

Universidad de Puerto Rico
RECINTO UNIVERSITARIO DE MAYAGUEZ
Departamento de Biología

BIOL 4428: Ornitología General

Instructor: Dr. Carlos A. Delannoy

PREGUNTAS GUIA PARA LECTURA MATERIAL SUPLEMENTARIO

Night Owls are Good Listeners

1. Describa el diseño experimental que usó Roger Payne para determinar que los múcaros de granero dependían de la audición para localizar su presa.
2. ¿Qué adaptaciones poseen los múcaros que reflejan su extraordinaria capacidad auditiva?
 - a) Cochlea
 - b) disco facial
 - c) amplia percepción de sonidos
3. ¿Cómo distinguen los múcaros sus presas? ¿Un ratón de una liebre?
4. ¿Cómo el múcaro logra conocer el origen de un sonido aun cuando cese el sonido?
5. ¿Cómo el múcaro reconoce que el sonido viene de la derecha - izquierda, abajo - arriba?
6. ¿Qué es el mapa neural que poseen los múcaros y cuál es su valor?

Glándula de Sal

1. Explicación al diagrama #1.
2. ¿Cómo se percató el investigador que era la glándula de sal y no el riñón del ave quien removía el exceso de sal en la sangre?
3. ¿Cómo logra la glándula de sal remover y producir un fluido tan concentrado de sal?
 - a) Comience con la morfología de la glándula.
 - b) Explicación proceso de coaster-current.
4. ¿Cómo se explica la transferencia de sal desde la sangre a los túbulos siendo el fluido en los túbulos de una concentración mayor?
5. Diferencias en el funcionamiento del riñón y glándula de sal.
6. Variación en la posición de la glándula en aves y cómo disponen del líquido.

Night Owls Are Good Listeners

Superb hearing enables the barn owl to hunt at night with deadly accuracy

by Masakazu Konishi

Favorite subjects in popular art and fables, owls have been cast in many roles—from messenger of death and evil omen to symbol of wisdom and good luck. Few people, however, actually see owls in the wild, and fewer still are familiar with their habits. For many, the hooting or screeching of an owl at night offers perhaps the most telling clue about owl behavior, suggesting as it does that the birds are nocturnal. To the human listener stumbling along in the dark, the obvious questions are, how do owls get about at night and how, in particular, do they manage to hunt down their prey?

Certainly the eyes of nocturnal owls are better adapted to dim illumination than are human eyes, but no animal can see in total darkness. Fortunately for the owls, their peak period of activity can vary from dusk to dawn, and even the middle of the night is seldom totally dark. The moon or the stars often provide enough light for nocturnal birds to fly by.

Nevertheless, there are times when owls are forced to operate in near-total darkness. In the early 1950s, Roger Payne and William Drury carried out experiments with barn owls (*Tyto alba*), among the most nocturnal of all owls, and live mice, which are typical of the small mammals on which these owls feed. The owls easily caught mice rustling among dead leaves on the floor of a totally darkened room. Subsequently, Payne found that an owl would strike a loudspeaker broadcasting tape-recorded mouse rustles. He then devised a clever test in which he attached a crumpled, noisy ball of paper to the tail of a mouse, which was walking noiselessly on sand; the owl attacked the paper, not the mouse. Without question, the owl was relying on sound—rather than smell or infrared waves from body heat—to locate its prey in the dark.

Because barn owls, unlike bats, do not use sonar, they are dependent on sounds produced by the movement of their prey. A mouse could escape death if it stopped making noises as soon as it noticed an approaching owl, but the bird's large wings, soft feathers, and small body enable it to fly silently. In addition, owls respond so fast that a mouse might not have a chance

to react: barn owls can take off from a perch within half a second of hearing a mouse, and they can fly about 12.5 feet per second in the dark.

To pinpoint a mouse's location by its noises alone, the barn owl needs an acute sense of hearing. Recently, its cochlea (the structure in the inner ear responsible for transforming sound waves into nerve impulses) has been found to be the longest of any bird's, and among the species studied so far, the barn owl can hear the widest range of frequencies. It can also hear extremely faint noises that are inaudible to humans.

The barn owl's hearing is aided by its facial ruff, a concave wall of stiff, dark-tipped feathers. The outer edges of the ruff, which encircle the two halves of the face separately, give the barn owl's face its distinctive heart shape. Like parabolic reflectors, the two halves of the ruff channel sound into the ears. (White, sound-transparent feathers that hide all but the outer rim of the ruff account for the barn owl's white face.) Other typically nocturnal owl species, such as the saw-whet, long-eared, and great gray owls, also have well-developed facial ruffs; diurnal species, such as the snowy and burrowing owls, do not.

But it is not enough to hear well: a barn owl hunting at night cannot afford to mistake a mature skunk for a mouse. Experiments have shown that these owls can remember complex noises and distinguish them from similar but different noises. Presumably, after many nights of sitting in a tree or cruising over fields, the barn owl learns to link the acoustic and visual characteristics of the animals in its environment, and eventually, it can identify appropriate prey by sound alone.

Once the barn owl recognizes a prey, it must determine exactly where the rustles come from. Pinpointing the source of a noise involves calculations in both azimuth (or left-right) direction and elevation (up-down) direction. Whether the barn owl also assesses the depth (or distance) of a sound is not known.

The barn owl reacts to a rustling noise by turning its face, with extreme accuracy and speed, toward the source of the sound. Once the source is directly in front of the

owl's face, the bird can pinpoint it with an error of less than 1.5° in both azimuth and elevation. Interestingly, for sounds originating within 30° of either side of the midpoint of the bird's face, the barn owl has an impressively good idea of where they are coming from even before turning its head. Payne originally thought that the barn owl determines the location of a sound by scanning with its head until it finds the right spot, but subsequent experiments have proved the owl to be much more sophisticated than that. When a noise is cut off before the barn owl has a chance to turn toward it, the bird still localizes accurately. It is able to do this by rapidly translating acoustic cues into a location, which it memorizes, even before turning. Not surprisingly, the farther away the sound source is from the midpoint of the face, the greater the chances that the owl will make a mistake.

To respond with such speed and accuracy, the barn owl needs both ears; with one ear plugged, it cannot localize sound at all. Experimental work during the last decade has shown that the cues used by the owl to determine the left-right position of a sound involve binaural time differences, that is, the difference in time it takes a sound to reach each of the two ears. When the sound source is located at the midpoint between the two ears, no time difference occurs, but a sound coming from the right, for example, reaches the right ear sooner than the left one.

The maximum binaural time difference for barn owls is about 150 microseconds (one microsecond being one-millionth of a second), compared with 570 microseconds for humans, who have larger heads. There is still some resistance to the idea that any animal can use such small time differences for sound localization, but recent studies in my laboratory have shown that the barn owl can actually use a binaural time lag as short as 10 microseconds.

The barn owl uses a different cue, known as binaural intensity difference, to figure out how far up or down, relative to its eyes, a sound is coming from. A head, whether a bird's or a human's, casts a sort of shadow in the sound field, interfering with the movement of sound waves. As a

Below: In this infrared photograph, taken in a soundproof, darkened room, a barn owl homes in on its unsuspecting victim. Just before striking, the owl adjusts its talons to the length and shape of the mouse. Right: A barn owl prepares to enjoy the fruits of its labors.

Masaakazu Kuroshi



result, a noise will sound less loud to the ear in the shadow than to the other ear. Humans, with ears placed at the same level on either side of the head, use both binaural time and binaural intensity cues for determining left-right direction. Barn owls, and most typically nocturnal owls, can use binaural intensity differences to determine elevation because their ear openings are asymmetrical. The nature of the asymmetry varies from species to species. In the barn owl, the asymmetry is restricted to the fleshy external part of the two ear holes: one is situated above the midpoint of the eye; the other, below. Similarly, the halves of the barn owl's facial ruff are slightly asymmetrical: the left one tilted downward; the right one, upward.

These asymmetries, which allow for the differential reception of sound waves, mean that sounds coming from below eye level will sound louder in the left ear and those coming from above will sound louder in the right. The differences in loudness allow the barn owl to pinpoint sound in the elevational plane. When a noise is equally loud in both ears, the owl knows that its source is at eye level.

The importance of hearing to the barn owl is reflected in its brain. Some of the brainstem regions devoted to binaural hearing are much larger in the barn owl

than in any other birds studied so far. In a special midbrain region, each cell is sensitive to a unique combination of binaural time and intensity differences and responds only to sound emanating from a single, small area in space. Recently, these locations in space have been found to correspond to specific locations within the brain: cells responsive to sounds in front of the owl occur in the anterior part of the brain, for example, while those sensitive to sounds from the side occur in the lateral part. Thus, the barn owl's brain contains a neural map of auditory space. The map provides the owl with a reference table that it can use to look up sound cues and assign each one a location. This is the first such map found in any animal, and undoubtedly, its evolution is closely related to the highly nocturnal nature of the barn owl's life style. Whether other birds or animals have auditory maps remains to be discovered.

Our growing ability to explain, in anatomical and neurophysiological terms, how barn owls localize sound may take away some of the mystery, but it in no way diminishes the impressiveness of their skill. The object of more than their share of superstition through the ages, owls have only in recent decades begun to receive recognition for their real talents. □

Knut Schmidt-Nielsen
January 1959

A special organ which eliminates salt with great efficiency enables marine birds to meet their fluid needs by drinking sea water. Similar organs have been found in marine reptiles

As the writers of stories about castaways are apt to point out, a man who drinks sea water will only intensify his thirst. He must excrete the salt contained in the water through his kidneys, and this process requires additional water which is taken from the fluids of his body. The dehydration is aggravated by the fact that sea water, in addition to common salt or sodium chloride, also contains magnesium sul-

fate, which causes diarrhea. Most air-breathing vertebrates are similarly unable to tolerate the drinking of sea water, but some are not so restricted. Many birds, mammals and reptiles whose ancestors dwelt on land now live on or in the sea, often hundreds of miles from any source of fresh water. Some, like the sea turtles, seals and albatrosses, return to the land only to reproduce. Whales, sea cows and some sea snakes, which bear

living young in the water, have given up the land entirely.

Yet all these animals, like man, must limit the concentration of salt in their blood and body fluids to about 1 per cent—less than a third of the salt concentration in sea water. If they drink sea water, they must somehow get rid of the excess salt. Our castaway can do so only at the price of dehydrating his tissues. Since his kidneys can at best se-

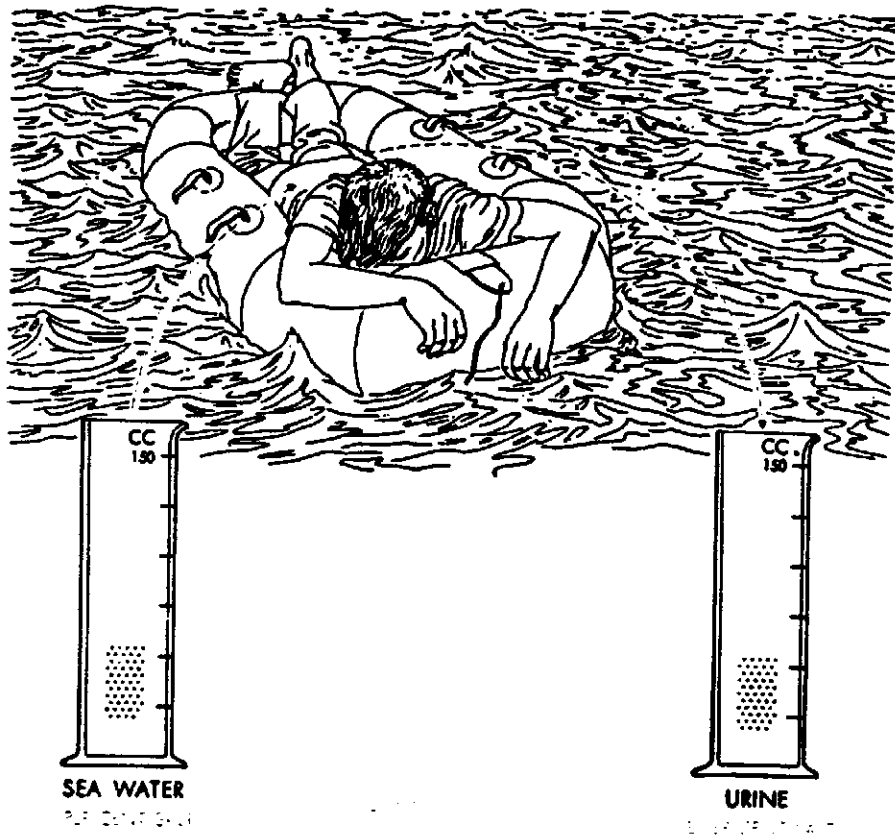


PETREL EJECTS DROPLETS of solution produced by its salt gland through a pair of tubes atop its beak, as shown in this high-speed photograph. The salt-gland secretions of most birds drip

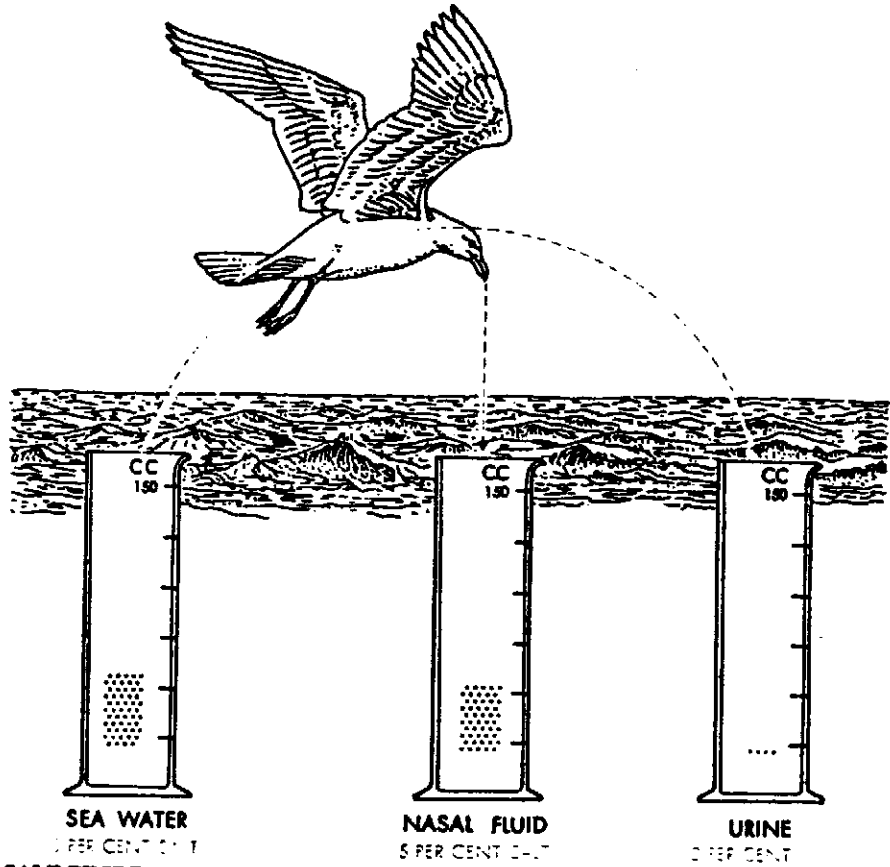
from the tip of the beak. The petrel, however, remains in the air almost continuously and has apparently evolved this "water pistol" mechanism as a means of eliminating the fluid while in flight.

crete a 2-per-cent salt solution, he must eliminate up to a quart and a half of urine for every quart of sea water he drinks, with his body fluids making up the difference. If other animals drink sea water, how do they escape dehydration? If they do not drink sea water, where do they obtain the water which their bodies require?

The elimination of salt by sea birds and marine reptiles poses these questions in particularly troublesome form. Their kidneys are far less efficient than our own: a gull would have to produce more than two quarts of urine to dispose of the salt in a quart of sea water. Yet many observers have seen marine birds drinking from the ocean. Physiologists have held that the appearance of drinking is no proof that the birds actually swallow water, and that the low efficiency of their kidneys proves that they do not. Our experiments during the past two years have shown that while the physiologists are right about the kidneys, the observations of drinking are also correct. Marine birds do drink sea water. Their main salt-eliminating organ is not the kidney, however, but a special gland in the head which disposes of salt more rapidly than any kidney does. Our studies indicate that all marine birds and probably all marine reptiles possess this gland.



The obvious way to find out whether birds can tolerate sea water is to make them drink it. If gulls in captivity are given only sea water, they will drink it without ill effects. To measure the exact amount of sea water ingested we administered it through a stomach tube, and found that the birds could tolerate large quantities. Their output of urine increased sharply but accounted for only a small part of the salt they had ingested. Most of the salt showed up in a clear, colorless fluid which dripped from the tip of the beak. In seeking the source of this fluid our attention was drawn to the so-called nasal glands, paired structures of hitherto unknown function found in the heads of all birds. Anatomists described these organs more than a century ago, and noted that they are much larger in sea birds than in land birds. The difference in size suggested that the glands must perform some special function in marine species. Some investigators proposed that the organs produce a secretion akin to tears which serves to rinse sea water from the birds' sensitive nasal membranes.



SALT EXCRETION IN MEN AND BIRDS is compared in these drawings. Castaway at top cannot drink sea water because in eliminating the salt it contains (colored dots) he will lose more water than he has drunk. His kidney secretions have a salt content lower than that of sea water. Gull (below) can drink sea water even though its kidneys are far less efficient than a man's. It eliminates salt mainly through its salt, or "nasal," glands. These organs, more efficient than any kidney, secrete a fluid which is nearly twice as salty as sea water.

We were able to collect samples of the secretion from the gland by inserting a thin tube into its duct. The fluid turned

out to be an almost pure 5-per-cent solution of sodium chloride—many times saltier than tears and nearly twice as salty as sea water. The gland, it was plain, had nothing to do with rinsing the nasal membranes but a great deal to do with eliminating salt. By sampling the output of other glands in the bird's head, we established that the nasal gland was the only one that produces this concentrated solution.

The nasal glands can handle relatively enormous quantities of salt. In one experiment we gave a gull 134 cubic centimeters of sea water—equal to about a tenth of the gull's body weight. In man this would correspond to about two gallons. No man could tolerate this much sea water; he would sicken after drinking a small fraction of it. The gull, however, seemed unaffected; within three hours it had excreted nearly all the salt. Its salt glands had produced only about two thirds as much fluid as its kidneys, but had excreted more than 90 per cent of the salt.

The fluid produced by the salt gland is about five times as salty as the bird's blood and other body fluids. How does the organ manage to produce so concentrated a solution? Microscopic examination of the gland reveals that it consists of many parallel cylindrical lobes, each composed of several thousand branching tubules radiating from a central duct like bristles from a bottle brush. These tubules, about a thousandth of an inch in diameter, secrete the salty fluid.

A network of capillaries carries the blood parallel to the flow of salt solution in the tubules, but in the opposite direction [see illustration on opposite page]. This arrangement brings into play the principle of counter-current flow, which seems to amplify the transfer of salt from the blood in the capillaries to the fluid in the tubules. A similar arrangement in the kidneys of mammals appears to account for their efficiency in the concentration of urine [see "The Wonderful Net," by P. F. Scholander, *SCIENTIFIC AMERICAN*, April, 1957]. No such provision for counter-current flow is found in the kidneys of reptiles, and it is only slightly developed in birds.

Counter-current flow, however, does not of itself account for the gland's capacity to concentrate salt. The secret of this process lies in the structure of the tubules and the cells that compose them.

The microscopic structure of a salt-gland tubule resembles a stack of pies with a small hole in the middle. Each "pie" consists of five to seven individual

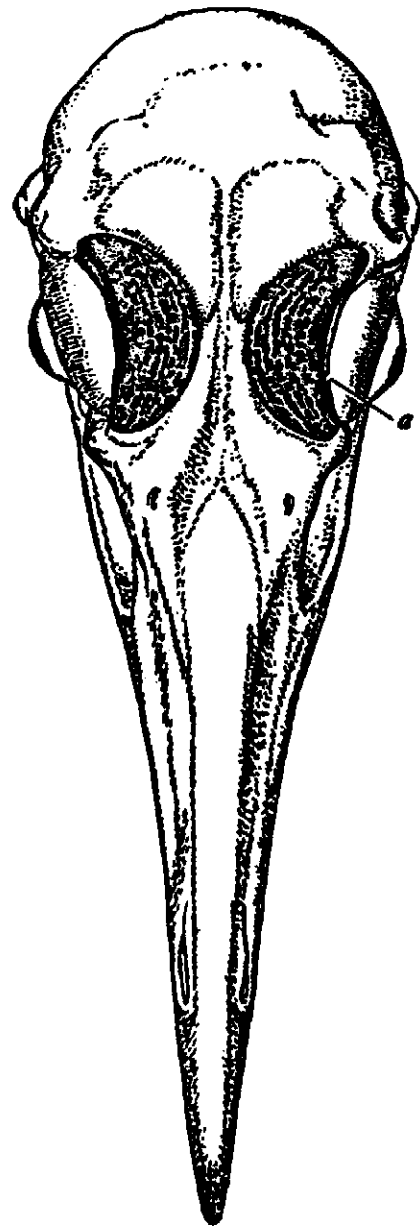
cells arranged like wedges. The hole, or lumen, funnels the secretion into the central duct. When we inject dye into the lumen, colored fluid seeps out into a system of irregular crevices in the walls of the tubule. More detailed examination with the electron microscope reveals a similar, interlocking system of deep folds which extend inward from the outer surface of the tubule. This structure may be important in that it greatly multiplies the surface area of the cell. It is worth noting that cells with similar, though shallower, folds are found in the tubules of the mammalian kidney.

Evidently some physiological mechanism in the cell "pumps" sodium and chloride ions against the osmotic gradient, from the dilute salt solution of the blood to the more concentrated solution in the lumen. Nerve cells similarly "pump" out the sodium which they absorb when stimulated [see "The Nerve Impulse and the Squid," by Richard D. Keynes; *SCIENTIFIC AMERICAN* Offprint 58]. Of course the mechanisms in the two processes may be quite different. In the tubule cells the transport of sodium and chloride ions seems to involve the mitochondria, the intracellular particles in which carbohydrates are oxidized to produce energy.

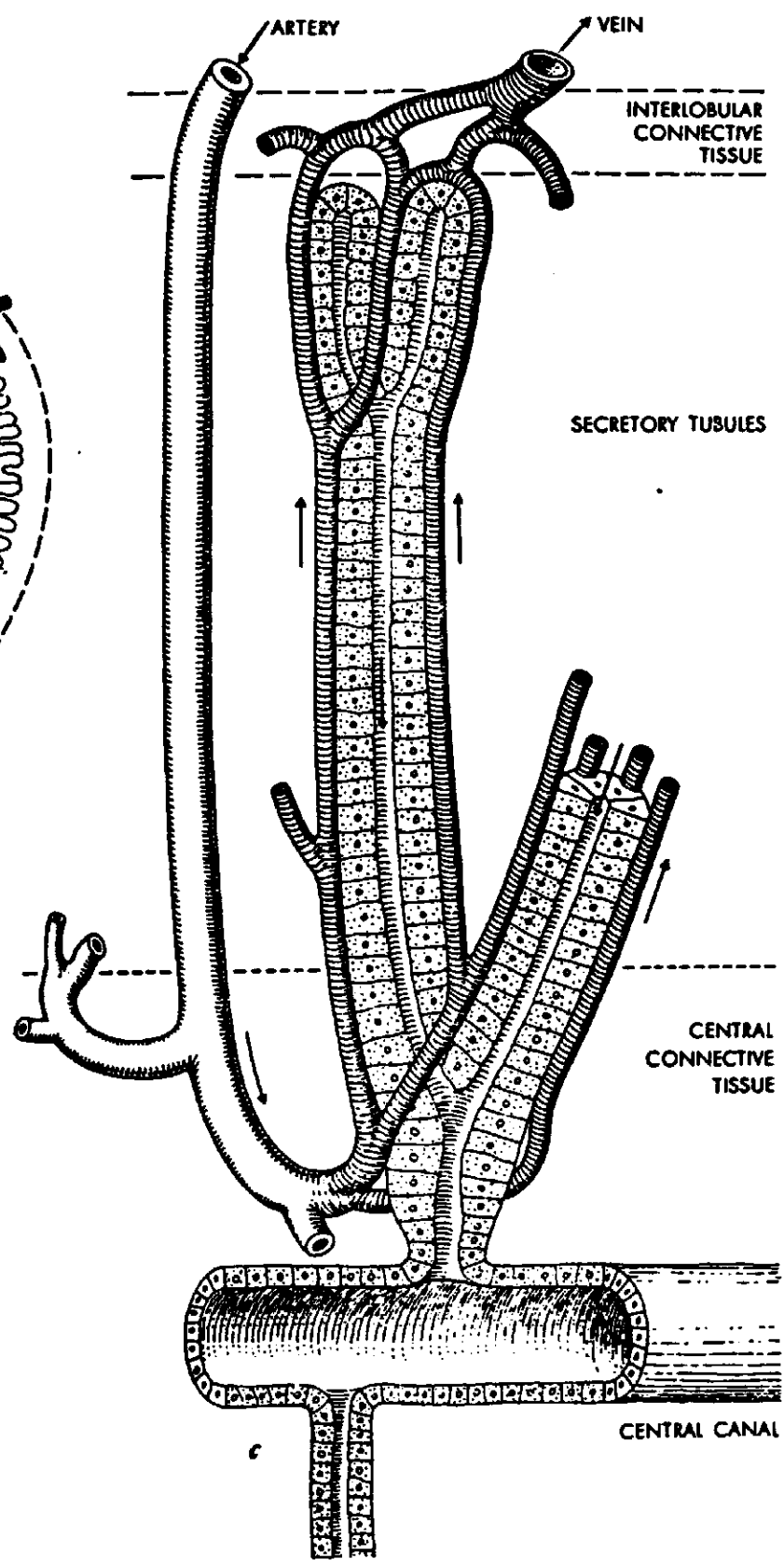
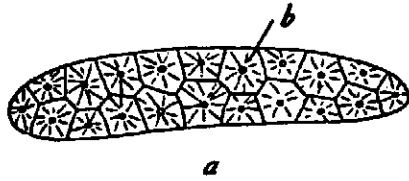
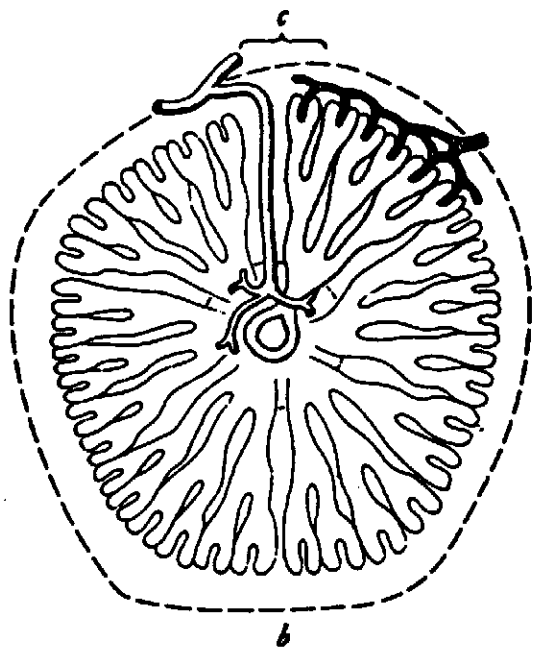
The similarities between the salt gland and the mammalian kidney should not obscure their important differences. For one thing, the salt gland is essentially a much simpler organ. The composition of its secretions, which apart from a trace of potassium contain only sodium chloride and water, indicates that its sole function is to eliminate salt. In contrast, the kidney performs a variety of regulatory and eliminative tasks and produces a fluid of complex and variable composition, depending on the animal's physiological needs at a particular time.

The salt gland's distinctive structure, elegantly specialized to a single end, enables it to perform an almost unbelievable amount of osmotic work in a short time. In one minute it can produce up to half its own weight of concentrated salt solution. The human kidney can produce at most about a twentieth of its weight in urine per minute, and its normal output is much less.

Another major difference between the two glands is that the salt gland functions only intermittently, in response to the need to eliminate salt. The kidney, on the other hand, secretes continuously, though at a varying rate. The salt gland's activity depends on the concentration of salt in the blood. The injection of salt solutions into a bird's bloodstream causes



STRUCTURE of salt gland is essentially the same in all sea birds. In the gull the glands lie above the bird's eyes, as shown at left. Cross section of a gland (a) shows that it consists of many lobes (b). Each of these



lobes contains several thousand branching tubules which radiate from a central duct like the hairs of a bottle brush. Enlargement of a single tubule (c) reveals that it is surrounded by capillaries in which blood flows counter to the flow of salt secretion in the tubule. This counter-current flow, which also occurs in the kidneys

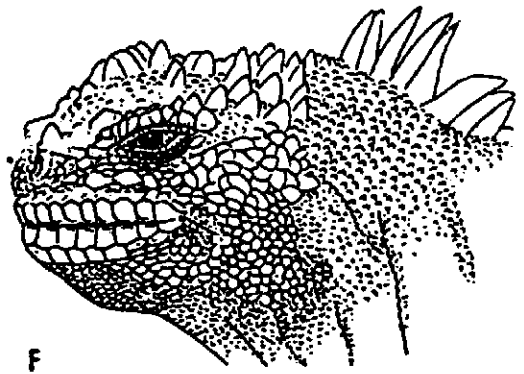
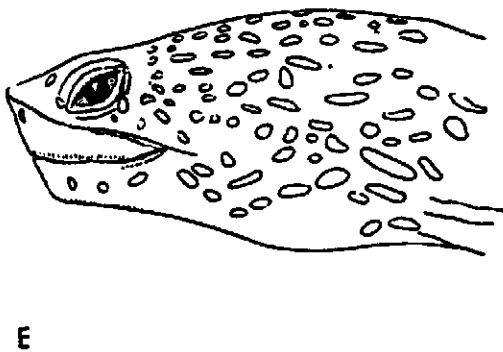
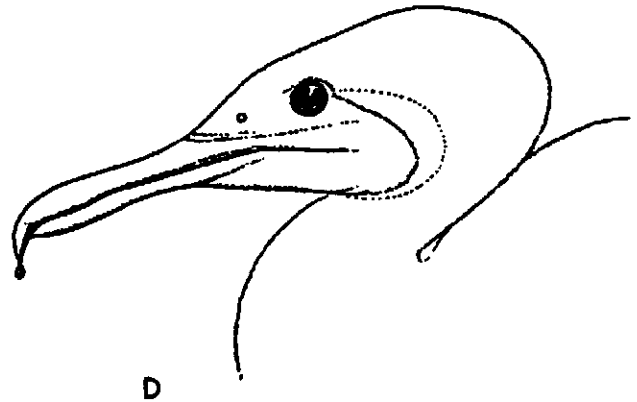
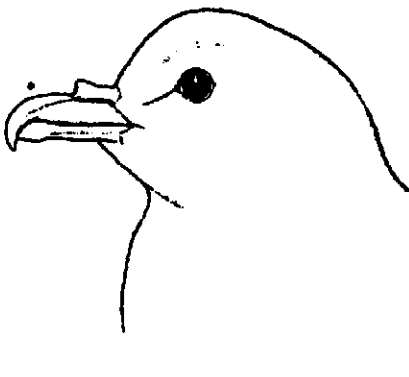
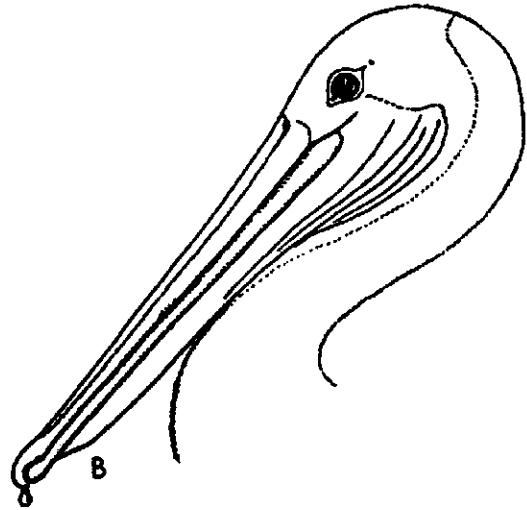
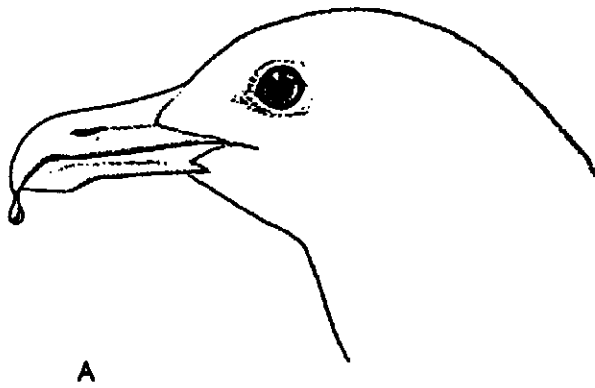
of mammals, facilitates the transfer of salt from the blood to the tubule. The tubule wall, only one cell thick, consists of rings of five to seven wedge-shaped cells. These rings, stacked one on top of another, encircle a small hole, or lumen, through which the salty secretion flows from the tubule into the central canal of the lobe.

the gland to secrete, indicating that some center, probably in the brain, responds to the salt concentration. The gland responds to impulses in a branch of the facial nerve, for electric stimulation of this nerve causes the gland to secrete.

While the structure and function of the salt gland is essentially the same in all sea birds, its location varies. In the

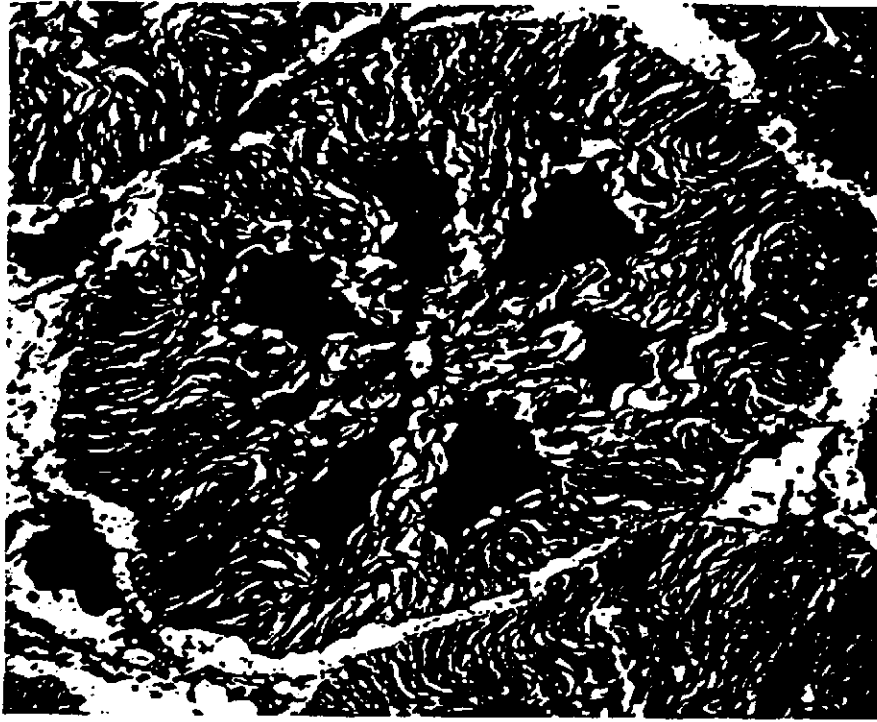
gull and many other birds the glands are located on top of the head above the eye sockets [see illustrations on this page]; in the cormorant and the gannet they lie between the eye and the nasal cavity. The duct of the gland in either case opens into the nasal cavity. The salty fluid flows out through the nostrils of most species and drips from the tip of the beak, but there are some interesting variations on this general scheme. The

pelican, for example, has a pair of grooves in its long upper beak which lead the fluid down to the tip; the solution would otherwise trickle into the pouch of the lower beak and be reingested. In the cormorant and the gannet the nostrils are nonfunctional and covered with skin; the fluid makes its exit through the internal nostrils in the roof of the mouth and flows to the tip of the beak.



LOCATION OF SALT GLAND (color) varies in different species of marine birds and reptiles. In the gull (A) the gland's secretions emerge from the nostril and drip from the beak; in the cormorant (D) the fluid flows along the roof of the mouth. The pelican (B)

has grooves along its upper beak which keep the fluid from dripping into its pouch; the petrel (C) ejects the fluid through tubular nostrils. In the turtle (E) the gland opens at the back corner of the eye; in the marine iguana (F) it opens into the nasal cavity.



CROSS SECTION OF SALT-GLAND TUBULE is shown magnified about 5,700 diameters in this electron micrograph made by William L. Doyle of the University of Chicago. To emphasize the cell-structure the specimen was kept in a solution which shrank and distorted the cells and their nuclei. Most of the material of the cells lies in folded, leaflike layers; cells with a somewhat similar structure are found in the kidney tubules of mammals.

The petrel displays an especially interesting mechanism for getting rid of the fluid. Its nostrils are extended in two short tubes along the top of its beak. When its salt glands are working, the bird shoots droplets of the fluid outward through the tubes [see illustration on page 186]. This curious design may reflect a special adaptation to the petrel's mode of life. Though the bird remains at sea for months at a time, it rarely settles down on the water to rest. Presumably the airstream from its almost continuous flight would hamper the elimination of fluid from the bird's nostrils, were it not for the water-pistol function of the tubes.

Our studies so far have demonstrated the existence of the salt gland in the herring gull, black-backed gull, common tern, black skimmer, guillemot, Louisiana heron, little blue heron, double-crested cormorant, brown pelican, gannet, petrel, albatross, eider duck and Humboldt penguin. These species, from a wide variety of geographical locations, represent all the major orders of marine birds. There is little doubt that this remarkable organ makes it possible for all sea birds to eliminate salt and live without fresh water.

The discovery of the salt gland in sea birds prompted us to look for a similar organ in other air-breathing sea animals.

In *Alice's Adventures in Wonderland* the Mock Turtle weeps perpetual tears because he is not a real turtle; real turtles, at least the marine species, also weep after a fashion. A. F. Carr, Jr., a distinguished specialist in marine turtles, gives us a vivid account of a Pacific Ridley turtle that came ashore to lay its eggs. The animal "began secreting copious tears shortly after she left the water, and these continued to flow after the nest was dug. By the time she had begun to lay, her eyes were closed and plastered over with tear-soaked sand and the effect was doleful in the extreme." Thus Carr makes it clear that the turtle's tears do not serve to wash its eyes free of sand, an explanation that otherwise might seem reasonable. The suggestion that the turtle weeps from the pangs of egg-laying is even wider of the mark.

With the loggerhead turtle as our subject, we have found that the sea turtle's tears come from a large gland behind its eyeball. The tears have much the same composition as that of the salt-gland secretions of the sea bird. Thus it would seem more than likely that the turtle's "weeping" serves to eliminate salt. The salt gland of the turtle has a structure similar to that of the gland in sea birds, with tubules radiating from a central duct, and it seems that this structure is

essential for the elaboration of a fluid with a high salt concentration. The similarity is the more striking because the location of the gland in the turtle indicates that it has a different evolutionary origin. Still a third independent line of evolution may be represented by the salt gland in the Galápagos marine iguana, the only true marine lizard.

Anatomical studies of the other marine reptiles—the sea snakes and the marine crocodiles—have established that their heads contain large glands whose function may be similar to that of the salt gland. When we succeed in obtaining living specimens of these creatures, we expect to determine whether their glands have the same function.

Investigations of marine mammals thus far indicate that these animals handle the elimination of salt from their systems in a more conventional manner. The seal and some whales apparently satisfy their need for water with the fluids of the fish on which they feed. The elimination of such salt as these fluids contain requires kidneys of no more than human efficiency. But other whales, and walrus, whose diet of squid, plankton or shellfish is no less salty than sea water, must surely eliminate large quantities of excess salt even if they do not drink from the ocean itself. Our knowledge of their physiology suggests that their kidneys, which are more powerful than ours, can eliminate all the salts in their food. Some mammalian kidneys do function at this high level. The kangaroo rat, whose desert habitat compels it to conserve water to the utmost, can produce urine twice as salty as the ocean, and thrives in the laboratory on a diet of sea water and dried soybeans [see "The Desert Rat," by Knut and Bodil Schmidt-Nielsen; SCIENTIFIC AMERICAN Offprint 1050].

We should like to study salt excretion in whales, but these animals are obviously not easy to work with. We have undertaken, however, some pilot studies on seals. When we injected them with salt solutions that stimulate the salt glands of birds and reptiles, they merely increased their output of urine. Methacholine, a drug which also stimulates the salt gland, gave equally negative results. Whatever the seal's need to eliminate salt, its kidneys are evidently adequate to the task. We must therefore assume that the salt gland has evolved only in the birds and reptiles, animals whose kidneys cannot produce concentrated salt solutions.