

Salt Gland Secretion by an Intertidal Lizard, *Uta tumidarostra*

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Many groups of reptiles possess cranial exocrine glands that supplement renal ion excretion by secreting highly concentrated salt solutions. In lizards, these salt glands are lateral nasal glands and are found in some or all members of several families (Dunson, 1976). Many herbivorous lizards (e.g., *Dipsosaurus*, *Sauromalus*, and *Uromastix*) have well-developed salt glands, and these glands secrete primarily potassium chloride (Dunson, 1976). Some lizards can also secrete bicarbonate in addition to chloride as the anion, though chloride generally predominates (Dunson, 1976). Insectivorous species possessing salt glands also secrete potassium chloride. Exceptions are found in species in marine habitats with high NaCl diets (e.g., *Amblyrhynchus*). We investigated salt gland secretion by a recently described intertidal lizard.

Grismer (1994) described the morphology, diet, and habitat of the insular side-blotched lizard *Uta tumidarostra* and its two close relatives, *U. encantada* and *U. lowei*, found on three islands of the Islas Encantadas Archipelago off the east coast of northern Baja California, México. These islands have little vegetation and, hence, few terrestrial arthropods. The lizards are found primarily in the intertidal zones of the islands, and a substantial component of their diet is the intertidal isopod *Ligia occidentalis*. All three species have enlarged rostral regions containing nasal salt glands that are nearly five times larger than the nasal glands of other *Uta*. A diet high in intertidal crustaceans would have high levels of sodium chloride, and there is little or no fresh water available on the islands to assist renal excretion of electrolytes. We hypothesized that the salt glands of these lizards secrete primarily sodium chloride and are responsible for a large proportion of the lizards' daily electrolyte excretion. We measured rates of secretion by the salt glands of freshly captured *U. tumidarostra* and a closely related insectivorous mainland species, *U. stansburiana*, and estimated the importance of the salt gland for electrolyte secretion. *Uta tumidarostra* secreted substantially more sodium than did *U. stansburiana*, and the salt gland of *U. tumidarostra* excretes at least a third of the salt intake.

MATERIALS AND METHODS

Uta tumidarostra (n = 50) were collected from Isla Coloradito, Baja California; and *U. stansbu-*

riana were collected from the adjacent Bahía de San Luis Gonzaga, Baja California (n = 6), and from inland Southern California (n = 20). Lizards were released at the capture sites. Salt gland secretion rates were measured by collecting secreted salt immediately after capture. Lizards were weighed and placed individually in collecting chambers (32 × 17 × 9 cm plastic boxes with raised wire mesh floors) for 24 h. Temperature ranged daily from 23–37 C for the Baja California animals; Southern California animals were kept in a controlled temperature chamber at 35 C. Secreted salt crystallized on the nares and then fell through the mesh to the bottom of the chamber. Salt could easily be separated from feces and urate and was swept into vials for later analysis. Salt gland secretions were dissolved in 1.0 mL of glass-distilled water and analyzed for sodium, potassium, and chloride using a Beckman flame photometer and a Buchler-Cotlove chloridometer.

About 100 *L. occidentalis*, the primary food item for *U. tumidarostra*, were collected from the intertidal zone of Bahía de San Luis Gonzaga, weighed, dried to constant mass, and finely ground. One portion of dried *Ligia* was hydrated with glass-distilled water and analyzed for sodium, potassium, and chloride. Energy content of another portion was measured via bomb calorimetry.

Data were analyzed using STATISTICA 4.1 (StatSoft, Inc., 1994, unpubl.) for the Macintosh. Samples for three lizards (two *U. tumidarostra*, one *U. stansburiana*) were apparently contaminated (NaCl about 2.5 times higher than any other secretion measured; L. C. Hazard, unpubl.), and were excluded from the analysis. Sodium, potassium, and chloride secretion rates for the two species were compared using two-tailed *t*-tests, with Bonferroni corrections for multiple tests (Zar, 1984). Within species, sodium and potassium were compared using paired two-tailed *t*-tests.

RESULTS

Uta tumidarostra secreted over twice as much potassium, 11 times as much chloride and over 27 times as much sodium as did *U. stansburiana* (Table 1). Sodium, potassium, and chloride secretion rates of *U. tumidarostra* were significantly higher than those of *U. stansburiana* ($P \leq 0.01$ for all tests).

TABLE 1. FIELD SALT GLAND SECRETION RATES AND ESTIMATED SALT INTAKE FOR *Uta stansburiana*, *U. tumidarostra*, AND *Amblyrhynchus cristatus*. Field sodium, potassium, and chloride secretion ($\mu\text{mol/g}\cdot\text{day}$; mean \pm SE and maximum) by the salt glands of *U. tumidarostra* ($n = 48$) and *U. stansburiana* ($n = 25$). Mean rate for each ion differed significantly between species ($P \leq 0.01$). Estimated average daily salt input was calculated based on estimated metabolic rate and salt and energy content of prey items. Diet for *U. tumidarostra* was 72% *Ligia occidentalis* and 28% nonmarine arthropods; diet for *U. stansburiana* was all nonmarine arthropods. Data for marine iguana were calculated from Dunson (1969) and Shoemaker and Nagy (1984).

	Sodium ($\mu\text{mol/g}\cdot\text{day}$)	Potassium ($\mu\text{mol/g}\cdot\text{day}$)	Chloride ($\mu\text{mol/g}\cdot\text{day}$)
<i>Uta stansburiana</i> ($n = 48$)			
Field salt gland secretion			
Mean (SE)	0.068 (0.02)	0.254 (0.08)	0.223 (0.08)
Maximum measured	0.32	1.56	1.54
Estimated mean daily input	1.1	1.7	1.1
<i>Uta tumidarostra</i> ($n = 25$)			
Field salt gland secretion			
Mean (SE)	1.84 (0.19)	0.61 (0.08)	2.52 (0.26)
Maximum measured	5.21	2.56	6.45
Estimated mean daily input	9.3	2.7	10.0
<i>Amblyrhynchus cristatus</i> ($n = 5$)			
Field salt gland secretion			
Mean (SE)	25.8 (12.8)	4.08 (2.3)	23.9 (11.9)
Maximum measured	61.2	12.2	56.9
Estimated mean daily input	14.5	3.63	15.7

Uta tumidarostra secreted more sodium than potassium ($P \leq 0.01$); 73% of the total cation secreted was sodium (Fig. 1). Chloride secretion was equal to the sum of sodium and potassium; thus, *U. tumidarostra* does not appear to secrete significant amounts of bicarbonate. In contrast, *U. stansburiana* secreted more potassium than sodium ($P \leq 0.01$; Fig. 1). Sodium made up only 11% of the total cation secreted. Nearly equal amounts of potassium and chloride were secreted: potassium made up 88% of cation secretion, whereas chloride was 91% of anion secretion. Bicarbonate probably accounts for the remaining 9% of anion secretion (see Dunson, 1976). For both species, ratios of sodium, potassium, and chloride to total secretion remain constant regardless of secretion rate.

Ligia occidentalis contained 0.69 mL water per gram wet mass and 850 μmol sodium, 190 μmol potassium, 900 μmol chloride, and 11.5 kJ per gram dry mass.

DISCUSSION

The greater total secretion rate seen in *U. tumidarostra* compared with the presumed ancestral species, *U. stansburiana*, is almost entirely a result of sodium chloride. Higher sodium chloride secretion is associated with higher dietary salinity. *Uta stansburiana* feeds on terres-

trial insects and has a very low salt gland secretion rate. However, *U. tumidarostra*, feeding on salty intertidal isopods, secretes over 11 times as much total salt and 27 times as much sodium as does *U. stansburiana*. There appears to be a close relationship between diet and salt gland function.

We calculated water, sodium, potassium, and chloride intake for each species based on their diets: 72% intertidal isopods and 28% nonmarine arthropods for *U. tumidarostra* (Grismer, 1994), and 100% nonmarine arthropods for *U. stansburiana*. For both species, we assumed a metabolic rate of 167 J/g \cdot day (Alexander and Whitford, 1968), assimilation efficiency of 83% (Bennett and Dawson, 1976), and metabolic water production of 0.029 ml/kJ (Eckert et al., 1988). Salt, water, and energy contents of *L. occidentalis* were from our measurements. Values for nonmarine arthropods were based on average data for insects: 0.70 mL water per gram wet mass and 20.5 kJ per gram dry mass (Mader, 1996), and 110 μmol sodium, 168 μmol potassium, and 115 μmol chloride per gram dry mass (Hillman and Pough, 1976). We estimated that *U. tumidarostra* ingested 0.037 mL water, 9.3 μmol sodium, 2.7 μmol potassium, and 10.0 μmol chloride per gram of lizard per day, whereas *U. stansburiana* ingested 0.028 mL wa-

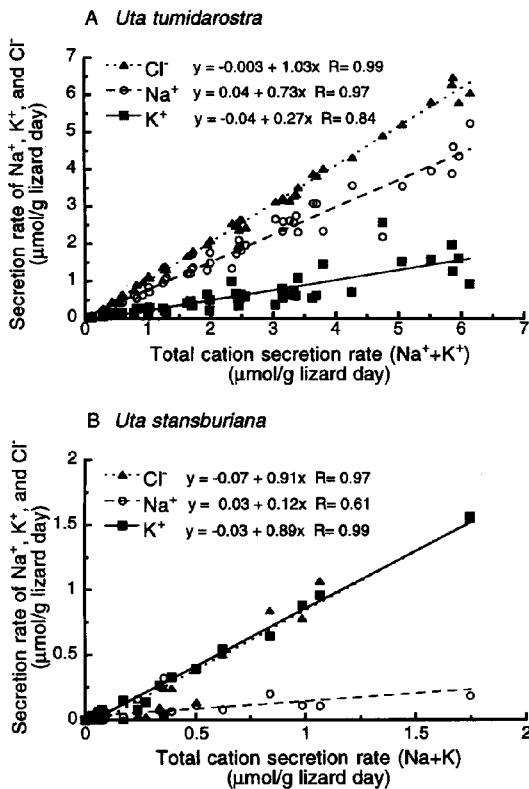


Fig. 1. Sodium, potassium, and chloride secretion rates versus total cation secretion rate (sodium + potassium) for (A) *Uta tumidarostra* ($n = 48$) and (B) *Uta stansburiana* ($n = 25$). Note that axes for the two species differ. Slopes indicate proportion of total cation (Na⁺, K⁺) or anion (Cl⁻) secretion accounted for by each ion. Ratios of sodium, potassium, and chloride to total secretion remain constant regardless of secretion rate.

ter, 1.1 μmol sodium, 1.7 μmol potassium, and 1.1 μmol chloride per gram of lizard per day.

Based on water intake from their insect diet, *U. stansburiana* can excrete up to 8.4 μmol/g · day of ions via the cloaca [assuming that all water taken in is excreted by the cloaca and that urine is maximally concentrated (300 mosM) and contains only sodium, potassium, and chloride]. This is over twice their estimated ion intake (3.9 μmol/g · day total sodium, potassium, and chloride); thus, all ions ingested can potentially be excreted via the cloaca. However, even at high humidity and low temperature, evaporative water loss can be 7% of the water intake we estimated (Roberts, 1968), which would decrease cloacal ion excretion. Under circumstances of reduced water availability or high evaporative water loss, the salt glands probably have a greater role in ion regulation for this species.

Using the same assumptions as above, *U. tumidarostra*, feeding mostly on isopods, can excrete at most 11.1 μmol/g · day of ions via the cloaca. Assuming this amount is evenly divided between anions and cations, 5.55 μmol/g · day of chloride could be excreted via the cloaca. This leaves 4.45 of the 10 μmol of chloride ingested to be excreted by the salt gland. Cations (sodium and potassium) must balance out the chloride (5.55 μmol/g · day in liquid urine; 4.45 μmol/g · day secreted by the salt gland), leaving 2 μmol/g · day of cation to be excreted as insoluble urate salts (Minnich, 1972). For this species, the salt gland must excrete at least 45% of the chloride and 37% of the cations ingested. The calculated daily chloride secretion rate (4.45 μmol/g · day) is well within the range of secretion rates measured (maximum = 6.45 μmol/g · day; Table 1), indicating that our calculations provide a reasonable estimate of daily salt budgets.

Uta stansburiana probably could not survive on the island diet. Estimated cation secretion by the salt gland would have to be 4.45 μmol/g · day at minimum; the highest secretion rate we have measured for salt-loaded *U. stansburiana* is about half of that (2.36 μmol/g · day; L. C. Hazard, unpubl. data). It is unlikely that the salt gland of *U. stansburiana* has the capacity to cope with the high-salt island diet.

The salt gland is crucial to *U. tumidarostra*, probably excreting at least one-third to one-half of all ions ingested. Few other lizards use the gland for sodium excretion. The Galápagos marine iguana (*A. cristatus*) feeds on seaweed and uses the salt gland to excrete both the potassium found in the seaweed and the sodium in the seawater it ingests (Dunson, 1969). The marine iguana excretes 95% of its sodium and chloride and 80% of its potassium via the gland (Shoemaker and Nagy, 1984). The marine iguana also has a higher rate of sodium secretion than does *U. tumidarostra*, with a maximum rate of 61.2 μmol sodium/g · day (Table 1; Dunson, 1969). Estimated ion intake rates for *U. tumidarostra* are comparable to those measured by Shoemaker and Nagy (1984) for the marine iguana (Table 1). Two other lizards also secrete more sodium than potassium: the rusty monitor (*Varanus semiremex*), which feeds in part on crabs and fish (Dunson, 1974), and a population of ameivas (*Ameiva quadrilineata*), which feeds in part on intertidal amphipods (Hillman and Pough, 1976). The rusty monitor has a slightly higher secretion rate than does *U. tumidarostra* (8.2 μmol sodium/g · day), whereas the ameiva's rate is far lower.

Uta tumidarostra is one of only a few lizard spe-

cies known to secrete more sodium than potassium under field conditions. Many lizards (including *U. stansburiana*; L. C. Hazard, unpubl. data) that normally secrete potassium in the field will switch to sodium if sodium-loaded for several days (Shoemaker et al., 1972; Dunson, 1976). This flexibility may have been important in allowing *U. tumidarostra* to switch from feeding on insects to feeding on isopods. The change from potassium to sodium secretion, in conjunction with the increase in salt gland size (Grismer, 1994), permits *U. tumidarostra* to use an abundant food source too salty for most other lizards to eat in large quantity. The ability to feed on isopods allows the island lizards to thrive in a restricted environment, the intertidal zone, where more typical insectivorous lizards probably could not survive.

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