

OSMOREGULATION BY ADÉLIE PENGUIN CHICKS ON THE ANTARCTIC PENINSULA

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ABSTRACT.—Physiologists have long contended that consumption of a diet of marine invertebrates imposes a high salt load on animals. I measured water and salt contents in the food, excreta, and body fluids of Adélie Penguin (*Pygoscelis adeliae*) chicks to determine patterns of osmoregulation in a bird that eats almost exclusively marine invertebrates. Adélie Penguins eat krill (*Euphausia* spp.) and feed the same to their chicks by regurgitation. Adélie chicks sometimes receive food that is significantly saltier than their body fluids, but on average the food has salt concentrations similar to those in their plasma. Adélie chicks excrete excess solutes via the salt glands, which are fully functional at hatching, and via the kidneys, which produce urine that is more concentrated relative to urine of other bird species. Larger chicks receive food that is drier than that eaten by smaller chicks, and larger chicks may compensate by excreting more of a given salt load via the salt glands, thus conserving water. Regurgitated food has significantly less Na⁺ than Cl⁻, but the salt glands secrete equal amounts of these two ions. Consequently, in larger chicks Na⁺ may be shunted from the urine to be excreted via the salt glands. The loss of this cation in the urine is compensated for by addition of NH₄⁺. Received 26 July 1996, accepted 1 February 1997.

ADÉLIE PENGUINS (*Pygoscelis adeliae*) live in an osmotically challenging marine environment. Adélie Penguins have little or no access to fresh water, and up to 99% of their diet is marine invertebrates, usually krill (mostly *Euphausia superba*; Volkman et al. 1980). Adélie chicks potentially face the same osmotic challenges as the adults, because the only food they receive is that regurgitated by their parents. Unless adults modify the composition of krill fed to chicks, then the chicks' osmoregulatory physiology must be sufficiently developed to handle potentially high salt loads delivered in the food within hours after hatching (Douglas 1963, 1968). The purpose of this study was to determine the magnitude of salt loads received by chicks, determine if adults alter the salt composition of food given to chicks, and measure the salt concentrations of chick excretions (e.g. urine and salt-gland secretion) to determine salt-output capability.

Adélie Penguins are good subjects for physiological studies of osmoregulation for four important reasons. First, their large size (adults weigh 4 to 5 kg) allows collection of relatively large samples of tissues and body fluids, which facilitates ion analyses. Second, Adélie Penguins are found in dense colonies near research

stations in Antarctica, and this abundance combined with their relative tameness permits acquisition of large sample sizes. Third, their life history is well known (Ainley et al. 1983). Fourth, all of the material input into chicks is regurgitated by the parents, simplifying measurements of water and salt influx.

METHODS

Adélie Penguin chicks were from colonies on Torgersen Island, near Palmer Station (64°46'S, 64°05'W) off the west coast of the Antarctic Peninsula. Regurgitated food spilled during feedings was collected throughout the nesting season from 52 adult penguins. Only food that was observed to be freshly spilled was collected. The chicks being fed were weighed using a Pesola spring scale. The regurgitated food was freeze-dried to determine water content, and the dried sample was homogenized and analyzed for Na⁺, K⁺, and Cl⁻ (see below). Twenty freshly collected krill were batched, homogenized, and analyzed for H₂O, Na⁺, K⁺, and Cl⁻ content.

In many birds, urine exits the ureters and is refluxed into the lower intestine in a retrograde direction before it is excreted from the vent. Dissections of Adélie chicks showed uric acid in the large intestine, indicating urinary reflux. Therefore, I distinguished between urine collected directly from the ureters (hereafter "urine," or "ureteral urine") and naturally voided fluid (hereafter "cloacal fluid"). Cloacal fluid was collected from 135 chicks by placing each chick in a clean plastic bucket with a wire-

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mesh floor. When excreta were produced, the chick was weighed and released back to its nest site. The fluid was aspirated with a Pasteur pipette, leaving the feces behind, and transferred to a screw-top plastic tube.

Urine was collected directly from the ureters in 13 chicks. First, naturally voided cloacal fluid was collected in a clean plastic bucket with a wire-mesh floor. Immediately after this excreta was voided, a glass cannula with a bulb on one end and a hole in the bulb was inserted into the vent. The hole was positioned dorsally, beneath the ureteral openings, and up to 250 μL of ureteral urine flowed directly into the cannula within two minutes. Ureteral urine was then transferred to glass capillary tubes that were flame-sealed. Salt-gland secretion was collected from chicks by holding a 75- μL glass capillary tube over one of the nares until the tube was at least half-full of secretion. The chicks were weighed after sampling, and the tubes were flame-sealed.

Blood was collected from 60 chicks of various sizes by puncturing a vein in the foot and drawing the blood into heparinized capillary tubes. The blood was centrifuged, the hematocrit measured, and the plasma kept in flame-sealed capillary tubes for later analysis. Seventeen chicks of various sizes were taken from the colony, killed by decapitation, and freeze-dried. The dried specimens were homogenized, and the dry homogenate analyzed for Na^+ , K^+ , and Cl^- content (see below).

For comparative purposes, samples of cloacal fluid, salt-gland secretion, and blood were also collected from adults as described above. To determine if adult penguins alter the chemical composition of the food before feeding it to their chicks, stomach contents of adults were sampled before and after an 8-h waiting period. Twelve adults were captured shortly after coming ashore and their stomach contents sampled by inserting a soft Tygon tube through the esophagus to the stomach and applying gentle suction using a 30-ml syringe. The penguins subsequently were held in a well-ventilated wooden box on Torgersen Island for 8 h, stomach contents were sampled again, and the penguins were released. In this manner it was easy to obtain 1 to 10 g of krill with no apparent damage to the penguin.

All liquid samples (urine and cloacal-fluid supernatant, salt-gland secretion, and plasma) were analyzed for osmolality and then frozen at -20°C for later analysis of Na^+ , K^+ , and Cl^- concentrations. Urine was also analyzed for PO_4^{3-} , SO_4^{2-} , urea, NH_4^+ , and urate. Osmolality was measured using a 5100B vapor-pressure osmometer (Wescor, Inc.). Sodium and potassium concentrations were measured using a Kline flame photometer (Beckman Instruments, Inc.). Chloride concentration was measured using a Buchler-Cotlove chloride titrator. Phosphate concentration was measured using a Sigma Diagnostics 670-C kit. Sulfate concentration was measured by

turbidimetry following addition of BaCl_2 to precipitate BaSO_4 (Goltermann et al. 1978). Urea and NH_4^+ concentrations were measured using a phenate-hypochlorite colorimetric procedure (Fawcett and Scott 1960). Urate concentrations were measured by dissolving and diluting the solid urate with KOH solution and measuring the absorbance at 293 nm. The molar absorptivity of uric acid ($1.22 \times 10^4 \text{ cm}^{-1}$) was used to calculate uric acid concentration (Worthington Enzyme Manual 1972).

All solid samples (regurgitated food, dried carcasses) were dried to constant mass to determine water content and then analyzed by leaching with distilled water and measuring the Na^+ , K^+ , and Cl^- concentrations in the leachate as described above for liquid samples. To test for complete leaching of Na^+ and K^+ , some samples were completely digested in concentrated nitric acid and the Na^+ and K^+ concentrations measured and compared with measurements made on the same samples leached with distilled water. No differences were seen between water-leached and acid-digested samples; therefore, all data presented are those from water-leached samples.

Data were analyzed using least-squares linear regression and *t*-tests in Statistica (StatSoft, Inc.), a statistics program for the Macintosh. Means are expressed ± 1 SD. Statistical significance was set at $P < 0.05$.

RESULTS

Regurgitated food was collected several times throughout the breeding season, and water content and salt concentration of the food did not exhibit consistent differences over the season. Water content of regurgitated food (range 2.2 to 6.9 g $\text{H}_2\text{O} \cdot \text{g}^{-1}$ dry mass) was negatively correlated with mass of the chick being fed ($r = 0.516$, $P < 0.001$; Fig. 1). Ion concentrations in regurgitated food ($\text{mmol} \cdot \text{kg}^{-1} \text{H}_2\text{O}$; see Table 1) were not correlated with chick mass. The batched sample of fresh krill was wetter and had higher concentrations of Na^+ , K^+ , and Cl^- than the averages for regurgitated food (Table 1). However, water content and concentrations of Na^+ , K^+ , and Cl^- in fresh krill were within the ranges measured for regurgitated food. The concentration of Cl^- in regurgitated food was higher than that of Na^+ in the same food samples ($P < 0.001$).

Osmolality of cloacal fluid was positively correlated with chick mass (Fig. 2). The shape of the curve appears to be due primarily to concentrations of NH_4^+ and PO_4^{3-} , both of which also were correlated with chick mass (Fig. 2). Urea and K^+ concentrations were positively

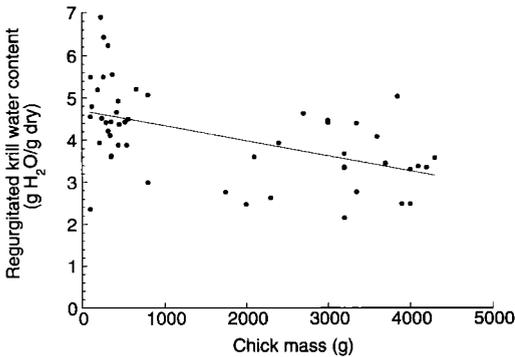


FIG. 1. Water content of regurgitated krill collected from adult Adélie Penguins feeding chicks of various sizes. Linear regression is significant ($r = 0.516$, $P < 0.001$).

correlated with chick mass, but Na^+ concentration was negatively correlated with chick mass (Fig. 2). Chloride, SO_4^{2-} , and urate concentrations were not correlated with chick mass. Mean cloacal-fluid solute concentrations (mmol/L) were as follows: Cl^- , 235 ± 69 (range 11 to 561, $n = 124$); SO_4^{2-} , 47 ± 23 (range 0 to 112, $n = 63$); and urate, 587 ± 582 (range 43 to 4,236, $n = 86$). Cloacal-fluid pH in 11 chicks of different sizes averaged 5.54 ± 0.277 (range 5.2 to 6.0). Concentrations of Na^+ , K^+ , and Cl^- in naturally voided cloacal fluid were not different from those in urine collected directly from the ureters of the same birds (Na^+ , $P = 0.57$; K^+ , $P = 0.18$; Cl^- , $P = 0.92$; Fig. 3).

Ion concentrations in salt-gland secretions (see Table 2) were not correlated with chick mass, nor were hematocrits and plasma-ion concentrations. However, the mean hematocrit for chicks in the colony ($36 \pm 3.9\%$, $n = 54$) was lower than that of fledglings standing on the beach waiting to go to sea ($45 \pm 3.7\%$, $n = 11$, $P < 0.0001$).

The concentrations (mmol \cdot kg $^{-1}$ wet mass) of Na^+ , K^+ , and Cl^- in chick carcasses were not correlated with chick mass, and were as follows: Na^+ , 71.2 ± 6.12 (range 58.6 to 83.6); K^+ , 46.9 ± 8.19 (range 34.5 to 59.8); and Cl^- , 59.5 ± 8.38 (range 38.6 to 68.7). Water content of chicks was negatively correlated with chick mass ($r = 0.85$, $P < 0.0001$). The linear regression between chick mass in grams (x) and % water content of chicks (y) was:

$$y = 79.7 - 0.00530x. \quad (1)$$

Na^+ and K^+ concentrations in food from

TABLE 1. Water (g $\text{H}_2\text{O}/\text{g}$ dry) and solute (mmol \cdot kg $^{-1}$ H_2O) contents of food pumped from the stomachs of adult Adélie Penguins (before and after an 8-h waiting period), food dropped by adults while feeding chicks (regurgitated food), and a batched sample of fresh krill. Data are $\bar{x} \pm \text{SD}$, with range in parentheses.

Water	[Na^+]	[K^+]	[Cl^-]
Stomach-pumped krill (initial; $n = 12$)			
7.2 ± 3.38 (3-16)	119 ± 30 (76-169)	40 ± 13 (13-61)	192 ± 38 (118-265)
Stomach-pumped krill (after 8 h; $n = 12$)			
11.1 ± 7.57 (4-30)	79 ± 24 (43-124)	19 ± 9 (0-34)	161 ± 40 (64-199)
Regurgitated food ($n = 89$)			
4.2 ± 1.15 (2.2-6.9)	146 ± 76 (5-586)	55 ± 26 (2-177)	205 ± 36 (136-348)
Fresh krill ($n = 20$)			
5.48	277	74.7	290

adult stomachs were significantly lower after an 8-h waiting period (Na^+ , $P < 0.01$; K^+ , $P < 0.001$), but water content and Cl^- concentration did not differ before and after the 8-h period (Table 1).

DISCUSSION

Physiologists have long contended that a diet of marine invertebrates constitutes a significant salt load to the animals consuming it (e.g. Green and Gales 1990). Adélie Penguins, with a diet composed almost exclusively of krill, therefore should experience appreciable salt loads on a regular basis. However, sodium concentrations in fresh krill are quite variable, ranging from 96 to 425 mmol \cdot kg $^{-1}$ H_2O (Mauchline 1980, Nicol et al. 1992). Although most of this range lies above the sodium concentration in the plasma of adults, it is difficult to state with certainty whether adult Adélies are continually salt-loaded in the field. Observations of chicks eating krill regurgitated by adults suggest that chicks receive the same salty diet as the adults, and therefore are subjected to the same ionic challenges. However, if the adults are not eating particularly salty krill, or if the adults can alter the composition of the krill, then the chicks may not have to handle a particularly large salt load.

In this study, it was not feasible to measure sodium concentration in the krill being eaten by the foraging adults. However, sodium con-

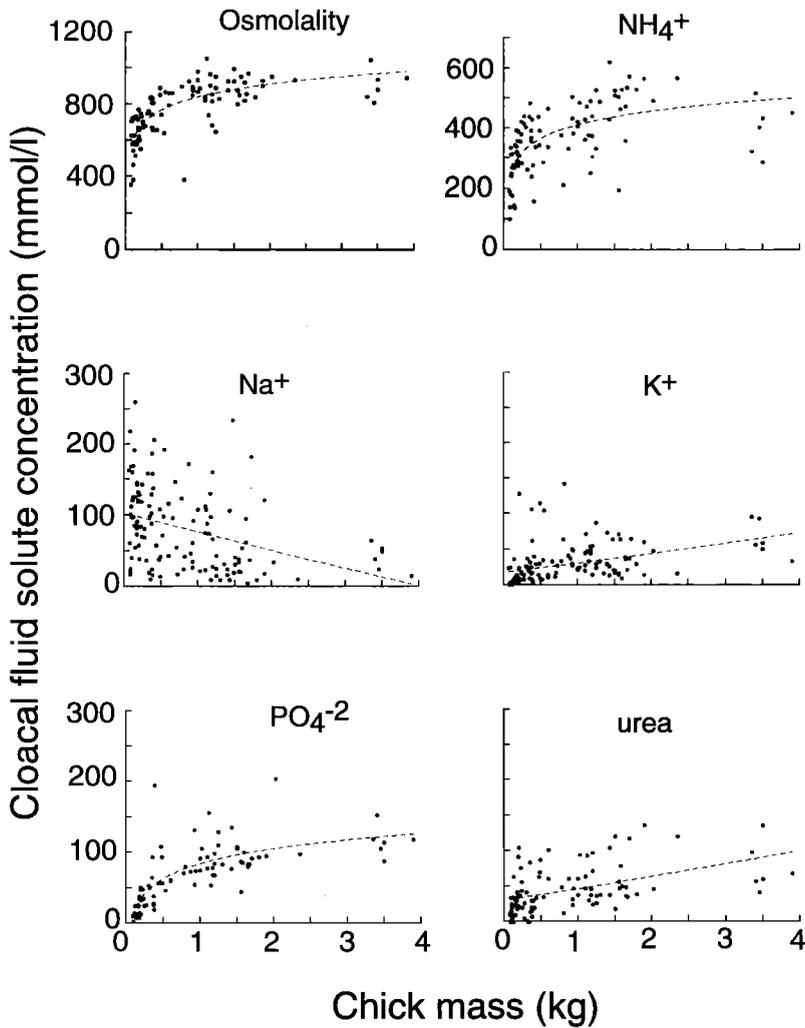


FIG. 2. Osmolality and concentrations of solutes in cloacal fluid collected from Adélie Penguin chicks of various sizes. All cloacal fluid was spontaneously voided and was collected within 10 min of capturing the chick. All regressions are significant at $P < 0.05$ or lower. Osmolality units are mosm/kg.

concentrations in regurgitated krill were measured, and although the range was considerable (5 to 586 $\text{mmol} \cdot \text{kg}^{-1} \text{H}_2\text{O}$), the mean was at the lower end of the range of concentrations in fresh krill (Mauchline 1980). Moreover, the mean sodium concentration in regurgitated krill was not significantly different from that in chick plasma, further suggesting that on average chicks did not receive particularly large salt loads relative to the salt concentration in their body fluids.

Whether adults alter the composition of krill may be related to how much time the krill spends in the adults' stomachs before it is fed

to their chicks. Stomach contents sampled before and after an 8-h waiting period did not differ in Cl^- concentration, similar to calculations by Douglas (1968). However, Na^+ and K^+ concentrations decreased, indicating that if the food resides in the stomach for sufficient time, it can be at least partially desalinated before being fed to the chicks.

Foraging adults apparently fill their stomachs with krill immediately before returning to the colony to feed chicks, and average travel time to the colony is about 1.15 h (range 10 min to 5 h; Chappell et al. 1993). After the adults return to the colony, the amount of time that

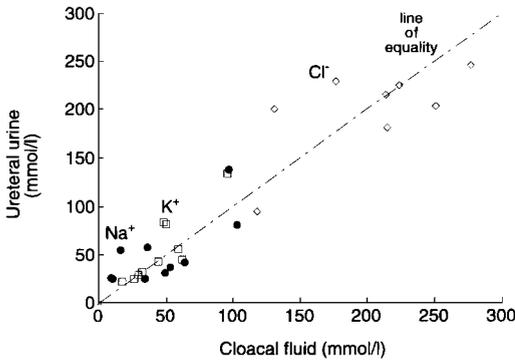


FIG. 3. Sodium, potassium, and chloride concentrations in urine and cloacal fluid collected from 10 Adélie Penguin chicks. Spontaneously voided cloacal fluid was collected first, immediately after which ureteral urine was collected. Concentrations of these ions did not differ between urine and cloacal fluid.

passes before the stomach contents are fed to the chicks depends on chick size. Small chicks are guarded continuously, and the guarding adults feed the chicks small amounts of regurgitated food throughout the day. Large chicks do not require guarding, and the adults feed them their entire stomach contents in a few minutes and usually depart the colony soon afterwards. Thus, food composition potentially can be altered more for smaller chicks than for larger chicks. However, salt concentrations did not differ in regurgitated food fed to small versus large chicks. Perhaps the adults' absorption of water exceeds salt absorption, causing the decrease in water content in the regurgitated food fed to large chicks, and masking any potential changes in salt concentration. Many birds, including Adélie Penguins, reflux urine anteriorly into the large intestine. Exposure to the mucosa of the intestine may result in modification of urine composition due to differential reabsorption of solutes and water (Anderson and Braun 1985). The cloacal fluid used for measurement of solute concentrations in the present study always was spontaneously voided and thus could have been refluxed and modified before excretion. However, urinary concentrations of Na⁺, K⁺, and Cl⁻ did not differ between ureteral and cloacal fluid, indicating that there was little, if any, postrenal modification of urine composition.

Adélie Penguin chicks have unusually high concentrations of urinary Cl⁻ compared with other species, and compared with Adélie

TABLE 2. Osmolality (mosm/kg) and solute concentrations (mmol/L) in salt-gland secretions, blood plasma, and urine of Adélie Penguin adults and chicks. Data are $\bar{x} \pm SD$ (range; *n* in parentheses).

Age	Osmolality	[Na ⁺]	[K ⁺]	[Cl ⁻]	Hematocrit	[PO ₄ ⁻²]	[SO ₄ ⁻²]	Urea	[NH ₄ ⁺]
Chick	1,421 ± 168 (712-1,767; 45)	722 ± 96.0 (340-895; 43)	24.0 ± 4.00 (15-40; 43)	743 ± 68.0 (563-914; 40)	—	—	—	—	—
	Adult	1,468 ± 104 (1,220-1,665; 21)	794 ± 69.1 (640-900; 14)	21.8 ± 1.46 (19-25; 14)	—	—	—	—	—
Chick	326 ± 9.9 (298-354; 66)	158 ± 5.86 (146-180; 57)	5.12 ± 2.14 (2-14; 57)	112 ± 6.77 (98-143; 56)	38 ± 4.9%	—	—	—	—
	Adult	329 ± 6.6 (314-344; 73)	165 ± 7.75 (152-186; 26)	4.43 ± 1.51 (1-8; 26)	116 ± 8.20 (92-165; 26)	54 ± 4.9%	—	—	—
Adult	805 ± 142 (429-1,011; 29)	20.3 ± 14.7 (5-45; 7)	98.0 ± 26.3 (52-125; 7)	68.3 ± 49.3 (16-141; 7)	—	84.2 ± 19.3 (57-111; 5)	75.0 ± 43.6 (33-120; 3)	83.1 ± 51.0 (11-144; 12)	237 ± 107 (139-327; 12)

TABLE 3. Avian cloacal-fluid osmolality (mosm/kg) and solute concentrations (mmol/L) in the field and laboratory (including salt-loading experiments).

Species	Age/ Type ^a	Osmolality						Reference
		Max.	Mean	[Na ⁺]	[K ⁺]	[Cl ⁻]	[NH ₄ ⁺]	
Adélie Penguin	C, F	1,055	777	81	30	235	270	This study
Adélie Penguin	A, F	1,011	805	20	98	68	237	This study
Adélie Penguin	C, L	—	—	—	—	247	—	Douglas 1968
Adélie Penguin	C, SL	—	—	—	—	249	—	Douglas 1968
Adélie Penguin	A, L	—	—	—	—	48	—	Douglas 1968
Adélie Penguin	A, SL	—	—	—	—	85	—	Douglas 1968
Leach's Storm-Petrel (<i>Oceanodroma leucorhoa</i>)	C, F	—	735	72	19	—	—	Goldstein 1993
California Gull (<i>Larus californicus</i>)	C, F	—	475	89	27	—	—	Mahoney and Jehl 1985
Glaucous-winged Gull	C, SL ^b	—	—	135	33	177	—	Hughes 1984
Glaucous-winged Gull	C, SL ^c	—	—	100	28	88	—	Hughes 1984
Gulls ^d	J, L	—	81	20	64	—	—	Ensor and Phillips 1972
Gulls ^d	J, SL	—	242	133	96	—	—	Ensor and Phillips 1972
Herring Gull	A, SL	680	385	60	11	—	88	Douglas 1970
Jackass Penguin	A, F	748	679	89	53	75	—	Oelofsen 1973
Jackass Penguin	A, SL	—	435	159	10	186	—	Erasmus 1978b
Jackass Penguin	A, L	—	160	31	3	115 ^e	—	Erasmus 1978b
American White Pelican (<i>Pelicanus erythrorhynchos</i>)	A, L	734	231	35	16	—	—	Calder and Bentley 1967
Greater Roadrunner (<i>Geococcyx californianus</i>)	A, L	736	453	70	43	—	—	Calder and Bentley 1967

^a C, chick; A, adult; J, juvenile; F, field study; L, laboratory study (not salt-loaded); SL, salt-loaded.

^b 1 to 16 days old.

^c 16 to 32 days old.

^d Data combined for *Larus argentatus* and *L. fuscus*.

^e Slightly salt-loaded.

adults (Table 3). The latter is puzzling, because the Cl⁻ concentrations in fresh krill and regurgitated food were not remarkably different. In addition, cloacal-fluid osmolalities are high in Adélie chicks and adults, averaging 800 mosm/kg (Table 3). Maximum cloacal-fluid osmolalities in Adélie Penguins (>1,000 mosm/kg) exceed any values reported for marine birds (Table 3), although they are comparable to maximum urine osmolalities measured in small passerines (e.g. 1,335 mosm/kg in a House Sparrow [*Passer domesticus*]; Goldstein and Braun 1989). However, maximum urine osmolalities in these passerines were determined from experimentally dehydrated birds.

The other urinary solutes that I measured (NH₄⁺, urea, PO₄⁻², and SO₄⁻²) have seldom been measured in other birds, with the exception of nitrogen excretion (see Table 4). Adélie Penguin chicks have urinary nitrogen compositions that are within the range measured in other birds.

Cloacal-fluid osmolality in the field increases with chick mass, and most of the increase in osmolality is due to an increase in NH₄⁺ concen-

tration (Fig. 2). Large chicks are fed significantly drier food than smaller chicks and therefore may require a mechanism to reduce water loss. Reduction of water loss can be achieved by excreting more of a salt load by the salt glands. Avian salt-gland secretion contains Na⁺ and Cl⁻ in nearly equal concentrations, but regurgitated food has a higher Cl⁻ concentration than Na⁺ concentration. Larger chicks reabsorb more Na⁺ from the urine (Fig. 2), possibly to provide the necessary cations to balance the excretion of Cl⁻ anions by the salt glands. There is a concomitant increase in urinary NH₄⁺ concentration with decreasing urinary Na⁺ concentration (Fig. 4), suggesting an exchange mechanism for the two ions. Similar results were obtained for Herring Gulls (*Larus argentatus*; Douglas 1970), and Erasmus (1978a) postulated such a mechanism for Jackass Penguins (*Spheniscus demersus*).

The composition of salt-gland secretion in Adélie Penguin chicks is comparable to that of other marine birds. Almost all of the osmotic concentration is due to Na⁺ and Cl⁻, with a relatively small concentration of K⁺ making up

TABLE 4. Relative amounts of nitrogenous compounds in avian urine. Units are expressed as percentage of total urinary nitrogen in each compound.

Species	Urate	NH ₄ ⁺	Urea	Reference
Adélie Penguin chicks	77	18	5	This study
Emu (<i>Dromaius novaehollandiae</i>)	79	5	10	Dawson et al. 1991
Chicken	75–80	10–15	2–6	O'Dell et al. 1960 ^a
Chicken	82	6	—	Katayama 1924 ^a
Chicken	66	8	6	Coulson and Hughes 1930 ^a
Chicken	63	17	10	Davis 1927 ^a
Chicken	60	23	6	Teekell et al. 1968 ^a
Chicken	55–72	11–21	1.5–11	McNabb and McNabb 1975 ^a
Duck	54	29	1.5	Stewart et al. 1969 ^a

^a In Shoemaker (1972).

most of the balance. Osmolality of salt-gland secretion was similar to that in other birds (Schmidt-Nielsen and Sladen 1958, Douglas 1970, Erasmus 1978b, Conway et al. 1988, Gray and Erasmus 1989, Hughes 1989, Hughes and Winkler 1990).

The blood of Adélie Penguin chicks was similar to that of adults in osmotic and ion concentrations, but hematocrit was significantly higher in adults. A similar result was seen in nestling Glaucous-winged Gulls (*Larus glaucescens*; Hughes 1984). Presumably, adult birds have a higher aerobic capacity required for flight or swimming and thus require a higher blood-oxygen carrying capacity. No gradual increase in hematocrit was observed in growing chicks, but fledglings standing on the beaches before going to sea had a significantly higher hematocrit ($\bar{x} = 45\%$) than younger chicks in the colonies ($\bar{x} = 38\%$, $P < 0.05$).

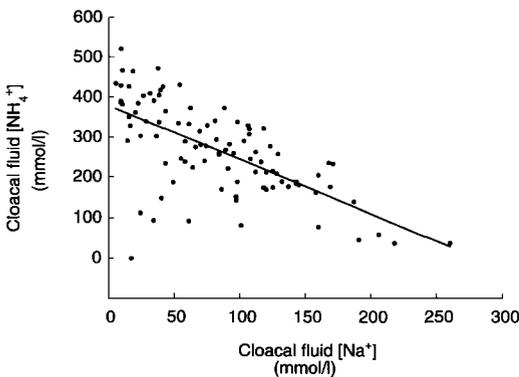


FIG. 4. Ammonium (y) and sodium (x) concentrations in cloacal fluid of Adélie Penguin chicks. Regression equation is $y = 378 - 1.35x$ ($r = 0.714$, $P < 0.0001$).

In summary, Adélie Penguin chicks consume a diet of regurgitated marine invertebrates, but on average the diet does not appear to entail a large salt load. Nevertheless, chicks have the ability to excrete excess solutes in salt-gland secretion and in urine that is more highly concentrated than that of most other bird species. Concentrations of salt-gland secretion are similar in many different bird species, and in Adélie chicks and adults. There are no significant ontogenetic changes in physiological capacity of Adélie chicks, but larger chicks receive drier food than smaller chicks and may conserve water by using their salt glands more than do smaller chicks.

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