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Sodium and Potassium Secretion by Iguana Salt Glands

ACCLIMATION OR ADAPTATION?

Lisa C. Hazard

THE MARINE IGUANA (*Amblyrhynchus cristatus*) is well known for its unusual diet and foraging mode. Feeding on subtidal/intertidal algae, it incurs a high load of salts (primarily sodium chloride, with some potassium) from its food (Dunson, 1969; Shoemaker and Nagy, 1984). To cope with this high-salt diet, the marine iguana uses large cranial salt glands that excrete most of the sodium, potassium, and chloride ingested; forceful expulsion of the secreted fluid is the cause of the dramatic snorting and sneezing observed in these animals (Schmidt-Nielsen and Fange, 1958). Other lizards also possess these extrarenal osmoregulatory organs (reviews in Peaker and Linzell, 1975; Dunson, 1976; Minnich, 1979, 1982). They are typically found in herbivorous or omnivorous lizards feeding on potassium-rich plants and secrete predominantly potassium chloride. Some lizards are found in marine or intertidal habitats and feed on sodium-rich foods; as in the marine iguana, their glands secrete primarily sodium chloride (Hillman and Pough, 1976; Hazard et al., 1998). An underlying, sometimes unstated, assumption of studies on marine species has

been that their glands are adapted for sodium excretion, whereas the glands of terrestrial herbivores are adapted for potassium secretion. However, it is possible that there is little or no difference in the actual secretory capabilities of the glands of marine and terrestrial species, and that the sodium or potassium secretion observed in the field is simply dictated by dietary ion content.

This chapter summarizes the distribution of salt glands among lizard taxa and evaluates aspects of salt secretion that might be important for the evolution of marine lizards. There are three major descriptive characteristics of salt secretion: secretion rate, composition of the secreted fluid, and concentration of the secreted fluid. As there are few data on secretion concentrations in lizards, this chapter focuses on the other two characteristics.

THE NEED FOR SALT GLANDS

Reptiles are not capable of creating liquid urine more concentrated than their body fluids, and are therefore limited in their urinary electrolyte

excretion. Like birds, many reptiles excrete nitrogenous waste as insoluble uric acid or urate salts (Minnich, 1972). This frees up osmotic space in the urine for electrolyte excretion. Some cations (predominately potassium) can also be bound as insoluble urate salts; however, anions (chloride) must be excreted in solution. Reptiles feeding on salty diets may take in ions in excess of renal excretion capacity. This is especially true if fresh water availability is limited, as is often the case in desert habitats.

There are two general ways in which reptiles can cope with high ion intake and concurrent low water availability: tolerate or regulate. Some species simply allow increases in blood ion levels, thereby storing ions until water becomes available for renal excretion. *Ctenophorus* (*Amphibolurus*) *ornatus* feeds primarily on sodium-rich ants and lacks salt glands. Plasma sodium levels of *C. ornatus* may increase from 166 mM when fully hydrated to 243 mM in the summer (Bradshaw, 1970). Plasma potassium levels in this species also increase (from 5.5 to 12.2 mM); both decrease within a few hours after rainfall. The desert tortoise (*Gopherus agassizii*) also lacks salt glands and feeds on desert plants high in potassium and low in water. These animals also tolerate large changes in plasma ion concentrations and osmolality and are dependent on periodic rainfall for excretion of excess ions (Peterson, 1996). Regulation is possible for species with specialized salt-excreting glands. These species may be able to excrete excess ions with minimal water loss, thus maintaining homeostasis and allowing them to continue feeding in the absence of available water. Reptiles particularly likely to incur high ion loads are those feeding on desert plants or marine diets.

HERBIVORY

Full herbivory is comparatively rare in lizards, occurring in only about fifty to sixty species of the approximately 3300 species known. All members of the family Iguanidae are large herbivores; other lizards considered to be fully herbivorous include those of the genera *Uromastix*

and *Hydrosaurus*, *Corucia zebrata*, and *Angolosaurus skoogi* (Iverson, 1982; Cooper and Robinson, 1990); many others are omnivorous. Herbivory presents special problems for osmoregulation and ion regulation. Plant foods tend to contain more potassium than do animal foods, and since plant food is generally of lower quality (nutritional content per gram), more of it must be taken in to meet energetic needs (table 6.1). Additionally, plants in arid environments may have low water contents. In reptiles, plasma potassium levels are much lower than sodium levels (3–8 mM K⁺ versus 131–243 mM Na⁺; Minnich, 1982), so that intake of a given amount of sodium or potassium results in a proportionally larger increase in plasma potassium level. Since extracellular and intracellular potassium must be tightly regulated to avoid disruption of nerve and muscle function, excess potassium loads must be excreted quickly (Minnich, 1979). Excess sodium is generally better tolerated.

MARINE DIETS

With marine or intertidal diets, water is not limited, but the concentration of sodium chloride and other ions is high (table 6.1). Several lizard species eat food from the intertidal or subtidal zones. The Galápagos marine iguana (*Amblyrhynchus cristatus*), which feeds on seaweed, takes in large amounts of both sodium and potassium from the seaweed and associated sea water (Dunson, 1969; Shoemaker and Nagy, 1984).

Several species of normally insectivorous lizards are known to feed on intertidal arthropods, which may have a high NaCl content. *Callisaurus draconoides* (Quijada-Mascareñas, 1992) and *Ameiva quadrilineata* (Hillman and Pough, 1976) feed in part on intertidal amphipods. The *Uta encantadae* group (three closely related species found on islands in the Gulf of California) feed almost exclusively on intertidal isopods (Grismer, 1994), and one of them, *U. tumidirostris*, takes in over eight times more sodium than its insectivorous mainland relative, *U. stansburiana* (Hazard et al., 1998).

TABLE 6.1
Ion Content of Lizard Plasma and Energy, Water, and Ion Contents of Selected Food Items of Lizards

	M.E. (kJ/g dry)	WATER (ml/g dry)	ELECTROLYTES (mm; μ mol/g dry)			REFERENCES
			Na	K	Cl	
Plasma (range)	—	—	130–240	3–8	92–163	1
Desert plants	8.7	1.36	33; 45	426; 579	198; 269	2, 3
Marine algae	8.2	5.9	300; 1770	196; 1156	444; 2620	4
Intertidal isopods	11.5	2.2	382; 840	85; 187	404; 888	5
Desert arthropods	—	1.9	75; 143	86; 163	67; 127	6
Insects	17.0	2.3	47; 108	72; 166	49; 113	7, 8
<i>Iridomyrmex</i> ants	—	3.0	290; 870	82; 246	—	9

Notes: M.E. = Metabolizable energy (total energy \times digestive efficiency). References: 1 = Minnich (1982); 2 = Nagy (1972); 3 = Nagy and Shoemaker (1975); 4 = Shoemaker and Nagy (1984); 5 = Hazard et al. (1998); 6 = Minnich and Shoemaker (1972); 7 = Mader (1996); 8 = Hillman and Pough (1976); 9 = Bradshaw and Shoemaker (1967). —, Not available.

IMPORTANCE OF SALT GLANDS

Field ion budgets have been constructed for several lizard species with salt glands (table 6.2). In most of these species, the gland is responsible for a significant proportion of the animal's daily sodium, potassium, and chloride excretion. Potassium and, to a lesser extent sodium, can be excreted both in liquid urine and as insoluble urate salts (Minnich, 1972). However, chloride can only be excreted in liquid urine or via the salt gland. If water is limited, the gland may be more important for chloride excretion than for cation excretion. This appears to be the case for *Ameiva*, *Uta tumidarostra*, *Sauromalus*, and *Dipsosaurus*, in which a greater proportion of the chloride intake is secreted by the gland than sodium or potassium (table 6.2).

DISTRIBUTION OF SALT GLANDS IN LIZARDS

Salt glands are found in some birds and reptiles; each group has modified a different cranial exocrine gland to serve as a salt-excreting gland. These include the lateral nasal gland (lizards; Philpott and Templeton, 1964), the lateral and

medial nasal glands (birds; Schmidt-Nielsen et al., 1958), the lachrymal gland (chelonians; Cowan, 1969), lingual glands (crocodilians; Taplin and Grigg, 1981), and sublingual glands (sea snakes; Dunson and Taub, 1967; Dunson, 1968). Among lizards, salt glands are found in some, but not all, species. The gland used is always the lateral nasal gland, which serves as a mucus-secreting gland in other species.

The known distribution of salt glands among lizard families is listed in table 6.3. Lizards are classified as having salt glands based on either histological or physiological evidence: salt-secreting cells of the lateral nasal gland have a characteristic striated appearance (Saint Girons and Bradshaw, 1987), and animals with salt glands will secrete a concentrated ion solution in response to an injected NaCl load or other stimulus (Minnich, 1979). One caution is needed: species currently listed as lacking salt glands could possibly have glands that are functional only at certain times of year, or after long-term salt exposure. For example, the sleepy lizard, *Tiliqua rugosa* (formerly *Trachydosaurus rugosus*), was thought to lack salt glands based on histology and lack of response to injected salt loads (Saint-Girons et al., 1977); however, other



TABLE 6.2
Role of Salt Gland in Lizard Electrolyte Budgets

SPECIES	DIET CATEGORY	DAILY INTAKE ($\mu\text{mol/g day}$)			SALT GLAND EXCRETION (% INTAKE)			REFERENCES
		Na	K	Cl	Na	K	Cl	
<i>Amblyrhynchus cristatus</i>	MH	14.5	3.63	15.7	95.2	80.4	93.6	4
<i>Ameiva quadrilineata</i>	MI	0.56	0.59	0.48	—	—	54.5 ¹	2
<i>Dipsosaurus dorsalis</i>	H	0.92	9.74	2.8	48.9	43.2	92.5	3
<i>Sauromalus obesus</i>	H	0.51	6.55	3.1	31.4	46.0	67.2	1
<i>Uta stansburiana</i>	I	1.1	1.7	1.1	renal output sufficient			5
<i>Uta tumidarostra</i>	MI	9.3	2.7	10.0	37.0 ¹ (Na+K)		44.5 ¹	5

Notes: Diet categories: M = marine/intertidal; H = herbivorous; I = insectivorous. References: 1 = Nagy (1972); 2 = Hillman and Pough (1976); 3 = Minnich (1976); 4 = Shoemaker and Nagy (1984); 5 = Hazard et al. (1998). —, Not available.

¹ Estimated minimum.

studies have shown that *T. rugosa* that are studied when they are active and feeding possess functional salt glands (Braysher, 1971; Bradshaw et al., 1984b).

Salt glands have apparently developed independently several times in lizards (Minnich, 1979), although no phylogenetic studies have been done. They are present in most Iguania (with the exception of the Agaminae) and Scincomorpha, and absent in Gekkota. Within the Anguimorphs, they only occur in the varanids (table 6.3). Despite the apparently independent origins, the gland used by lizards to secrete salt is always the lateral nasal gland. Salt glands are generally associated with herbivorous or marine/intertidal species, though many other species also possess them. I am unaware of any herbivorous or marine lizard that lacks salt glands, although some frugivorous geckos (e.g., *Phelsuma*) have yet to be examined. In general, the herbivorous and marine species possess larger glands that secrete salt at a higher rate than do the glands of insectivorous or carnivorous lizards (Minnich, 1982).

COMPOSITION OF SECRETED FLUID

In most birds and reptiles with salt glands, the glands secrete concentrated solutions of sodium chloride (Peaker and Linzell, 1975). The ability of lizard salt glands to secrete large amounts of potassium is highly unusual among animals with salt glands (with one exception among the birds: ostriches secrete primarily potassium; Schmidt-Nielsen et al., 1963; Gray and Brown, 1995). Furthermore, some lizards are capable of varying the composition of the secreted fluid in response to varying ion intake.

SPECIES COMPARISON

Most lizards with salt glands typically secrete potassium chloride under natural conditions (Dunson, 1976); this is true even for insectivorous species without high potassium intake. In species that feed on marine or intertidal foods, sodium excretion predominates. Individual lizards can vary the composition of the secreted fluid. With long-term (several days) exposure to NaCl loads, potassium-secreting animals will



TABLE 6.3
Distribution of Salt Glands Among Lizards

FAMILY	SALT GLANDS PRESENT	SALT GLANDS ABSENT
Iguania		
Chamaeleonidae		
Chameleontinae	Not studied	
Leiolepidinae	<i>Uromastix</i> spp.	
Agaminae	None known	<i>Agama</i> spp. <i>Ctenophorus</i> spp. <i>Diporiphora australis</i> <i>Lophognathus longirostris</i> <i>Moloch horridus</i> <i>Pogona minor</i>
Iguanidae	All <i>Amblyrhynchus cristatus</i> <i>Brachylophus fasciatus</i> <i>Conolophus subcristatus</i> <i>Ctenosaura</i> spp. <i>Cyclura cornuta</i> <i>Dipsosaurus dorsalis</i> <i>Iguana iguana</i> <i>Sauromalus</i> spp.	
Phrynosomatidae ¹	All <i>Phrynosoma</i> spp. <i>Sceloporus</i> spp. <i>Uma</i> spp. <i>Uta stansburiana</i> <i>Uta tumidarostra</i>	
Corytophanidae ¹	Not studied	
Crotaphytidae ¹	All <i>Crotaphytus collaris</i> <i>Gambilia wizlizenii</i>	
Polychridae ¹	<i>Anolis carolinensis</i> <i>Liolaemus</i> spp.	
Hoplocercidae ¹	Not studied	
Opluridae ¹	Not studied	
Tropiduridae ¹	Not studied	
Gekkota		
Gekkonidae	None known	<i>Coleonyx variegatus</i> <i>Gecko gecko</i> <i>Crenodactylus ocellatus</i> <i>Diplodactylus stenodactylus</i> <i>Gehyra variegata</i> <i>Heteronotia binoei</i> <i>Oedura lesueuri</i> <i>Rhynchoedura ornata</i> <i>Underwoodisaurus milii</i>
Pygopodidae	None known	<i>Lialis burtonis</i>

TABLE 6.3 (continued)

FAMILY	SALT GLANDS PRESENT	SALT GLANDS ABSENT
Scincomorpha		
Gymnophthalmidae	Not studied	
Teiidae	<i>Ameiva quadrilineata</i> <i>Cnemidophorus</i> spp.	<i>Tupinambis teguixin</i>
Lacertidae	<i>Acanthodactylus</i> spp. <i>Eremias guttulata</i> <i>Aporasaura</i>	<i>Lacerta viridis</i>
Xantusiidae	<i>Xantusia vigilis</i>	None known
Scincidae	<i>Tiliqua rugosa</i> <i>Eumeces skiltonianus</i> <i>Carlia fusca</i> <i>Carlia rhomboidalis</i> <i>Ctenotus taeniolatus</i> <i>Cryptoblepharus litoralis</i> <i>Egernia kingii</i> <i>Hemiergis peronii</i> <i>Menetia greyi</i> <i>Tiliqua occipitalis</i>	None known
Cordylidae	<i>Angolosaurus skoogi</i>	<i>Cordylus cataphractus</i>
Anguimorpha		
Xenosauridae	Not studied	
Anguidae	None known	<i>Elgaria multicarinatus</i> <i>Anniella pulchra</i>
Dibamidae	Not studied	
Amphisbaenia	None known	<i>Bipes biporus</i>
Helodermatidae	None known	<i>Heloderma suspectum</i>
Lanthanotidae	Not studied	
Varanidae	<i>Varanus semiremax</i> <i>V. gouldii</i> <i>V. salvator</i> <i>V. flavescens</i> <i>V. griseus?</i> <i>V. acanthurus</i> <i>V. rosenbergi</i> <i>V. giganteus</i>	

Sources: Data from Lemire and Deloince (1977); Minnich (1979, 1982); Saint Girons and Bradshaw (1987); Cooper and Robinson (1990); Clarke and Nicolson (1994); taxonomy from Estes et al. (1988); Frost and Etheridge (1989).

¹ Formerly included in Iguanidae; all iguanids were presumed to have salt glands, but not all of these groups have been examined.

gradually increase sodium output (Shoemaker et al., 1972). This phenomenon is controlled by the endocrine system: aldosterone and prolactin both decrease sodium excretion; absence of aldosterone increases sodium excretion (Shoemaker et al., 1972; Bradshaw et al., 1984a; Hazard, 1999).

The ability to modify the composition of the secreted fluid may give animals flexibility in acclimating or adapting to changes in dietary salinity. Several studies have been done on the secretion rates and sodium:potassium ratios secreted by lizards. To evaluate the extent to which

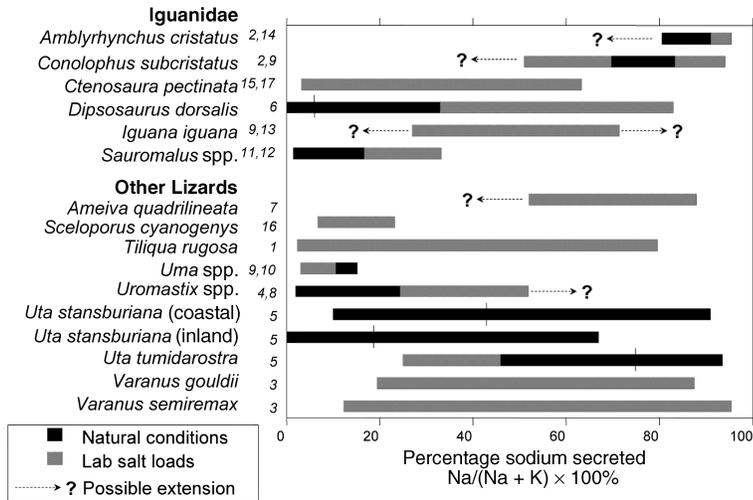


FIGURE 6.1. Range of relative sodium and potassium secretion for iguanids and other lizards. Percentage sodium (sodium/[sodium + potassium] \times 100%) was calculated when necessary from reported Na:K or K:Na ratios. Black bars indicate ranges seen under natural conditions; gray bars indicate extensions beyond the field ranges seen in response to ion loads. Vertical lines indicate mean percentage sodium secreted under natural conditions, where reported. Arrows indicate that individuals may not have been sufficiently challenged (through long-term NaCl or KCl loading) to determine the actual range possible for the species. Data for *Sauromalus hispidus*, *S. obesus*, and *S. varius* are pooled, as are data for *Uromastix acanthinurus* and *U. aegyptius* and for *Uma scoparia* and *U. notata*. Key to reference numbers to the right of the taxa: 1 = Braysher (1971); 2 = Dunson (1969); 3 = Dunson (1974); 4 = Dunson (1976); 5 = Hazard et al. (1998) and unpubl. data; 6 = Hazard (1999); 7 = Hillman and Pough (1976); 8 = Lemire et al. (1980); 9 = Minnich (1979); 10 = Minnich and Shoemaker (1972); 11 = Nagy (1972); 12 = Norris and Dawson (1964); 13 = Schmidt-Nielsen et al. (1963); 14 = Shoemaker and Nagy (1984); 15 = Templeton (1964); 16 = Templeton (1966); 17 = Templeton (1967).

different species can modify their sodium and potassium output, in figure 6.1 I summarize data from several such studies. Minnich (1979) reported single values for spontaneous secretion by about two dozen otherwise unstudied species; these species are not included in the figure. Most were iguanians and secreted predominately potassium; some were varanids and secreted predominately sodium.

Most researchers have reported the relationship between sodium and potassium secretion using a ratio, typically the Na:K ratio. However, this approach skews the relationship at very high or low ratios. If the ratio is 1:1, the animal is secreting equal amounts of sodium and potassium. As the fraction of potassium increases, the Na:K ratio decreases to a minimum of zero.

However, if the fraction of sodium increases, the Na:K ratio can increase indefinitely. To avoid this problem, I have converted the reported ratios to percentages (sodium/[sodium + potassium]) ranging from 0 to 100% sodium.

In *Dipsosaurus*, a normally potassium-secreting individual that is given a sodium load takes several days to adjust to the load and increase sodium secretion. Maximal sodium secretion is seen after 4–6 days of sodium loading (Hazard, 1999). Other species (e.g., *Tiliqua rugosa*) react in much the same way (Bradshaw et al., 1984b). Therefore, the ranges reported here may not reflect the true range of secretion possible for a species. Where animals may not have been given sufficient ion loads to determine a maximum or minimum, I have indicated the

possibility of a wider range for that species (figure 6.1). Ranges shown are for species, not individuals; individuals within a species may have more restricted ranges of excretion composition than does the species as a whole.

Different species are able to modify the composition of the secreted fluid to different extents; reported field ranges are generally more restricted than what the animals are capable of when subjected to ion loads in the laboratory (figure 6.1). For example, *Dipsosaurus dorsalis* secretes less than 33% sodium in the field (usually less than 5%), but can secrete solutions with cation compositions ranging from 0% to 83% sodium when given NaCl or KCl loads. Interestingly, they appear to have some obligatory potassium secretion even when given very high loads of NaCl (Hazard, 1999). *Sceloporus cyanogenys* only secretes from 6.7% to 16.6% sodium even when given long-term sodium loads in the laboratory (Templeton, 1966). Dramatic differences can be seen even in closely related species, such as *Uta stansburiana*, an insectivorous species, and *U. tumidarostra*, an insular species that feeds on intertidal isopod crustaceans (Grismer, 1994). Here, the ranges overlap substantially, but the mean field percentages differ, with the island species secreting more sodium than the mainland species (figure 6.1). *Sauromalus*, *Uma*, and *Sceloporus* appear to be limited primarily to potassium secretion, but other genera, such as *Iguana*, may have wider ranges than are currently known.

Because individual lizards of some species can modify the composition of their salt gland secretions, field secretion of sodium and potassium likely reflects the ion content of the diet of an individual, rather than the absolute capability of the gland to vary cation secretion. Examining the range of Na:K values possible under laboratory conditions gives a better indication of the extent to which populations are potentially able to respond to changes in the salinity of their diet. Further investigation of the underlying mechanisms of secretion may give insight into why some species are more limited than others in their ability to vary cation secretion.

REPEATABILITY OF SECRETORY ABILITY IN DESERT IGUANAS

With the possible exception of the varanids, the sodium-secreting marine species (such as *Amblyrhynchus* and *Uta tumidarostra*) are thought to be derived from mainland potassium-secreting species. The transition from a primarily potassium-secreting species to a primarily sodium-secreting species could involve natural selection on the capacity of the gland to secrete sodium. One way to determine whether natural selection can act on a trait is to examine within-individual repeatability of the trait over time. Repeatability ranges from 0 to 1, where 0 is not repeatable, and 1 is perfectly repeatable (each individual performs identically each time it is tested; Lessells and Boag, 1987).

Ion secretion by desert iguanas was repeatable over both short periods (weeks) and long-term (years; Hazard, 1999). In response to NaCl loads, sodium secretion rate, potassium secretion rate, and the cation ratio (percentage sodium) were all repeatable over a two-week period (repeatabilities of 0.44, 0.71, and 0.59, respectively). Secretion rates varied more over the long term, and only cation ratio was repeatable over a two-year period (repeatability of 0.60). Individuals that respond to NaCl loads by secreting high (or low) proportions of sodium tend to do so consistently over time.

Repeatability sets an upper limit to heritability, and the actual heritability may be much lower if repeatability is due to phenotypic effects rather than genotypic effects. Duck embryos preexposed to NaCl had higher secretion rates than control animals when subjected to intravenous NaCl 6–10 days later (Lunn and Hally, 1967). The ontogeny of salt glands in lizards has not been studied, and it is possible that individuals exposed to different ions early in life may retain a tendency to secrete different ions in a laboratory situation. However, the endocrinological system involved in modifying the cation ratio is likely to have variable and heritable components, including prolactin, aldosterone, and

associated receptors and intracellular signaling proteins. Further studies on heritability of secretion ability are needed.

SECRETION RATE

Salt gland secretion rate in birds is related to salt gland size (Holmes and Phillips, 1985); the same may be true for lizards. In most birds with salt glands, the salt gland lies on top of the skull in a depression over the orbit, and individuals can acclimate to salt loads by increasing gland size (Peaker and Linzell, 1975). In lizards, however, the gland is contained within the rostrum (Philpott and Templeton, 1964), and gland size is constrained by the size of the cartilaginous capsule that encloses the gland. Therefore, a short-term increase in gland size in an individual due to environmental effects is unlikely. However, increases over evolutionary time would be possible.

Secretion rates vary among lizard species (Minnich, 1979). Species needing higher secretion rates due to high ion diets should have relatively larger glands. Data on relative salt gland sizes in lizards are limited, but in two marine species with diets high in NaCl, the gland is larger than in relatives with less salty diets. The gland of *Amblyrhynchus* is enlarged such that the bulk of it is located over the eye (Dunson, 1969), and the gland of *Uta tumidarostra* is nearly five times larger than that of its mainland relative *U. stansburiana* (Grismer, 1994).

CONTROL OF SECRETION RATE

Initiation of secretion by lizard salt glands has been shown to be under the control of the parasympathetic nervous system; treatment with acetylcholine (ACh) or ACh analogs induces secretion in non-salt-loaded animals (Templeton, 1964; Shuttleworth et al., 1987). The environmental factors that stimulate secretion have been determined for the desert iguana (Hazard, 2001). In this species, secretion is increased specifically in response to potassium and chloride ions. Sodium alone, and general osmotic loads (e.g., sucrose) have no effect. This contrasts with other

taxa possessing salt glands; in birds and sea snakes, secretion is increased in response to any osmotic load (Minnich, 1979; Holmes and Phillips, 1985), whereas in green sea turtles, sodium appears to be the relevant secretagogue (Marshall and Cooper, 1988). Interestingly, the two relevant secretagogues for desert iguanas (potassium and chloride) are also the primary ions secreted by this species in the field. The environmental stimuli involved in initiating secretion by the salt glands of other lizard species have not been well studied, and it would be interesting to determine whether secretion by marine lizards is also stimulated by potassium and chloride, or whether these species are more similar to other marine animals.

CONCLUSIONS

Salt glands supplement renal salt excretion, and provide a means for lizards to feed on diets or live in environments high in sodium or potassium. The differences seen under field conditions may reflect a direct effect of diet on secretion, rather than different abilities of the various species. Although most species secrete either primarily potassium or primarily sodium under natural conditions, many appear to be capable of a wide range of cation secretion when subjected to experimental ion loads. This includes *Conolophus* and *Uta stansburiana*, close relatives of the marine/intertidal forms *Amblyrhynchus* and *U. tumidarostra*, respectively. This suggests that selection for the ability to secrete sodium may not have been necessary for the ancestors of these marine species to switch from a more typical terrestrial diet to a marine diet. Secretion of sodium by these species may simply reflect acclimation of the glands to a sodium-rich diet. However, it does appear that some species are more specialized than others, and that selection could act on secretion. *Sauromalus* and *Sceloporus* have a much lower capacity for sodium secretion than do the other species examined, and the ability of *Amblyrhynchus* to reduce sodium secretion is not known. *U. tumidarostra* appears to be unable to reduce sodium secretion below about 25%.

Secretion by *Dipsosaurus* in response to NaCl or KCl loads is repeatable, suggesting that natural selection could potentially act on cation secretion. Regardless of the current level of specialization of the marine species, the flexibility of the related terrestrial species appears to have served as a preadaptation that allowed these animals to secondarily invade marine habitats and specialize on marine foods.

Virtually all of the NaCl-secreting lizards with marine diets (e.g. *Amblyrhynchus*, *Uta tumidarostra*, *Ameiva*) are derived from species that are primarily potassium-secreting. However, even groups without herbivorous ancestors, such as the varanids, are capable of secreting potassium (figure 6.1). To better understand differences among species, more information is needed about the mechanisms underlying secretion. It may be that the ion transport proteins involved in secreting sodium and potassium somehow constrain the system to require some potassium secretion, even when sodium is the relevant dietary ion.

A second factor important to the evolution of marine lizard species is secretion rate. Marine foods are saltier overall than most terrestrial foods (table 6.1), and a higher secretion rate is necessary to cope with the higher salt load. Both the marine iguana and *Uta tumidarostra* have higher secretion rates than related species and

have hypertrophied salt glands (Dunson, 1969; Grismer, 1994; Hazard et al., 1998). For the evolution of primarily sodium-secreting glands of marine lizards to occur, a change in the overall capacity of the gland (in part through an increase in relative gland size) may have been more important than evolutionary changes in the ability to excrete sodium specifically.

To better evaluate the evolution of ion secretion by lizard salt glands, more data are needed on field and maximum rates and ratios of cation secretion, ion compositions of diets, and mechanisms of control of secretion. It would be particularly interesting to examine groups other than the Iguania, such as the varanids, and to clarify the presence or absence of salt glands in families that have not been thoroughly examined.

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