NASAL SALT SECRETION IN FALCONIFORM BIRDS

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Falconers have long known that various raptors, especially accipiters and eagles, exude a clear fluid from their nares while eating. We were reminded of this fact while handling a melanistic Gabar Goshawk (*Micronisus gabar*), which we trapped in the Kalahari Desert in August 1964. As the hawk ate his prey, the small droplets of fluid that collected on our gloves had a strong salty taste. This discovery led us to look for nasal secretions in 16 species and 10 genera of Accipitridae and in eight species and three genera of Falconidae. We have studied behavioral and physiological aspects of nasal secretion in these raptors with reference to Schmidt-Nielsen's (1964) hypothesis regarding the general necessity for birds to utilize an extrarenal mechanism of salt excretion, as an adjunct to efficient water reabsorption from the cloaca in concentrating uric acid, and also in connection with the overall water economy of carnivorous birds.

MATERIALS AND METHODS

We obtained birds and information from various sources. Our initial observations were made on an adult male Gabar Goshawk, an adult female Red-necked Falcon (*Falco chiquera*), and a pair of adult Pigmy Falcons (*Polihierax semitorquatus*), which we trapped in the Kalahari Gemsbok National Park in the Republic of South Africa and subsequently transported to our laboratory at Syracuse University. In addition, we obtained the following hawks from a bird dealer in New York: an immature Savannah Hawk (*Heterospizias meridionalis*) and a juvenile Yellow-headed Caracara (*Milvago chimachima*), both from South America, and an immature Saker (*Falco cherrug*) and an adult Laggar (*Falco jugger*) from India. Heinz Meng kindly permitted us to obtain some samples from a trained Peregrine (*Falco peregrinus*), Goshawk (*Accipiter gentilis*), and Red-tailed Hawk (*Buteo jamaicensis*). We also made some observations and measurements on a female American Kestrel (*Falco sparverius*), an immature Red-tailed Hawk, and an immature Sharp-shinned Hawk (*Accipiter striatus*), all from the vicinity of Syracuse, New York. Walter R. Spofford and Morlan W. Nelson made some observations for us on their captive Golden Eagles (*Aquila chrysaëtos*), and Archie White and George Goode, taxidermists of the Transvaal Museum, and O. P. M. Prozesky, ornithologist there, noted secretions for us in a number of captive South African eagles and hawks. We have also been able to observe secretions at close hand in caged specimens of the Lappet-faced Vulture (*Torgos tracheliotus*), Cape Vulture (*Gyps coprotheres*), and White-backed Vulture (*Gyps africanus*) at the Pretoria Zoo, and recently we have had a tame Bateleur (*Terathopius ecaudatus*) under close observation. Thus, our material has been drawn from four continents and represents a fairly wide taxonomic sampling of species within the Falconiformes.

When a hawk expelled nasal secretions, the fluid could be collected for analysis in various ways. The simplest method was to place a sheet of aluminum foil in front of the bird at the level of its feet and wait for it to sneeze or sling the fluid that collected in its nares onto the foil. The droplets were immediately collected with small, volumetric pipettes ranging from 1 to 25 μl in capacity. With docile birds a 10 or 25 μl pipette could be inserted into one of the hawk's nares to collect the secretion before it was voided (fig. 1).

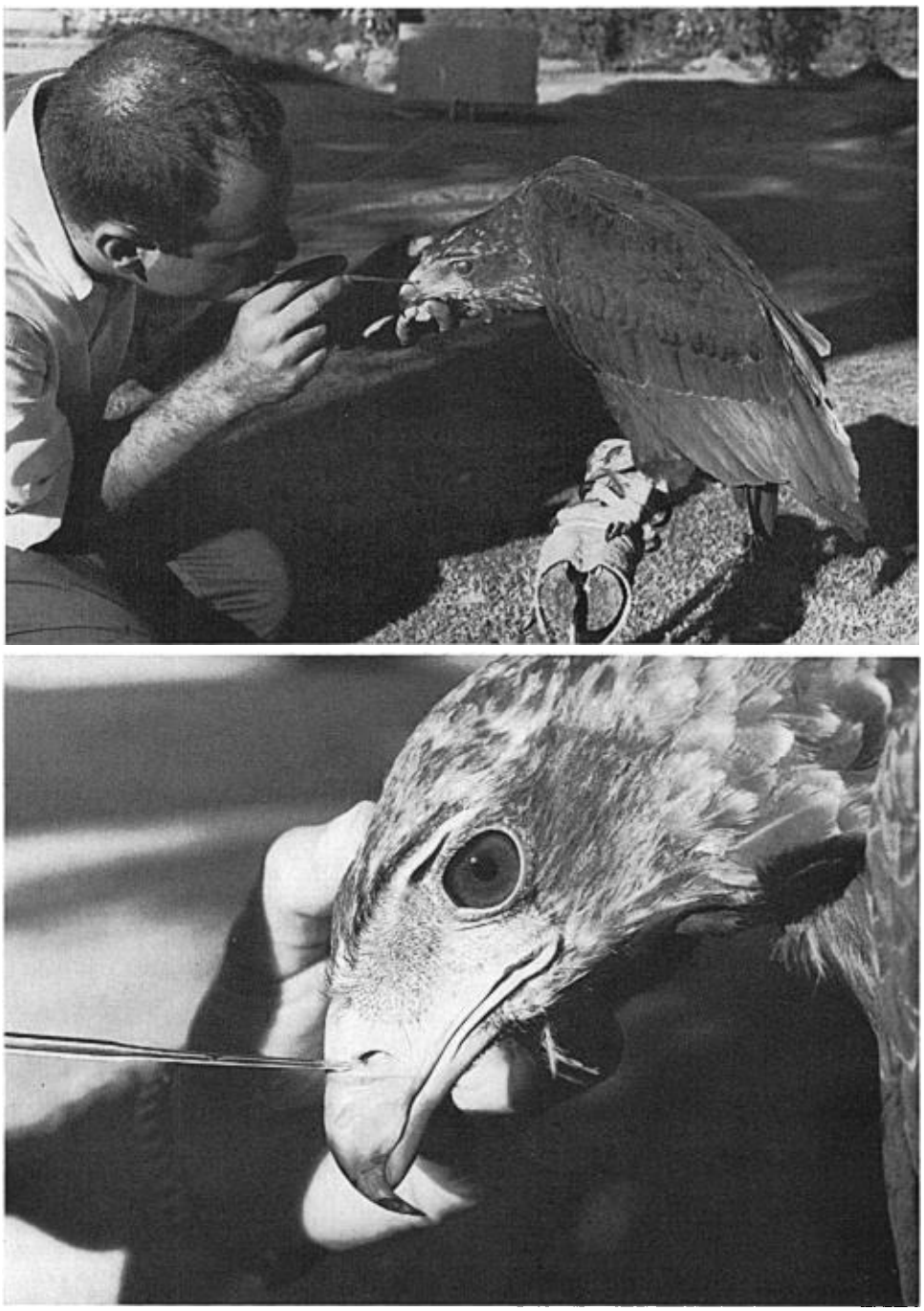

Figure 1. Method of taking samples of nasal secretion directly from the nares of a Bateleur. Note shape of nare and the secretion that has drooled onto beak. In the normal head-up posture, the secretion drains directly down to the tomium and drips off the hooked tip of the beak.

Urine samples were collected on aluminum foil sheets placed beneath the birds. If the urine had a distinct, clear, and liquid portion, this fluid was collected in a pipette in the same way the nasal secretions were taken. More often, whole urine was sucked into a small capillary tube, one end was flame sealed, and the tube was centrifuged. The clear, liquid supernatant was used for ion analysis.

Blood was obtained from a wing vein and drawn into a heparinized capillary tube. The tube was centrifuged, and the plasma supernatant was blown into a depression slide and taken up in a volumetric pipette.

After any of the samples had been measured in a volumetric pipette, the contents were blown out into 2 ml of distilled water. These diluted samples were then analyzed for Na^+, K^+, and Ca^{++} on a Coleman flame photometer, and for Cl^- on an Aminco electric chloride titrator. Phosphate determinations were made using the method of Fiske and Subbarow (1925).

Nasal glands were dissected from the Gabar Goshawk, the Sharp-shinned Hawk, the Red-tailed Hawk, the Savannah Hawk, the American Kestrel, one of the Pigmy Falcons, the Yellow-headed Caracara, and from a Lappet-faced Vulture collected in South West Africa and a Black Kite (*Milvus migrans*) collected in the western Transvaal. These glands were fixed in formalin.

RESULTS AND DISCUSSION

The Gabar Goshawk. Micronisus gabar. This bird, which weighed 175 to 180 g, nearly always exuded a salty tasting secretion from its nares while eating and for some time after finishing a meal. Most often the fluid, which collected in the orifices of the external nares, was eliminated by vigorous head-shaking and was frequently associated with ruffling of the plumage, but sometimes this hawk also sneezed the fluid out in fine droplets. We never saw any nasal secretions except during the brief period of feeding each day, but the encrustations of salt crystals around its nares led us to believe that the bird must have secreted for some time after the meal was over. When fed a laboratory mouse, the bird secreted 10 to 15 μl of fluid, about half of which was voided while eating the mouse, the other half within five minutes after finishing. Fluid could be seen forming in the bird's nares within nine minutes after it started eating. When this hawk was fed raw meat from a chicken wing, he usually did not secrete any nasal fluid at all; on a few occasions somewhat less than 2 μl were obtained. An intact sparrow carcass stimulated as much secretion as a mouse. Adding 0.1 g of NaCl to a mouse produced no marked change in the secretory pattern of this hawk. Salted chicken was not tried.

We collected 23 nasal samples from this accipiter. The high, low, and mean values for the ionic concentrations in these samples are shown in table 1. The lowest concentrations of Na^+ and Cl^-, the predominant ions in the secretion, were well above the blood concentrations. The first secretion voided by the bird was usually of much higher concentration than subsequent samples; this occurred because the first secretion dissolved and mixed with crystals of salt that had accumulated in the nares from the previous day. As an example, one initial sample had a Na^+ concentration of 2316 mmole/liter and Cl^- concentration of 2441 mmole/liter. Crystals of salt were visible in the nares before the drop of fluid formed. The next secretion was less than half the concentration of the first, 1039 mmole/liter for Na^+ and 770 mmole/liter for Cl^-.

Because of the formation of salt crystals from evaporation in the nares, it is impossible to make an unequivocal statement about the osmotic concentration of

TABLE 1

SUMMARY OF IONIC CONCENTRATIONS IN BLOOD, URINE, AND NASAL SECRETION OF FALCONIFORM BIRDS, AS MILLIMOLES PER LITER

Species	Blood				Urine				Nasal			
	Na^+	K^+	Ca^{++}	Cl^-	Na^+	K^+	Ca^{++}	Cl^-	Na^+	K^+	Ca^{++}	Cl^-
Micronisus gabar												
High	—	—	—	—	190	100	17	67	2316	128	56	2441
Mean	160	—	—	127	73	48	6	48	1023	45	21	983
Low	—	—	—	—	24	12	2	32	440	16	3	416
Number	1			1	9	9	5	5	23	18	6	20
Accipiter gentilis												
High	—	—	—	—	—	—	—	—	620	200	—	502
Low	—	—	—	—	130	128	—	31	380	100	—	339
Number					1	1		1	2	2		2
Buteo jamaicensis												
Number = 1	—	—	—	—	206	76	—	21	380	20	—	226
Heterospizias meridionalis												
High	—	—	—	—	135	150	32	47	890	30	10	949
Mean	170	8	3	123	88	123	19	43	433	16	3	455
Low	—	—	—	—	40	96	6	39	255	6	1	263
Number	1	1	1	1	2	2	2	2	7	5	5	7
Terathopius ecaudatus												
High	—	—	—	—	100	144	—	138	520	15	—	505
Mean	—	—	—	—	45	77	—	40	259	9	—	256
Low	—	—	—	—	10	18	—	5	176	6	—	185
Number	—	—	—	—	9	9	—	9	10	10	—	10
Falco cherrug												
Number = 1	—	—	—	—	234	268	—	155	920	170	—	851
Falco peregrinus												
Number = 1	—	—	—	—	120	232	—	14	—	—	—	—
Falco sparverius												
High	190	16	—	157	340	92	6	237	—	—	—	—
Mean	187	14	5	152	103	41	4	89	—	—	—	—
Low	184	12	—	147	13	9	1	23	—	—	—	—
Number	2	2	1	2	12	10	9	12				
Polihierax semitorquatus												
High	—	—	—	—	150	300	10	71	—	—	—	—
Mean	—	—	—	—	94	115	7	34	630	40	42	397
Low	—	—	—	—	56	46	2	13	—	—	—	—
Number					6	5	5	7	1	1	1	1

the actual secretion without cannulation of the gland. We feel, however, that the minimum values, about 450 to 500 mmole/liter for both Na^+ and Cl^-, approximate closely the true concentrating ability of the nasal gland in this species.

There were never any definite proportions between the concentrations of the various ions; cations were always in excess. Since the amount of phosphate in the

secretion was below our limit of analysis, some other anion, such as sulfate or bicarbonate, must have been present.

The fact that this goshawk responded by secreting when given an intact mouse or bird carcass to eat but not when fed plain chicken muscle can be explained by differences in the composition of water and electrolytes in the two kinds of food. On the average, raw chicken wing meat has more preformed water in it than the average for various mouse tissues (3.38 mg H_2O/mg dry wt of chicken versus 2.83 mg H_2O/mg dry wt of whole mouse), but the differences in ionic composition are even more important. The total body store of Na^+ is about 60 mmole/kg or roughly 90 mmole/liter of total body water; for K^+ the comparable figures are 42 mmole/kg and 63 mmole/liter; but for muscle the Na^+ concentration is only about 10 mmole/liter of water, whereas the K^+ concentration averages 160 mmole/liter (from Pitts, 1963). The excretion of Na^+ is much less of a problem on a diet of pure muscle, but the reverse is true for K^+.

On the other hand, the nasal secretion begins to form within a few minutes after food has been swallowed, while the bulk of it is still in the crop and before any appreciable amounts of ions, water, or other materials could have passed from the gut into the general circulation. The idea of a direct sensory stimulation (from tactile or chemical receptors in the mouth or via ocular routes) is suggested and is consistent with Schmidt-Nielsen's (1960) finding that the nasal gland of the Herring Gull (*Larus argentatus*) is controlled by parasympathetic fibers associated with the facial nerve. Such innervation indicates control by a higher central nervous organization, into which various sensory inputs could be directed. Our observations indicate that in this species, as in other falconiforms (see below), the nasal secretion is normally stimulated to flow by sensory inputs originating directly from the gustatory process, as well as by blood-borne chemical stimuli acting on osmoreceptors in the central nervous system. McFarland (1965) has recently shown that both photic and auditory stimuli can produce an increase in the rate of flow of the nasal secretion in minimally salt-loaded "sea-gulls."

In general, the concentrations of Na^+ and Cl^- in the urine of the Gabar Goshawk were less than those of its blood, while the urine concentration of K^+ (48 mmole/liter) was much higher than one would expect for plasma (around 5 mmole/liter). It also appears that phosphate is a major anion in this bird's urine, as we obtained a value of 158 mmole/liter. There was no obvious or consistent relationship among the various ions, but the blood concentrations of Na^+ and Cl^- were in the range to be expected for birds.

The Savannah Hawk. Heterospizias meridionalis. This bird submitted to having a small pipette inserted into its nares, either for the purpose of washing them free of salt crystals or to withdraw the nasal secretion as it accumulated at the orifice. This was the closest we could come to a direct cannulation. Also, because this hawk, which weighed about 1 kg, swallowed laboratory mice whole, it was possible to salt-load the bird by putting NaCl into the body cavity of an eviscerated mouse. We also salt-loaded the bird by means of a tube directed into its crop, into which we introduced salt solutions.

Like the Gabar Goshawk, the Savannah Hawk eliminated its nasal secretions as they collected in large drops at the orifices of its nares by slinging its head from side to side as it ate. We never saw it sneeze out the fluid. Sometimes the drops drooled down the sides of its beak and dripped off. Fluid was observed in the nares

within 30 seconds after the bird began to eat, but the bird never showed a response just at the sight of food.

Secretions were collected during and immediately after feeding the hawk some mice. The ionic concentrations in the secretions were less than those from the Gabar Goshawk but greater than the concentrations in the Savannah Hawk's blood (table 1). In all of these determinations, the secretion was obtained by inserting a 10 μl pipette into one of the hawk's nares in order to minimize the effect of evaporation. The concentration of phosphate ion was again below the limit of the technique of analysis (0.05 mmole/liter). The average equivalents of anions and cations balanced each other almost perfectly, but this was usually not the case for any given sample. The urine samples were similar to those of the Gabar Goshawk in that they were hypotonic to blood for Na^+ and Cl^- but hypertonic for K^+.

Because of the relatively high rates of secretion, which were estimated at about 100 μl per minute during the time of eating, we regard it as unlikely that the samples represent secretions contaminated by dissolved salt crystals lodged in the nares. In all cases, the first secretion from the Savannah Hawk was omitted, and only secretions that formed after the feeding of the first mouse were analyzed. Copious secretion stopped in a few minutes after the last mouse was eaten, but intermittent secretion may have occurred subsequently, as the bird often had an encrustation of salt in its nares the following day.

To see whether or not the nasal secretion could be stimulated by an osmotic stress, we fed the hawk 0.5 g of NaCl placed in the body cavity of a mouse. The bird's nares were previously washed free of salt crystals by flushing with distilled water. After a drying period the hawk was given the salted mouse. Within 30 seconds after the mouse had been swallowed, a nasal secretion formed in the nares and was collected for analysis. This sample had the highest ionic concentrations obtained for this bird, 1010 mmole/liter for Na^+ and 1040 for Cl^-. Moreover, about five minutes after eating the mouse, the hawk passed an extremely liquid urine of large volume. This was the only hyperosmotic urine sample collected from the bird, 346 mmole/liter for Na^+ and 173 for Cl^-. After 12 hours of rest without food, the hawk had a heavy encrustation of salt crystals on the cere around both nares. Similar encrustations occurred after injecting 5 ml of 100 mmole/liter NaCl into the bird's crop with a tube, even though in this case the solution was hypotonic to the hawk's blood.

The Bateleur. Terathopius ecaudatus. We were attracted to this species when we saw a tame, immature individual begin to secrete at the mere sight of food in the trainer's hand, again indicating the importance of nonosmotic stimuli in the production of this secretion among falconiform birds. Moreover, the secretion was copious and salty tasting. We were subsequently able to observe this bird in detail and to obtain both urine and nasal samples (table 1). The volume of secretion produced by this bird was quite high by comparison with the other birds we handled: assuming about 20 drops per ml, the fluid secreted during feeding usually amounted to about 2 or 3 ml. We also saw the Bateleur secreting at other times of the day, especially when lying on the ground sunning and panting. The concentration of ions in the secretion was, however, rather low, the lowest values being not much above expected concentrations of Na^+ and Cl^- in blood.

The nares of the Bateleur are dorso-ventrally elongated and taper to a point at the ventral end (see fig. 1). This shape appears to be a structural arrangement that

TABLE 2

OCCURRENCE OF NASAL SECRETION IN FALCONIFORM BIRDS

Taxon	Secretion present	Observers
Accipitridae		
Torgos tracheliotus	yes	Cade
Gyps coprotheres	yes	Cade
Gyps africanus	yes	Cade
Aquila chrysaëtos	yes	Spofford and Nelson
Aquila verreauxi	yes	Goode, Cade, and Greenwald
Aquila rapax	yes	Goode, Cade, and Greenwald
Aquila wahlbergi	yes	Cade and Greenwald
Polemaëtus bellicosus	yes	Goode, Prozesky, and White
Terathopius ecaudatus	yes	Goode, Cade, and Greenwald
Buteo jamaicensis	yes	Cade, Greenwald, and Meng
Buteo rufofuscus	yes	Goode, Prozesky, and White
Accipiter gentilis	yes	Geenwald and Meng
Accipiter striatus	yes	Cade
Micronisus gabar	yes	Cade and Greenwald
Melierax musicus	yes	Goode and Prozesky
Heterospizias meridionalis	yes	Cade and Greenwald
Falconidae		
Milvago chimachima	no	Cade and Greenwald
Falco cherrug	yes	Cade and Greenwald
Falco jugger	no	Cade and Greenwald
Falco biarmicus	yes	Goode
Falco peregrinus	yes	Greenwald and Meng
Falco chiquera	yes	Cade
Falco sparverius	no	Cade and Greenwald
Polihierax semitorquatus	yes	Cade and Greenwald

permits the secretion to accumulate in the lower part of the nares and to drain out without obstructing the air passages.

Average values for urine concentrations of Na^+ and Cl^- in the Bateleur are hypotonic to expected values for blood, whereas the concentration of K^+ is much higher. It is interesting, however, that the maximum values for all three ions differ from the minimum values by a full order of magnitude. The ionic composition of hawk urine changes markedly through the day, apparently in relation to the time of feeding and to uric acid production; but only after samples for the entire day have been analyzed will it be possible to work out the details.

Other species of Accipitridae. For both the American Goshawk (*Accipiter gentilis*) and the Red-tailed Hawk (*Buteo jamaicensis*), the urine concentrations of Na^+ and Cl^-, but not of K^+, were lower than the expected values for blood, whereas the nasal secretions of both species were hypertonic for Na^+ and Cl^-. All the observed species of Accipitridae showed definite signs of nasal secretion while eating (table 2). The aegypine vultures, like the Bateleur, produce an especially copious secretion that is salty tasting. They also secrete when panting and have dorso-ventrally elongated nares. These accipitrid species typically eliminate the secretion from their

nares by head-shaking. The Gabar Goshawk is the only one we have observed to sneeze out the fluid.

The Falconidae. A male and female Pigmy Falcon (*Poliheirax semitorquatus*), each weighing between 50 and 55 g, were observed for several months; both birds occasionally sneezed out minute and uncollectable droplets of secretion while feeding. The total amount voided during a meal was probably always less than 5 μl. A sample of one secretion was finally obtained. It was hyperosmotic to blood for Na^+, Cl^-, and other ions, whereas Na^+ and Cl^- in the urine were hypotonic to the expected blood values, while the concentration of K^+ was much higher. One hundred milligrams of NaCl added to 10 g of chicken meat produced a somewhat more copious secretion from the female, but she nevertheless died from the treatment.

A female American Kestrel (*Falco sparverius*) produced rather concentrated urine, by comparison with the other species, and the ionic concentrations of her blood plasma were unusually high also (table 1). This increased blood concentration may have significance in explaining the fact that this kestrel was never observed to secrete nasal fluid.

Our observations on the Pigmy Falcons, Meng's Peregrine Falcon, the Saker, and the Red-necked Falcon indicate that those species of Falconidae that secrete a nasal fluid typically eliminate the material by sneezing rather than by head-shaking, as in the Accipitridae. Furthermore, the amount of secretion voided during a meal is considerably less for falcons than for accipitrids of comparable size. Some species apparently do not secrete at all (table 2). Our data also indicate the possibility that the urine of members of the Falconidae is more concentrated in electrolytes than the urine of the Accipitridae. While this point requires further investigation, we suggest that the Falconidae may have largely obviated the need for an extrarenal mechanism of salt excretion by enhancing the ability of their kidneys to concentrate. If the high blood values of the kestrel are typical of falcons, then this would be another physiological attribute of this family that would reduce the need for an extrarenal excretion of salt.

Anatomical considerations. Presumably the secretions that we have observed come from the nasal glands, although we have no direct evidence that this is so. Except for the aegypine vultures, the nasal glands of the Falconiformes are much smaller than the functional salt-secreting glands of marine birds (Technau, 1936). Moreover, the shape and position of these glands in the orbital region vary considerably among the groups of falconiform birds. We found that the general shape and position of the glands from the Pigmy Falcon, American Kestrel, Greater Kestrel (*Falco rupicoloides*), and Yellow-headed Caracara correspond closely to those given for the Gyrfalcon (*Falco rusticolus*) by Technau (1936:571). The glands of these falcons are rather ovoid in shape, only slightly flattened, and lie with approximately the anterior half in the orbital sinus and the posterior half in the orbit itself (position IIa, preorbital-interorbital, of Technau's classification, p. 594). Technau gives the weight of the preserved Gyrfalcon gland as 25 mg (approximately 2 mg of gland per 100 g body weight), whereas the wet weight of the Pigmy Falcon gland was 5 mg (approximately 10 mg per 100 g body weight). Although the American Kestrel, Greater Kestrel, and Yellow-headed Caracara are considerably larger in body size, their glands are not much larger than that of the Pigmy Falcon. It may be a significant association that neither the American Kestrel nor the caracara was observed to secrete, but caution should be exercised in generalizing from observations based on single individuals of a species. We have some evidence that the influences of

captivity on a wild hawk may inhibit secretion. The hand-reared Bateleur referred to previously always secreted copiously when fed, but a wild-caught and untamed individual of the same age did not secrete at all for the first two weeks after capture. Even after a month of captivity, although calm enough to feed freely from the hand, this bird secreted only a few drops of fluid during a meal. All of the birds listed in table 2 as not secreting were wild-caught individuals that were always nervous when handled. All of those that secreted copiously were quite tame.

The shape of the glands from the Gabar Goshawk and the Sharp-shinned Hawk correspond closely to the description given by Technau for the glands of *Accipiter nisus* and *A. gentilis*. These accipiterine glands are thin, elongate strips of tissue, but whereas Technau (p. 595) gives the position for the two species he observed as IId, exorbital, the position of ours corresponds more closely to position IIb, interorbital. They lie entirely in the orbit, appressed against the ventral surface of the frontal bone and near the bony septum between the two orbits. Technau gives the weight of the Goshawk's gland as 20 mg, about the same relative size as the Gyrfalcon's, and of the European Sparrowhawk as 6 mg. A freshly preserved gland from *Micronisus gabar* weighed about 7 mg (approximately 4 mg of gland per 100 g body weight).

The gland of the Black Kite is also elongate but thicker than the accipiterine glands. It lies with part of its body against the bony rim of the orbit and part against the connective tissue sheath that stretches between the dorsal edge of the orbit and the frontal shield, in a position approximating IIc, interorbital-exorbital.

The glands of the Red-tailed Hawk and the Savannah Hawk also lie in position IIb, interorbital, but in each of these species there is a distinct depression in the ventral surface of the frontal bone, in which the glands are lodged. Moreover, the glands are thicker and oval in shape rather than thin and elongated. Examination of a mummified head of a Bateleur found dead in the Kalahari revealed a similar shape and location, also with a depression in the frontal bone.

An 8.5-kilogram Lappet-faced Vulture collected in the Namib Desert had a nasal gland weighing approximately 400 mg—an elongate kidney-shaped organ 25 x 8 x 5 mm, lying in position IIa. The gland of this vulture is larger than any listed by Technau for members of the Pelecaniformes and is close to the size of the Herring Gull's (*Larus argentatus*) supraorbital gland.

This cursory examination of morphology indicates that a detailed study of nasal glands in the Falconiformes might yield some useful taxonomic information. The fact that the gland of the Savannah Hawk is like that of the Red-tailed Hawk and not like the glands of the accipiters is another suggestive reason for removing *Heterospizias* from the Accipitrinae, where it is usually placed, and including it with the Buteoninae instead.

GENERAL DISCUSSION

In early studies on the function of nasal salt glands in pelecaniform and charadriiform birds, it became evident that these glands serve as organs of osmotic regulation, secreting hyperosmotic solutions of NaCl in response to salt-loading (Schmidt-Nielsen *et al.*, 1958; Fänge *et al.*, 1958). It was later shown that these glands are under central nervous, cholinergic control and respond to any increase in blood osmolarity by secreting salt solutions that are hyperosmotic to the blood (Schmidt-Nielsen, 1960). The general conclusion from this fascinating work seemed to be that functional nasal glands represent a specialized adaptation for marine existence.

Nasal salt secretions have now been described in 10 avian orders and in a few species of reptiles (Schmidt-Nielsen, 1960; Schmidt-Nielsen *et al.*, 1963; Cooch, 1964; Norris and Dawson, 1964; and our study). Although the nasal glands of marine birds are most conspicuously developed (Technau, 1936) and are capable of high rates of flow (Schmidt-Nielsen, 1960), there is no a priori reason why the smaller nasal glands of many terrestrial birds should not also be functional; that is, capable of secreting a salty fluid hyperosmotic to the blood. Schmidt-Nielsen *et al.* (1963) have recently reported that this is indeed the case for two terrestrial birds of desert habitat, the Ostrich (*Struthio camelus*) and a North African partridge (*Ammoperdix heyi*); but they presented no data on either the concentrations of the ions or on the rates of flow of the solutions secreted by these birds. We are now able to provide some corroborative data on 21 terrestrial species in the order Falconiformes. It may be that the relative size of the nasal gland is associated primarily with rates of flow and not at all, or only to a small extent, with concentrating ability.

As a result of his recent experience with terrestrial birds and lizards, Schmidt-Nielsen (1964) has broadened his concept of the extrarenal mechanism for reducing plasma osmotic pressure to include the interesting idea that such a mechanism may have been a prerequisite for birds to take full advantage of the water economy inherent in uric acid excretion. His argument is approximately as follows: Uric acid cannot be concentrated to the maximum degree in the kidney tubules without clogging them and the ureters; hence, the uric acid arrives in the cloaca with a large amount of water. This water is probably removed from the uric acid by an active transport of sodium with a passive following of water, in accordance with the prevailing notion that active transport of water is energetically improbable and not yet convincingly demonstrated in any biological system. Such a mechanism leaves the bird or reptile with the problem of excreting the salt that is moved across the cloaca into the blood. Schmidt-Nielsen's scheme further suggests that it is necessary for the water and salt voided from the cloaca to form at most an isotonic solution with respect to blood, since a greater concentration of salt would hold back water and militate against the water-conserving properties of uric acid. There are some difficulties with this hypothesis, not the least of which is the fact that it remains to be shown unequivocally that there is a concentration or precipitation of uric acid in the cloaca, but the scheme seems reasonable and worth pursuing.

Implicit in Schmidt-Nielsen's thinking is the idea that as a result of the movement of sodium *and water* across the cloaca the blood becomes concentrated with respect to sodium. It is not immediately clear from Schmidt-Nielsen's presentation why this should be so; it is because birds lose large amounts of ion-free water by evaporation from their respiratory systems (see Bartholomew and Cade, 1963). Thus, if a bird's urine is usually hypotonic or isotonic to its blood and it acquires appreciable quantities of electrolytes from ingested food or water, then—quite apart from any mechanism involving the movement of sodium from the cloaca to concentrate uric acid—the organism must have an extrarenal route for excreting salt in order to remain in water and salt balance; or it must drink a sufficient amount of ion-free water to compensate for the evaporative loss.

Carnivorous birds provide an instructive case in point. Our data indicate that falconiform birds typically pass a cloacal fluid with hypotonic concentrations of Na^+ and Cl^-. Although sometimes drinking free water, these birds are quite capable of maintaining water balance with only the preformed water taken in their fleshy food (Bartholomew and Cade, 1963). Since raptors eat freshly killed prey with water

TABLE 3

WATER AND SALT REGULATION IN A SMALL ACCIPITER

Item considered	Computation or measurement	Value
(1) Total body weight	Direct weighing	150 g
(2) Wet weight of daily food ration	Direct weighing	30 g
(3) Water content of food	66⅔%, standard value[1]	20 g
(4) Dry weight of food	Item (2) minus item (3)	10 g
(5) Oxidative water from 10 g of protein	Item (4) x 0.449, based on uric acid end product[1]	5 g
(6) Total water from food	Item (3) plus item (5)	25 g
(7) Evaporative loss of water	2.5% body wt/day, from generalized wt relative curve[2]	3.75 g
(8) Water available for excretion	Item (6) minus item (7)	21.25 g
(9) Total Na^+ content of food	60 mmole/kg wet wt[3]	1.8 mmole
(10) Average Na^+ conc. in urine	Flame photometer	75 mmole/liter
(11) Estimated total Na^+ excreted by kidney/day	Item (8) x item (10)	1.59 mmole
(12) Excess Na^+ to be excreted extrarenally	Item (9) minus item (11)	0.21 mmole
(13) Volume of nasal secretion required	1000 mmole/liter = 0.21 mmole/$X\mu$l, $X = 210$ μl	
(14) Estimated total K^+ content of food	42 mmole/kg wet wt[3]	1.26 mmole
(15) Average K^+ conc. in urine	Flame photometer	50 mmole/liter
(16) Estimated total K^+ excreted by kidney	Item (15) x item (8)	1.06 mmole

[1] Schmidt-Nielsen, 1964. [2] Bartholomew and Cade, 1963. [3] Pitts, 1963.

and electrolyte compositions similar to their own, the salt and water obtained from their food should be essentially isosmotic to their own body fluids. With evaporation as a significant factor in the total loss of water, but not of ions, these birds must acquire a salt load from their food; and it seems plausible that the nasal glands play a role in eliminating the excess sodium chloride. Such a mechanism has even greater significance for a raptor living in the desert, where rates of evaporation are high and where ion-free drinking water is of limited occurrence.

Let us consider a small accipiter weighing 150 g. Under moderate conditions of temperature and humidity, for instance 20° to 25°C and 30 to 40 per cent relative humidity, such a hawk can maintain body weight indefinitely on about 30 g of whole mouse tissues per day without drinking. Certain quantitative implications of this ration for the regulation of water and salts are shown in table 3. The hawk ingests approximately 1.8 mmoles of Na^+ per day in its food. Although most of these ions can be eliminated by a copious flow of hypotonic urine, about 0.21 mmoles remain to be accounted for. Given an average Na^+ concentration of 1000 mmole/liter for the nasal secretion, these excess ions could be excreted in a volume of 210 μl. Our observations during the feeding of the Gabar Goshawk, for instance, did not suggest a volume of secretion of this magnitude, but it is not unreasonable to suppose that hawks secrete at other times of the day also, as indicated by the accumulation of salt crystals in the nares.

Potassium is excreted mainly through the urine. The total intake in the food is about 1.26 mmole, of which we can account for 1.06 mmole assuming an average urine concentration of 50 mmole/liter. Since individual samples of urine frequently contain much higher concentrations and since there is the distinct possibility of a

24-hour cycle of changes in these concentrations, we believe it is safe to assume that the kidney of hawks is able to handle the entire potassium load from the food, although the nasal secretion does carry a small amount.

It is also interesting to consider the implications of a 30 g ration of butchered meat (muscle). The water content amounts to about 78 per cent of the wet weight, the Na^+ concentration is very low, about 10 mmole/liter of water in the muscle, and the K^+ concentration is very high, about 160 mmole/liter (Pitts, 1963). The bird has about 23 g of water available for excretion, giving a potential Na^+ excretion from the urine alone of 1.15 mmoles per day, whereas the food ration contains only about 0.234 mmoles. Obviously, sodium is no problem with this type of food. The ingested potassium, on the other hand, amounts to about 3.74 mmoles. To excrete this amount with the water available from the food, the average urine concentration of K^+ must be around 162 mmole/liter. Again, since we often obtained values for individual urine samples well over 200 mmole/liter, we believe the falconiform kidney is able to handle a potassium load of this magnitude. Occasional nasal secretions also contain rather high concentrations of K^+ and may sometimes contribute significantly to the removal of this ion.

The most critical factor in all of this regulation is the rate of evaporation. In falconiform birds, the upper limit to the amount of the total available water (preformed and oxidative) that can be lost by evaporation without producing a water deficit seems to be determined by the volume and concentration of the nasal secretion for Na^+ and by the concentrating ability of the kidney for K^+. If the evaporation from our hypothetical hawk is increased to 10 per cent of its body weight per day under conditions of high temperature and low humidity, a rate of evaporation quite to be expected for a small bird living under desert conditions, then only 10 g of water are available for urine formation and nasal secretion on the mouse ration. The average concentration of Na^+ in the urine would allow only for the excretion of 0.75 mmoles out of the total 1.8 mmoles ingested, if all of this water were used for urine. At a concentration of 1000 mmole/liter, it would take about 1 ml of nasal secretion to excrete the remainder. The urine concentration of K^+ would have to average about 126 mmole/liter.

We do not know for sure that these concentrations and volumes can be realized by an actual hawk of the size considered, but these simple calculations do illustrate the obvious adaptive advantage, in terms of water conservation, of a functional salt-secreting gland for terrestrial, carnivorous birds that are not drinking. In fact, this function may well have its greatest adaptive significance for nestling hawks, which, as Gordon (1934) pointed out long ago, are absolutely dependent upon the water in their fleshy food and which are often exposed to rather intense heating by radiation in their open nests. A recent observation on a three- to four-day-old Bateleur chick in Kruger Park is indicative. When the bird was exposed to sunlight in its nest, it soon began to pant, and in less than one minute thereafter a salty-tasting fluid appeared in its nares.

SUMMARY

Many birds of prey exude a clear fluid from their nares while eating. In an examination of 16 species of Accipitridae and 8 species of Falconidae, we found these secretions to contain high concentrations of Na^+ and Cl^-, which were always hypertonic to known values for blood. Potassium ions were excreted mainly in the urine. The gustatory process seems to provide some nonosmotic stimuli that promote secretion.

Presumably the secretion comes from the nasal glands, but we have no direct proof that this is so. Except for the aegypine vultures, the nasal glands of falconiforms are much smaller than the functional salt-secreting glands of comparable-sized marine birds, but there is no a priori reason why a small gland should not be functional. Size of the gland may be associated only with the volume of secretion and not with concentrating ability. The morphology of falconiform nasal glands shows considerable differences among species groupings and might serve as a useful tool for taxonomic considerations. The accipitrid species typically void the secretion by shaking their heads from side to side, and they secrete larger volumes than the falcons, which sneeze out the fluid.

The main adaptive value of a functional salt gland for terrestrial, carnivorous birds seems to be associated with the fact that they acquire a sodium load from their food that is not easily excreted by their typically hypotonic urine. Evaporation results in a further concentration of the ingested electrolytes, but the salt gland may function effectively enough in some species to permit them to remain in water balance solely on the preformed and oxidative water associated with their food, even in the face of relatively high rates of evaporative loss. We have examined some quantitative aspects of this problem.

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