

Ion Secretion by Salt Glands of Desert Iguanas (*Dipsosaurus dorsalis*)

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ABSTRACT

Unlike the NaCl-secreting salt glands of many birds and reptiles, the nasal salt glands of lizards can secrete potassium as well as sodium, with either chloride or bicarbonate as the accompanying anion. The factors responsible for initiating secretion by the gland and the rates of cation and anion secretion were studied in the desert iguana, *Dipsosaurus dorsalis*. Lizards were given combinations of ions for several days, and secreted salt was collected daily and analyzed for sodium, potassium, chloride, and bicarbonate. Maximum total cation secretion rate was $4.4 \pm 0.38 \mu\text{mol/g/d}$. Cation secretion ranged from 24% to 100% potassium; even high NaCl loads did not abolish potassium secretion. Maximum bicarbonate secretion was about $0.5 \mu\text{mol/g/d}$; chloride was the predominant anion. Secretion rate increased only in response to those treatments that included potassium and/or chloride; sodium ions and other osmotic loads (e.g., sucrose) did not increase secretion. This is in contrast to birds and some other reptiles with salt glands, which initiate NaCl secretion in response to any osmotic load. The specificity of the response of the salt gland of *Dipsosaurus* may be related to the ecological importance of dietary potassium and chloride for herbivorous desert lizards.

Introduction

Salt glands, used by some nonmammalian vertebrates to supplement renal ion excretion, are cranial exocrine glands that secrete hyperosmotic electrolyte solutions. Most animals with salt glands (e.g., marine birds, sea turtles, sea snakes) secrete NaCl via the gland, with little or no variation in the composition of the secreted fluid.

In contrast, the salt glands of lizards secrete potassium as

well as sodium, and the relative amounts of the two cations can be altered. Marine lizards such as the marine iguana secrete primarily sodium but also secrete appreciable quantities of potassium. Terrestrial lizards generally secrete potassium under natural conditions but will also secrete sodium when given NaCl loads. The ability to secrete sodium appears to vary across species and among individuals.

Lizards can also secrete bicarbonate as well as chloride as the anion accompanying sodium or potassium. Chloride and bicarbonate secretion have been measured in only a few studies to date (Schmidt-Nielsen et al. 1963; Norris and Dawson 1964; Templeton 1967; Shoemaker et al. 1972). For most species, chloride balances most of the sodium and potassium secreted, especially if animals are given NaCl or KCl loads. However, some bicarbonate may be secreted, especially by *Sauromalus* (Norris and Dawson 1964; Nagy 1972).

In addition to the differences in ions secreted, lizards also appear to control secretion differently than other groups with salt glands. In marine birds and sea snakes, secretion of NaCl can be initiated by general osmotic loads, including NaCl, sucrose, and mannitol, and salt loads are thought to be detected by osmoreceptors (Minnich 1979; Holmes and Phillips 1985). However, Shoemaker et al. (1972) showed that *Dipsosaurus* increased secretion in response to NaCl, KCl, potassium acetate, potassium bicarbonate, and potassium succinate loads (though the responses to the organic salts of potassium were lower) but that other osmotic loads (sucrose and mannitol) did not increase secretion rate. Their general conclusion was that lizard salt glands responded only to stimulation by alkali metal ions (sodium, potassium, and rubidium). This suggests a unique mechanism for detecting salt loads and initiating secretion. However, Peaker and Linzell (1975) suggested that the osmotic loads and organic salts of potassium may have taken longer to be absorbed by the lizards, resulting in lower observed secretion rates.

The goals of this study were to clarify what osmotic or ionic stimuli initiate secretion by the salt glands of *Dipsosaurus* and to determine the degree to which *Dipsosaurus* salt glands are capable of secreting four ions (sodium, potassium, chloride, and bicarbonate).

Material and Methods

Animals

Desert iguanas were collected from Cathedral City, California, in April, May, and July 1995 and April 1996 under a California Department of Fish and Game scientific collecting permit and ranged from 20 to 100 g. Animals were maintained in groups

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in the University of California, Riverside, Biology Vivarium in large cages (1 × 2 m) with a sand substrate (UCR Animal Care Protocol A-M9504026-3). Heat lamps and full-spectrum UV lighting (Repta-Sun; Fluker Laboratories, Baton Rouge, La.) were provided 12–14 h/d. Lizards were fed a diet consisting of fresh greens and mealworms, occasionally supplemented with fresh fruit, crickets, and commercial iguana diet (ZooMed); water was provided ad lib. Lizards were maintained in captivity long term. Only healthy lizards were used in experiments.

Experiments

To test the effects of ionic and osmotic loads on secretion, lizards were fasted for at least 2 d and then weighed, and a 24-h pretreatment collection of secreted salt was made (day 0). Lizards were then given intraperitoneal ion loads daily for 4 d, and secreted salt was collected for 5 d (except where noted). To collect salt secreted by the nasal glands of *Dipsosaurus*, I placed individual lizards in collecting chambers (32 × 17 × 9-cm plastic boxes with raised wire-mesh floors). Lizards were kept in a temperature cabinet (38°C day/28°C night; 12 h each), with fluorescent light provided during the day. Secreted salt crystallized on the nares of the lizards and then fell through the mesh to the bottom of the chamber. Salt was separated from feces and urate and swept into glass or plastic vials daily.

To test the effects of sodium, potassium, and chloride separately and in combination, several treatments were given ($n = 5\text{--}7$ per group): potassium chloride, sodium chloride, histidine chloride, potassium acetate, sodium acetate, histidine acetate, sucrose (isoosmotic to ion loads), saline control, and sham-injected control. Histidine and acetate were not expected to stimulate the salt gland and were used to resolve the roles of potassium, sodium, and chloride. The histidine acetate treatment served as a control for effects of histidine and acetate and also as an osmotic load lacking sodium, potassium, or chloride. To reduce the possible problem of different rates of absorption of the various solutions from the peritoneal cavity, and to allow time for hormonally mediated changes in the composition of the secreted fluid, ion loads were given daily for ≥ 4 d, and plasma ion levels were monitored during some experiments. Lizards were given 5 μmol of salt/g lizard (0.01 mL of 0.5 M solution/g lizard) daily for 4 d.

To further examine the range of secretion rates and ion ratios possible, lizards were given doses of NaCl, KCl, and potassium acetate twice as high as those above (10 $\mu\text{mol/g}$; 0.02 mL of 0.5 M solution/g lizard for 4 d) and the lower dose of NaCl for an extended period (5 $\mu\text{mol/g}$; 0.01 mL 0.5 M NaCl/g lizard for 6 d). For the high-dose KCl treatment, daily collections were continued for an additional 3 d posttreatment. During the high-dose potassium acetate experiment, one lizard developed muscle tremors (a possible sign of hyperkalemia or hypochloremia) after three injections. The fourth injection was omitted, though samples were collected on days 4 and 5.

Sample Analyses

Salt samples were hydrated with 1.0 mL of glass-distilled water and analyzed for sodium and potassium using a Beckman flame photometer and for chloride using a Buchler-Cotlove chloridometer. Field secretion rates were estimated by collecting secreted salt for 24 h immediately after lizards were captured.

Bicarbonate content of some samples was also measured. After hydration of the dry salt samples, a portion was placed in a 140-mL syringe, which was then filled with CO₂-free air. The sample was acidified with 0.2 M HCl to evolve carbon dioxide, and after a 1-h equilibration period, the gas contents of the syringe were flushed through a carbon dioxide analyzer (LiCor) and percentage carbon dioxide was measured. The amount of CO₂ (μmol) was calculated from percentage CO₂, accounting for syringe volume, water vapor, temperature, and barometric pressure. This test did not distinguish between bicarbonate and carbonate, but previous studies suggest that lizards secrete primarily bicarbonate rather than carbonate (Norris and Dawson 1964). Preliminary tests of known samples showed that this method measured about $96\% \pm 3\%$ of the bicarbonate present.

Blood samples were collected during some experiments (NaCl, KCl, sodium acetate, potassium acetate, and high NaCl treatments) to determine the effects of ion loading on plasma ion levels. Blood samples were taken immediately before injection, 3–4 h after the first injection, 3–4 h after the last injection, and at the end of the experiment. Blood was collected from the postorbital sinus in 70- μL heparinized capillary tubes (ammonium heparin) and immediately centrifuged. Packed blood cells were broken off and plasma samples were refrigerated until analyzed for sodium, potassium, and chloride.

Data Analysis/Statistics

Secretion in response to treatments was evaluated using three variables: total secretion rate (sodium + potassium rates), percentage potassium ($100\% \times \text{K}^+ / [\text{Na}^+ + \text{K}^+]$), and percentage chloride ($100\% \times \text{Cl}^- / [\text{Na}^+ + \text{K}^+]$). Secretion on the day following the fourth injection (day 4) was used for analysis. Data are presented as mean \pm SE except where noted. Statistical analyses were performed using STATISTICA 4.1 (Statsoft, Tulsa, Okla.) for the Macintosh. To reduce heterogeneity of variances, rates were square root transformed and percentages were transformed to the arcsine of the square root (Zar 1984). Tests with $P \leq 0.05$ were considered statistically significant.

Results

Field Secretion

During the 24 h immediately postcapture, lizards secreted primarily potassium chloride; very little sodium was present (Fig. 1). There was no relationship between total secretion rate and

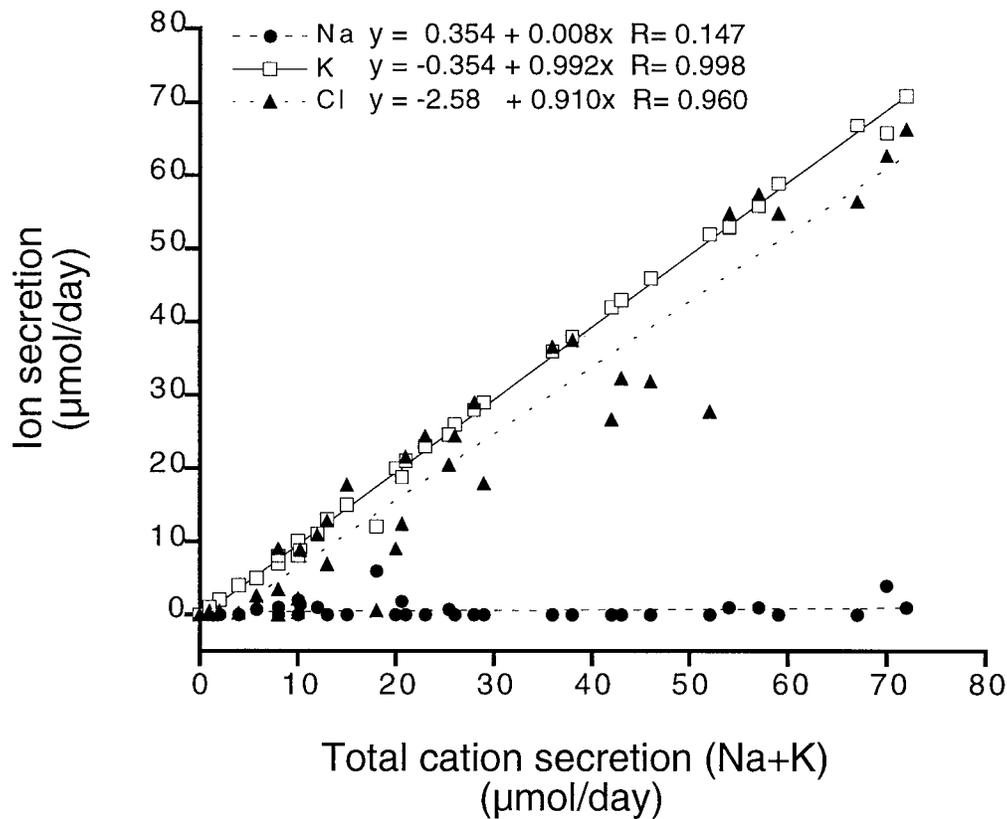


Figure 1. Sodium, potassium, and chloride secretion by *Dipsosaurus* salt glands in the 24 h immediately postcapture ($n = 39$). Individual ion rates are plotted versus total secretion rate (sodium + potassium). Slopes indicate proportion of total cation (Na^+ , K^+) or anion (Cl^-) secretion accounted for by each ion. Ratios of sodium, potassium, and chloride secretion remain constant regardless of secretion rate.

lizard mass (range 8.7–92.3 g), so field rates were not corrected for mass. Chloride balanced roughly 90% of the secreted cations (as determined by the slope of the correlation between chloride and total cation secretion; Fig. 1), suggesting that small amounts of bicarbonate were secreted by some lizards. Mean mass-specific rates were calculated for comparison with mass-specific secretion rates of lizards given ion loads in the laboratory: postcapture lizards secreted $0.035 \pm 0.008 \mu\text{mol sodium/g/d}$ (range 0.0–0.28), $0.703 \pm 0.118 \mu\text{mol potassium/g/d}$ (range 0.01–3.27), and $0.621 \pm 0.114 \mu\text{mol chloride/g/d}$ (range 0.01–3.13).

Ion Loads

Blood Ion Levels. Plasma ion concentrations generally responded as expected to the ion loads for which blood was sampled (Fig. 2). Because of low sample sizes, not all of these changes were statistically significant, but the trends were apparent. Plasma sodium increased in response to NaCl and sodium acetate but not KCl or potassium acetate. Plasma potassium increased in response to KCl and potassium acetate but not NaCl or sodium

acetate. Plasma chloride increased in response to NaCl and KCl and decreased in response to sodium acetate and potassium acetate, from a normal range of 125–135 mM to as low as 101 mM in one individual.

Total Secretion Rate. Secretion in response to ions and other treatments was compared via ANOVAs and Tukey's t -tests (Table 1). Control lizards (isoosmotic saline, sham injection) maintained total cation secretion rates well below $1.0 \mu\text{mol/g/d}$, comparable to preinjection rates. The rate of secretion for lizards given sucrose was significantly lower than for control lizards. Histidine acetate-treated lizards also maintained very low secretion rates (not significantly different from sucrose rate), indicating that neither histidine nor acetate initiates secretion. This allows the use of histidine chloride, sodium acetate, and potassium acetate to evaluate effects of the individual ions on secretion. Of these treatments, sodium acetate did not significantly increase secretion rate (not significantly different from sucrose and histidine acetate rates), while potassium acetate and histidine chloride did. Lizards secreted more in response to histidine chloride ($2.56 \pm 0.18 \mu\text{mol/g/d}$) than in

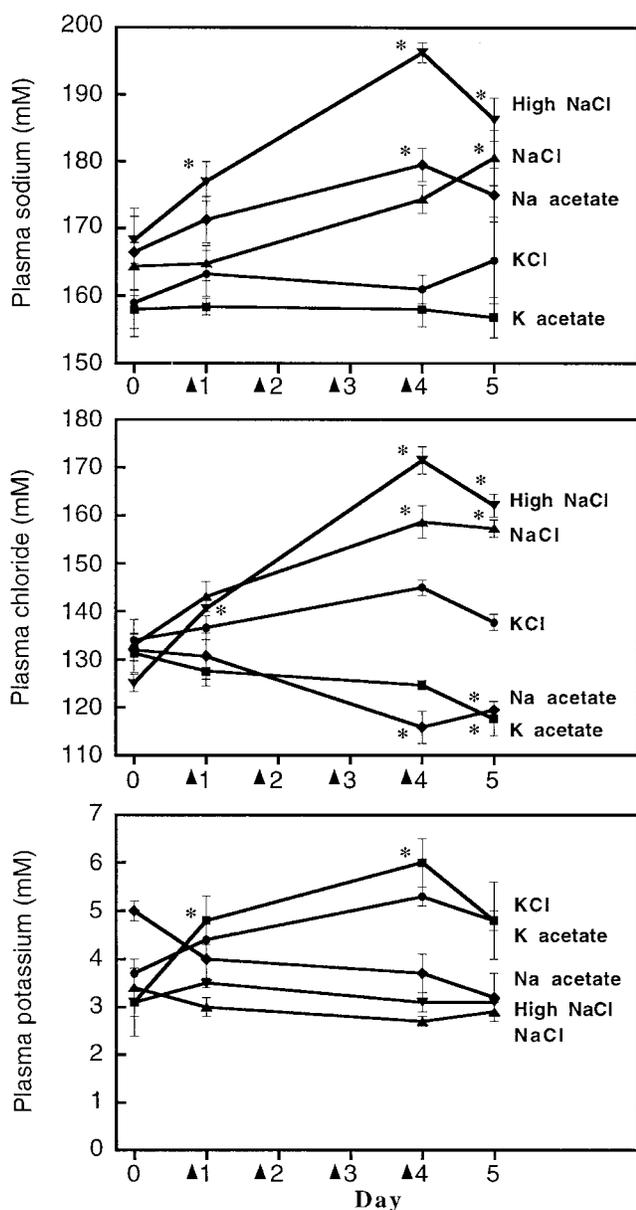


Figure 2. Plasma ion levels (mean [SE]) during ion treatments. *Dipsosaurus* were given 5 μmol salt/g/d for 4 d (indicated by triangles), except the high-NaCl group (10 μmol /g/d for 4 d). Ion levels were measured before injection, after the first injection, after the fourth injection, and at the end of the experiment. Asterisk indicates levels significantly higher than initial concentrations (ANOVA and Tukey's *t*-tests, $P < 0.05$). Several trends were not significant because of low sample sizes (potassium acetate, $n = 5$; potassium chloride, $n = 3$; sodium acetate, $n = 3$; sodium chloride, $n = 5$; high sodium chloride, $n = 3$).

response to potassium acetate ($1.58 \pm 0.16 \mu\text{mol}/\text{g}/\text{d}$). Giving sodium in combination with chloride (NaCl treatment) resulted in a mean secretion rate of $2.47 \pm 0.21 \mu\text{mol}/\text{g}/\text{d}$, not significantly different from the histidine chloride rate. The KCl-

treated lizards had the highest secretion rates, reaching $4.39 \pm 0.38 \mu\text{mol}/\text{g}/\text{d}$ after four injections. Only treatments that included potassium and/or chloride (KCl, potassium acetate, NaCl, histidine chloride) resulted in increased secretion rates.

The time course of the response to ion loading and secretion of individual ions (sodium, potassium, and chloride) was examined for each treatment that significantly increased secretion rate (Fig. 3). Potassium chloride-treated lizards increased secretion most rapidly, whereas sodium chloride- and histidine chloride-treated lizards did not increase secretion substantially for 2 or 3 d. Even lizards receiving a high dose of NaCl did not secrete on the first day postinjection, though rates were higher than for the low NaCl dose after that and were comparable to KCl rates by the end of the experiment. A high potassium acetate dose did not increase secretion rate above the rate seen in response to the lower potassium acetate dose. Secretion in response to histidine chloride and NaCl loads remained constant or increased even after treatment ended (day 5). Secretion in response to the lower potassium chloride dose and to potassium acetate began more quickly and dropped off sharply after the last injection. Secretion in response to the higher KCl dose also decreased after treatment ended, but more slowly.

Cation Secretion. Potassium, sodium, and histidine chloride treatments were compared to evaluate the effect of cation load on ratios of cations secreted (Table 1). Potassium chloride-loaded lizards secreted $93\% \pm 4\%$ percent potassium, significantly higher than other treatments. Sodium chloride-treated lizards secreted $41\% \pm 4\%$ potassium on day 4, and histidine chloride-treated lizards secreted $60\% \pm 11\%$ potassium. Histidine chloride and sodium chloride treatments did not differ significantly from one another. For the histidine chloride-treated lizards, mean percentage potassium remained similar to starting levels, but percentage potassium increased in some lizards and decreased in others. The resulting high variance (significantly higher than the variance of the NaCl treatment; variance ratio test $P < 0.05$) may account for the lack of a statistically significant difference between histidine chloride and sodium chloride treatments.

Higher sodium loads were used to determine how much sodium secretion is possible for *Dipsosaurus*. In lizards that received four NaCl injections (5 mol/g/d), percentage potassium was $41\% \pm 4\%$ on day 4 and decreased to $36\% \pm 3\%$ on day 5 (Fig. 3C). Lizards given the same dose for 6 d reduced the ratio to $25\% \pm 2\%$ by day 8 (Fig. 3H). In both of these groups, potassium secretion remained relatively constant once ion loading began, at about $1.0 \mu\text{mol}/\text{g}/\text{d}$, while sodium secretion gradually increased. Lizards given a higher dose of NaCl (10 $\mu\text{mol}/\text{g}/\text{d}$) for 4 d had sodium secretion rates that were about twice as high as for the lower dose, but the rate of potassium secretion again remained the same (Fig. 3G). Per-

Table 1: Rate and composition of salt secreted by *Dipsosaurus* salt glands (means \pm SE) following 4 d of ionic or osmotic loads

Treatment (<i>n</i>)	Total Secretion Rate ($\mu\text{mol cation/g/d}$)	Cation Ratio ($\text{K}^+ / [\text{Na}^+ + \text{K}^+] \times 100\%$)	Anion Ratio ($\text{Cl}^- / [\text{Na}^+ + \text{K}^+] \times 100\%$)
Sham injection (6)	.56 \pm .10 ^D	63 \pm 7	91 \pm 2
Isoosmotic saline (7)	.60 \pm .08 ^D	62 \pm 3	78 \pm 5
Sucrose (7)	.14 \pm .02 ^E	67 \pm 6	30 \pm 10
Histidine acetate (5)	.06 \pm .02 ^E	53 \pm 15	19 \pm 14 ^C
Na acetate (5)	.14 \pm .03 ^E	46 \pm 3	17 \pm 9 ^C
K acetate (6)	1.58 \pm .16 ^C	99 \pm 1	67 \pm 4 ^B
Histidine Cl (6)	2.56 \pm .18 ^B	60 \pm 11 ^B	100 \pm 2 ^A
NaCl (6)	2.47 \pm .21 ^B	41 \pm 4 ^B	98 \pm 1 ^A
KCl (6)	4.39 \pm .38 ^A	93 \pm 4 ^A	94 \pm 1 ^{A,B}
High K acetate (3)	1.02 \pm .47	90 \pm 4	65 \pm 17
High KCl (3)	4.04 \pm .33	98 \pm 0	100 \pm 3
High NaCl (3)	4.08 \pm .41	25 \pm 4	99 \pm 2
Extended NaCl (6):			
Day 4	1.97 \pm .22	43 \pm 5	94 \pm 1
Day 6	3.58 \pm .21	30 \pm 3	97 \pm 2

Note. Dose for all treatments was 5 $\mu\text{mol/g/d}$, except for sucrose, high KCl, high K acetate, and high NaCl (10 $\mu\text{mol/g/d}$) and isoosmotic saline (1.5 $\mu\text{mol/g/d}$). Treatments sharing the same letter are not statistically different from one another (ANOVA and Tukey's *t*-tests). Treatments without letters were not included in the statistical analyses.

centage potassium fell to 24% \pm 4% by the end of the high-NaCl treatment.

Anion Secretion. Mean percentage chloride ranged from 39% to 65% on day 0, before ion injections were given. In chloride-loaded lizards (KCl, NaCl, and histidine chloride treatments), percentage chloride increased to 94%–100% by day 4 and was significantly higher for those treatments than for sodium or histidine acetate, which decreased to 17% \pm 9% and 19% \pm 4%, respectively (Table 1). Percentage chloride decreased to 67% \pm 4% for potassium acetate–injected lizards, significantly lower than histidine chloride and sodium chloride and higher than sodium acetate and histidine acetate, but not significantly different from potassium chloride.

Salt samples from lizards given the higher dose of potassium acetate were analyzed for bicarbonate as well as sodium, potassium, and chloride. Bicarbonate measured by evolution of carbon dioxide was about 76% of the bicarbonate predicted by subtraction of chloride from total cation secretion (Fig. 4). This is a lower recovery rate than that found during preliminary tests of the method (96% \pm 3% recovery from test samples with known amounts of bicarbonate) but suggests that bicarbonate makes up most of the anion deficit (total cation – chloride). Bicarbonate secretion (measured directly or estimated by subtraction of chloride rate from total cation rate) never increased above 0.6 $\mu\text{mol/g/d}$ for any treatment. Low-

percentage chloride measurements were only found with low total secretion rates.

Discussion

Initiation of Secretion

Studies of other taxa with salt glands (e.g., birds, turtles) have determined that in these groups, secretion by the glands is initiated by osmotic challenges (Minnich 1979; Holmes and Phillips 1985). Changes in plasma osmotic concentration could be detected by plasma volume receptors, by osmoreceptors, or by ion-specific receptors. Birds secrete in response to any osmotic load, including NaCl, sucrose, sodium bicarbonate, and arginine chloride (Erbe et al. 1988); osmoreceptors and possibly plasma volume receptors are thought to be involved in activating neural stimulation of secretion (Bennett et al. 1997). In lizards, Shoemaker et al. (1972) found that osmotic loads (sucrose or mannitol) were not sufficient to initiate secretion.

This study gives further evidence that osmotic loads are insufficient to stimulate secretion by lizard salt glands. Several treatments (sucrose, histidine acetate, and sodium acetate) presented osmotic challenges but did not increase secretion rate. Further, while secretion was initiated by both NaCl and KCl, the same osmotic load did not result in the same total secretion rate. KCl-treated lizards secreted at higher rates than sodium chloride– or histidine chloride– treated lizards. It has been

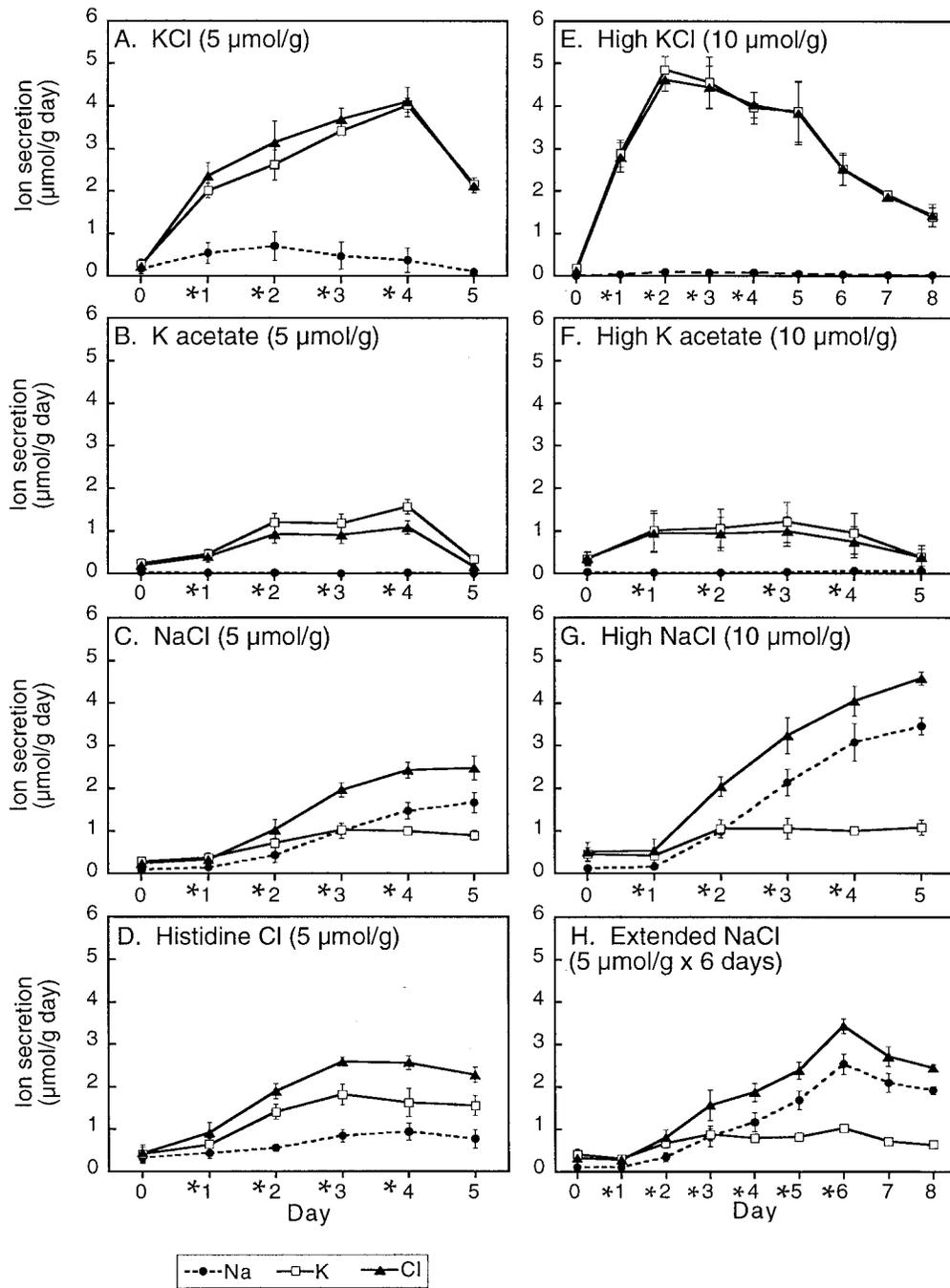


Figure 3. Sodium, potassium, and chloride secretion by *Dipsosaurus* salt glands for those ion treatments that significantly increased total secretion rate. Symbols represent mean \pm SE. Treatments (indicated by an asterisk) were given for 4 d except where noted.

suggested that differing effects of the different ion solutions on secretion rate might be caused by different rates of absorption from the peritoneal cavity and that the lack of effect of sucrose and mannitol might be caused by the same problem (Peaker and Linzell 1975). This study used chronic loads (≥ 4 d) to

reduce that possibility. Plasma cation levels in potassium acetate- and sodium acetate-treated lizards changed similarly to those in KCl- and NaCl-treated lizards, respectively, indicating that absorption rates were not an issue.

Shoemaker et al. (1972) concluded that alkali metal ions

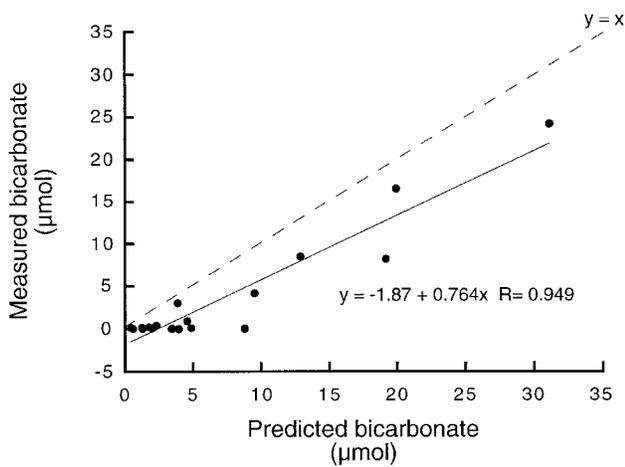


Figure 4. Measured versus predicted ([sodium + potassium] – chloride) bicarbonate secretion by salt glands of *Dipsosaurus* given a high potassium acetate load (10 µmol/g for 4 d). Data for three lizards and 5 d of collection were pooled.

(sodium or potassium) were needed to initiate secretion, since NaCl, KCl, and organic salts of potassium increased secretion rate while sucrose and mannitol did not. However, I found that sodium acetate does not stimulate secretion, while histidine chloride and potassium acetate do. Thus, only treatments including potassium and/or chloride initiate secretion; initiation of secretion by NaCl is caused by the presence of chloride. The effects of potassium and chloride on secretion appear to be additive. Secretion in response to KCl is higher than that in response to the same dose of either potassium acetate or histidine chloride. When the mean secretion rates for the two ions given alone are added, the sum is similar to the rate seen when both ions are given at the same time (Fig. 5). A higher dose of chloride (the double NaCl load) resulted in an approximate doubling of total secretion rate. It would be interesting to give higher doses of the individual ions to determine whether either one alone can stimulate the gland to its maximal rate. However, doing so with a potassium acetate load is problematic, given the limited capability of *Dipsosaurus* for bicarbonate secretion (see below). These results strongly suggest that *Dipsosaurus* uses ion-specific receptors for potassium and chloride, rather than osmotic or volume receptors, to detect and respond to an ion load. Similar ion-specific systems have been described; for example, mammalian adrenal glomerulosa cells secrete aldosterone in response to increased extracellular potassium (but not sodium) outside the cells (Bentley 1971).

Interestingly, despite the differences in the receptors used to detect an ion load, lizards appear to initiate secretion via the same neuronal mechanism used by other taxa. As in birds, exogenous acetylcholine (ACh) and ACh analogs such as methacholine stimulate secretion by lizard salt glands (Templeton

1964; Shuttleworth et al. 1987), and the ACh blocker atropine reduces secretion (Templeton 1972). Acetylcholine is the primary neurotransmitter of the parasympathetic nervous system, which suggests parasympathetic control of secretion. Histological and other studies support the possibility that salt glands are under nervous control (Peaker and Linzell 1975).

Cation Secretion

Despite the lack of effect of sodium on initiation of secretion, sodium loading does affect the composition of the secreted fluid. *Dipsosaurus* are relatively flexible in their ability to vary which cations (sodium or potassium) are secreted. The proportion of total cation secreted as potassium ranged from about 100% to 25% but never fell to zero. Even after 6 d of NaCl loading or 4 d of a higher dose of NaCl, potassium secretion remained relatively steady at about 1.0 µmol/g/d. The decrease in percentage potassium was largely achieved by increasing sodium secretion rather than by decreasing potassium. It may be that while secreting, *Dipsosaurus* cannot reduce potassium secretion below about 1.0 µmol/g/d. If total secretion rate in response to chronic NaCl loading could eventually reach the apparent maximum seen in response to KCl loading (5.0 µmol/g/d), the minimum possible percentage potassium would be about 20% ([1.0 µmol/g/d potassium]/[5.0 µmol/g/d total cation]). This is close to the cation ratio observed after 6 d of NaCl loading and after 4 d of a higher dose of NaCl. This apparent obligatory minimum potassium secretion may be related to the mechanisms of sodium and potassium secretion by lizard salt glands, which have not been determined.

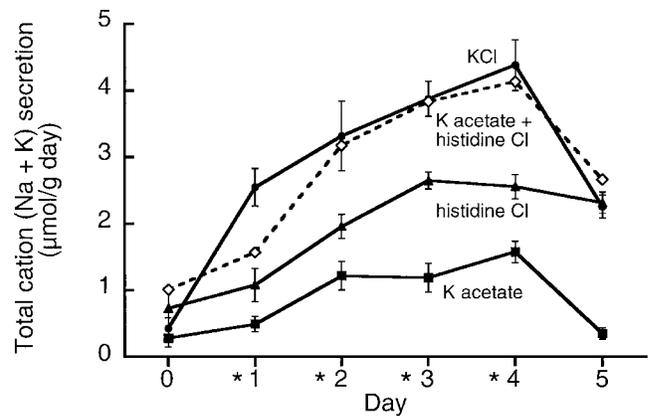


Figure 5. Total cation secretion (sodium + potassium) by *Dipsosaurus* salt glands in response to potassium chloride, potassium acetate, and histidine chloride treatments (5 µmol/g for 4 d; n = 6 per group). Symbols represent means ± SE. The sums of the daily means of the potassium acetate and histidine chloride treatments are also plotted (dashed line) for comparison with the KCl treatment. Asterisk indicates ion injections.

Other species, such as the marine iguana (*Amblyrhynchus cristatus*) and an intertidal lizard, *Uta tumidarostra*, are able to secrete more sodium. The marine iguana can secrete as much as 95% sodium (Dunson 1969), and *U. tumidarostra* can secrete up to 94% sodium (Hazard et al. 1998). However, these species are apparently not capable of secreting large proportions of potassium. In contrast, species such as *Uromastix acanthinurus* (Lemire et al. 1980) and *Sceloporus cyanogenys* (Templeton 1966) secrete predominantly potassium and have a limited ability to secrete sodium. *Dipsosaurus*, which can secrete 25%–100% potassium, has one of the broadest ranges reported for lizards (Minnich 1982). However, individuals need several days to alter cation secretion, and measuring secretion after a single NaCl or KCl load (as has been done in most studies) is probably not sufficient to determine the range of cation secretion possible for a species. Even after 6 d of NaCl loading, the cation ratio for *Dipsosaurus* was still decreasing (Fig. 3H). Therefore, it is likely that other species are capable of greater flexibility than has been reported.

Anion Secretion

Chloride secretion is not always sufficient to balance out total cation (sodium and potassium) secretion. Evolution of carbon dioxide from salt secreted by lizards given potassium acetate confirms that the remaining anion is either bicarbonate or carbonate. Half as much carbonate as bicarbonate would be needed to balance the cation charge, as carbonate is divalent. The carbon dioxide measured was about 76% that predicted by the anion deficit calculated from measured sodium, potassium, and chloride. This strongly suggests that the anion secreted is bicarbonate (or perhaps a mix of bicarbonate and carbonate), as this molar amount of carbonate would exceed the charge needed for electrical neutrality of the secreted fluid. These results agree with those of Norris and Dawson (1964), who measured the amount of evolved carbon dioxide and the pH of secretions in solution and concluded that bicarbonate, rather than carbonate, was secreted.

Dipsosaurus appears to be limited in its ability to secrete bicarbonate. The ratio of chloride to bicarbonate could be reduced in response to potassium acetate loads but only by decreasing chloride secretion. Even with high potassium acetate loads, secretion of bicarbonate was low. In some potassium acetate experiments, overall secretion decreased even while ion loads were still being given. Plasma chloride levels decreased in lizards given acetate loads (Fig. 2). This suggests that lizards secreted primarily KCl until plasma chloride levels decreased below some threshold but that after this they were unable to secrete potassium bicarbonate in sufficient amounts to cope with the potassium load given and, therefore, stopped secreting rather than allowing further chloride depletion.

Sauromalus, a close relative of *Dipsosaurus*, is reported to secrete high proportions of bicarbonate in the field (Norris and

Dawson 1964; Nagy 1972). However, Norris and Dawson (1964) only report ratios measured from scrapings of nasal secretions from around the nares, not actual secretion rates. It is possible that while the ratio of chloride to bicarbonate is very low, the overall secretion rates of these animals were also low and that at higher secretion rates, they would secrete primarily chloride. Nagy (1972) found chloride percentages of 60%–77% in field secretions of *Sauromalus*. *Sauromalus* fed their natural diet in the laboratory secreted about 1.1 μmol bicarbonate/g/d. This rate of bicarbonate secretion is higher than that observed for *Dipsosaurus* in this study (maximum of about 0.6 μmol /g/d) but still low relative to the overall rate of secretion. There have apparently been no measurements of chloride or bicarbonate secretion by *Sauromalus* given ion loads such as potassium acetate to determine whether they are able to secrete more bicarbonate under those conditions.

Field Secretion

In the field, *Dipsosaurus* secreted primarily KCl, with small amounts of sodium and bicarbonate. Field cation and anion ratios were comparable to those measured by Minnich (1970), who found that *Dipsosaurus* secreted 98% potassium and 61% chloride in field secretions. Field rates were not correlated with lizard mass but, rather, may have been more affected by how recently before capture an individual had fed. Field secretion rates were relatively low compared with rates seen in response to ion loading in the laboratory. The mean rate of cation (sodium + potassium) secretion was 0.74 μmol /g/d; the highest rate measured was 3.6 μmol /g/d. Lizards given 4 d of KCl loading in the laboratory secreted a mean of 4.4 μmol /g/d. The maximum reported field secretion rate for *Dipsosaurus* is 4.7 μmol /g/d (calculated from data in Minnich 1982), comparable to both the maximum field rate in this study and the mean rate measured in the laboratory.

Minnich (1976) constructed electrolyte budgets for *Dipsosaurus* in the field during their summer activity period. He determined that they take in 0.92 μmol Na, 9.74 μmol K, and 2.80 μmol Cl per gram daily and that they excrete 0.45 μmol Na, 4.21 μmol K, and 2.59 μmol Cl per gram daily via the salt gland (the rest is excreted in feces and urine). These estimated rates are well within the range of secretion rates found in this study. However, the rate of chloride secretion is much lower than the total cation secretion. If a lizard actually secreted this amount of each ion daily, it would have to secrete bicarbonate at a rate of 2.07 μmol /g/d, far above their apparent capacity. Either *Dipsosaurus* has a greater capacity for bicarbonate than this study determined or the estimated budget is inaccurate. As Minnich's estimated salt gland excretion was calculated by subtraction of fecal and urinary excretion from estimated intake, this result could be caused by measurement errors.

Ecological Importance

Desert iguanas take in potassium on a daily basis during their active season and need to be able to excrete it quickly and with minimal water loss to maintain plasma potassium within tolerable limits. The rapid response time and high rate of secretion of the salt gland allow this. The salt glands of *Dipsosaurus dorsalis* provide an important avenue for electrolyte excretion in the field. Minnich (1976) determined that the gland is responsible on average for 43% of their potassium excretion, 49% of sodium excretion, and 93% of chloride excretion and hypothesized that the gland was especially important when lizards were feeding on dry plant material in the summer. Nagy (1972) had similar findings for the chuckwalla, *Sauromalus obesus*, which relies on its gland for 46% of potassium, 31% of sodium, and 67% of chloride excretion. The salt glands of these herbivorous desert species are clearly most important for excretion of potassium and chloride. Potassium levels in plants can be very high, and plasma potassium levels must be maintained within fairly narrow limits (3–8 mM). Assuming a plasma volume of 5% of body mass and plasma potassium concentration of 3.4 mM (Minnich 1970), a lizard secreting at a relatively high rate of 4.7 $\mu\text{mol/g/d}$ could clear the plasma of potassium in <1 h. However, the gland may be even more important for excretion of chloride. If nitrogen intake is sufficient, sodium and especially potassium can be excreted as insoluble urate salts (Minnich 1972) with very little water lost. Chloride, however, can only be excreted in liquid urine, which in reptiles can only be as concentrated as the body fluids, or via the salt gland. If a desert lizard has a diet high in chloride, the salt gland may be the most important route for its excretion. In addition, lizards given chloride without sodium or potassium (histidine chloride treatments) seem to be able to secrete sodium or potassium chloride without becoming hyponatremic or hypokalemic. However, lizards given potassium without chloride (potassium acetate loads) quickly become hypochloremic and cease secretion, apparently allowing plasma potassium to increase rather than lose more chloride. As chloride content of plants may be low relative to potassium (Minnich 1976), excretion of potassium by lizard salt glands may be limited by availability of chloride.

Given the importance of the gland for potassium and chloride secretion, rather than sodium secretion, it is interesting that secretion by *Dipsosaurus* glands is stimulated specifically by these two ions rather than osmotic loads. Osmotic loads are sufficient to initiate secretion by the salt glands of birds (Peaker and Linzell 1975). However, these are marine species that use their salt glands to secrete exclusively sodium chloride. They have no need for differential responses to different types of ion loads because the electrolyte composition of their diet is relatively invariant. Terrestrial lizards, especially herbivores, have more use for a gland that only responds to particular ions. Lizards are unique among birds and reptiles with salt glands

in their flexibility of cation secretion (and possibly anion secretion).

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