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ENVIRONMENTAL SODIUM AS A FACTOR IN THE BEHAVIOR
AND DISTRIBUTION OF AFRICAN ELEPHANTS

by Naomi D. Wheelock

Abstract: African elephants ingest substances which are rich in sodium. High sodium levels in available water also attract elephants. Overall distribution of elephants is controlled primarily by game park managers. It is suggested that manipulation of the sodium variable may be a useful tool in development of more efficient management schema.

Introduction: Salt appetite has been observed in many mammals including snowshoe hares, elk, reindeer, gorillas (Blair-West *et al.*, 1968), sheep, cattle (Denton, 1965), giraffe and elephants (Weir, 1969, 1972, 1973, and Poche, 1975). African elephants eat soils, termitaria, tree bark and wood ash which have been shown to be rich in sodium, as well as preferentially visit water holes where sodium content is high (Weir, 1969, 1972, 1973). Asian elephants are also known to utilize salt licks (Hubback, 1939). The function of sodium in ruminant digestion has been investigated (Denton, 1965) and is discussed in light of the fact that elephants approach the ruminant mode of digestion (Weir, 1972). This review explores the relationship between environmental sodium and elephant behavior and distribution, as well as physiological requirements for sodium balance and its control.

Elephant distribution: Although highly specialized in some parts of their anatomy, elephants are relatively unspecialized ecologically. They are able to occupy a wide variety of habitats, from sea level to montane and from desert to tropical rain forest (Laws, 1970a). Sikes (1971) postulated that their natural pattern was semi-aquatic. She noted that great numbers of *Loxodonta africana* were once permanently associated with large year-round swamps such as Lake Chad.

The present distribution of *Loxodonta africana* is determined largely by man, without regard for the preference of the animals. Consequently, populations are under varying degrees of stress (Weir, 1972). During this century, the elephants have been steadily concentrated into areas unsuited to human occupation due to low or variable rainfall and to the presence of few permanent rivers (Glover, 1963). These areas, originally a mosaic of woodland, high forest, gallery forest and scattered grassland (Laws *et al.*, 1975), are in the process of conversion to uninterrupted grassland due to the influence of elephants and fire (Buechner and Dawkins, 1961).

When possible, elephants move naturally in response to availability of water, food and shade. They spend the dry season in gallery forest. During the rainy season, they leave permanent water (Bax and Sheldrick, 1963) for the newly sprouted grasses of the savannah. When the rains cease, large herds are observed moving back to their former forest ranges (Sikes, 1971).

In restricted habitats, researchers have been unable to find convincing evidence of any regular seasonal movements greater than 15 km. Major seasonal patterns can no longer be an important feature of elephant behavior due to

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concentration of the animals in reserves and parks (Laws et al., 1975). The elephants are forced to congregate in marshes during the dry season. Their movements are related to rains but do not follow an annual cycle (Buechner et al., 1963).

Diet: Discrepancies exist in the literature regarding Loxodonta's seasonal preferences for food types and ratio of grass to woody material in the diet, and the definition of woody material is not made clear. Buss (1961) observed that grasses were selectively utilized. Glover (1963) observed that grass was nutritionally adequate only when green; when dry, elephants shunned it. Bax and Sheldrick (1963) claimed that woody vegetation was utilized only during drought. Freshly sprouted grasses predominate in the diet in the wet season; bark, leaves, creepers and herbs in the dry season. According to Laws, woody material from young regenerating trees and shrubs was preferred. When available, browse and herbs constitute 50 to 70% of the food intake (Laws, 1970a, and Laws et al., 1975). Laws stated that optimal grass consumption should not exceed 50% except when high nutrition sprouts are available (1970b). Sikes (1971) felt that elephants were browsers by nature and that the adaptation to grass was forced. Field (1971) noted that browse intake rises sharply when precipitation falls below 50mm/month but that herbs are frequently eaten during the rainy season. It is clear that grasses, herbs, twigs, fruit, bark and roots are all consumed at times (Schaaf, 1972).

Minerals: Sodium may be depleted in arid regions. At great distances from the sea, the sodium content of rain water is decreased. Where water tables are low, soluble minerals are leached out of the soil in which fodder plants grow. On the other hand, the deep water may be extremely high in minerals (Denton, 1965). Game park managers provide artificial water supplies in the dry season, some of which are pumped from sodium rich underground supplies.

Elephants seek out certain foods for their mineral content. One attraction of tree bark may be its high level of calcium (Bax and Sheldrick, 1963), yet Weir (1972) did not find calcium content of water to affect elephant distribution. When dietary intake of sodium is low, elephants eat soils high in water soluble sodium. During the rainy season these salt licks become favored drinking spots. Sodium intake may be further supplemented by eating termite mounds or wood ash. This selective utilization of sodium rich soils and water results in the ingestion of calcium, magnesium, potassium and other minerals with which the sodium is associated. Blair-West et al. (1968) postulated that changes in the sodium/potassium ratio in ruminant saliva was the principal adaptive mechanism in hot, dry, mineral deficient environments. Although elephants are not ruminants, there is some fermentation in their caeca and colons and production of phenyl substituted fatty acids which resembles the ruminant pattern (Hungate et al., 1959 and Cmelik, 1964 both cited in Weir, 1972).

Soil: Weir (1969) reported that during the dry season elephants in Wankie National Park, Zimbabwe-Rhodesia, excavated steep sided pits of 0.5 to 1.5 m depth and 3 to 25 m width, ingesting some of the excavated material. These pits are found in grassy plains and sometimes at the bases of termite mounds but not in thickets which occur on the plains. This behavior was also reported for elephants in Kabalega (Murchison) Falls National Park, Uganda (Weir, 1973).

At the height of the dry season water was pumped into concrete reservoirs and pans to sustain the animals and keep them in the park. When water was more abundant, fewer elephants were seen in the park and much less activity was noticed at the pits. Nonetheless, elephants have been observed drinking both rain water from the excavations and artificially supplied water in preference to rain water in other areas (Weir, 1969, 1972).

Weir's chemical analyses of the soils of these areas, examining absolute mineral values and conductivity, revealed that high sodium levels were found in material from the sides of the pits. Loose excavated material which was not ingested had a sodium content higher than that of surrounding soils but lower than that of the pit walls. Some non-excavated areas show high sodium content, especially where borehole water had been pumped. Most other samples were sodium poor although some had high levels of calcium, magnesium and potassium. Strong indications that sodium was the attractant, rather than other minerals, came from the fact that areas exposed by road making were only utilized as (salt) licks if their sodium content was high.

Where termite mounds showed demolition and pawing by elephants, surrounding soils had been scraped for areas of one to five meters but not dug to any depths. Chemical analyses revealed very low sodium levels in these areas. In areas of high sodium and soil excavation, termite mounds were undisturbed and scrapes were absent. Elephants also excavate and ingest wood ash in areas far from sodium rich soils (Weir, 1969, 1972). (See Table I).

Weir (1969) stated categorically that sodium content was the most important factor in salt lick soils and that no soils sampled were found to have higher sodium content. Salt lick areas contained the highest concentrations of elephant dung, while the dung of other mammals was more often concentrated at the edge of grassy or wooded areas. Weir (1969) suggested two alternative explanations of the dung build-up. On the one hand, it could be a straightforward indication of the amount of time spent at the salt lick, representing a focus of elephant social interaction similar to that provided by drinking and bathing spots. On the other hand, the possibility cannot be ruled out that the behavior pattern at salt licks is different. The dung deposition might facilitate relocation of rich sodium sources.

The availability of highly saline water, pumped from boreholes, may affect both the social pattern of the elephants and their recourse to the salt licks. Sodium rich soils were present near all areas where water was pumped. Where sodium content of the water was high, elephant numbers were also high and excavation was limited. Where sodium content was low, the reverse was observed (Weir, 1972).

Water: An analysis of large mammals at dry season water holes in Wankie (Weir, 1972) indicated that elephant distribution varied from that of other animals. No correlations were found with geological, climatic or vegetational variables. Nonetheless, high correlations were shown between elephant frequency and sodium content of supplied water. For instance, two waterholes only 4 km. apart, a short distance for elephants in search of water, showed a marked difference in: a) the average number of elephants per census (233 vs. 125); and b) the proportion of elephants to all species observed (42.9 vs. 28.3%). Elephants

Table I. Soil sodium availability and utilization by elephants in two African game parks.

A. Wankie National Park, Zimbabwe-Rhodesia (after Weir, 1969.)

Site	[Na] ppm in aqueous 1:5 extracts of dry soil	Notes
Scrape at Jambile	8.0	Sites investigated by elephants, presumably as potential licks
	8.0	
	8.6	
	7.5	
Slope above "pumped" pan, 0.5 m depth	6.4	Sites investigated by Weir as potential licks
	8.0	
	7.0	
Termite mounds at Jambile: sides "pawed"	10.4	Material "used" by elephants instead of licks
	10.4	
Termite mound, Makwa basin:		Equivalent termite mound material not used as licks
	top	
	base	
	base (0.5 m depth)	
Termite mounds, Main camp basin:		Equivalent termite mound material not used as licks except where sodium content in mound rises above 320 ppm
	top	
	top	
	sides	
	sides	
	base	
	base	

B. Kabalega Falls National Park, Uganda (after Weir, 1972.)

1 & 2	Surface soil	20.6	Ambient levels - higher than those in Kalahari sand areas. Termite mounds not utilized
	Sub soil	25.5	
3 & 4	Surface soil	25.0	not utilized
	Sub soil	23.8	
	Exposed scrapes	29.0	
5	Soil above slit	35.0	Elephants removing soil
	Soil from slit	177.5	
	Soil below slit	115.0	
6	Soil from wallow	190.0	Elephants drinking
	Soil near wallow	66.0	
7	Overlying soil	75.0	Elephants digging, trampling
	Exposed crumbling rock	128.0	
	Basal debris and clay	98.5	
	Rock sample	116.0	
	Rock sample	107.0	

drink 180-230 liters of water daily. The difference in sodium intake from high sodium sources (60 g/day) to low (7.6 g/day) is enormous. Ingestion of one kilogram of salt lick soil might provide 20 g of sodium. If soil sodium was available, elephants were found drinking at water holes with low sodium content. If neither soil nor water contained appreciable sodium, few elephants were reported even where foodstuffs were abundant. These areas showed signs of shallow elephant scrapes but no excavation. Termite mounds also showed pawing. Weir (1972) described the sodium budget of the elephants at Wankie as precarious and proposed a dependency of population density on environmental sodium. (See Table II).

In Kabalega Falls, Weir (1973) found that sodium in available water was abundant and soil ingestion was limited to seepage areas. Throughout the park both water and food contained higher levels of minerals than at Wankie and the concentration of sodium did not determine elephant distribution. No signs of elephant demolition were found at termite mounds.

Utilization of water holes at Tsavo National Park, Kenya, was studied by Ayeni (1975, 1977). Here the dry season was short and water tables remained near the surface of river beds even in the dry season and elephants could reach water by digging. Away from the rivers there were some water holes which had been dug out by elephants that remained throughout the year. Other areas were supplied with highly saline borehole water.

Ash: Tsavo, formerly covered by dense brush with scattered large trees, is now extensively long grass. This vegetation turns to straw in the dry season (Glover, 1963). As soon as the straw is combustible, fires are set by honey hunters and poachers (Bax and Sheldrick, 1963). The entire countryside is burned over within a short period. Where forest fires occur in Wankie, elephants were observed digging and ingesting the ash. Analysis showed sodium to be present in the ash and absent in the surrounding soil and yet the sodium content is only on the order of 0.05 g/kg. Ash ingestion was also observed at Kruger National Park, Republic of South Africa, and on the shore of Lake Kariba, Zimbabwe-Rhodesia (Weir, 1972).

Physiological requirements for sodium balance and its control: Denton (1965) reviews salt appetite in all phyla and examines the effects of adrenocorticotrophic hormone (ACTH) secretion of the anterior pituitary as a stimulus to aldosterone secretion. Other stimuli to aldosterone secretion are low sodium concentration or high potassium concentration in the adrenal arteries, angiotensin and renin levels, action of the pineal gland, and conditions of stress, such as pregnancy and thirst. Aldosterone secretion reduced sodium excretion but not urine volume. Its effect is on distal tubular activity. The parotid gland is particularly sensitive to sodium deficiency. In sheep with parotid fistula, sodium is lost and aldosterone secretion soars. Sheep experimentally deprived of sodium and then exposed to solutions of varying concentrations of sodium, are able to make up the deficit by adjusting the volume of solution consumed (Denton, 1965).

Sodium is required by all terrestrial mammals and sodium storage schema are advantageous to animals who may encounter shortages in their environment (Weir, 1972). Furthermore, if the central nervous system can trigger

Table II. Water sodium availability and occurrence of elephants at Wankie National Park, Zimbabwe-Rhodesia (after Weir, 1972.)

Site	Description	[Na] ppm *mean value	Average number elephants/census
Guvalla I	Reservoir at pumped pan	2620*	
Guvalla I	Pumped pan	1165*	297
Guvalla II	Pumped pan	970*	
Nyamandhlovu	Pumped pan	933*	233
Nyamandhlovu	Reservoir I at pumped pan	790	
Nyamandhlovu	Reservoir II at pumped pan	750	
Shapi pan	Pumped pan	237	185
Sidina	Deepened and pumped pan	227	
Ngwashla pan	Pumped pan	138*	221
Kennedy I	Pumped pan	74*	72
Kennedy I	Reservoir at pumped pan	19	
Dom	Pumped pan	70	125
Makwa 5	Reservoir at pumped pan	28*	
Makwa 5	Pumped pan	42*	60
Makwa 8	Pumped pan	29*	
Makwa 8	Reservoir at pumped pan	26	
Balla Balla	Deepened pan	17	
Livingi	Deepened pan	10*	
Jambile I	Pumped pan	11	(>25 figure taken from graph)
Jambile II	Pumped pan	6	
Natural pan		50*	
Natural pan		45	
Natural pan		36	
Natural pan		15*	
Natural pan		23*	
Natural pan		28	
Natural pan		10	
Natural pan		10	
Deepened pan		10	
Deepened pan		4	

Censuses in September 1959, October 1959, November 1960, October 1961 and October 1962. Water analyses between 1961 and 1966.

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appetitive behavior leading to detection and ingestion of sodium rich soils, water or plants, an animal can survive even in a severely depleted environment. Sodium depleted sheep exhibit restlessness and exploratory behavior, especially tasting (Denton, 1965). This is probably analagous to the scraping by elephants in search of soil worth digging. Salt appetite is common among higher mammals, particularly ruminants who selectively utilize sodium rich vegetation. In rats, sodium appetite has been shown to relate to bodily need rather than taste (Denton, 1965). Aldosterone production is the probable mechanism for adjustment of sodium to potassium ratio of ruminant saliva (Blair-West et al., 1968). Salivary secretion in ruminants is constant and copious. A dessicated, coarse diet requires increased mastication and additional salivary secretion (Denton, 1965). The severely dry and mineral-deficient conditions in Wankie accentuate these requirements. The relative inefficiency of elephant digestion can be compensated for by efficiency in detection and utilization of environmental sodium (Weir, 1972).

Benedict (1936 cited in Weir, 1972) measured energy, water and mineral budgets with a captive Asian elephant of 3.175 kg. He calculated a sodium chloride input of 182 g/day in water and food. Output amounted to 195 g/day in feces and urine. Fecal analysis of a 2,041 kg African elephant in Tsavo (Dougall, 1963 cited in Weir, 1972) showed 0.143% dry weight of sodium. The daily output of feces (dry weight) in this animal was 21 kg, contributing to a 30 g daily sodium loss. If Benedict's (1936) figures for urine are applied proportionately, another 120 g of sodium are lost (Weir, 1972).

Analysis of sodium content of elephant foodstuffs (Dougall et al., 1964 cited in Weir, 1972) shows a dry weight of 0.165% as compared to 0.065% in other animals. The indication is of selective utilization of sodium rich plants, rather than a random feeding pattern. Dry season browse provides much more sodium than grass does. Perhaps the roots can reach the level at which sodium has been leached.

In a sodium-deficient Australian environment, Blair-West et al. (1968) found that cattle were more apt to experience sodium deficiency than sheep, who can reduce the sodium content of their feces. Morphologically, the adrenal glands of animals in sodium poor areas are larger than those in sodium rich areas. The salivary glands showed increased development of parotid ducts with enhanced vascularization, suggestive of chronic hyperactivity and sodium reabsorption. Emotional stress of exams triggers increased aldosterone production in medical students (Denton, 1965). Aumann and Emlen (1965 cited in Blair-West et al., 1968) reported an increased salt intake for a laboratory population of crowded microtine rodents. Crowding and stress in the artificially restricted game parks may also contribute to elephant sodium requirements.

Summary: Whatever the natural pattern of distribution of Loxodonta africana may have been, they are now concentrated in game parks and reserves which are managed by humans. The use of woody material as a food source has been shown to increase in dry seasons, possibly as a direct result of high sodium content. Other sources of sodium are soils, wood ash, termite mounds and borehole water. Management schema involving sodium manipulation in the already artificially

supplied water could facilitate a more favorable distribution in terms of maximizing food utilization and minimizing habitat destruction.

Hormonal and neural bases for sodium regulation implicate control of excretory loss by aldosterone secretion and stimulation of salt appetite. In addition, stress is likely to increase aldosterone secretion and salt intake. Most of the research in this area has been conducted on ruminants, rats, dogs and humans. It would be interesting to investigate whether elephants have control over sodium content of their feces, and to examine directly parotid development and aldosterone production in a variety of sodium availability circumstances. Furthermore, Benedict's 1936 study stands alone in quantifying overall physiological behavior of elephants. Surely, the experimental problems presented by the largest terrestrial animal can be overcome. It would be fascinating to approach the problem with contemporary technology.

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