Road salt offers insights into the connections between diet and neural development

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Ecologists have long studied how temperature and precipitation generate patterns in the abundance and diversity of life on Earth. Biogeochemistry, moreover, is increasingly seen as a third major driver of ecological pattern from the local to the global scale (1). Shortfalls of any of the 25 or so essential chemical elements—responsible for building tissue, enzymes, and electrolytes—can cause pathology (2). Like temperature and precipitation, these elements can combine to colimit populations and ecosystems, and are nonrandomly distributed across the planet as a result of a variety of natural and anthropogenic drivers (3, 4). Up to now, ecology's focus has been on carbon, nitrogen, and phosphorus—so-called macronutrients—as ecological drivers, given their large contribution to biomass (1). In PNAS, Snell-Rood et al. (5) support a rising tide of evidence showing that micronutrients like sodium (Na) can shape the biology of individuals, communities, and ecosystems. Moreover, the authors suggest that the availability of Na dictates how developing organisms invest in different organ systems. In doing so, they open a new front for ecologists interested in the link between organismal performance and biogeochemistry.

Sodium is unique because it combines relative rarity over much of the terrestrial world with absolute need by animals. Homer called it "the divine substance"; the word salubrious derives from Latin's *salus* for health; Roman soldiers were paid a salar(y)ium to buy sal(t). Sodium's uniqueness likely starts in Earth's deep history. Early cells faced the problem of diffusion: the more a cell accumulated metabolically useful molecules and particles from outside its plasma membrane, the faster water would leak into the cell through that plasma membrane—the familiar process of osmosis. How to keep these primordial cells from bloating and bursting? Probably the first solution, used by microbes and plants, was to build cell walls (6). These walls surrounded the plasma membrane and prevented it from popping despite internal pressures of 10 atmospheres or more (the crunch of an apple results from millions of tiny explosions when cell walls are breached).

Fig. 1. Sodium chloride, a key ingredient of road salt, often accumulates on roadside plants like *Asclepias*. There it acts like a catalyst to development in the caterpillars of the Monarch Butterfly *Danaus plexippus*, promoting the development of thoracic muscles in males and eye size in females. Illustration by D. Kaspari.

Animals, instead, exploited diffusion's numbers game; osmosis ceases when the number of particles on either side of the membrane is equalized. The challenge was to find a particle that was unnecessary to run the cell and could hence be ejected without depleting an essential metabolite. Na—ionic and abundant in ocean water—fit the bill. Sodium-potassium pumps ejected 3 Na out of the cell for every 2 K pumped in. Embedded in cell membranes, Na-K pumps generated a salty interstitial fluid that bathed animal cells, inhibiting osmotic leakage and performing a variety of other useful functions. Na-K pumps allowed for the construction of multicellular, flexible (and hence mobile) heterotrophs, a rather successful design in the history of life on Earth.

Ecologists are increasingly fascinated with the Na-K pump, a Faustian bargain that ties organismal performance to environmental sodium stocks (3, 7–9). Na-K pumps are costly in a variety of ways (10). First, as much as one-third of the resting ATP budget of an animal cell can go into running Na-K pumps. Second, we animals have a hard time hanging onto sodium; because we constantly dump it into our interstitial fluids we are also constantly excreting it. Finally, plants are virtually sodium-free compared with the animals that consume them (11). Plant-eaters need to hunt and ingest adequate quantities of sodium even as they constantly leak it in their pee, sweat, and feces.

Snell-Rood et al. (5) studied how a common activity in the industrialized northern regions—applying road salt when the weather gets icy—affects the plants that grow along roadsides and the butterflies that depend on them for food. The authors made three significant discoveries.

The first finding deals with the distribution of sodium in the butterfly's environment. Biogeochemistry's role in ecology plays out at

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a variety of spatial scales. At the continent scale, sodium inputs from aerosols decline exponentially with distance from the ocean (4). Within a landscape, sandy soils lose sodium faster than clay soils (3) and plants passively accumulate Na given its similarity in size to plant-essential K ions (11). Snell-Rood et al. (5) worked in a sandy Minnesota savannah far inland from the ocean, what should be a Na-poor ecosystem. The authors revealed considerable variability in the sodium content of four common potential food plants. The four differed only approximately twofold in sodium content on control prairies, but varied nearly 10-fold in sodium next to salted roads. The milkweed *Asclepias*, a host plant for Monarch butterflies (Fig. 1), was the big sodium accumulator. It is unclear why the four plants varied in uptake ability. There are many possible mechanisms (11), and which ones predominate has implications for the availability of Na to prairie herbivores. The authors suggest one possibility: *Asclepias* leaves are covered with hairs that may catch and hold aerosol minerals. If furry leaves are more likely to accumulate sodium from road salt, or a good spray of bison urine (9), then accumulated Na would act primarily to attract Na-deprived herbivores, a bad deal for the plant. However, there is another possibility. If *Asclepias* harvest significant quantities of Na through their roots (11) they can spike their nectar with sodium and attract Na-craving pollinators, like butterflies (12) and social insects (13). Increases in pollination may make up for any loss, fitness-wise, to herbivory. The distribution and implications of Na in nectar are ripe for exploration.

Second, a growing body of work shows that Na-shortfall inhibits organisms and ecosystems. Salt-craving moose risk icy waters to get salty aquatic plants (7); crickets engage in cannibalism to acquire salty flesh (8). The western Amazon is the home of old leached soils: when fertilized with water mimicking Na-rich coastal rain, detritivore densities and decomposition rates both increase (9, 10). However, Snell-Rood et al. (5) point to a new and underappreciated effect of sodium limitation: sodium may also be a catalyst for development (Fig. 1). Monarch caterpillars raised on roadside milkweeds bioaccumulated six times more Na than control populations. Cabbage white caterpillars also bioaccumulated when raised on a laboratory diet with high Nacontent. Both species of caterpillars invested more in Na-rich tissues when on a high Na diet: males built more thoracic muscle and females built bigger eyes. In similar fashion, human cravings for salt peak in adolescence

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(14), at the same time as the volume of frontal, parietal, and temporal gray matter reaches its maximum (15). Although their findings are still preliminary, Snell-Rood et al. (5) show that traits with clear effects on performance may show norms of reaction along gradients of sodium, a new and exciting front in "Eco-Devo" (16).

A third twist to this story is that larvae of both butterfly species suffered higher mortality on high Na diets. This result comes with a proviso. Butterflies can discriminate foods by their saltiness (12) but in both experiments individual caterpillars were provided with only one Na dose; they could not self-regulate Na intake relative to other nutrients. If the caterpillars provided high Na foods had also been offered low Na foods, these mortality differences may have thus attenuated. However, at least one other such study found that colonies of ants given a range of Na-rich foods still appeared to "overdose" when high Na foods were provided ad libitum (17). When resources are in chronic short supply, perhaps the benefits of resource bonanzas are so rare that organisms lose the ability to say "enough."

A reading of Snell-Rood et al. (5) suggests many productive lines of research. Here are two. First, because coastal habitats are less Na-limited (13), do coastal butterfly populations produce males with larger thoraces and females with larger eyes compared with their inland cousins? If so, biogeochemists may want to start a conversation with neurobiologists (see also ref. 18). Second, road salt is considered a pollutant to aquatic systems (19) but can also supply terrestrial consumers with a much needed nutrient (7, 20). In this era of tightening research budgets, a fertilization experiment, geographically replicated throughout the temperate and boreal regions of Earth, is waiting to be exploited: a grand latticework of salted roads.

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