moose eat 7 kg browse/day during a 241-day non-summer period and 4.8 kg forage/day, including 0.6 kg aquatic vegetation, during summer (Belovsky et al. in prep.). We do not attempt estimating how much sodium becomes available through digestion; net intake is determined simply by subtracting fecal sodium from forage sodium.

While usage of mud-lick water apparently varies a great deal among individual animals, we assign an approximate average usage to our hypothetical adult -- 2.25 l. of mud-lick water per day. This rate is based on water intake in domestic and wild ruminants and on the arbitrary assumption that one-quarter of all the animal's water is from licks. If lick waters contain 25 ppm sodium, the animal acquires 20 g of sodium per year.

The balance sheet (Table 2) suggests that moose at Isle Royale have no net surplus of sodium over the year. That our estimates of input and requirements appear to be equal was a chance occurrence; we do not claim precision necessary for balancing sodium budgets within 1 g or even within 10. Although our computations are rough, we believe they indicate that moose at Isle Royale may be compelled to expend considerable extra time and energy to maintain their sodium balance. Within the population the lactating cow, with its higher requirement, should be the first to experience effects of sodium shortage. As such, this animal, whose budget we are now estimating, will indicate the threshold of availability at which sodium shortage begins to affect population dynamics.

Storage of Sodium by Moose

If aquatic plants provide most of a moose's sodium, then, according to the annual budget, in order to overcome the next 9 to 10 months' negative balance, the animal needs a strategy for storing some of the summer's intake. Sodium in the body can be efficiently protected from being lost through urine; the ecological implications of this are discussed by Denton

(1965), Bott et al. (1964), and Scoggins et al. (1970). However, fecal losses cannot be similarly reduced. Mammalian physiologists have not generally discussed the possibility that, as a strategy against periods of negative balance, animals accumulate excess sodium. Because supra-normal concentrations in body fluids are toxic, accumulation of sodium is generally regarded as a detrimental rather than a beneficial adaptation.

We have been exploring two possible storage strategies: mineralization of extra sodium in hard tissue for release on demand, i.e., as with calcium and phosphorus; and substitution of potassium for sodium in saliva by the parotid gland so that sodium in rumen fluid can be expended as from a reserve. If there is seasonal storage and release of sodium in hard tissue, then observed concentrations in bone should vary correspondingly: we are currently analyzing bones and teeth to test this.

Denton (1957) showed that when sheep are kept on sodium-deficient rations for a number of weeks, they do not suffer reduction of body-fluid sodium. He attributed this to conservation of sodium by the kidney, and more importantly, to substitution of potassium for sodium in parotid saliva. Because sodium is normally the principal action in saliva, a great deal is drawn from the circulatory system for salivary production, the daily amount of which equals or exceeds the animals' blood via intestinal reabsorption against a concentration gradient, this recovery brings tract-contents concentration down only to around 100 ppm (dry-wt basis). Thus, even in deprivation, ruminants apparently lose sodium through feces at about 100 ppm. However, if these losses can be compensated for by potassium substitution in rumen fluid, then the sodium level in circulatory fluids, maintenance of which is crucial to well-being, is protected. Such protection lasts until the substitutable sodium in the rumen is used up. Otherwise, when sodium intake again rises, the substitution is reversed, and sodium is restored in the rumen fluid.

If moose are similar to sheep with respect to substituting potassium, then, extrapolating from Denton's sheep on a live-weight basis, we calculate that our adult equivalent moose has 274 g sodium to contribute annually from its rumen pool. This 274 g exceeds what we estimate is our moose's total 12-month requirement (Table 2), thus suggesting that Isle Royale moose would maintain year-round balance using this strategy. We analyzed rumen contents from the adult male autopsied in winter. Adjusting for sodium and potassium contributed by forage, we calculated that the animal's salivary Na^+/K^+ ratio had been 0.45. This value is intermediate between Denton's 18.0 for those sheep which were on an adequate intake and 0.055 for those on low sodium for 14 days. It is consistent with the substitution hypothesis and has prompted us to further study.

Our balance figures (Table 2) suggest that during summer Isle Royale moose may not be replacing their full capacity for sodium. We estimated that the hypothetical moose obtains a total of 210 g during summer, 199 of which is from aquatics; on the other hand it may have a capacity to store 274 g. If this is the case, then the sodium question is more one of ecological availability than of physiological capacity.

Were moose physiologically nonadapted to withstand the sodium shortages imposed by the fundamental environment, i.e., that set of factors which underlies the fundamental niche, then the species ought not to be found at all in such habitats. The fact of their presence serves to corroborate our calculation that they are adapted to withstand prolonged sodium shortage -- so long as their deficits can be made up during some season of the year. A downward trend in available sodium may lead then to loss of the opportunity of each individual to restore its annual deficit. The consequences of this should be a population decline.

The Role of Sodium Shortage in Limiting Numbers of Moose

It has been stated elsewhere that the Isle Royale moose herd is held from further growth by a combination of food limitation and wolf predation (Mech 1966, Shelton 1966, Jordan et al., 1967). There has been an increase in the population since the mid 1960's (Jordan and Wolfe in prep.), during which period we have observed a concommitant increase in foraging pressure by moose on the vegetation. This pressure will eventually reduce productivity in those plant species most preferred by moose. Peterson and Allen (unpubl. reports, Purdue Univ.), studying the wolves, have not found a corresponding increase in wolf numbers during the same period. They find that, compared to the period 1959-1966 when Mech (1966), Shelton (1966) and Jordan et al., (1967) were working at Isle Royale with D.L. Allen, wolves now require less effort to kill moose and that more moose are dying from non-predatory causes. Wolfe (unpubl. reports, Purdue Univ.) witnessed a transition period during 1967-70.

Our investigations are not to the point where we can specify the role of sodium in population changes at Isle Royale. The following observations, however, in light of the measurements discussed above, permit tentative conclusions about its importance. By the early 1930's, moose at Isle Royale, having successfully established themselves some 25 years earlier in the absence of predators, reached the peak of a population eruption. Die-offs followed during the mid-1930's, and were attributed to gross shortage of forage during winter (Hickie n. d.) -- suggesting that the animals could not maintain a positive energy balance. At the same time, Murie (1934) and Brown (n. d.) provide records suggesting that shortage of some mineral such as sodium was affecting population processes: aquatic vegetation, mud-licks and tree bark were being used heavily.

Impact of moose on ponds was causing severe destruction of these habitats (Murie 1934), and leading to the virtual disappearance of several aquatic species. We have examined a series of photographs taken by Dr. Frank R. Oastler during the 1930's. These show aquatic sites whose substrate was churned up and whose shoreline vegetation was denuded more than at any pond we have observed recently -- even where we consider usage to be heavy. The extent to which mud licks were being used in 1929, according to Murie's (1934) description, appears much greater than at present. He reports seeing as many as 20 animals together at a lick. Murie (1934) and Brown (n. d.) recorded that moose commonly stripped bark from _Populus tremuloides_ as well as from _Sorbus americana_ and occasionally from _Abies balsamea_. Even today virtually all medium-sized, mature _Populus_ show scars between 1 and 2 or 3 m high -- sign, we believe, of past barking by moose.

From 1963 through 1973, Jordan made ecological observations on the island as well as communicating with others making similar records. Intensity of summer aquatic feeding has increased: whereas in the mid-1960's moose generally started feeding in ponds in mid-June and stopped in late July or early August, now they start somewhat earlier and continue until late August or early September. In the mid-1960's at the end of each aquatic feeding season, generally there remained large quantities of submerged and floating plants ungrazed. In recent years, however, ponds appear virtually cleared of all such vegetation by September. Likewise, mud-lick usage was essentially not recorded during the mid-1960's, whereas it is recorded at a variety of sites today: our data for this comparison, however, are not sufficient yet for a firm conclusion. Usage of bark during the past decade has unquestionably increased; our first substantial record was in May 1970 when, in various sites within the widespread 1936 burn, we noted barking on pole-sized _Populus tremuloides_. During the past 3 or 4 years, moose have been using the bark of _Alnus rugosa_ also. Use of bark in 1973 is probably much less than during the late 1920's and early 1930's; the interesting point is the emergence of a definite trend.

We believe that current impact of moose on aquatic sites will lead to lower primary productivity and perhaps will interfere with sodium cycling. Besides destroying plants, moose greatly disturb the substrate by their trampling. Organic sediments in ponds contain up to 300 ppm sodium (Table 1) which we suspect is a major source for plants (Botkin et al. ms.). If the sediment sodium were not available, aquatic plants would have as their source only the pond water which contains just 2 ppm. If the trampling of moose releases more sodium from the sediments than is being replaced, then the pool of sodium available to aquatics is reduced. We do not know whether this would lead to lower total production or lower sodium concentrations in plant tissues.

During the 1930's, and perhaps now as well, limitation of the moose population seemed more attributable to the supply of food than to any other factor. Heavy usage on all forms of forage in all seasons provides strong, indirect evidence for this. Today, as preferred plants are heavily exploited, their subsequent productivity will be reduced, i.e., the annual supply of nutritious food will progressively decline. It is more difficult to establish whether there is but one nutritional component accounting for undernutrition or several. The issue has been discussed elsewhere in terms of energy vs. protein (cf. Bell 1971). The pattern of year-round heavy exploitation of preferred plants at Isle Royale suggests that shortage of either or both energy and protein may be operative, perhaps alternatively between seasons or between years. If the moose population is presently prevented from further growth solely by a sodium shortage, then we would not expect to see the extensive competition for browse which is apparently now occurring. Perhaps nutritional resources for moose at Isle

Royale exist in a well-balanced array so that with over-exploitation, scarcity develops uniformly among all components. Obviously, more study, including experiments, is needed.

Meanwhile, we do observe that, regardless of the relative importance of sodium, the apparent drive in moose for sodium may of itself act to set future environmental capacity for the island's population. Assume that sodium is the primary factor stimulating moose to seek aquatics, and assume that productivity of aquatic habitats declines more under moose impact than does the base for productivity of any other resource. Then, during a period of general overexploitation, aquatics, the primary source of sodium, will be the first resource to fail. With failure of aquatics, there would result a nutritional crisis for moose in which sodium becomes the primary limiting factor.

CONCLUSIONS

In exploring the overall flux of materials and energy in an undisturbed terrestrial ecosystem, in combination with natural-history observations, we have generated intriguing questions about physiological adaptations in moose and the ecological status of a mineral nutritionally essential to that herbivore. Rarely is it shown that growth of an animal population is limited solely by the supply of a single chemical element. Nevertheless, each possible limiting factor should be investigated in depth. Our study so far has shown that availability of sodium is potentially a key factor in setting the upper limit on Isle Royale's moose population.

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