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INSIGHTS

Lust for Salt in the Western Amazon

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ABSTRACT

Although the use of mineral licks by diverse Amazonian birds and mammals is well-known, the ultimate motivation for such behavior remains unclear. As aerosol deposition of salts declines with distance from oceanic sources, lick visitation in the western Amazon can be explained by demand for sodium, given the low concentration of this micronutrient in the plant tissues consumed by these taxa. Sodium limitation also influences ant foraging behavior, and impinges on ecosystem rates of carbon cycling. The biogeographical context of sodium availability has been largely overlooked, but has substantial pantropical implications for herbivore and decomposer performance in inland rain forests.

Abstract in Spanish is available in the online version of this article.

Key words: ant; decomposition; geophagy; herbivory; licks; litter; sodium; vertebrate.

Ecological research in the tropics often involves studies of herbivory. We suggest that an important feature of this plant–animal interaction, namely salt limitation, has been neglected by such studies, and yet has important implications for the physiological condition of herbivores, as well as for litter decomposition and carbon cycling more generally within inland tropical forests. Animals need dietary salt to maintain homeostasis, and exhibit corresponding behaviors to offset metabolic loss of sodium, chloride, and potassium ions (Denton 1982). This phenomenon is particularly pronounced in herbivores, for which dietary ingestion of intrinsically low-sodium plant tissue is often insufficient to meet nutritional requirements (National Research Council 2005). In consequence, taxa as diverse as African elephants (Holdø *et al.* 2002), moose (Risenhoover & Peterson 1986), and mountain gorillas (Rothman *et al.* 2006) seek out dietary supplementation of sodium. The use of mineral licks worldwide is well-documented for ungulates and other herbivorous mammals, although the role of compounds supplemental to sodium cannot necessarily be excluded (Jones & Hanson 1985, Klaus & Schmid 1998). Here, we propose that the diverse vertebrate visitors to the well-known mineral licks of the western Amazon have a common goal of sodium supplementation in a region deprived geographically of salt. Moreover, the outcome of sodium deprivation extends to the phytophagous arthropod community, including key taxa in the decomposition ecology of leaf litter.

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SALT-SEEKING IN THE AMAZON BASIN

Mineral licks of the western Amazon represent premier examples of geophagy; together with mineral-enhanced seepages and pools to which animals are attracted, these sites are known in Spanish as *collpas*, *saladeros*, and *salados*. Known sites on riverbanks to which parrots flock to ingest soil are prominent tourist destinations, and exceed fifty in South America (Brightsmith & Muñoz-Najar 2004, Lee *et al.* 2009). Less appreciated but equally relevant are comparable behaviors at clay and mineral licks reported for Amazonian primates (Ferrari *et al.* 2008, Blake *et al.* 2010), phyllostomid bats (Bravo *et al.* 2008), and various other mammals (see Izawa 1975, Brightsmith *et al.* 2008). Multiple hypotheses not mutually exclusive to sodium seeking have been proposed to explain these behaviors, including the use of clays to facilitate alkaloid detoxification, and medicinal functions of ingested soil (Table 1). Correlational analyses between salt content at licks and attraction behavior cannot rule out such alternative motivating factors. For the iconic geophagy exhibited by Amazonian parrots, however, recent studies have concluded that sodium acquisition is the primary motivating factor. Clay licks occur primarily in the western Amazon, with limited occurrence in the central and northern regions of the basin, but never near the Atlantic shoreline (Lee *et al.* 2009). Analysis of soil content at licks confirms elevated sodium levels (and in some cases magnesium levels) relative to control sites (Brightsmith *et al.* 2008, Powell *et al.* 2009). Geophagy by other sympatric avian taxa, such as columbids and cracids (Brightsmith & Muñoz-Najar 2004), is similarly consistent with sodium seeking associated with obligately phytophagous diets.

TABLE 1. *Non-mutually exclusive hypotheses for mineral lick visitation and geophagy by vertebrates (see also reviews by Kreulen 1985 and Klaus & Schmid 1998).*

Hypothesis	References
1. Detoxification of plant secondary compounds, especially alkaloids	Oates (1978), Gilardi *et al.* (1999)
2. Mineral supplementation of diet, especially with sodium and calcium ions	Jones and Hanson (1985), Powell *et al.* (2009)
3. Acquisition of soil to supplement mechanical grinding in the avian crop	Gionfrido and Best (1996)
4. Zoopharmacognosy, with particular reference to internal parasites and alleviation of diarrhea	Knezevich (1998), Vermeer and Ferrell (1985)
5. Buffering of gastric pH	Oates (1978), Mahaney *et al.* (1999)

Extensive work on bat attraction to salt licks in Amazonian Peru has also implicated sodium deprivation as a motivating factor. Pools and depressions in soil, some of which are created by terrestrial geophagous taxa, are visited by no fewer than 26 species of phyllostomid bats (Bravo *et al.* 2008, 2010b). Water from the bat-visited *collpas* is enhanced in sodium, and (less so) in calcium and potassium; bats prefer to drink water from the lick sites when matched with controls (Bravo *et al.* 2010a). Using nitrogen isotope ratios, Voigt *et al.* (2008) showed that short-tailed fruit bats (*Carollia perspicillata*, Phyllostomidae) with plant-dominated diets were more likely to be captured at salt licks in Ecuador, and concluded that calcium seeking and buffering of plant secondary compounds were likely explanations for this behavior. However, given that plant tissues typically contain orders of magnitude less sodium compared with animals, this finding also supports a conclusion of sodium deprivation among more phytophagous individuals.

Visitors to mineral licks in the Amazon can also be found among some primates and arthropods. Geophagy in New World monkeys is well-documented, but its restricted occurrence in Amazonian as opposed to Central American forests has not been well-understood (Izawa 1993, Campbell *et al.* 2005, Ferrari *et al.* 2008). We suggest that this behavior in frugivorous primates is driven by a search for sodium, and is unlikely to occur in most of lowland Central America or near the South American littoral, given their proximity to oceanic sources. Moreover, ants in the western Amazon favor low-concentration sodium solution relative to either carbohydrate or protein baits, and the intensity of this response varies inversely with distance from oceanic sources at continental scales (Kaspari *et al.* 2008). Inland attraction to sodium is, however, substantially diminished for ant taxa that are predominantly carnivorous, as would be predicted given their animal prey (Kaspari *et al.* 2008). Insects from at least five other orders have also been observed engaging in geophagy at mineral licks in Peru (Brightsmith *et al.* 2008, Molleman 2010). These behaviors are not confined to the tropics; the attraction of some temperate-zone swallowtail butterflies to various sodium salts is well-known (Arms *et al.* 1974).

THE GEOGRAPHY OF SALT

In aggregate, the evidence supporting vertebrate attraction to salt in the Amazon basin is both compelling and geographically constrained. The vast majority of mineral licks utilized by parrots and other vertebrates are in the western part of the basin thousands of kilometers from the Atlantic Ocean. Directly to the west of these sites, the Andean range has precluded influx of marine aerosols from the Pacific since the late Miocene (Graham 2009). Sodium concentrations in Amazonian river waters are accordingly highest at the Atlantic, and decline monotonically with increasing distance upriver (Stallard & Edmond 1981, Tardy *et al.* 2005). This geographical gradient suggests that the western Amazon is salt-deprived, and that an increasing physiological demand for dietary salt supplementation is correspondingly manifested by herbivores at mineral licks. Carnivorous and omnivorous taxa, by contrast, are less likely to be sodium-stressed, and one commonality of all documented vertebrates that visit Amazonian salt licks and *collpas* is a predominantly phytophagous diet.

Altitudinal variation in salt availability may similarly be relevant to animal nutritional ecology, given greater leaching by precipitation at higher elevations. Differential responses of herbivores from lowland and alpine regions may correspondingly ensue (Blair-West *et al.* 1968). The eastern slopes of the Andes should be particularly susceptible to sodium deprivation, to which end an elevational transect of environmental availability would be informative. Water at salt licks consumed by the mountain tapir in Colombia is enhanced in both nitrogen and sodium relative to a control stream (Lizcano & Cavelier 2004), but no further information is available on such behaviors in Andean contexts.

ECOLOGICAL IMPLICATIONS

As behavioral attraction to salt represents a temporary but intentional switch from macronutrient to micronutrient consumption, a number of ecological consequences may ensue. Metabolic costs of movement to mineral licks, together with an opportunity cost in time otherwise spent foraging, indicate net energetic losses. Exposure to predators may ensue at licks, particularly for arboreal taxa that otherwise rarely venture to the ground (Link *et al.* 2010), whereas mixed-species groups visiting salt licks may benefit from an overall enhanced group alertness to potential predators. Although the adverse physiological consequences of extreme sodium deprivation are clear (Denton 1982), chronic effects of suboptimal levels may cascade into other aspects of herbivore ecology, including reproductive and population dynamics (Freeland *et al.* 1985, Batzli 1986). This outcome would pertain to tropical as well as extra-tropical sites that, for reasons of physical geography, are sodium-restricted (*e.g.*, Aumann & Emlen 1965).

Additional contexts can be identified within tropical forests that provide for enhanced sodium. The activity of fungal decomposers concentrates sodium within leaf litter, and also within

decomposing logs (Cromack *et al.* 1977). Chimpanzees in central Africa consume decaying palm pith that is high in sodium (Reynolds *et al.* 2009), and this behavior may be more widespread among primates in tropical forests (Kaplin & Moermond 2000, Pinto & Setz 2004, Rothman *et al.* 2006). Non-trivial consumption of decaying wood has also been noted for spider monkeys at various Amazonian sites (Suarez 2006, Di Fiore *et al.* 2008) and, as with geophagy, is generally confined to the western parts of the basin.

Indigenous Amazonian peoples would also be predicted to seek out dietary supplements of sodium. Kayapó Indians in central Brazil have been reported to burn leaves of three palm species to obtain salt-enhanced ash (Posey 2002), but the geographical distribution of such activity has not been studied.

At the broader ecosystem scale, sodium availability may also influence rates of litter decomposition and carbon cycling in inland tropical forests. Low-level addition of 0.5 percent sodium chloride solution to standardized leaf litter bags in the Peruvian Amazon resulted in a marked increase in termite numbers and in overall mass loss relative to bags treated with stream water controls (Kaspari *et al.* 2009). These effects occurred over a timespan of only several weeks, and were attributed to effects of sodium enhancement alone given results with different salt combinations. Sodium limitations on decomposition in tropical rainforests may in fact be widespread given that approximately 80 percent of such humid regions lie more than 100 km inland. In sodium-limited temperate-zone ecosystems, anthropogenically supplemented salts may also have the potential to alter insect behavior and population growth rates (Braun & Flückiger 1984, Kaspari *et al.* 2010). The consequences of salt supplementation in both tropical and temperate zones represent an intriguing target for experimental work at behavioral and ecological scales.

CONCLUSIONS AND FUTURE DIRECTIONS

Evidence to date suggests that visitation by diverse mammalian and avian taxa to mineral licks in the western Amazon can be at least partially explained by the geographically imposed outcome of sodium deprivation. Alternative hypotheses, and, in particular, detoxification of alkaloids and other toxins, are not necessarily generalizable to the broad diversity of plant secondary compounds consumed by animal taxa, and also do not explain restriction of these behaviors to only the western parts of the Amazon basin. The recently observed geographical gradient in ant behavioral responses to salt baits extends the concept of sodium deprivation to a key invertebrate group, and indicates a more general phenomenon in herbivorous taxa. The Amazon represents the largest tract of inland rain forest on the planet. Identification of sodium as a potentially constraining physiological and ecological factor for herbivores has important implications for animal population dynamics as well as broader features of carbon cycling within this vast region.

To move beyond correlational interpretations of animal foraging behavior at salt licks, additional evidence should be obtained to test the hypothesis of sodium deprivation. For example, demonstration of an inverse relationship between behavioral attraction to sodium and its excretory loss (Holdø *et al.* 2002), as well as differential responses to multiple sodium- and chloride-containing compounds (Blair-West *et al.* 1968, Arms *et al.* 1974), can be used to hone in on particular ions as primary attractants. In the tropical regions characterized by a dry season and reduced deposition of salt via rainfall, behavioral responses to sodium may correspondingly become more pronounced. Inland salt licks at tropical sites in the Old World (Klaus *et al.* 1998, Matsubayashi *et al.* 2007) would also be appropriate for characterization of mineral content relative to herbivore behavior and distance from oceanic sources. In contrast to various alternative hypotheses (see Table 1), we predict sodium deprivation to be the one common factor underlying these otherwise taxonomically and geographically disparate phenomena.

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