Iodine as a Possible Controlling Nutrient for Elephant Populations

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ABSTRACT

The geography and physiology of iodine deficiency in humans and domestic ungulates suggests that the nutritional content of ground water may hold a key to humane and efficient management of population sizes of elephants. Artificial bore water in dry climates in southern Africa appears to be, on average, a good supplement of this easily leached element, and may have inadvertently boosted the reproductive rates of elephants in several conservation areas. The largest land mammals are likely to be limited by deficiency of iodine, inasmuch as their plant foods are deficient in this element relative to the hormonal requirements associated with exceptional brain size and relatively great thyroid size. Extrapolation from domestic ecosystems suggests that elephants exceed medium-sized wild herbivores in the sensitivity of their reproductive rates to subclinical deficiency of iodine, partly because the rate of loss of iodine from the body is likely to be hyperallometric to those of energy, protein, and water, with increasing body size. Elephants pass food and water rapidly for their body size, but this allows maximal intakes of iodine, which can potentially be further supplemented by absorption through the skin. The great variation in concentrations of iodine between adjacent aquifers suggests a versatile approach to population control. Closure of iodine-rich bore holes in overpopulated areas may reduce rates of sexual maturation, conception, birth, and weaning, with minimum artificial distress to adults or surviving juvenile elephants. Conversely, selection of the bore waters richest in iodine may help to promote population growth in areas recently restocked with elephants. All proboscideans became extinct in the Americas and temperate Eurasia at the end of the Pleistocene, when glacial melting had profoundly depleted iodine, and humans had the means to monopolize the remaining sources of supplementary iodine. The maximal intelligence and fecundity of those megaherbivores which have survived the era of domestication may have made these species depend on supplementation of iodine.

RESUME

La géographie et la physiologie de la déficience en iode chez les humains et les ongulés domestiques suggère que le contenu nutritionnel de la nappe phréatique puisse détenir la clé d’une gestion humaine et efficace de la taille des populations d’éléphants. L’eau de forages artificiels dans les climats secs d’Afrique australe semble apporter en moyenne un complément conséquent de cet élément facilement éliminé par filtration. Elle est susceptible d’avoir fait augmenter par inadvertance les taux de reproduction des éléphants dans plusieurs zones de protection. Il est probable que les plus grands mammifères terrestres seraient limités par une déficience en iode, attendu que leurs aliments végétaux ne peuvent couvrir les besoins hormonaux associés à une taille de cerveau exceptionnelle et une taille de thyroïde relativement grande. Une extrapolation à partir de systèmes domestiques suggère que les taux de reproduction sont plus sensibles à une déficience en iode en dessous du seuil clinique chez les éléphants que chez les herbivores sauvages de taille moyenne ; ceci est en partie dû au fait que le taux d’élimination de l’iode du corps est susceptible d’être hyperallométrique par rapport à celui de l'énergie, des protéines et de l'eau lorsque la taille corporelle augmente. Les éléphants évacuent les aliments et l'eau rapidement pour leur taille corporelle, mais ceci permet une consommation d'iode maximale, qui peut être encore complétée par une absorption à travers la peau. Les grandes variations des concentrations en iode entre des aquifères adjacents suggèrent une approche versatile du contrôle des populations. La condamnation de forages riches en iode dans les régions surpeuplées pourrait réduire les taux de maturité sexuelle, de conception, naissances et sevrage avec un impact minimum sur les adultes ou les jeunes éléphants survivants. Inversement, la sélection des forages riches en iode pourrait aider à encourager la croissance de la population dans les régions où des éléphants ont récemment été réintroduits. Tous les proboscidiens se sont éteints sur le continent américain et en Eurasie tempérée à la fin du Pléistocène, lorsque la fonte des glaciers avait largement réduit la quantité d'iode et que les humains avaient les moyens de monopoliser les sources complémentaires d'iode restantes. L'intelligence maximale et la fécondité des méga herbivores qui ont survécu à l'ère de la domestication pourraient avoir rendu ces espèces dépendantes de la fourniture en iode.

INTRODUCTION

There is an urgent need for humane methods of population control for elephants. Populations of the African elephant, *Loxodonta africana (*Blumenbach, 1797) have increased rapidly in southern Africa, despite their artificial confinement to conservation areas. Public sentiment for elephants is partly based on a perception that, like whales, they are among the most intelligent of animals, with relative brain size exceeding those of all other ungulates (Quiring, 1950; Bauchot, 1978). Elephants share the longevity, measured reproduction, social bonds, dexterity and tool use, management of food resources, potential destructiveness of vegetation, and mining activities which characterize humans. Elephants also have a striking affinity with water, and are able to swim farther than any other land mammals (Johnson, 1980).

Elephants reproduce and grow far more slowly than do like-size whales, suggesting that the poor quality of plants as food limits the maximum body sizes of animals on land. Further suggesting nutritional constraints are the extreme behaviours of elephants foraging for inorganic nutrients: excavation of large caves (Bowell et al., 1996), digging of seepage pits in preference to drinking adjacent running water (Spinage, 1994), and conversion of large termitaria to concave wallows (K.L. Tinley, pers. comm., 1999). I suggest that a critical nutrient is iodine, of proven importance in domestic, but neglected in wild, ecosystems (Milewski, 1999). This is based on my integration of the medical and veterinary literature, in relation to several paradoxes of elephant anatomy and behaviour.

EFFECTS OF DEFICIENCY OF IODINE ON MAMMALIAN REPRODUCTION

Among the many nutrients with their complex interactions, iodine most closely approaches the status of a metabolic megacatalyst (Milewski and Diamond, in press). Iodine is essential to mammals in quantities great enough to produce frequent deficiency in herbivores. It is needed by plants in negligible quantities, and has never been shown to be deficient for plant physiological functions (Shkolnik, 1984).

Iodine, the neglected nutrient in wildlife ecology

Iodine incorporated in thyroid hormones has control over exceptionally many enzyme reactions in the mammal body (Underwood, 1981, Hetzel and Maberly, 1986, McDowell, 1992). Iodine is the only nutrient used mainly in an endocrine gland and its hormones. It has the greatest concentration of any micronutrient in one organ relative to the rest of the body: more than 70% of iodine in the body is stored in nontoxic form in the thyroid (Prasad, 1978), which has the only extracellular store of hormones contained in any endocrine gland (Lee and Knowles, 1965). It was the first micronutrient to be recognized as such, and is responsible for the first disease (goitre, *viz* increase in the mass of the thyroid which compensates to some degree for iodine deficiency) scientifically attributed to the environment rather than infection (Oliver, 1997). It has the greatest atomic mass and ionic radius among nutrients (Plant and Raiswell, 1983), yet (like chlorine and bromine), is mobile regardless of environmental pH and E_h (Plant et al., 1996). It is the only nutrient which is more concentrated in soils than in parent rocks, but not actively retrieved from the gaseous state (Plant and Raiswell, 1983; Stewart and Pharoah, 1996; Milewski and Diamond, in press). Of all micronutrients, it has the greatest ease in passing from blood to milk, and the greatest degree to which concentration in milk reflects maternal nutrition (Prasad, 1978; Underwood, 1981). It also has the most categorical separation of any nutrient between animals (required) and land plants (not required) (Sauchelli, 1969; Shkolnik, 1984). Despite its high rank in the nutritional hierarchy, iodine is the least frequently analyzed of all important nutrients for wild ungulates (see McNaughton, 1989).

Iodine as a key nutrient for brain growth

Iodine is directly and indirectly essential for the brain, although not concentrated in this energy-demanding organ (Wayne et al., 1964; Prasad, 1978). Brain tissue has rapid metabolism, and requires thyroid hormones indirectly for maintaining its thermal homeostasis (Quiring, 1950; Sokoloff et al., 1977; Hetzel and Maberly, 1986). A reduced metabolic rate of the cells of the cerebral cortex results in prolonged reaction time, and brain function is sensitive to the supply of thyroxine, even in normal persons (Lee and Knowles, 1965; Stewart and Pharoah, 1996). However, thyroid hormones control normal brain function and development, and affect neuronal activity, even in poikilothermic vertebrates (Lee and Knowles, 1965; Stewart and Pharoah, 1996). The priority taken by the brain in ontogenetic growth means that the supply of iodine affects reproduction.

Nearly one in three humans living today is deficient in iodine, to the degree of risking retarded metabolism and reduced intelligence (WHO, 1996). There is a continual gradation of effects between sufficiency and clinical deficiency. The children of clinically deficient parents risk permanent damage to the brain, even when the parents are otherwise well-nourished (Stewart and Pharoah, 1996). The largely irreversible defects of cretinism are life-threatening even with intensive social support.

Iodine as a key nutrient for reproduction

The supply of iodine affects reproductive rate, since age of sexual maturation, and frequency of oestrus, depend on hormonal sufficiency, and are, in turn, dependent on the thyroid as an integral part of the endocrine system. Thyroxine is required in relatively large quantities for the rapid metabolism and growth of mammalian offspring, which depend on the mother for iodine until weaned. Milk contains minimal thyroxine, and is rich in iodine only where maternal intake of this nutrient is ample. Human milk has a concentration of iodide 20-30-fold that in blood plasma (Wayne et al., 1964), and the daily requirement for iodine of cows successfully weaning their offspring is five-fold that of non-lactating, non-pregnant cows (Campbell, 1983). However, the quantity of iodine in cows' milk varies greatly, from being deficient for calves, to being excessive for human consumers (Hemken, 1980; Underwood, 1981; McDowell, 1992). This is because subclinically deficient cows produce milk deficient in iodine, although sufficient in energy, protein, and other nutrients. Domestic ungulates have been selectively bred for production of meat and milk, which has been possible by virtue of supplementing their supply of iodine. I suggest that, in wild ungulates, the mother takes priority in providing for her own thyroid, partly by delaying her reproductive attempts until she has access to sufficient iodine to support offspring.

Iodine is the micronutrient most frequently deficient among domestic ungulates worldwide, despite their relatively small brains (Underwood, 1981; McDowell, 1992). Mild clinical deficiency of iodine, undiagnosed in adults, produces goitre in neonates, and goitre in adults produces mortality of foetuses and neonates (Sauchelli, 1969; McDowell, 1992). My inference from a voluminous veterinary literature is that reproductive rates may be reduced by subclinical deficiency which does not necessarily produce ill-health in adult cattle and sheep. No other micronutrient appears to affect either brain function and development, or reproduction, to the degree that iodine does.

ENVIRONMENTAL SUPPLY OF IODINE

Recent data have shown that potable ground water under dry climates in southern Africa is rich in iodine on average, even in areas of Kalahari sand (Table 1), and that concentrations vary greatly among adjacent aquifers (CSIR, 1982). This suggests that the provision of artificial bores has boosted the original availability of a valuable supplement of iodine for herbivores. In order to understand the potential power of this mode of supplementation of a megacatalyst in wildlife management, one must understand the limitations on the supply of iodine to terrestrial ecosystems in general.

Iodine nutrition is precariously balanced, because of the narrow tolerances of this potentially toxic nutrient in animal bodies, and the boosting of requirements by goitrogens and other antagonistic substances, ranging from simple elements to complex organic compounds (Stewart and Pharoah, 1996; Oliver, 1997). Slight excess of iodine (absolute or relative to other elements) may produce similar effects to its deficiency (Hetzel and Maberly, 1986). Although the thyroid stores a certain amount of iodine, this delays deficiency by only weeks or months, once daily intakes become deficient.

Availability of iodine from plants

No data appear to be available for the concentrations of iodine in plants eaten by elephants or other herbivores in elephant habitats, or the proportions of iodine derived from soil as opposed to atmosphere. However, wild plants are likely to be a deficient source of iodine, because of the inutility of iodine for their metabolism. Land plants have no reason to translocate iodine from roots to foliage, except possibly in mutualism with their consumers (e.g. in domestication). Certain crops selectively bred as human foods are possibly among the few plants conveying iodine from soil to leaves and fruit. Because iodine is incorporated by land plants mainly from the atmosphere, partly *via* precipitation intercepted on foliage and stems (Whitehead, 1984), this element is likely to reach fibrous tissues, other than bark, in minimal concentrations. Perhaps to compensate for the inevitable passive absorption of certain amounts of iodine, many plant genera produce goitrogenic secondary chemicals, which reduce the amount or effectiveness of iodine taken up by the thyroid, thus boosting requirements for iodine several-fold in domestic herbivores (WHO, 1996; Milewski and Diamond, in press).

Human requirements for iodine are met mainly from non-plant sources: sea food and bovine milk (Hetzel and Maberly, 1986; WHO, 1996). Artificially iodized salt has demonstrated the potential simplicity of supplementation of iodine, but deficiency prevails in many human populations because of political factors (Stewart and Pharoah, 1996). Several species of cultivated herbaceous plants have sufficient iodine relative to goitrogens, as foods for humans (Sauchelli, 1969; Oliver, 1997). Elephants frequently risk their lives to raid human crops (Spinage, 1994), possibly because these are profitable sources of iodine compared to wild plants (Table 2). However, many species (e.g. legumes, brassicas, cassava, sorghum) remain goitrogenic even after selective breeding for

Table 1. Mean concentrations of iodine in potable ground waters from natural springs and artificial bore holes, under dry climates far inland but not separated from the sea by high mountains. Salt refers to total dissolved solids except where asterisked (sodium only), using sea water for comparison. Sources are CSIR (1982), McCaffrey (unpubl.), and sources cited by Milewski and Diamond (in press).

Source of water		Dissolved content	
		Iodine [mg/l]	Salt [mg/l]
Sea		0.05	34,500
Southern Africa:			
Springbok Flats, north of Pretoria (rainfall ca 700mm/year)			
	Ecca shale	0.07	<1,100*
	Irrigasie shale	0.12	<3,570*
	granite	<0.01	<300*
Southeast Namibia (rainfall 150-350 mm/year)			
	Kalahari sand	0.10	826
	quartzite	0.10	987
	sandstone	0.14	1,440
	gravel	0.09	530
	granite	0.37	1,200
Central Australia:			
west and northwest of Alice Springs		0.25	1,060
border, Northern Territory/South Australia		0.05	1,090
mound springs, south and west of Lake Eyre		0.1	1,000

agriculture (Stewart and Pharoah, 1996; WHO, 1996). Partly for this reason, deficiency of iodine remains widespread in human populations which rely on plant foods, even near the coast (WHO, 1996).

The iodine cycle

It is time for wildlife ecologists to assess the degree to which the elusiveness of iodine on land, and its redundancy in the sea, have limited herbivory (Milewski and Diamond, in press). Analytical techniques may soon be available and affordable for an element found in extremely small concentrations, and able to diffuse through plastic (Plant et al., 1996).

The mobility of iodine explains its continual supply and depletion at the land surface. A combination of solubility (as iodide) and volatility (as elemental iodine and methyl iodide) ensures that concentrations of iodine occur naturally only in certain situations. Iodine is easily leached, and is lost into the atmosphere once exposed to oxygen and light, and certain microbes found in acidic substrates (Whitehead, 1984). Iodine is rapidly and thoroughly absorbed by the body from food and water, but is also eas-

Table 2. Potential sources of iodine for elephants, showing the importance of ground water where this is available. Assumptions are that an average adult elephant of body mass 3,000 kg requires 10 mg of iodine per day, eats 30 kg/day dry matter, and drinks 30 litres/day of water. Quantity required/day is a maximum, based on iodine being supplied only by the substance in question. Real quantities required would be less than the stated values, in proportion to the contributions of various substances via oral consumption, and potentially also percutaneous absorption.

Substance		Iodine [mg/kg]	Quantity required/day	Comment
Organic matter (dry state):				
	Cultivated herbaceous leaves	0.3	20 kg	incurs risk
	Goitrogenic wild leaves	0.2	>60 kg	requires suppl.
	Seaweed	500	12 g	ample
	Marine organic sediment	50	120 g	inaccessible
Rocks and soils:				
	Volcanic rock	0.1	60 kg	impossible
	Shale	5	1.2 kg	impracticable
	Sandstone	0.1	60 kg	impossible
	Selected soil	8	0.75 kg	possible
	Salt crust in volcanic cave	1,000	6 g	ample
Waters:				
	Sea water	0.05	120 l	too saline
	River/ground water in moist areas	0.003	2,000 l	impossible
	Melted snow	0.002	3,000 l	impossible
	Ground water in dry areas	0.1	60 l	possible

ily lost in urine (Wayne et al., 1964; Prasad, 1978; Stewart and Pharoah, 1996).

The main supply of iodine to terrestrial ecosystems is atmospheric, decreasing with distance from the coast, and with altitude (Whitehead, 1984; Stewart and Pharoah, 1996). Gaseous and aerosol iodine are deposited in rain, but rapidly drained back to the sea (Whitehead, 1984). Iodine deficiency is widespread among humans living in mountains and along floodplains of major rivers. The melting of glaciers can thus deplete iodine profoundly across whole landscapes, as indicated by modern deficiency in areas last glaciated thousands of years ago (Hetzel and Maberly, 1986).

Iodine is potentially enriched on land relative to sodium chloride, because iodine is exceptionally volatile at the sea surface, and aerosol is fractionated in favour of iodine (Whitehead, 1984). Iodine accumulates in soil organic matter, perhaps by virtue of its uninvestigated use as a nutrient by fungi, as much as from its passive uptake by plant roots. However, iodine incorporated in humus is exposed, like nitrogen, to depletion by fire. Iodine is not known to be replenished by microbes such as those which actively concentrate atmospheric nitrogen (Oliver, 1997).

Although the cycling of iodine is imperfectly known, several anomalies may be explained by the hypothetical supply of this element to continental interiors by repeated volatilization of iodine from the land surface (Fuge, 1996). Salinas (e.g. Kalahari pans) accumulate sodium chloride of ultimately marine origin, but the accompanying iodine tends to accumulate in subsurface brine toxic to herbivores. Concentrations of iodine found recently in potable ground water in the dry interiors of southern Africa and Australia (see Table 1) appear to have no precedence in well-studied North America. This reflects the blockage of iodine from sea air from reaching the dry interiors of Asia and the Americas, by mountain barriers (Fuge, 1996). Iodine tends to accumulate in alkaline earths, because of its conversion to iodate, which does not easily volatilize (Whitehead, 1984; Fuge, 1996). The apparent tendency for limestone areas to be deficient in iodine (Edmunds and Smedley, 1996; Fuge, 1996) may be a result of poor volatilization from the ground surface, hence poor absorption from the atmosphere by plants (R.Fuge, pers. comm., 2000). However, iodate is available in natural mineral licks, possibly explaining much of the geophagia (earth-eating) observed in elephants and other herbivores (Bowell and Ansah, 1994).

The nutritional value of ground water

The greatest concentration of iodine relative to salts in ground water appears to have been achieved in those dry areas receiving considerable input of gaseous iodine. Potable ground water in most of Namibia contains on average double the concentration of iodine, at less than 5% of the concentration of salt, found in sea water (CSIR, 1982), including areas far too far inland to receive marine aerosol (see Table 1). This suggests that ground water over a wide area of the interior of southern Africa may contain an average of 0.1 mg/l of iodide, equivalent to the sufficient concentrations in milk, and the dry plant matter eaten by non-lactating cattle (Underwood, 1981; WHO, 1996). Under modern conditions, the ubiquity of artificial bores may allow ungulates in dry areas routinely to obtain as much iodine from drinking water as from food (see Table 2). Ground water may be as valuable a supplement of iodine inland as seaweed is at the coast (Underwood, 1981; Whitehead, 1984). It is unknown whether natural springs far inland produce iodine-rich water for native herbivores, or whether elephants utilize iodine-rich springs.

ARE EXTREMELY LARGE MAMMALS PRONE TO DEFICIENCY OF IODINE?

Although the scaling of nutrient requirements with body size has been neglected in wildlife ecology, one study of domestic herbivores suggests that a widening disparity between micronutrients, including iodine, and other food resources may arise with increasing body mass (Milewski and Diamond, in press). Use of energy, protein and water all scale to the logarithmic exponent of ca 0.75 when daily total requirements of the body are plotted against adult body mass among species of mammalian herbivores (Calder, 1984). Requirements for iodine are poorly known for wild ungulates, and unknown for any species larger than cattle. However, food intake and thyroid size indicate that nutritional allometry affects the requirements for iodine by the largest species.

Rate of consumption of food relative to body mass decreases four-fold with increasing body mass of ungulates (Owen-Smith, 1988). The proportion of the diet consisting of fibre also increases with increasing body size, because even the elephant trunk is less efficient than small mouthparts in selecting the smallest, least ligneous part of plants. Large herbivores compensate partly by releasing energy from cellulose to a degree thermodynamically uneconomical for even those small herbivores with elaborate fermentation chambers in their guts (Owen-Smith, 1988). However, I suggest that elephants risk iodine deficiency if they do not supplement the limited quantity and quality of plant matter they eat, with respect to this element.

Scaling of thyroid mass (Quiring, 1938; Calder, 1984) and requirements for iodine (Smith, 1980, 1981) among herbivores follow an allometric exponent of ca 0.9, exceeding those of other metabolic organs (adrenal, liver) as well as those of metabolism and food intake. Brain and thyroid mass are relatively great in elephants, despite their relatively low body temperature (Quiring, 1950). Based on available data, the thyroid mass of the African elephant is double that predicted for a herbivore of its body mass (Milewski and Diamond, in press).

The biogeography of proboscideans in relation to iodine

Any allometric tendency for iodine to be most deficient in the largest herbivores would be critical, because of regimes of predation by modern humans. It is anomalous that elephants survive only on two continents, in view of their wide distribution only 10,000 years ago. Climate changes, and extermination by humans, are only partial, and proximate, explanations of their sudden disappearance in the Americas and temperate Eurasia, in view of the survival of proboscideans through several previous glacial cycles, and through the era of domestication in Africa and parts of Asia. I suggest that an ultimate explanation is nutritional: megaherbivores in periglacial areas had a precarious iodine sufficiency, which failed at the end of the last Ice Age with the combination of widespread melting and leaching, and competition for the remaining sources of iodine with predatory and technologically advanced humans. The affinity of proboscideans for islands, on which they have been among the most successful of mammalian colonizers (Johnson, 1980), is consistent with the importance of iodine. Most of the Americas is likely to be relatively poor in iodine, because the Rockies and Andes are not only deficient, but have isolated the dry interiors (e.g. Great Basin desert, Sonoran desert, Monte desert) from atmospheric iodine (see Whitehead, 1984). Furthermore, both the mountains and most areas above latitude 35 degrees (north and south) were glaciated in the Pleistocene. Most of low-altitude North and South America is drained by rivers arising in mountain snows, and tropical South America is additionally leached by heavy rainfall.

When humans developed the tools routinely to kill healthy adults of even the largest species of elephantids, only species with maximal fecundity and maximal intelligence survived. Many species of megaherbivores (e.g. ground sloths) with both small brains and slow reproduction had survived natural predation, but were hunted to extinction by humans at the start of the Holocene (Milewski and Diamond, in press). If extant elephants exceed extinct proboscideans in relative brain (and thyroid) size in response to selective pressure by human predation, the cost in terms of iodine may be unaffordable in many environments.

I suggest that southern Africa provided a particularly suitable environment for elephants, because of its topography and freedom from past glaciation. The African plateau is uplifted and dissected enough to produce leakage of ancient ground water at the surface, without having mountains high enough to block the atmospheric supply of iodine. Before the advent of artificial bore holes, herbivores far from the sea depended on scattered patches of earth impregnated with iodate, and possibly natural springs and termitaria. Thus, original populations of elephants may have been sparser, reproducing at lesser rates, than those in several conservation areas in southern Africa today.

SUPPLEMENTATION OF IODINE BY ELEPHANTS

I hypothesize that elephants rely on three concurrent pathways of intake of iodine:

1) rapid consumption of plants, favouring species and plant parts with maximum ratios of concentration of iodine to goitrogens,
2) routine oral consumption of inorganic supplements, by geophagia and drinking of mineralized water, and
3) absorption of iodine through the complex

skin, by wallowing, bathing, and spreading dust on the wet body.

Evidence of iodine in geophagia by elephants

Geophagia appears to be normal behaviour of elephants in most of their habitats (Sikes, 1971; Hanks, 1979; Spinage, 1994). Generations of elephants have excavated large caves on volcanic slopes in East Africa, by consuming salt crusts precipitated by seepage of ground water on rocks within, where the iodine content is protected from light and heat. The concentration of iodine attained (ca. 1,140 mg/kg, Bowell et al., 1996) in this supplement rivals that in seaweed (Whitehead, 1984), and is more than 100-fold the mean concentrations of iodine in the richest rocks or soils (Milewski and Diamond, in press). Water rich in iodine outside the caves is contaminted with fluoride, which becomes less concentrated as iodine becomes more concentrated, in the formation of salt crusts in the caves (Bowell et al. 1996).

Although megaherbivores may depend to an extreme degree on iodine extraneous to their food, even medium-size herbivores may show geophagia for this nutrient as much as for any other. Neglect of iodine in the many published analyses of mineral licks may help to explain the generally inconsistent compositions of earths eaten, and the emphasis, partly by default, on sodium in the literature (e.g. Weir, 1972; Jones and Hanson, 1985).

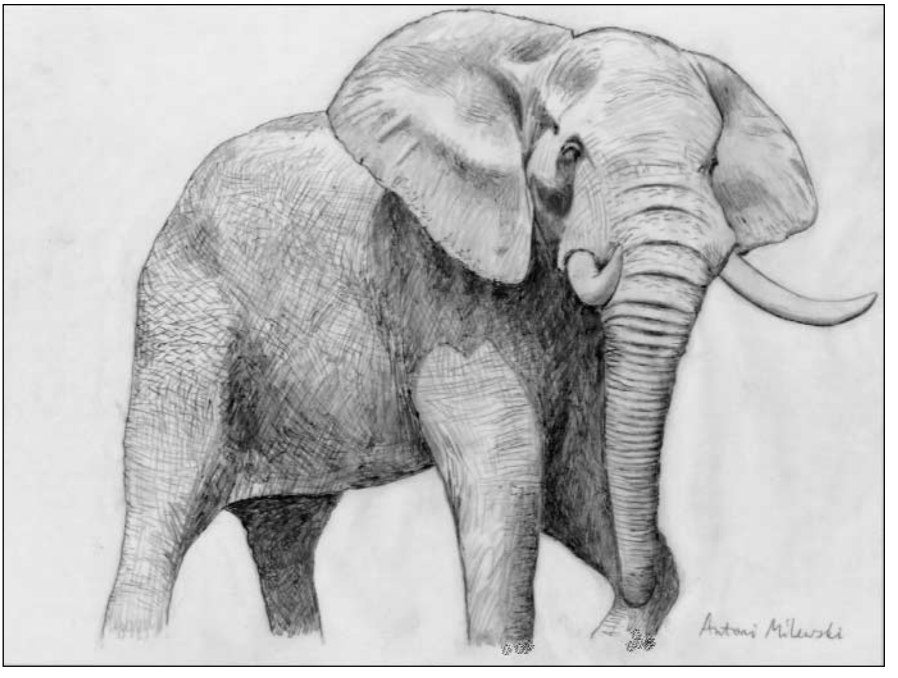
Drinking of iodized water by elephants

Where iodized ground water is available, drinking is likely to be as efficient a means of supplementing iodine as is geophagia, because of the relative quantities which can be consumed. For example, ground water in the area where elephants utilize large caves (Bowell et al., 1996) is at least 50-fold richer in iodine than the worldwide average for ground water (Edmunds and Smedley, 1996), despite the poverty of basalt for iodine. Iodine is concentrated a further ten-fold in water percolating into the caves to evaporate (forming the iodine-rich salt crust eaten by elephants here), and up to 100-fold in the saline pore waters of surface soils also utilized for geophagia in the general vicinity of the caves (Bowell et al., 1996). At this location, even non-saline surface pools have concentrations of iodine exceeding those of sea water ca. ten-fold, suggesting an additional potential for supplementation of iodine by immersion of the body.

Percutaneous absorption of iodine by elephants

The complex skin of the African elephant constrasts with its simple gut, and is potentially an organ of nutrition as well as thermoregulation. Although wallowing has usually been assumed to control ectoparasites, it is paradoxical that the elephant skin is so complicated as to provide refuge for parasites, and so well vascularized and enervated that elephants are vulnerable to mosquitoes, and do not tolerate oxpeckers (Maclean, 1985; Spinage, 1994). Folding, wrinkling and papillation of the dermis, and the sizes of ears, trunk, tail, and genital organs, compensate for the allometric reduction of the ratio of surface area to body mass which accompanies increasing body size (Calder, 1984). Percutaneous absorption has an advantage over drinking, in reducing the inevitable margin of loss of iodine in urine, and possibly excluding fluorine.

Iodine in topically applied iodophor disinfectants is proven to diffuse rapidly through the intact epidermis into the blood, increasing the supply of iodine to thyroid and milk of domestic ungulates (Hemken, 1980). In human infants, this inadvertent supplementation is sometimes so great as to be toxic (Cohen, 1996). Iodide is known to diffuse slowly through micropores in wet skin (Milewski and Diamond, in press), which may be significant relative to oral consumption where pools are too saline or contaminated to be potable. However, I suggest that conversion of iodate (likely to be available in surface mud) to methyl iodide (volatile enough to penetrate skin), is promoted by microbes harboured in the acidic microenvironment of skin folds, based on processes known to occur in soils (see Whitehead, 1984).



Nutrient control as a means of population control?

Populations of apparently healthy elephants are flexible in their reproductive rates (2-7% per year), partly because elephants exceed medium-size herbivores in the variation of age at onset of sexual maturity, and of intervals between pregnancies (see Owen-Smith, 1988; Whyte et al., 1998). If reproductive rates reflect the supply of key resources as I hypothesize, population increases may be minimized by enforcing subclinical deficiency of iodine, at levels calculated to ensure minimum distress in adults and offspring. Conversely, where elephants have been recently reintroduced, or the habitat is deficient in iodine, managers may find that artificial supplementation with iodine boosts reproduction. Populations can possibly be maintained static in the long-term at reproductive rates of ca. 3% per year, balanced by episodic natural mortality on an acceptable scale. The water supply offers a way of controlling reproductive rates of elephants without affecting smaller herbivores to the same degree. Available data suggest that adjacent bore holes may have iodine concentrations ten-fold different (CSIR, 1982), potentially allowing the deliberate reduction or increase of the supply of iodine to elephants, by the appropriate selection of water points.

The literature on iodine deficiency in humans and cattle differs in emphasis, and in neither case quantifies effects on reproductive rates directly. The best-known effects of iodine deficiency are on development and function of the brain in humans, and on the viability of offspring in cattle selectively bred for fecundity and rapid growth. Human culture may obscure the biological effect of iodine deficiency on human reproductive rates, whereas the relative decephalization of cattle may reduce effects on bovine intelligence.

In Hwange National Park in Zimbabwe, the combination of sandy soils and dry climate suggests that ground water has been a critical resource for wildlife, and elephants here are known for their attraction to sodium-rich earths and bore waters (Weir, 1972). At both Addo and Knysna in South Africa, small populations of elephants were spared a half-century ago, followed by opposite reproductive trends after effectively being cut off from the coast. In Addo National Park, the dry climate and brackish ground water suggest that bore hole establishment provided a critical supply of iodine at the time the population was confined by fencing.

RECOMMENDATIONS FOR FURTHER RESEARCH

The remarkable frequency and impact of iodine deficiency in humans and cattle indicates the potential importance of iodine deficiency in elephants, which are highly encephalized, and apparently reproduce as rapidly as is possible for land animals of their body size. The possible allometric divergence between iodine and other nutritional factors, and the extreme selective pressure on megaherbivores at the end of the Pleistocene, add to the likelihood that iodine is a controlling nutrient for populations of the largest herbivores. However, this proposal remains mainly circumstantial until tested.

Basic surveys are required: of concentrations of iodine in waters, earths, and muds utilized for drinking, bathing and wallowing; of concentrations of iodine and goitrogens in woody plants and bark; and of relative brain and thyroid sizes of extinct proboscideans. Experiments need to be performed: on preference for iodine-rich water sources; on passage of iodine from mud, through skin, into blood; and on the long-term effect of subclinical deficiency on reproductive rate. Assumptions should be tested: of the greater incidence of surface sources of iodine inland in Africa and India than elsewhere; of relatively great requirements for iodine by the large thyroids of elephants; and of the greater requirements for iodine by extant than by extinct species of proboscideans. The following are suggested research topics in this context:

- Verification of the concentration of iodine in bore water artificially provided in conservation areas.
- Quantification of the contributions of bore holes, natural mineral licks, and natural springs in parts of northern Botswana where elephant populations have increased rapidly in the last two decades.
- Verification of percutaneous absorption of iodine by elephants (e.g. utilizing isotopes as markers), including whether micropores enhance capillarity and diffusion of iodide, and whether microbial symbioses in skin folds enhance generation of methyl iodide and other volatile forms of iodine.
- Quantification of the mass-balance of iodine in the elephant body, by characterization of thyroid mass according to sex and age, concentration of iodine in the thyroid, and rates of loss of iodine in urine and faeces (see Mahaney and Hancock, 1990).
- Investigation of the incidence of goitre in relation to iodine supply, in captive populations of elephants.
- Evaluation of the availability of iodine from various tissues of woody plants, by analysis of concentrations (including bark and shed leaves), and quantification of the incidence and effects of goitrogens, e.g. cyanogenic glycosides.
- Quantitative analysis of the effects of subclinical deficiency of iodine in reducing rates of oestrus, ovulation, conception, pregnancy, birth, lactation, and weaning in elephants, in comparison to other ungulates including equids.
- Experimentation on the effects of supplemental iodine in triggering musth in male elephants.
- Preference by elephants for water rich in iodine over water poor in iodine, when presented with a choice of drinking waters in captive and free-range situations.
- Comparison of cranial volumes of extinct and extant species of proboscideans, to test the possible increase of brain sizes relative to body sizes in response to increased predation pressure from humans in the late Pleistocene.

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REFERENCES

Bauchot, R. (1978) Encephalization in vertebrates. *Brain, Behav. and Evol.* 15, 1-18.

Bowell, R.J. and Ansah, R.K. (1994) Mineral status of soils and forage in the Mole National Park, Ghana, and implications for wildlife nutrition. *Environ. Geochem. Health* 16(2), 41-58.

Bowell, R.J., Warren, A. and Redmond, I. (1996) Formation of cave salts and utilization by elephants in the Mount Elgon region, Kenya. In: *Environmental geochemistry and health with special reference to developing countries* (Ed. J.D. Appleton, R. Fuge and G.J.H. McCall). Geological Society of London Special Publication no. 113, pp. 63-80.

Calder, W.A. (1984) *Size, function and life history*. Harvard University Press, Cambridge, Massachusetts.

Campbell, E.A. (1983). Animal health in Australia, vol. 3: *Nutritional deficiencies and diseases of livestock*. Australian Bureau of Animal Health.

Cohen, B.A. (1996) Pediatric dermatology. In: *Cutaneous medicine and surgery: an integrated program in dermatology*, vol. 2 (Ed. K.A. Arndt, P.E. Le Boit, J.K. Robinson and B.U. Wintroub), chapter 184. W.B. Saunders, Philadelphia, pp. 1889-1899.

CSIR (1982) ‘n Waterkwaliteitskaart van die ondergrondse waters in Suidwes-Afrika, met spesifieke verwysing na die benuttingswaarde van die water. Regional Lab., National Institute for Water Research, Council for Scientific & Industrial Research, Windhoek.

Edmunds, W.M. and Smedley, P.L. (1996). *Groundwater geochemistry and health: an overview*. In: Environmental geochemistry and health with special reference to developing countries (Ed. J.D. Appleton, R. Fuge and G.J.H. McCall). Geological Society of London Special Publication no. 113, pp. 91-106.

Fuge, R. (1996) Geochemistry of iodine in relation to iodine deficiency diseases. In: *Environmental geochemistry and health with special reference to developing countries* (Ed. J.D. Appleton, R. Fuge and G.J.H. McCall). Geological Society of London Special Publication no. 113, pp. 201-212 .

Hanks, J. (1979) *A struggle for survival: the elephant problem*. Struik, Cape Town.

Hemken, R.W. (1980) Milk and meat iodine content: relation to human health. *J. Am. Vet. Med. Ass*. 176 (10), 1119-1121.

Hetzel, B.S. and Maberly, G.F. (1986). Iodine. In: *Trace elements in human and animal nutrition*, vol. 2 (Ed. W. Mertz). Academic Press, Orlando, pp. 139-208.

Johnson, D.L. (1980) Problems in the land vertebrate zoogeography of certain islands and the swimming powers of elephants. *J. Biogeog.* 7, 383-398.

Jones, R.L. and Hanson, H.C. (1985) *Mineral licks, geophagy and biogeochemistry of North American ungulates*. Iowa State University Press, Ames, Iowa.

Lee, J. and Knowles, F.G.W. (1965) *Animal hormones*. Hutchinson University Library, London.

Maclean, G.L. (1985) *Roberts’ birds of southern Africa*. The Trustees of the John Voelcker Bird Book Fund, Cape Town.

Mahaney, W.C. and Hancock, R.G.V. (1990) Geochemical analysis of African buffalo geophagic sites and dung on Mount Kenya, East Africa. *Mammalia* 54, 25-32.

McCaffrey, L.P. (unpubl.) Distribution and causes of high fluoride groundwater in the western Bushveld area of South Africa. PhD Thesis, 1998. University of Cape Town.

McDowell, L.R. (1992) *Minerals in animal and human nutrition*. Academic Press, San Diego.

McNaughton, S.J. (1989) Interaction of plants of the field layer with large herbivores. Zoological Symposium no. 61. *Zool. Soc.*

Lond. pp. 17-29.

Milewski, A.V. (1999) Iodine as an important nutrient for elephants. *Newsletter of the Zoo Nutrition Center of the Wildlife Conservation Society* (New York) 9, 2-3.

Milewski, A.V. and Diamond, R.E. (in press) Why are very large mammals absent from Australia? A new hypothesis of micronutrients. *J. Biogeog*.

Oliver, M.A. (1997) Soil and human health: a review. *Eur. J. Soil Sc*. 48, 573-592.

Owen-Smith, N. (1988) *Megaherbivores: the influence of very large body size on ecology*. Cambridge University Press, Cambridge.

Plant, J.A. and Raiswell, R. (1983) Principles of environmental geochemistry. In: *Applied environmental geochemistry* (Ed. I. Thornton). Academic Press, London, pp. 1-39.

Plant, J.A., Baldock, J.W. and Smith, B. (1996) The role of geochemistry in environmental and epidemiological studies in developing countries: a review. In: *Environmental geochemistry and health with special reference to developing countries* (Ed. J. D. Appleton, R. Fuge and G. J. H. McCall). Geological Society of London Special Publication no. 113, pp. 7-22.

Prasad, A.S. (1978) *Trace elements and iron in human metabolism*. Plenum Medical Book Co., New York.

Quiring, D.P. (1938) A comparison of certain organ and body weights in some African ungulates and the African elephant. *Growth* 2, 335-346.

Quiring, D.P. (1950) Functional anatomy of the vertebrates. McGraw-Hill, New York.

Sauchelli, V. (1969) *Trace elements in agriculture*. Van Nostrand Reinhold, New York.

Shkolnik, M. (1984) *Trace elements in plants*. Developments in Crop Science 6. Elsevier, Amsterdam.

Sikes, S.K. (1971). *The natural history of the African elephan*t. Weidenfeld and Nicolson, London.

Smith, R.M. (1980) Trace element requirements. *Proc. Nutr. Soc. Aust.* 5, 36-43.

Smith, R.M. (1981) Trace element needs of species in relation to body size. *Proceedings of the Fourth International Symposium on Trace Element Metabolism in Man and Animals*. Australian Academy of Science, Canberra, pp. 9-13.

Sokoloff, L., Fitzgerald G.G. and Kaufmann E.E. (1977) Cerebral nutrition and energy metabolism. In: *Nutrition and the brain*, vol. 1 (Ed. R.J. Wurtman and J.J. Wurtman). Raven Press, New York, pp. 87-139.

Spinage, C.A. (1994) *Elephants.* T. and A.D. Poyser, London.

Stewart, A.G. and Pharoah, P.O.D. (1996) Clinical and epidemiological correlates of iodine deficiency disorders. In: *Environmental geochemistry and health with special reference to developing countries* (Ed. J.D. Appleton, R. Fuge and G.J.H. McCall). Geological Society of London Special Publication no. 113, pp. 223-230.

Underwood, E.J. (1981) *The mineral nutrition of livestock*. 2nd ed. Commonwealth Agricultural Bureaux, Farnham Royal, England.

Wayne, E.J., Koutras, D.A. and Alexander, W.D. (1964) *Clinical aspects of iodine metabolism*. Blackwell, Oxford.

Weir, J.S. (1972) Spatial distribution of elephants in an African national park in relation to environmental sodium. *Oikos* 23, 1-13.

Whitehead, D.C. (1984) The distribution and transformation of iodine in the environment. *Environ. Int*. 10, 321-339.

WHO (1996) *Trace elements in human nutrition and health*. World Health Organization, Geneva.

Whyte, I., van Aarde, R. and Pimm, S.L. (1998) Managing the elephants of Kruger National Park. *Anim. Conserv*. 1, 77-83.