OBSERVATIONS ON METABOLISM OF SODIUM CHLORIDE IN THE RED CROSSBILL

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Over the past five years the capacities of several land birds for obtaining osmotically unobligated water from saline solutions have been evaluated (see Bartholomew and Cade, 1963). Such studies have contributed to an understanding of the water economies of species inhabiting salt marshes (Cade and Bartholomew, 1959) and to some assessment of the potential of species inhabiting deserts for gaining water from saline sources (Bartholomew and Cade, 1958). Studies of utilization of saline solutions have recently been supplemented by analysis of kidney function in the House Finch (*Carpodacus mexicanus*) and certain subspecies of the Savannah Sparrow (*Passerculus sandwichensis*) by Poulson and Bartholomew (1962a, b).

Despite significant advances in the understanding of electrolyte metabolism of wild land birds, many additional studies are needed. The high order of interspecific and even intraspecific variability in this area hinders generalizations concerning salt tolerances of these animals. Moreover, studies of electrolyte excretion should be extended beyond the two species on which data are now available. For these reasons we undertook this investigation of the Red Crossbill (*Loxia curvirostra*). We considered this bird of particular interest because of its habit of eating salt in the wild—most of our experimental birds were obtained with a trap baited with a block of salt. The observations reported here concern capacities of individuals of this species for utilizing sodium chloride solutions of various concentrations and their response to injected loads of this salt.

Materials and Methods

The Red Crossbills used in this investigation are referable to the subspecies *Loxia curvirostra sitkensis*. Birds of this form are resident along the Pacific coast of North America, including islands, from central southern and southeastern Alaska south to northwestern California. However, they may wander widely, chiefly in winter, and have been recorded as far south as Arizona and as far east as New York and Massachusetts. The 48 individuals studied were captured in the Huron Mountains, Marquette County, Michigan, in the summer and fall of 1960, and in the winter of 1960–61 both at this place and on the University of Michigan campus, Washtenaw County, during a large-scale invasion of the state by crossbills.

Except during experiments, the Red Crossbills were housed out-of-doors in flight cages, the smallest of which measured $4 \times 6 \times 9$ feet. In these cages they were exposed to photoperiods natural for the latitude of Ann Arbor (approximately 42°

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N) and to ambient temperatures that generally fluctuated between -10° and 0°C in the winter and occasionally reached 33°C in the summer. The crossbills were provided with snow or water for drinking, with food consisting of sunflower seeds, piñon nuts, and hemp seeds, and with salt blocks. The individuals studied generally maintained their normal weight (about 30 g) under these conditions and remained in excellent condition over the two years in which the studies here reported were conducted.

EXPERIMENTS

Utilization of salt solutions by crossbills.—Birds to be used in experiments on utilization of salt solutions were brought indoors and, in most cases, placed in groups of six within cages measuring 24 × 36 × 48 inches. However, for some experiments involving 0.2 to 0.3 M salt solutions, birds were placed individually in cages measuring 24 × 24 × 24 inches. The larger cages were each provided with two drinking devices consisting of inverted graduated cylinders equipped with "L"-shaped drinking tubes (see Bartholomew and Dawson, 1954). Only one drinker was used in each of the smaller cages. The birds were restricted to a diet of piñon nuts and were deprived of salt blocks throughout these experiments. The temperature in the room housing these cages ranged from 23° to 28°C and the relative humidity remained below 30 per cent during winter and early spring when these experiments were performed. Photoperiod varied from 10 to 13 hours, being keyed to that prevailing outside. Natural daylight entering the room through the windows was augmented by daylight fluorescent lights.

Crossbills from outdoor flight cages frequently gained weight following transfer indoors. In the week or so required for them to reach a new, stable weight (mean, 31.9 g), they learned to use the drinking devices which contained tap water (sodium content, 1.5 mEq/liter).

At the beginning of an experiment, the crossbills were weighed and the tap water in the drinking devices replaced with distilled water or an NaCl solution of a given molarity. The birds were thereafter weighed daily to the nearest 0.1 g and the amount of fluid drunk during the previous 24 hours was determined. Before the birds were returned to the cage, the drinking device was refilled with the appropriate fluid and food was replenished. Thus we determined changes in weight of all birds and the average daily intake of fluid within a group of six birds in the larger cages, or the actual fluid intake of birds in the smaller cages. At salinities as high as 0.2 M, the experiments lasted about three weeks. At higher salinities, experiments were continued until the birds appeared severely stressed.

Plasma samples were obtained for sodium determinations. Control samples were taken from birds that had been drinking tap water for several weeks. The other samples were obtained at the completion of experiments; control samples had previously been obtained from some of the animals studied. For sampling, the crossbills were immobilized on their backs and a wing extended so the brachial vein was visible. The skin covering it was cleaned with ethanol. When the surface had dried the vein was punctured with a fine needle. As blood appeared, a 0.05 ml sample was collected in a heparinized capillary tube (1.5 mm in diameter). One end of this tube was flame-sealed and the other provided with a plastic cap. The sample was centrifuged and the plasma removed to be refrigerated until analysis.

Fluid intake and urine production.—On a number of occasions, birds being maintained in the previously described experiments were removed to separate cylindrical cages, 6 inches in diameter and 10 inches high, in which their fluid consumption could be measured and their urine collected after they had fasted overnight (this to minimize fecal contamination of the urine samples). The point in the experiment at which this was done varied with the concentration of the solution that the birds were drinking, but it was late enough so that they had developed a well-defined response (e.g., significant loss of weight, markedly increased fluid intake, etc.). The birds were transferred to the small cages at the end of the day before observations were to be made. Voided urine fell through a wire platform onto parafilm covering the bottom of the cage. As soon as this occurred, the parafilm was removed and the urine collected in a capillary tube, the ends of which were then flame-sealed. In all these experiments, the observer was concealed to minimize disturbance of the birds. Collections were continued for two or three hours, after which the birds were returned to their cages. They suffered no apparent ill-effects from the period of fasting. Urine samples were subsequently centrifuged to settle the uric acid present. This allowed us to estimate the volume of the fluid column within the capillary. The urine was refrigerated until it could be analyzed for sodium.

Fluid preferences of crossbills.—In view of the ingestion of salt by crossbills in nature, it was thought that they might prefer sodium chloride solutions to distilled water. We noticed that certain of the crossbills housed in cages with tap water available in more than one place consistently drank from particular drinkers regardless of where these devices were placed, or at particular positions regardless of the drinkers available there. Consequently, experiments to test the preferences of crossbills between distilled water and 0.100 M or 0.200 M NaCl were designed taking these behavioral tendencies into account. The birds were placed in separate cages measuring 24 × 24 × 24 inches, as soon as they had learned to use drinkers. Each cage was provided with two superficially identical drinkers, one containing distilled water and the other 0.100 or 0.200 M NaCl. In the tests, the positions of the solutions, the drinkers, or both were interchanged every three days. Each test lasted 9 or 12 days, and the volume consumed from each drinker was recorded daily.

Acute loads of sodium chloride.—Acute salt loads were administered by injection of a 10 per cent (about 1.7 M) solution of NaCl into birds that had fasted overnight. This fluid was injected through a needle-tipped capillary tube into the brachial vein. Tubes of this type, also used to obtain blood samples, were prepared from pyrex melting point capillaries 11.5 mm in outer diameter. These were drawn out into two 6-cm segments on a Livingston micropipette puller after being heated with a dental blow pipe. The thin tips thus produced were sharpened further by grinding them on a rotating glass plate covered with a paste containing exceedingly fine particles of diamond (Diaplast). When completed, the chisel-like tips of the capillaries approximated 30 μ in diameter.

For venipuncture, the needle-tipped capillaries were mounted in a simple electrode holder that could be advanced by a screw mechanism. This holder was in turn mounted on a cathetometer stand, which allowed smooth movement in the vertical plane. The blunt end of the capillary tube was connected via polyethylene tubing to the components for injection or blood sampling. The bird was enclosed in a paper cylinder containing a slit through which a wing protruded. This wing was placed in a restraining device with the ventral surface exposed. Just before venipuncture, the bird was lightly anesthetized with ether. The hole left in the vein was so fine that it tended to close with little loss of blood.

For injection of the NaCl solution, the needle-tipped capillary tube was connected, with polyethylene tubing, to a small glass bulb almost filled with this fluid. The upper end of this bulb was in turn connected via polyethylene tubing to a 1 ml tuberculin syringe. The portion of the bulb above the level of the NaCl solution, the connection, and the syringe were all filled with paraffin oil. Injection through the microneedle was controlled by advancing the plunger of the syringe.

For sampling the blood of injected birds the needle-tipped capillary tube was flushed with a solution of potassium heparin and then dried. It was then fitted in the electrode holder as described previously and connected to a 50 ml syringe, with polyethylene tubing. Suction was applied by withdrawal of the plunger of the syringe. When approximately 0.02 ml of blood had been obtained, the needle-tip was removed, and the two ends of the tube flame-sealed. Several samples could be thus obtained without harming the birds. The blood was centrifuged and the hematocrit determined. The capillary tube was then broken just above the boundary between the cells and plasma, and the segment containing

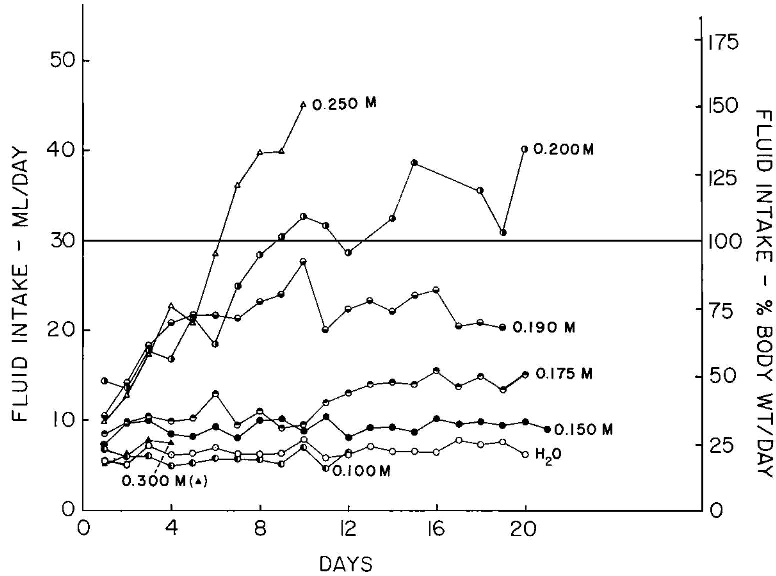

Figure 1. Mean amounts of various solutions of NaCl taken *ad libitum* by Red Crossbills. These are also expressed on the right hand ordinate as percentages of the body weight of a 30-g bird.

the plasma resealed. This plasma was kept refrigerated until analyzed for sodium.

In the salt-loading experiments, the birds were weighed and an initial blood sample taken. After this the sodium chloride load was injected. The birds were then repositioned in the restraining device so that a blood sample could be taken from the other wing 10 to 20 minutes after injection, after which they were placed in observation cages.

After a bird had received a salt load, it was generally maintained in the observation cage for 6 to 7 hours. During this time urine samples were collected and treated as previously described. At the end of the experiment another blood sample was taken and the bird was again weighed.

Analysis of blood and urine samples.—Blood and urine samples were analyzed for sodium using a Coleman model 21 flame photometer. About 0.001 ml of fluid was diluted in 5 ml of water and compared with similar dilutions of standard NaCl solutions.

RESULTS

Relation of fluid intake to concentration of salt solutions.—At moderate temperatures, the daily intake of distilled water by Red Crossbills averaged 6.6 ml/day, or 0.22 ml/g body weight/day (Figure 1). Their intake of 0.100 M NaCl was about the same and of 0.150 M somewhat higher. At each of these concentrations, the drinking rates remained essentially constant throughout the experiments. Fluid intake tended to increase between 0.175 M and 0.250 M. At each of the concentrations in this range, the rate of drinking rose dramatically during the first few days of the experiment; the birds finally came to drink daily amounts of 0.200 and 0.250 M NaCl exceeding their body weight. Crossbills remained in good condition on sodium chloride solutions as highly concentrated as 0.200 M, throughout the 20 days of the experiments. However, their appreciable loss of weight on 0.250 M NaCl necessitated termination of the experiments with this concentration after 8 to 10 days. They responded erratically to 0.300 M solutions; the average daily intake was little higher than that observed when the birds were maintained on tap water. However, some individuals consumed little or none of this salt solution, whereas others drank large amounts—in the case of one bird, 39 ml/day (164 per cent body weight/day). The serious losses of weight incurred by the animals maintained on 0.300 M, regardless of drinking pattern, necessitated termination of the experiments after only four days.

Relation of body weight to the concentration of salt solutions.—Birds provided with distilled water or with sodium chloride solutions up to 0.190 M, at the end of the experiment weighed on the average as much or more than they did at the beginning (Figure 2; Table 1). With 0.200 M, their final mean weight was still more than 90 per cent of the original. At higher concentrations, the birds progressively lost weight. On the average those maintained on 0.250 M lost nearly 20 per cent of their original weight at the end of 10 days. Birds maintained on 0.300 M lost almost 30 per cent in 4 days. Despite the sharp decline of weight on this latter concentration, these birds still fared better on the average than individuals maintained without any fluid whatever. After returning to drinking tap water, all birds showed normal levels of weight and fluid intake within a few days.

Concentrations of sodium in plasma and urine.—The concentration of sodium in the plasma of crossbills supplied with tap water, salt blocks, and the various seeds, averaged 161.2 mEq/liter (Table 2). Six birds were maintained for several months on distilled water and piñon nuts alone. These nuts contained 0.03 mEq of sodium and 0.17 mEq of potassium/g wet weight. After almost three months, each of the six birds showed a lower plasma concentration of sodium than initially. The decline was 6 to 20 mEq/liter in all except one bird in which it was more than 30 mEq/liter (this bird had a plasma sodium concentration of only 117 mEq/liter and died shortly after blood sampling). Nine months after the birds had been deprived of salt blocks, blood samples were

TABLE 1

WEIGHTS OF RED CROSSBILLS WHILE DRINKING VARIOUS FLUIDS AND DURING DEHYDRATION[1]

Fluid (M NaCl)	Day							
	1	2	3	4	5	10	15	20
[Distilled H_2O]	101 ± 3 (16)	102 ± 4 (16)	103 ± 6 (16)	102 ± 5 (16)	103 ± 5 (16)	102 ± 6 (16)	103 ± 6 (15)	106 ± 7 (9)
0.150	101 ± 2 (17)	101 ± 3 (17)	101 ± 3 (17)	99 ± 4 (17)	99 ± 5 (17)	97 ± 6 (17)	98 ± 9 (16)	101 ± 10 (10)
0.175	100 ± 3 (11)	100 ± 2 (11)	100 ± 3 (11)	100 ± 2 (11)	99 ± 3 (10)	100 ± 4 (11)	102 ± 4 (8)	100 ± 4 (5)
0.190	99 ± 4 (9)	99 ± 7 (9)	103 ± 7 (9)	103 ± 4 (9)	104 ± 4 (9)	106 ± 3 (9)	107 ± 5 (9)	109 ± 6 (8)
0.200	99 ± 3 (14)	97 ± 3 (14)	96 ± 6 (14)	95 ± 6 (14)	97 ± 6 (14)	93 ± 4 (14)	93 ± 5 (13)	91 ± 5 (10)
0.250	97 ± 2 (12)	95 ± 2 (12)	95 ± 3 (12)	91 ± 3* (12)	89 ± 4* (12)	81 ± 10 (6)		
0.300	92 ± 3* (12)	85 ± 5** (12)	79 ± 6** (11)	73 ± 5** (9)				
[No fluid]	86 ± 3** (10)	76 ± 3** (10)						

[1] Mean weight and standard deviation expressed as percentages of initial mean weight. N given in parentheses.
* Significantly different from initial weight at 5 per cent level.
** Significantly different from initial weight at 1 per cent level.

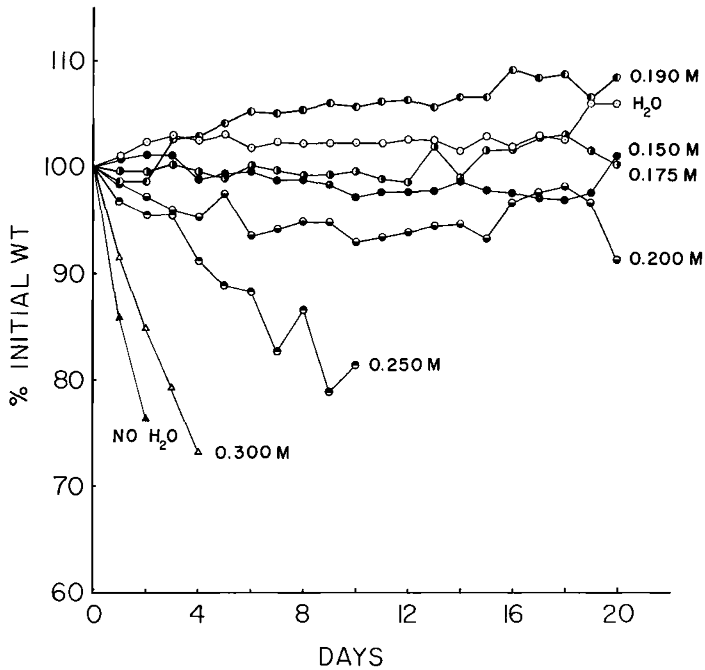

Figure 2. Mean body weights of Red Crossbills (as per cent of initial weight) during *ad libitum* drinking of water and NaCl solutions of various concentrations and during dehydration.

again taken for the remaining birds. At this time, the concentrations ranged from a decline of 7 mEq/liter to an increase of 4 mEq/liter, as compared with the initial values for these birds.

The concentration of sodium in the plasma remained at near-normal levels when the crossbills were maintained on sodium chloride solutions as concentrated as 0.200 M. However, it rose significantly as birds provided with only 0.250 or 0.300 M solutions for drinking lost weight. The highest plasma level of sodium tolerated by these animals approximated 210 mEq/liter.

Observations on output of urine by crossbills supplied with various fluids for drinking are summarized in Table 3. Mean concentrations of sodium in urine, obtained over several hours, tended to exceed only slightly the concentrations of this cation in the solutions used for drinking (Table 3). This occurred despite the ability of some crossbills, at least, to produce urine containing about 500 mEq of sodium/liter (no. 289, Table 3). The relatively dilute urine produced by two birds drinking

TABLE 2
SODIUM CONCENTRATIONS IN THE PLASMA OF RED CROSSBILLS AFTER MAINTENANCE ON VARIOUS FLUIDS OR DEHYDRATION

Fluid (M NaCl)	*Period (days)*	*N*	*Plasma sodium concentration (mEq/liter)*		
			Mean	*s*	*Range*
[Tap water]	20	22	161.2	6.2	148–171
0.150	20	6	159.2	10.7	150–180
0.175	20	5	158.4	2.3	155–160
0.190	20	9	171.4	7.0	164–188
0.200	20	3	160.0	—	158–162
0.250	8	3	194.7	—	178–208
0.300	2	5	185.6	16.5	170–211
0.300	4	6	204.7	12.0	189–226
[No fluid]	2	3	194.3	—	188–205

0.175 M may reflect the fact that they happened to be in positive water balance when urine was collected on the twentieth day (see Table 2).

The rate of urine output by crossbills tended to rise as the sodium concentration of the drinking water increased between 0 and 0.250 M NaCl (Table 3). Considerable variation was evident among birds drinking 0.300 M NaCl, but three of the four values were at the lower limit of or below the range of those observed with 0.250 M NaCl. As previously noted, most birds supplied with 0.300 M NaCl drank little or none of it over part or all of the four-day experimental period. Urine was scanty in these "non-drinkers" and, in the majority of instances, low in sodium. In one case, a bird (no. 110) subsequently began drinking appreciable quantities of the salt solution, and both the volume and sodium concentration of its urine increased.

Preferences between distilled water and 0.100 or 0.200 M NaCl.—The fluid intake of crossbills given access to both distilled water and 0.100 M or 0.200 M NaCl is summarized in Table 4. In tests with the lower salt concentration, one bird (no. 271) showed a consistent preference for distilled water. However, the rest showed no clear preference and some tended to drink consistently from the same drinker regardless of its position and contents, or at the same position regardless of the drinker or fluid there. In tests with 0.200 M NaCl, the birds, with one exception, showed a strong preference for distilled water. The exception (no. 989) drank consistently at the same position.

Responses of crossbills to acute salt loads.—The response of seven crossbills, several studied two or more times, to injections of NaCl amounting to 0.09 to 0.59 mg/g of body weight are summarized in Table 5. In periods generally lasting six hours, the birds never eliminated much more than half the salt load received by injection. Despite plasma con-

TABLE 3
URINE PRODUCTION OF RED CROSSBILLS DRINKING VARIOUS FLUIDS

Bird	Fluid	Period on fluid (days)	Urinary sodium concentration (mEq/liter) Mean	Range	Urine production (Cubic mm/hr)
944	Tap water	20	4.1	3.0–4.5	34
101	"	20	7.3	3.0–11.5	38
000	"	20	12.0		14
213	"	20	4.9	3.0–10.0	119
300	"	20	3.5	3.0–10.0	82
104	"	20	71.1	27–140	339
107	"	20	5.6	5–6	7
117	"	20	2.6	2–3	44
288	"	20	67.5	25–110	49
989	0.175 M NaCl	21	157	131–245	124
992	" "	21	203	170–256	473
285	" "	20	201	117–310	172
929	" "	21	163	110–254	201
233	0.200 M NaCl	20	244	169–324	498
260	" "	20	256	217–287	120
259	" "	21	247	168–430	118
216	" "	21	210	196–264	2,250
225	0.250 M NaCl	5	332	297–382	235
257	" "	5	257	237–363	370
217	" "	7	263	230–415	409
214	" "	7	263	223–345	308
266	" "	7	325	273–457	418
110	0.300 M NaCl	2	157	30–277	24*
115	" "	2	15	–	10*
985	" "	2	129	78–176	18*
932	" "	3	155	72–242	23*
990	" "	3	29	24–36	12*
113	" "	3	18	11–22	17*
116	" "	3	13	–	9*
115	" "	4	10	7–13	12*
985	" "	4	314	242–414	33*
289	" "	2	430	395–510	252
927	" "	3	328	178–400	26
951	" "	4	282	252–346	753
110	" "	4	378	300–487	124

* Drinking amounts of 0.300 M NaCl amounting to less than five per cent of body weight/day.

centrations of sodium ranging up to more than 200 mEq/liter, the maximum concentrations of this cation in the urine did not reflect the full power of the concentrating mechanism in these birds (see Table 3). Moreover, the maximal concentrations were highly variable—the highest being quadruple the lowest—and did not appear to be correlated with the sodium concentration of the plasma. The inability of the birds to reduce appreciably the concentration of sodium in the plasma by urine production is probably due mainly to the reduction of body water by evaporation.

TABLE 4
FLUID INTAKE OF RED CROSSBILLS GIVEN ACCESS TO DISTILLED WATER AND 0.100 M OR 0.200 M NACL

Bird	*Mean fluid intake (ml/day)*							
	0–3 days		*3–6 days*		*6–9 days*		*9–12 days*	
	H_2O	*NaCl*	*H_2O*	*NaCl*	*H_2O*	*NaCl*	*H_2O*	*NaCl*
			0.100 M NaCl					
989[1]	5.0	4.0	0.5	7.2	8.5	0.3	1.5	7.8
226[1]	6.5	0.8	7.2	0	0	8.2	6.2	0
285	2.3	4.7	4.7	3.0	4.3	1.7	4.3	1.3
260	4.3	0.7	5.0	1.0	1.0	5.0	5.7	1.0
271	5.7	0.7	6.0	2.3	6.0	1.0	6.7	2.0
952[2]	6.3	0.7	7.3	1.0	0.7	7.3	1.0	8.7
			0.200 M NaCl					
107	5.7	0.5	5.8	0.2	5.3	0.8	4.9	1.0
213	4.7	0	4.5	0.2	4.4	0	4.5	0.8
000	3.8	0.8	5.5	0	5.2	0.3	4.5	0.2
300	3.7	0.8	4.3	0.8	3.2	0.5	3.3	0.8
992	4.7	0	3.3	1.2	4.0	0.2	—	—
989[1]	3.2	0	0	10.3	0	7.8	—	—

[1] Consistently drank at one position.
[2] Consistently drank from one drinker.

The maximal plasma concentration of sodium tolerated by injected crossbills approximates 210 mEq/liter. The bird that died as an apparent result of injection of NaCl showed plasma sodium concentrations of 206 and 212 mEq/liter immediately and four hours after injection, respectively. Another bird survived an initial plasma concentration of 210 mEq/liter and one a terminal concentration of 206 mEq/liter.

DISCUSSION

Crossbills, like other cardueline finches, avidly eat salt whenever it is available, and there are many records of these birds ingesting rock salt placed on roads to melt snow, material from salt blocks of the type supplied for cattle, salt spilled around ice cream freezers, material leached out of cement, wood ashes, and urine-stained snow (Tordoff, unpublished observations; see Tordoff, 1954: 17). We wondered whether this curious behavior might allow the birds to satisfy a requirement for some mineral that they do not obtain in sufficient quantity in their food. Our results do not exclude this possibility. However, they suggest that the ingestion of salt beyond that present in the food is unnecessary for maintenance of sodium balance and apparent good health by crossbills (even though they are fed only piñon nuts, which are relatively high in potassium and low in sodium, for many months). The finding (Table 3) of urinary sodium concentrations as low as 3 mEq/liter suggests that highly effec-

TABLE 5
RESPONSES OF RED CROSSBILLS TO INJECTIONS OF A HYPEROSMOTIC SOLUTION (10 PER CENT) OF SODIUM CHLORIDE

	Individuals									
Bird	*A*			*B*	*C*	*D*	*E*		*F*	*G*
Date	*11/19/61*	*11/27/61*	*12/5/61*	*11/30/61*	*12/12/61*	*1/4/62*	*2/6/62*	*2/9/62*	*2/8/62*	*2/13/62*
Duration of expt.(hr)	3	4.5	6	6	6	4	6		6	4
Weight (g)										
Pre-	25.9	27.5	28.6	25.1	23.7	27.9	34.4	32.5	32.2	25.5
Post-	25.9	25.7	25.9	22.6	22.6	26.9	33.0	30.8	30.2	25.5
Salt load										
Volume (ml)	0.06	0.25	0.40	0.35	0.30	0.40	0.26	0.49	0.24	0.20
Amount (mg)	6	25	40	35	30	40	26	49	24	20
mg Na/g body weight	0.09	0.36	0.55	0.55	0.50	0.56	0.30	0.59	0.29	0.31
Plasma Na (mEq/liter)										
Pre-	—	160	160	166	164	168	159	158	164	160
10 to 20 min	170	182	210	194	189	206	177	190	184	177
Post-	173	176	196	198	206	212	186	193	177	184
Hematocrit (per cent)										
Pre-	—	51	57	55	48	55	54	49	56	53
10 to 20 min	43	43	53	51	50	40	46	45	48	50
Post-	46	52	54	56	45	46	54	41	52	48
Urinary Na (mg/g)	0.01	0.20	0.17	0.18	0.06	0.10	0.04	0.15	0.15	0.04
Max. Na concen. (mEq/liter)	118	249	210	472	151	276	310	407	318	280
per cent Na load excreted	11	56	31	33	12	18	13	25	52	13
Urinary water loss										
ml	0.27	1.05	1.25	0.65	0.56	0.70	0.48	0.88	0.91	0.42
cubic mm/g	10	38	44	26	24	25	14	27	28	16

tive means of conserving this ion are present. It seems certain that these birds must have ready access to water when they ingest any appreciable quantity of sodium chloride, for, as subsequently discussed, they do not excrete electrolytes economically with respect to water.

Crossbills show no fluid preference when given both 0.100 M NaCl and distilled water for drinking, but they will generally drink the latter to the virtual exclusion of 0.200 M NaCl (Table 4). The absence of a preference for either molarity of sodium chloride over distilled water and the fact that the amounts of these solutions ingested daily do not provide similar quantities of this compound provide no support for the hypothesis that crossbills have a requirement for sodium chloride beyond that which they can obtain in their food. The results obtained for these birds in the fluid preference experiments are reminiscent of those reported for House Finches (Bartholomew and Cade, 1958). These other carduelines showed no preference between distilled water and sodium chloride solutions as concentrated as 0.15 M, but they strongly preferred the former in comparison with concentrations of 0.20 M or higher. When representatives of two subspecies of Savannah Sparrows were each given equal access to distilled water and 0.25 M NaCl, they drank more distilled water than salt water. However, the ratio between the amounts of these fluids ingested was such that the weight-relative salt intake of the salt marsh form, *P. s. beldingi*, was about three and a half times that of *P. s. brooksi*, which breeds in freshwater marshes (Poulson and Bartholomew, 1962b). Bartholomew and Cade (1963) conclude from a review of the experiments on fluid preferences cited here and on preferences of Mourning Doves (*Zenaidura macroura*), and California Quail (*Lophortyx californicus*), for various dilutions of sea water, that birds distinguish different salt concentrations and, if given a choice, will drink solutions of concentrations they can readily tolerate.

The *ad libitum* intake of distilled water by Red Crossbills (22 per cent body weight/day) is of the same order as that of most other passerines of comparable size for which data are available (see Bartholomew and Cade, 1963, Table 1). It is probably in excess of their minimal daily needs, for Poulson and Bartholomew (1962a) have noted that House Finches can manage in the absence of thermal stress on a water intake equivalent to 10 per cent body weight/day, whereas their *ad libitum* intake averages 16 per cent body weight/day. *Ad libitum* water consumption has also been shown to be in excess of minimal needs for several other birds (Bartholomew and Cade, 1963).

The *ad libitum* utilization of sodium chloride solutions by crossbills conforms qualitatively to the pattern observed in the Mourning Dove (Bartholomew and MacMillen, 1960), and several passerines including the House Finch (Bartholomew and Cade, 1958; Cade and Bartholomew, 1959; see also Bartholomew and Cade, 1963). These birds increase the rate of fluid intake with salinity up to a point, and individuals may come to ingest more than their body weight of salt water daily. Beyond a certain concentration (between 0.250 and 0.300 M in Red Crossbills), drinking tends to be reduced, and some individuals may not ingest any fluid even though they are undergoing severe weight loss. Bartholomew and Cade (1963) point out that the increase of water consumption with increased salinity of the solution is consistent with a familiar concept of the thirst mechanism in vertebrates. Ingestion of salt increases the osmotic concentration of the body fluids, and this results in stimulation of osmoreceptors that ultimately leads to a drinking response by the birds.

This response with solutions at favorable concentrations results in a restoration of internal osmotic pressure to the original level. This mechanism suffices as long as the water is not highly saline; at higher concentrations the birds obtain progressively smaller quantities of osmotically unobligated water from the fluid they drink, and eventually, despite ingestion of extraordinary volumes of salt solutions in some cases, they cannot maintain water balance. This leads to the elevated sodium concentrations observed in the plasma of crossbills drinking sodium chloride solutions more concentrated than approximately 0.200 M. As noted previously, individuals of this species did not survive either long-term drinking or salt injection experiments if the plasma sodium concentration exceeded approximately 210 mEq/liter, or 1.3 times normal (161 mEq/liter). Since other conditions, e.g., water content of the birds, differ between the two types of experiments, this appears to be an actual expression of the maximal sodium tolerance of the Red Crossbill.

Although the use of saline water by crossbills conforms to an apparently widespread pattern, the capacities of these carduelines for maintaining weight while drinking sodium chloride solutions appear lower than those of most other species for which data have been obtained (see Bartholomew and Cade, 1963, table 3). The maximum concentration that crossbills can drink and still maintain weight is in the vicinity of 0.20 M. Comparable values reported for other species are: Mourning Dove, 0.15 M (Bartholomew and MacMillen, 1960); Budgerygah, *Melopsittacus undulatus*, <0.20 M (Cade and Dybas, 1962); Zebra Finch, *Taeniopygia castanotis*, 0.60 M (Oksche *et al.*, 1963); House Finch, 0.25 M (Bartholomew and Cade, 1958); two races of the Savannah Sparrow that breed in salt marshes, 0.55 and 0.60 M (Cade and Bartholomew, 1959); White-crowned Sparrow, *Zonotrichia leucophrys gambelii*, 0.20–0.30 M (Oksche *et al.*, 1963); and Song Sparrow, *Melospiza melodia cooperi*, 0.40 M (see Bartholomew and Cade, 1963).

Data on excretory function over periods in which crossbills are dependent upon salt solutions for water have some curious features. The mechanism for concentrating urine in these birds does not work at full capacity steadily even when they appear to be gaining insufficient water from the fluid they are ingesting. Concentrations of sodium were observed to reach approximately 500 mEq/liter in individual samples of urine, yet the mean concentration tended to exceed only slightly that of the fluid ingested.

The maximal concentration of sodium found in any urine sample from a crossbill, 510 mEq/liter (bird no. 289, Table 3), amounts to about 2.7 times the concentration of this cation in the plasma (estimated as 186 mEq/liter from Table 2). However, the highest *mean* concentration of sodium for any set of urine samples collected over two or three hours, 430 mEq/liter (also bird no. 289, Table 3), amounts to only 2.3 times the plasma concentration. Urine to plasma ratios for sodium are unavailable for other passerine birds. The highest ratio of this type for chloride, indicated by any urine sample, from a House Finch was 3.1. In this species the highest *mean* ratio for chloride was 2.4 (Poulson and Bartholomew, 1962a). These birds, like crossbills, do not sustain their renal concentrating mechanism at the highest level of which it is capable, even when water balance cannot otherwise be maintained without prodigious intake of fluid.

The abilities of crossbills and House Finches to produce urine concentrated with respect to electrolytes are overshadowed by that of Savannah Sparrows, particularly representatives of subspecies breeding in salt marshes. Poulson and Bartholomew (1962b) found urine to plasma ratios for chloride as high as seven and averaging as much as five in *P. s. beldingi.* The renal capacities of all these passerines also appear to surpass those of marine birds in which the maximal urine to plasma ratios for sodium or chloride appear barely to reach two (Schmidt-Nielsen and Fänge, 1958; Schmidt-Nielsen *et al.*, 1958). However, these marine birds possess salt-secreting glands which allow extra-renal excretion of salts with relatively small loss of water (Schmidt-Nielsen, 1960), as discussed subsequently.

Administration of loads of sodium chloride to crossbills by injection markedly increased the plasma concentrations of sodium. The observed concentrations were much lower than those estimated on the assumption that the sodium becomes equilibrated only with the extracellular fluid (estimated as 25 per cent of body weight). However, they approximate closely concentrations estimated on the assumption that this cation becomes equilibrated with the total body water (estimated as 70 per cent of body weight). This also appears to be the case in other animals such as domestic cats (Conway and McCormack, 1953), lizards, *Tiliqua [Trachysaurus] rugosa* (Bentley, 1959) and toads, *Bufo marinus* (Shoemaker, 1964). Presumably, the administered salt largely remains in the extracellular space, equilibration with the intracellular fluid occurring osmotically. Such an osmotic movement of water into the extracellular fluid compartment probably contributes to the drop in hematocrit noted in crossbills shortly after injection of the 10 per cent saline (Table 5), both through increasing plasma volume and decreasing erythrocyte volume.

Red Crossbills eliminate loads of sodium chloride very slowly when deprived of water for drinking, and they are less effective in this regard than either Rock Doves, *Columba livia,* or various aquatic birds having salt-secreting glands (Scothorne, 1959; Schmidt-Nielsen *et al.*, 1958;

Schmidt-Nielsen, 1960). The latter use these glands to a significant and in some cases predominant extent in excreting this salt (see Schmidt-Nielsen, 1960). Such structures appear to be absent from passerines (Schmidt-Nielsen, 1963), despite their recent discovery in some terrestrial birds of other orders (Schmidt-Nielsen *et al.*, 1963).

ACKNOWLEDGMENTS

Birds used in this study were obtained through the courtesy of Percival Dodge, William P. Harris, Jr., and other members of the Huron Mountain Club, and the Huron Mountain Wildlife Foundation. Bertram G. Murray, Frank B. Gill, and Larry L. Wolf rendered valuable assistance. Our work was supported in part by grants from the National Science Foundation (G-9238, GB-1455, and G-19812) and from the Horace H. Rackham School of Graduate Studies, The University of Michigan.

SUMMARY

This study deals principally with analysis of the capacities of Red Crossbills for obtaining osmotically unobligated water from solutions of sodium chloride and of responses of these birds to acutely applied loads of this salt. The *ad libitum* intake of tap water by crossbills is equivalent to 22 per cent body weight/day, a value in the same range as those reported for other passerines of comparable size. When deprived of fresh water, their utilization of sodium chloride solutions as fluid sources conforms to the pattern observed in the Mourning Dove and several passerines. The rate of fluid intake increases with salinity up to a point and individuals may come to ingest more than their body weight of salt water daily. Beyond approximately 0.250 M NaCl, crossbills tend to reduce their drinking, and some individuals may not ingest any fluid even though they are undergoing severe weight loss. The maximum concentration in which these birds can maintain body weight is near 0.2 M. They had to be returned to drinking tap water after four days of drinking 0.3 M NaCl, because of severe weight losses.

Red Crossbills show no significant preference between distilled water and 0.100 M NaCl when supplied with both for drinking. However, they strongly prefer water to 0.200 M NaCl.

The plasma sodium concentration of Red Crossbills in water balance is 161.2 ± 6.2 mEq/liter. A significant rise in this concentration develops when the birds are forced to obtain their fluid from NaCl solutions more concentrated than 0.200 M. Urinary sodium concentrations for birds maintained on tap water were well below plasma concentrations of this cation. The respective urinary concentrations for birds drinking 0.175 to 0.300 M NaCl averaged slightly higher than the sodium concentration of the fluid ingested. The maximum urine to plasma ratio observed for this cation approximates 2.7.

Acute salt loads were applied by forcing the birds to ingest NaCl pills or by injection of 10 per cent NaCl into the brachial vein. The latter method provided more useful information from an analytical standpoint. The injected NaCl appears to equilibrate with the total body water rather than with just the extracellular fluid. Birds receiving 0.5 to 1.1 mg of sodium/g by pill never excreted more than 18 per cent of this load over 6 to 7 hours. Birds receiving 0.1 to 0.6 mg/g by injection did somewhat better over the same period, excreting up to half of the load. The associated urinary water loss and evaporative water loss prevented this excretion from alleviating the hypernatremia induced by salt loading.

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