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SODIUM DYNAMICS AND ADAPTATIONS OF A MOOSE POPULATION

GARY E. BELOVSKY AND PETER A. JORDAN

ABSTRACT.—A “balance sheet” for sodium losses and intakes was developed for moose (*Alces alces*) at Isle Royale National Park, Michigan. This technique emphasized potential times of the year and avenues of sodium loss that might be limiting. A mechanism for sodium storage was proposed which involves the replacement of sodium in the salivary-rumen fluids with potassium during periods of sodium deficiency (September to May).

Annual sodium “balance sheets” for adult moose (*Alces alces*) bulls, barren cows, cows with a single calf, and cows with twins were constructed to compare sodium retention with acquisition at Isle Royale National Park, Michigan. The ability to acquire sodium obviously must be greater than or equal to losses; otherwise, moose could not exist in the area because sodium is required for osmotic homeostasis, buffering of body fluids, nerve transmission, reproduction, hair production, lactation, growth, and the maintenance of body weight and appetite (Church et al., 1971; Smith et al., 1972). A sodium budget, at best, is crude because of the variability in field measurements and, in many cases, their approximate nature. However, the budgets demonstrated when sodium availability during a year or from year to year might be limiting to moose.

Sodium was chosen as a likely limiting nutrient to moose because it is considered to be a rare element in northern ecosystems that do not receive oceanic salt impaction (Botkin et al., 1973; Jordan et al., 1974). Botkin et al. (1973) found at Isle Royale that the average sodium content of terrestrial vegetation was 3 to 28 parts per million (ppm), while that of aquatic macrophytes was 2 to 9,400 ppm. Based upon dietary sodium requirements of domestic livestock, they demonstrated that a moose could satisfy only 7 to 14% of its sodium requirements by feeding on terrestrial plants. Consequently, the remaining requirement must be acquired from sodium in aquatic vegetation. Aho and Jordan (1979) documented that moose at Isle Royale consumed from 63 to 95% of the annual production of submerged aquatics, and we have observed that moose on the island appeared to have a “drive” for aquatics to the point of ignoring danger (loud noises, presence of humans, and motorboats).

In addition, several investigators examined sodium as a potentially limiting nutrient for herbivores. Hutchinson and Deevey (1949) suggested that sodium might account for herbivore cycles in northern regions; Aumann (1965) and Aumann and Emlen (1965) showed a positive correlation between peak microtine population densities and the concentration of sodium in soils. Furthermore, captive *Microtus pennsylvanicus* exhibited a reduced fecundity and density tolerance as dietary sodium levels decreased. Krebs et al. (1971) countered these arguments by demonstrating no correlation between soil sodium levels and microtine densities in Indiana. Nevertheless, other studies indicated that herbivorous mammals modified their behavior in response to sodium: East African ungulates sought surface water high in sodium (Weir, 1972a, 1973; Jarman, 1972); Australian herbivores sought foods high in sodium and excreted very little sodium (Denton et al., 1961; Denton, 1956, 1957, 1965; Bott et al., 1964; Scoggins et al., 1970); *Odocoileus virginianus* had seasonal adaptations to sodium retention linked with availability and requirements (Weeks and Kirkpatrick, 1976); *Marmota monax* and *Sciurus niger* had seasonal predilections for sodium salts (Weeks and Kirkpatrick, 1978); and *Cynomys gunnisoni* and *C. ludovicianus* possibly alleviated a potential sodium deficit by feeding on insects (Bakko, 1977). Finally, Jordan

et al. (1972) demonstrated that sodium was the least stable mineral, as yet studied, in forest biogeochemical cycles.

METHODS AND RESULTS

The adults, for which annual Na^+ "balance sheets" were constructed, were assumed to be of average weight, 358 kg (Jordan et al., 1971). Two separate sets of data were required to construct "balance sheets:" the Na^+ content of materials ingested, excreted, or stored, and the rates of ingestion, excretion, and storage of Na^+ .

The study areas were described in greater detail elsewhere (Belovsky and Jordan, 1978). The study was conducted at Isle Royale National Park, Michigan, between 1972 and 1974 on an upland forest site, the canopy of which was composed primarily of deciduous species, and on a coastal forest, the canopy of which was dominated by conifers.

Na⁺ content of materials.—The Na^+ content of moose tissue, feces, and urine (Table 1) was measured by use of the same analytical techniques employed by Botkin et al. (1973) for vegetation. Samples were collected with plastic gloves, distilled in purified-silica flasks and analyzed by atomic absorption spectrophotometry. The mean Na^+ concentrations of food plants were computed from vegetation Na^+ values reported by Botkin et al. (1973) and the observed moose diet at Isle Royale (Belovsky and Jordan, 1978).

The small number of urine samples (Table 1) was unavoidable, given the protected status of moose in national parks and the unavailability of captive individuals. Urine in summer was collected by catheterization of immobilized moose. Of seven moose immobilized, only three had not emptied their bladders. Winter samples were even more difficult to collect, because the study period was only 2 weeks and samples were available only from moose shot for another study. Only one of the three moose shot had urine in its bladder. The individual was healthy as determined by bone marrow condition and was considered typical of adult moose in February.

Additional winter urine samples were obtained by watching moose at close range (3–15 m) and collecting frozen urine-snow samples within several min of an observed urination. This was possible because the urine-snow mixture froze before the urine melted to the soil. The moose urine-snow was compared with controls of human urine and urine-snow to estimate dilution. Two such samples analyzed had Na^+ concentrations that were approximately 1 ppm, suggesting that the Na^+ concentration of the single winter urine sample collected from the bladder was reliable (Table 1).

Rates of storage, excretion, and ingestion.—The rate of Na^+ storage (Table 1) by a moose depends upon its growth rate and offspring production. The model of moose-biomass dynamics presented by Jordan et al. (1971) was used to estimate adult body growth, most of which arose from fat storage for winter and from recovery from weight losses after winter when food was scarce. Reproductive cows require Na^+ to produce fetuses, amniotic fluids, and milk to feed calves. Variation in milk production during lactation was not included in the "balance sheet;" rather a total production value for the period was used.

Na^+ is lost by moose primarily through excretion because cervids do not normally sweat as a means of thermoregulation (Irving, 1964) and artiodactyl sweat is low in Na^+ (MacFarlane, 1964). Furthermore, losses of Na^+ through "drooled" saliva was considered unimportant, because moose were seldom observed to salivate on themselves or their food plants. Defecation and urination rates (Table 1) were obtained by observing moose over more than 80 h at distances of 3 to 15 m. The number of fecal groups produced/day was computed from these observations. The urination rate was measured by one observer timing the duration of urination and closely watching urine flow, while a second person cut holes of different sizes in plastic bags, that were

TABLE 1.—Parameters ($\bar{X} \pm SD$) employed in constructing the Na^+ "balance sheets" for reproductive and nonreproductive adult moose, with sources of values.

Category	Estimates
Forage plants	
Terrestrial	
Summer	9 ppm ^a
Winter	7 ppm ^a
Aquatic	2,950 ppm ^a
Moose materials	
Urine	
Summer	44 ppm \pm 28 (n = 3)
Winter	1 ppm (n = 1)
Feces	
Summer	85 ppm \pm 55 (n = 26)
Winter	112 ppm \pm 39 (n = 7)
Tissue (muscle, fat, and hair) ^b	1,000 ppm ^a
Milk	1,576 ppm ^c
Outputs	
Urine	
Summer	131 s/day \pm 56 \times 0.1 l/s \pm 0.02 = 13.1 l/day (n = 5) (n = 6)
Winter	73 s/day \pm 7 \times 0.1 l/s \pm 0.02 = 7.3 l/day (n = 3) (n = 6)
Feces	
Summer	6 pies/day \pm 2 \times 178 g dry wt/pie \pm 36 = 1,068 g dry wt/day (n = 7) (n = 35)
Winter	17 pellet groups/day \pm 7 \times 178 g/pellet group \pm 35 = 3,026 g/day (n = 3) (n = 23)
Storage	
Growth	45 kg/yr ^d
Lactation	70 l/calf/yr ^e
Amniotic fluids	4.4 l/calf ^f
Fetal growth	11.2 kg/fetus ^e
Consumption	
Terrestrial plants	
Summer	4,030 g dry wt/day ^g
Winter	4,647 g dry wt/day ^e
Aquatic plants	
Bulls	655 g dry wt/day ^g
Cows	1,081 g dry wt/day ^g

^a Botkin et al., 1973; ^b assuming that the tissue added by a moose each year is composed of 90% muscle and fat and 10% hair; ^c Cook et al., 1970; ^d Jordan et al., 1971; ^e Knorre, 1959; ^f Austin and Short, 1972; ^g Belovsky and Jordan, 1978.

maintained at a constant volume of water. By comparison, the observer matched the proper flow from the bags to estimate the rate of urine flow.

The daily consumption of food by adult moose measured at Isle Royale by Belovsky and Jordan (1978) was used in the "balance sheet" computations (Table 1).

Ability to find Na^+ .—Buckets of salt solutions (KCl, $KHCO_3$, KSO_4 , NaCl, $NaHCO_3$, $NaSO_4$) of 1, 10, and 100 milliequivalents/l (meq/l) concentrations were set at a natural mud lick to determine whether moose had a predilection for Na^+ salts and to determine the minimum salt concentrations that they could detect. One hundred twenty-six presentations, which were divided equally among all six salts and concentrations, were made.

TABLE 2.—Annual Na^+ (in g) “balance sheets” for moose of different sexes and reproductive classes at Isle Royale.

Na ⁺ factor	Bulls	Cows		
		Barren	With 1 calf	With twins
Outputs				
Excretion	157.6	157.6	157.6	157.6
Tissue growth	45.0	45.0	45.0	45.0
Total	202.6	202.6	202.6	202.6
Reproduction				
Amniotic fluid			4.4	8.8
Fetus			11.2	22.4
Milk			112.0	224.0
Total			127.6	255.2
Total outputs	202.6	202.6	330.2	457.8
Inputs				
Aquatic consumption	208.7	344.4	344.4	344.4
Terrestrial consumption				
Summer	4.5	4.5	4.5	4.5
Winter	8.4	8.4	8.4	8.4
Total inputs	221.6	357.3	357.3	357.3
Net balance	+19.0	+154.7	+27.1	-100.5

Chronology of Na⁺ “balance sheet.”—Moose were observed to feed only on aquatic vegetation for 108 days (early June through mid-September); this time limit possibly was imposed by excessive heat losses by moose to cold pond water during other periods. Because aquatic plants have the highest water and sodium content of forage plants, it was assumed that the high output of urine during summer was restricted to the aquatic feeding period. Summer fecal production was considered for 124 days, the period that deciduous leaves and herbs were consumed (mid-May through mid-September).

Na⁺ “balance sheets.”—With the above chronology and the values in Table 1, the annual Na^+ requirements (losses plus storage) and intakes (food) were computed for adult moose of different reproductive classes (Table 2).

DISCUSSION AND CONCLUSIONS

Although we cannot show irrefutably that the “balance sheets” (Table 2) present minimum Na^+ losses and requirements, two additional sets of observations suggest that they were minimal. First, moose on another area at Isle Royale, where aquatic macrophytes were unavailable, “slurped” water containing filamentous algae, *Spirogyra* sp., (Belovsky and Jordan, 1978), which was approximately 0.0146 g Na^+ /g dry wt (Boyd and Lawrence, 1966). The annual Na^+ intake for moose on this second area was computed to be 177 g/yr for a bull and 338 g/yr for a cow, comparable to values presented in Table 2. Second, moose have an energy-maximizing foraging strategy (Belovsky, 1978). This strategy suggests that moose should not consume more aquatic plants than necessary to supply Na^+ requirements, because aquatics have the lowest net energy content per unit of rumen filled of any summer forage plant. Therefore, a moose at Isle Royale should use the least amount of Na^+ to minimize aquatic consumption and maximize daily energy intake.

Because the “balance sheets” appeared to present minimum Na^+ requirements, several points can be made. First, there were striking differences in Na^+ requirements

between reproductive and nonreproductive moose (Table 2). A reproductive moose required 128 to 255 g/yr more Na^+ than nonreproductive individuals, depending upon whether one or two calves were produced. Cows with twins did not seem to be able to satisfy their Na^+ requirements by food intake; perhaps they mobilized Na^+ stored from foods consumed in previous years. Furthermore, 94 to 96% of an adult moose's Na^+ intake came from aquatic plants, which were available only for 30% of the year. These observations suggested that moose may have evolved adaptations to reduce excretory Na^+ losses, to increase intake of aquatic plants, and to store Na^+ for periods when aquatic plants were not available (70% of year). In addition, they suggest that moose growth rates and reproduction, especially for reproductive cows, may be limited by Na^+ availability.

Na⁺ retention adaptations.—Moose lost less Na^+ through urine than by any other route (7%), suggesting an efficient excretory system. In summer, the Na^+ concentration of urine was 1.9 meq/l, while in winter it declined to 0.00004 meq/l. Na^+ values for moose urine were equal to or less than Na^+ urine values measured for other Na^+ -deprived herbivores: *Odocoileus virginianus*, 1.7 meq/l (Weeks and Kirkpatrick, 1976); *Cynomys ludovicianus* and *C. gunnisoni*, 4.5 meq/l (Bakko, 1977); and Australian mammals, including *Vombatus* sp., *Oryctolagus cuniculus*, *Macropus* sp., and sheep, 0.3 to 0.5 meq/l (Scoggins et al., 1970). Ability of a moose to reduce renal Na^+ was impressive because its large daily intake of water in summer (28.7 l) required a large urine output and renal filtration rate, thereby demanding that renal Na^+ conservation mechanisms operate quickly and efficiently. Other mammals studied for renal Na^+ retention were from dry environments, where urine was concentrated at slow filtration rates making Na^+ retention easier (Gordon et al., 1968).

Although Na^+ losses were greatest in feces, there was evidence for a well developed fecal- Na^+ conservation mechanism. During winter, moose lost 4.9 meq Na^+ /kg dry wt of feces and the same per liter of fecal water; in summer, 3.7 meq/kg dry wt or 1.2 meq/l of fecal water were lost. The fecal- Na^+ values for moose were equal to or less than values measured for other Na^+ -deprived herbivores: domestic cow, 196 meq/kg dry wt or 7.6 meq/l (Renkema et al., 1962); *Loxodonta africana*, 78.3 meq/kg dry wt (Weir, 1972b); and Australian domestic rabbits, 5 meq/kg dry wt for soft feces or 2 meq/kg dry wt for reingested feces (Scoggins et al., 1970). White-tailed deer, however, conserved fecal Na^+ 58% better than moose (Weeks and Kirkpatrick, 1976).

Adaptations for Na⁺ intake.—The Na^+ content of forage necessary to satisfy requirements of moose was 90 to 200 ppm, depending upon reproductive status, far less than the 1,000 ppm suggested for livestock (Hafez and Dyer, 1969). Nevertheless, moose appeared to possess several adaptations for feeding upon plants high in Na^+ . Female moose have a rumen volume 1.2 times larger than that of a bull of the same weight, based upon the wet weight of rumen contents (Belovsky, 1978). The greater volume permitted cows, whose Na^+ requirements were greater, to consume more bulky aquatics for Na^+ content, and still have rumen capacity for energy-food (leaves) (Belovsky, 1978).

The ability to detect low Na^+ concentrations in foods was another adaptation. Studies cited by Arnold and Hill (1972) demonstrated that Na^+ solutions were detected by ruminants between 85 and 100 meq/l concentrations; moose were found to consume only 100 meq/l solutions of Na^+ and K^+ ($\chi^2 = 22.7$, $P < 0.005$, $df = 1$). Moose were expected to prefer Na^+ solutions, however, almost as many K^+ buckets were utilized as Na^+ buckets (7 K^+ :8 Na^+). Moose were either unable to distinguish specific ions and concerned themselves only with minimum concentrations, or the experiment was not definitive.

Natural mud licks at Isle Royale were not important sources of Na^+ ; they contained only 0.4 to 2.2 meq Na^+ /l, which was less than concentrations detectable by moose.

TABLE 3.—A comparison of moose preference for aquatic plants (% by weight in diet \times % occurrence in diet/% by weight availability \times % occurrence in the environment: Krueger, 1972), based on data collected at Isle Royale (Belovsky and Jordan, 1978), with their Na⁺ content (Botkin et al., 1973; Boyd and Lawrence, 1966).

Species	Preference index	Na ⁺ (ppm)
<i>Utricularia</i> sp.	5.73	8,048
<i>Potamogeton</i> sp.	5.78	7,230
<i>Nitella</i> and <i>Chara</i> sp.	3.39	2,850
<i>Equisetum</i> sp.	0.96	1,574
<i>Carex</i> sp.	0.27	390
<i>Spirogyra</i> sp.	11.11	14,600

If moose were to use licks as substitutes for aquatic plants, 15 to 83 l/day of lick water would be needed to supply Na⁺ requirements. This amount of water intake would pose a serious reduction in rumen volume for feeding and increase the renal filtration rate, which might lead to greater losses of Na⁺ in urine. Furthermore, licks were distributed too widely for all moose to have access to them. Concentrations of Na⁺ in licks at Isle Royale may not be abnormal, because all reported lick-Na⁺ concentrations found in the literature were below 20 meq/l (Weeks and Kirkpatrick, 1976; Knight and Mudge, 1967; Hebert and Cowan, 1971; Cowan and Brink, 1949; Murie, 1934; Dalke et al., 1965; Stockstad et al., 1953).

Moose demonstrated preferences for species of aquatic plants, the main Na⁺ sources, based upon their Na⁺ concentration (Table 3). Furthermore, a preference index of 1, indicating a neutral reaction to a food, was found at Na⁺ concentrations of 65 meq/l, a value close to the level of Na⁺ detection by moose.

Na⁺ storage adaptations.—Moose may store Na⁺ in the saliva-rumen fluid system during the aquatic feeding period (early June to mid-September) for later withdrawal. Denton (1956, 1957) and Bott et al. (1964) demonstrated for sheep and cattle that K⁺ replaced Na⁺ in saliva-rumen fluids during Na⁺ deprivation and liberated Na⁺ to maintain the body's ionic balance. The process was reversed when Na⁺ was no longer deficient.

About 15% of the body mass of a ruminant is ingesta and fluids in the rumen (Denton, 1956, 1957; Church et al., 1971), and an average adult moose (358 kg) displaces 33.6 l of rumen volume with food (Belovsky and Jordan, 1978). If moose replace Na⁺ with K⁺ in rumen-saliva fluids at the same rate as sheep, 5,100 ppm (Denton, 1956, 1957), an adult bull would have a Na⁺ reserve of 93 g, while a cow would have 112 g—the sex difference arises from the different rumen capacities. These potential Na⁺ reserves would fulfill requirements for bulls and for cows with single calves, but would fall 17 g short annually for a cow with twins. This may explain why twinning was not more common at Isle Royale.

The rumen-fluid composition for a moose shot in February was 6,221 ppm Na⁺ and 49,510 ppm K⁺; a Na⁺/K⁺ ratio of 1:8. Because ruminants seem to have similar saliva-rumen fluid compositions (Johnson, 1966), the Na⁺/K⁺ ratio was compared with those observed for sheep: 18:1 for non-Na⁺ deprived and 1:18 for severely deprived (Denton, 1956). The ratio for the single moose fell at the lower end of the sheep values, suggesting that moose may replace Na⁺ with K⁺.

The factors in Table 1 along with moose and vegetation K⁺ values (D. Botkin, pers. comm.) were used to compute a K⁺ budget. During summer, moose did not gain K⁺; the intake was excreted or used for growth and reproduction. In winter, however, 360 g were accumulated and available for substitution with Na⁺. Furthermore, in winter, moose urine contained 800 ppm K⁺, a value comparable with the 1,170 ppm of a Na⁺-

deprived cow (Bott et al., 1964), and the 741 ppm of sheep (Denton, 1956). Therefore, moose seemed to increase K^+ reserves under conditions of Na^+ deprivation.

While Na^+ -deprived, a moose's rumen reservoir would need to release 0.4 g/day of Na^+ , far less than the several g/day response elicited for sheep and cattle (Denton, 1956, 1957; Bott et al., 1964). In terms of total response, the experimental short-term Na^+ released (30 days) by sheep and cattle was equivalent to the amount required during the period of chronic deprivation for moose.

In summary, our study suggests that in regions where primary foods contain nutritionally inadequate levels of sodium, moose circumvent sodium stress by consuming aquatic plants in midsummer. These generally have Na^+ levels an order of magnitude or two higher than terrestrial plants. Moose then retain enough sodium during the rest of the year to avoid deficiency, to support new growth in spring, and to support gestation and early lactation in reproducing females. Essentially nothing is known about Na^+ physiology of other nonaquatic herbivores of the boreal region; it has been observed that white-tailed deer apparently consume more aquatics than has commonly been reported (Hennings, 1977). There is a marked need to verify the hypothesized Na^+ - K^+ shift in moose and other ruminants that are seasonally restricted in their access to sodium.

Because sodium drive in moose at Isle Royale is so pronounced, and their consumption of aquatics sometimes approaches 100% (Murie, 1934; Aho and Jordan, 1979), it would appear that a relatively small decline in aquatics could have a major impact on the herd; implications of this are explored in a sequel paper (Belovsky, 1981). Furthermore, in regions where terrestrial environments are the same but aquatic resources are not as abundant nor as evenly dispersed, capacity of the environment to support moose may be correspondingly lower than at Isle Royale.

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