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By KENNETH E. STAGER

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DAVID K. CALDWELL, *Editor*

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THE ROLE OF OLFACTION IN FOOD LOCATION BY THE TURKEY VULTURE (*CATHARTES AURA*)[1]

By KENNETH E. STAGER[2]

ABSTRACT: An experimental approach to the problem of the olfactory ability of the turkey vulture, correlated with morphological studies, has provided evidence of a well-developed sense of smell in this species.

Information is presented concerning the ethology of cathartine vultures. The flight, food- locating habits, agonistic and predatory behavior of the five cathartine vultures are compared. The king vulture (*Sarcoramphus*) of tropical America, although its behavior is poorly known, appears, on the basis of present ethological and morphological data, also to utilize olfaction in its location of food. The need for a detailed study of the food-locating habits of *Sarcoramphus* is thus indicated. There is no evidence, either ethological or morphological, to indicate that olfaction plays more than a minor role, if any, in food location by *Coragyps, Gymnogyps,* and *Vultur.* There likewise are no data to indicate that the Old World vultures employ any sense other than vision in the location of food.

INTRODUCTION

The subject of olfactory ability in vultures has been commented upon since the time of Aristotle and Pliny ((Soudek, 1927) and debated pro and con by zoologists in general and by ornithologists in particular since 1826 (Audubon, 1826).

The degree of olfactory acuity possessed by any particular group of animals is a most difficult subject to investigate. Compared with our knowledge of the visual and auditory senses of animals, we know practically nothing with respect to the sense of olfaction. The subjective nature of olfaction makes it one of the most difficult of the senses to measure in terms of degree or nervous response.

Compared with the demonstrated macrosmatism of certain insects and mammals, it can be safely stated that the Class Aves on the whole is microsmatic, but to accept the belief that birds are anosmatic is comparable to arguing that the Class Mammalia is incapable of flight, thus ignoring the highly specialized mammalian Order Chiroptera.

The question of olfactory ability among vultures, or the lack thereof, has been complicated by the tendency of early investigators to apply a too generalized interpretation to their findings, both for and against, and their failure to realize that they were dealing with two entirely different kinds of vultures. In the past there has been a tendency for investigators of the be-

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[1] This study was submitted to the Graduate School, University of Southern California in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

[2] Senior Curator of Ornithology, Los Angeles County Museum.

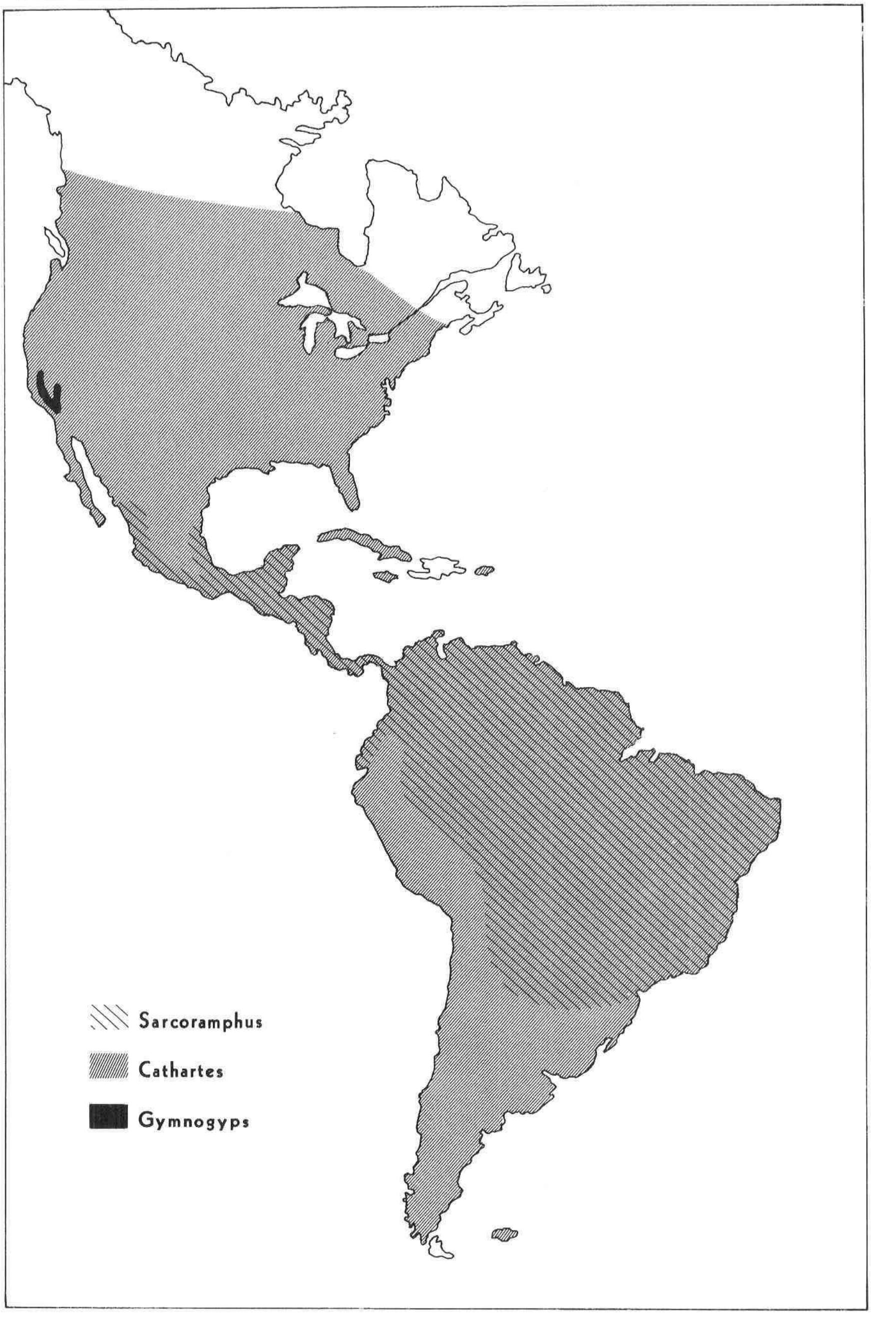

Figure 1. Geographical distribution of *Cathartes, Gymnogyps,* and *Sarcoramphus.*

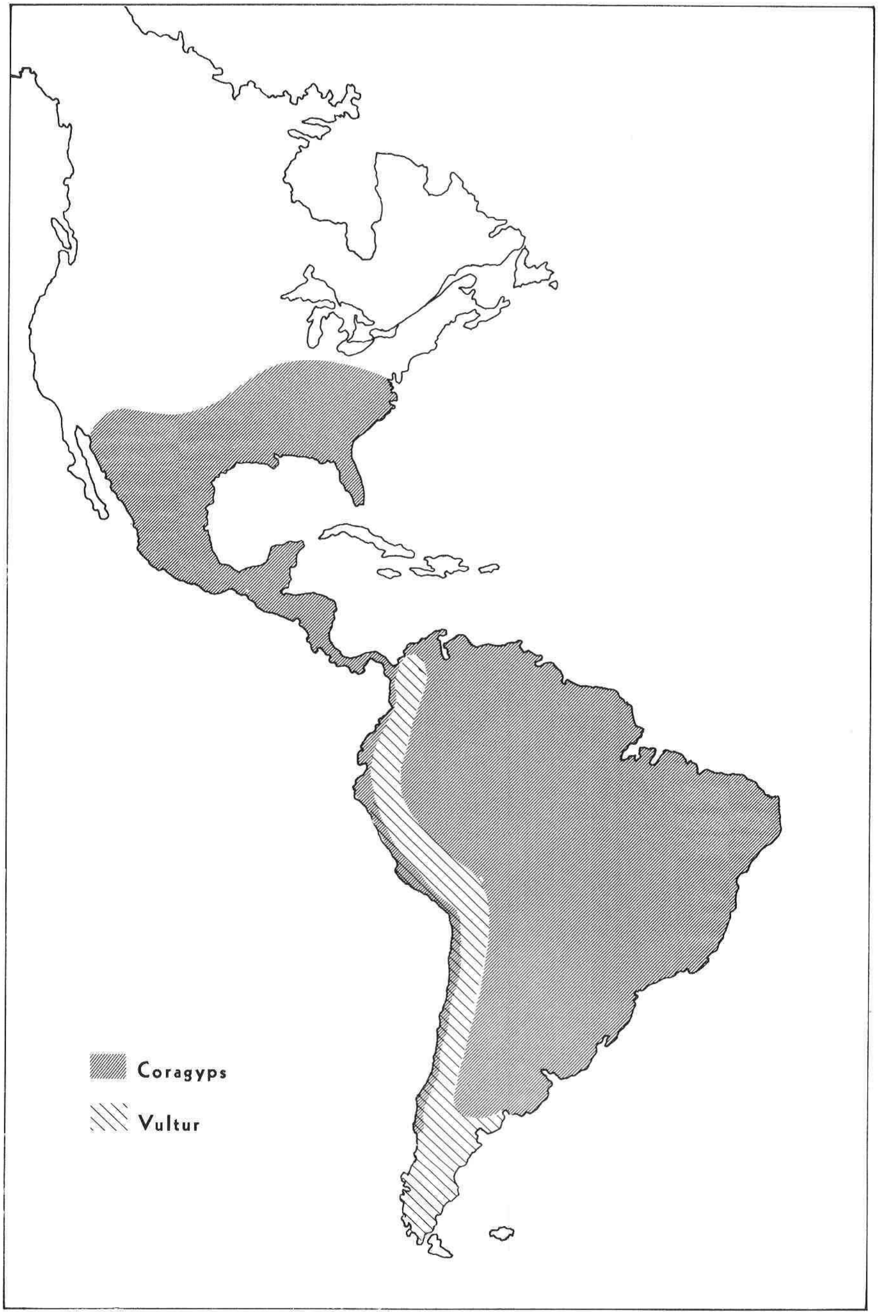

Figure 2. Geographical distribution of *Coragyps* and *Vultur*.

havior of aegypiine vultures of the Old World to include the cathartine vultures of the New World in their conclusions. The inverse mistake has been made by students of cathartine vulture behavior in the interpretation of their data. The resultant confusion has greatly delayed the solution of the entire problem.

The purpose of this study is to place the problem of olfaction in vultures in its correct perspective and to consider morphological and behavioral evidence to determine if there are, within the family Cathartidae, certain genera that possess and utilize a well-developed sense of smell.

A. THE CATHARTINE VULTURES

The Suborder Cathartae includes but one living family, the Cathartidae, although it contains two monotypic extinct families, the Teratornithidae and the Neocathartidae. The living family Cathartidae, commonly referred to as the New World vultures and sometimes known as the pseudo-vultures, resembles superficially the true vultures, or Old World vultures of the Suborder Falcones. The differences between the two groups, however, are profound. The internal structure of the two involves differences not only in the skeletal framework, but also in the musculature and other portions of the soft anatomy as well. As pointed out by Friedmann (1950:6), the general resemblance is adaptive, as both groups perform the same service as scavengers in the niche they inhabit.

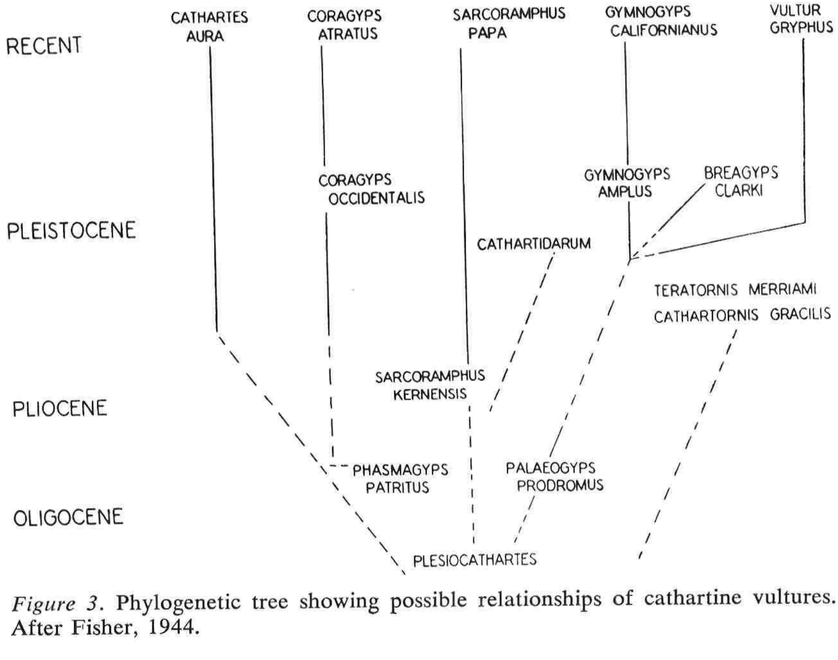

Figure 3. Phylogenetic tree showing possible relationships of cathartine vultures. After Fisher, 1944.

The family Cathartidae is restricted to North and South America and certain adjacent islands. The family comprises five living genera: the turkey vulture (*Cathartes*); the black vulture (*Coragyps*); the king or royal vulture (*Sarcoramphus*); the Andean condor (*Vultur*); and the nearly extinct California condor (*Gymnogyps*). All references in this work to the genus *Cathartes* refer to the species *Cathartes aura* and do not include the small, and little-known, yellow-headed vulture *Cathartes burrovianus.*

B. PALEONTOLOGICAL RECORD

The earliest known representative of the cathartine line in North America is *Neocathartes,* a long-legged vulture of the Upper Eocene (Wetmore, 1956). At the same time a similar vulture (*Plesiocathartes*) appeared in France. *Plesiocathartes* was indistinguishable from the cathartids and continued into the Lower Oligocene. During this time the family Cathartidae was becoming established in North America, being represented by two genera, *Paleogyps* and *Phasmagyps.* There is an absence of records of Miocene vultures throughout the world, but according to Howard (1950:12), the cathartine vultures are restricted to the New World from the Pliocene on. All cathartine genera of the Pliocene and Pleistocene are represented by living forms today except for the large condor-like vulture, *Breagyps,* which is known only from the late Pleistocene of California and Nevada. Ancestral relationships of the Cathartidae are best shown by Fisher (1944:294), who presented them in the form of a phylogenetic tree (Fig. 3). The rise and decline of cathartine species in North America is well shown by Miller (1942:212), in his diagram indicating abundance and the geologic history of the family (Fig. 4).

C. HISTORICAL REVIEW

The literature pertaining to olfaction in birds is relatively sparse before 1834. References to the sense of smell in vultures consist chiefly of scattered notes relative to the remarkable powers of scent possessed by all vultures.

In 1826, however, John James Audubon, appearing before the Natural History Society of Edinburgh, read his classic paper (Audubon, 1826) entitled: "Account of the Habits of the Turkey Buzzard (*Vultur aura*), particularly with the view of exploding the opinion generally entertained of its extraordinary power of smelling." Audubon was of the firm opinion that vultures lacked a sense of smell and that they relied solely upon remarkable vision as a means of locating their food. To substantiate his argument, Audubon conducted a number of poorly contrived experiments which in reality tended to test the visual acuity of vultures rather than their possible olfactory ability.

The experiments of Audubon (1826) were supposedly conducted with the turkey vulture, but a critical examination of his remarks reveals that he was concerned chiefly with the actions of the black vulture (*Coragyps*), rather than the turkey vulture. The aggressive behavior of the birds used in

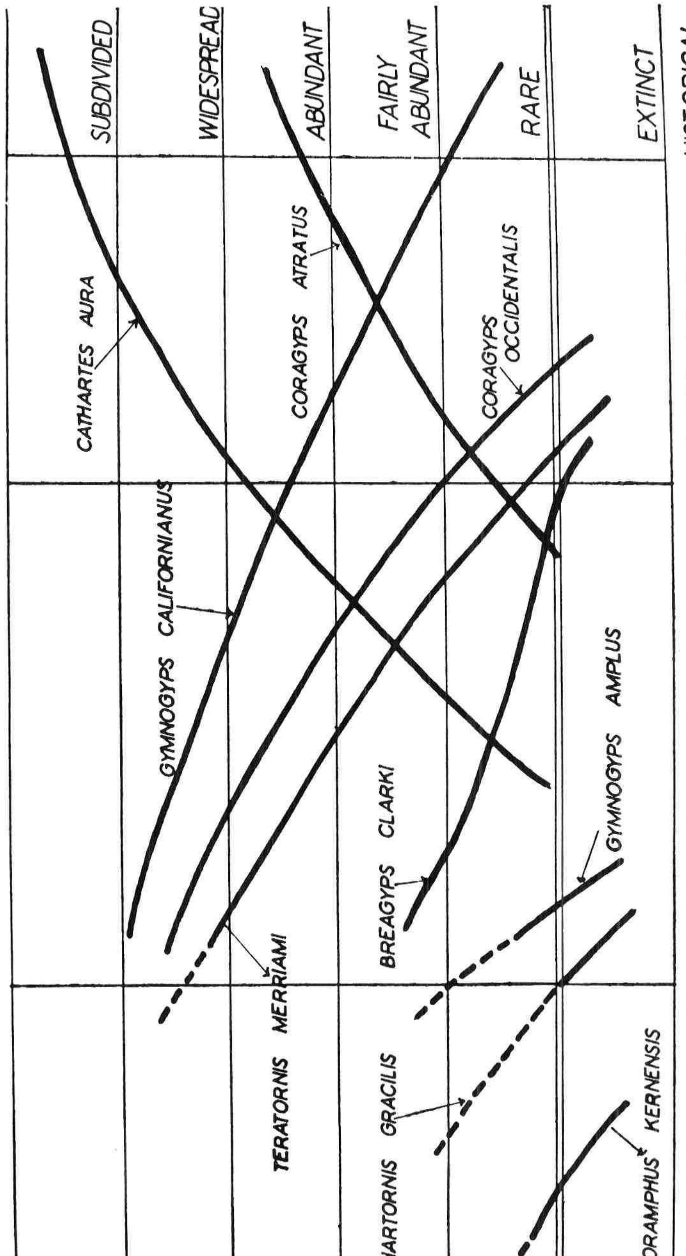

Figure 4. Diagram showing abundance and geologic history of cathartine vultures. After Miller, 1942.

his experiments are typical of *Coragyps,* and in sharp contrast to the shyness so characteristic of *Cathartes.* Although Audubon believed that his experiments had conclusively settled the question of olfaction in vultures, he was soon to learn that his paper had initiated an argument among ornithologists—an argument that is still alive today. As criticism of the Audubon experiments mounted, a friend of Audubon, John Bachman, came to his rescue. Bachman (1834) repeated the experiments of Audubon in the presence of a learned group of citizens. These observers then signed a document to the effect that they had witnessed the tests and were thoroughly convinced that the vulture lacked a sense of smell and was attracted to its prey entirely by vision. The Bachman experiments also failed to quiet the critics of Audubon, the most vigorous of whom was a Mr. Charles Waterton (1830; 1832; 1833; 1834; and 1870). In his efforts to discredit Audubon, however, Waterton made several misleading statements and presented arguments as confusing as those of his opponents.

Since Audubon's time there has accumulated a rather extensive amount of literature on the olfactory ability of birds in general and vultures in particular. Most of the early literature is anecdotal, being sight observations of vultures in the wild, supported at best with simple uncontrolled tests.

Gurney (1922) was the first student of avian olfaction to indicate that the cathartine vultures of the New World were unrelated to the aegypiine vultures of the Old World and that the two groups should be studied independently. There are numerous observations on the lack of olfactory ability among the vultures of the Old World (Adams, 1858; Chapman, 1921; Dresser, 1875; Hadfield, 1875; Hill, 1905; Hunter, 1883; Hutton, 1837; Kirk, 1864; Lilford, 1893; Macgillivray, 1837; Meinertzhagen, 1959; Soudek, 1927; and Stewart, 1959). It is interesting to note, however, that all of these references pertain to casual or accidental observations on the behavior of Old World vultures and do not involve any controlled experimentation.

A review of the literature concerned with observations on the behavior of cathartine vultures reveals that, in spite of the negative findings of Audubon (1826) and Bachman (1834), the observations are singularly balanced in the affirmative for a sense of smell, especially as they apply to observations on the turkey vulture (*Cathartes aura*). Observations indicative of a sense of smell and worthy of mention are those of Bent (1937); Bishop (1921); Dickey and van Rossem (1938); Earl (1929); Forbush (1927); Gill (1904); Gosse (1847); Grinnell (1913); Hall (1925); Hopkins (1887); Howell (1932); Lewis (1928); Rhoads (1883); Sayles (1887); Schomburgk (1839); Sells (1837); Taylor (1923); and Williams (1922). Observers who were of the opinion that cathartine vultures lacked a sense of smell are as follows: Audubon (1826); Bachman (1834); Barrows (1887); Bedichek (1960); Housse (1949); Hoxie (1887); Lehmann (1940); and Leighton (1928).

Charles Darwin (1841), while in Valparaiso, Chile, during the cruise of H.M.S. *Beagle,* made a crude olfactory experiment with captive Andean condors (*Vultur gryphus*) that left him believing that this species lacked a sense of smell. At the same time, however, he stated his belief that the turkey vulture has a sense of smell.

Various observers have presented ideas for the purpose of explaining the ability of turkey vultures to find hidden baits by means other than a sense of smell. One hypothesis widely quoted in the literature and attributed to Darlington (1930) suggests that the turkey vulture locates hidden food by hearing the buzzing of flies and other necrophagous insects, and that they may then observe the concentration of these insects about a hidden item of food and thereby detect its location. The hypothesis should be attributed to Taber (1928) rather than to Darlington, however, as it was he who first proposed it. Taber also expressed the opinion that the turkey vulture may observe the movements of carrion-eating mice and ground squirrels to and from a hidden carcass and, "having perceived these signs, the vulture through long experience *knows* [my italics] that this means food." Here, too, is an interesting hypothesis, but with no evidence to support it. Lehmann (1940) was of the opinion that turkey vultures sit about watching the movements of domestic dogs in the forested areas. The dogs, with their keen sense of smell, locate the hidden carrion and thus disclose its location to the keen-eyed vultures.

Not willing to accept the senses of smell, vision or hearing as the means whereby the turkey vulture locates its hidden food, Beck (1920) proposed the presence of a fourth sense that he termed the occult sense, or food-finding sense. Beck never quite describes this food-finding power but sums up his discussion of this illusive fourth sense by stating:

> Unfortunately, research on these occult senses is difficult —often impossible. Theories have to be based upon analogies and chance observations. Under these conditions chance observation must assume a somewhat greater significance than ordinarily is placed upon it.

Another hypothesis is that proposed by McKechnie (1923) in which he suggested that the true purpose of well-developed olfactory tracts in soaring birds, such as the turkey vulture and the albatross, may be for the purpose of detecting the direction and quality of air currents rather than for the detection of food. McKechnie offered no evidence to support this idea but suggested the need for experiments to determine the validity of the hypothesis.

An olfactory experiment performed by Hill (1905) is of interest because of the rather startling results obtained and the wholly unwarranted conclusions given. Placing a domestic turkey in an enclosure, the investigator first subjected it to the fumes of carbide and water, followed by carbon bisulphide and then a sponge soaked in chloroform. His final test was to place a saucer filled with hot dilute sulphuric acid in the enclosure with the turkey. To the saucer of acid he then added one ounce of potassium cyanide. The reaction resulting in prussic acid became so violent that the experimenter considered the neighborhood unsafe. The turkey became violently ill and died. From this test the author concluded that birds cannot smell.

During the 136 years that have elapsed since Audubon stirred up the controversy over the presence or absence of a sense of smell in New World vultures, it is most surprising to find that very little actual study has been made of the behavior of the turkey vulture and the role played by olfaction in its economy. Beebe (1909) conducted experiments with captive turkey and black vultures in the New York Zoological Gardens. Negative responses were obtained from the black vultures, but the turkey vultures readily located the hidden but odoriferous bait. The experiment was not repeated, nor was it properly controlled.

Strong (1911) attempted some simple experiments to test the olfactory acuity of the turkey vulture, using meat wrapped in paper. His results were negative, and he believed that the conditions of his experiments did not warrant the conclusion that the meat was not smelled by the turkey vulture.

In Panama, Chapman (1929) conducted a number of experiments with non-captive turkey vultures and obtained very positive responses showing olfactory prowess. He failed to carry his tests to a desired conclusion, however; and he never had an opportunity to resume the tests.

Coles (1938), in an unpublished doctoral thesis, gave a good review of earlier experimentation with the turkey vulture, and then described the experimentation he undertook to further test the olfactory acuity of this species. Using captive turkey vultures, Coles contrived a number of different tests that he hoped might settle the question of olfaction. His first test consisted of placing leather hoods over the heads of the captive birds to prevent vision but still allow freedom of the nostrils and mouth. After being conditioned without food for thirty-six hours, the birds were introduced into a pen containing a pan of decomposed meat. The birds never succeeded in locating the meat or subsequent samples of strong chemicals. Instead of acting normally, the hooded birds crouched with heads down or walked in ever-decreasing smaller circles. From this behavior the writer decided that the test techniques were too foreign to the normal environmental conditions of the vulture to be of value and the experiment was terminated.

The second experiment consisted of placing two crocks of fresh water in the cage with the vultures after the birds had been fed heavily salted food and denied drinking water for forty-eight hours. One crock was treated with concentrated ammonia that, according to the author, filled the entire room with strong fumes. With this condition prevailing, the vultures were still expected to be able to distinguish, through olfaction, the crock that was free of ammonia. Negative results were reported for this experiment, as the birds showed no discrimination and drank readily from the ammonia filled crock.

The third experiment performed by Coles was of a multiple-choice type. The captive vultures were conditioned to eat out of three metal containers, each of which had a removable metal collar that hid the contents from view. The vultures soon learned to open the containers and obtain the food contained therein. The test was accomplished by placing food in one of the three containers, placing the containers in the experimental pen and then introducing the hungry vultures. Coles found that the vultures would investigate each container, but opened only the one containing the hidden food. Trials of this type were repeated a sufficient number of times to provide valid data regarding the possession of a sense of smell by turkey vultures.

The fourth experiment performed by Coles was designed to test olfactory sense perception within a given area. For this test, a 6-foot square, wooden frame was placed on the floor of the vulture cage. The frame was covered with paper, with poultry wire above the paper so that the vultures could walk upon it without breaking through the paper. A pan of meat could then be placed under the frame at any point of the 36-square-foot grid. It was hoped by the investigator that the vultures would be able to detect the exact point on the grid where the meat pan had been hidden. Only negative results were obtained as the vultures were unable to locate the pan.

The latter experiment described above was the last of the series performed by Coles, and from the results of all of his tests he concluded that the turkey vulture possesses a sense of smell, but that it is of limited use and secondary to the well-developed sense of vision possessed by the species.

Owre and Northington (1961) have recently published on a series of controlled feeding experiments performed by them on captive turkey vultures in Florida. Two captive birds were used in the feeding trials. Each of the vultures was presented with leaf-filled pans, one of which contained meat concealed from view. The pans were presented to the birds in the open, concealed from direct view behind screens, or concealed in boxes with single openings. In each of the experiments, pans containing food were selected first a significant number of times. Evidence of olfactory acuity is thus believed afforded. Owre and Northington concluded that the interpretation of their results suggests that smell may be of a degree of importance varying with the situation confronting the birds. They also found that the vultures showed a preference for freshly-killed chicks over other types of fresh and decaying food.

The literature bearing upon the sense of smell and olfactory organs of birds in general is too exhaustive to treat in this survey, and is best summarized in a few key papers: Raspail (1899); Strong (1911); Gurney (1922); Soudek (1927); Ishihara (1932); Technau (1936); Walter (1943); and Pumphrey (1948).

D. EARLY PERSONAL OBSERVATIONS

My observations on food location by turkey vultures began in the summer of 1935. While conducting field work in the lower Colorado River valley of eastern Riverside County, California, an opportunity presented itself which enabled me to conduct a simple experiment involving the turkey vultures of that desert area. On this occasion the skinned carcass of a badger (*Taxidea taxus*) was carefully concealed in the heart of a thick-foliaged creosote bush (*Larrea*) on the flat desert floor, one mile west of the river valley proper. The carcass was securely wrapped in newspapers and placed in the bush just after dawn. A close watch was kept on the bait site throughout the day. In the afternoon of the second day a lone turkey vulture was observed circling in the area where the bait was concealed. A gentle wind was blowing from the west and the vulture sailed around the bait site in decreasing circles until a landing was made approximately thirty feet up-wind of the bait-containing bush. The vulture walked back and forth in the up-wind area for several moments, launched itself into the air again and resumed circling the bait site. After completing a series of low-level circles about the bush, the vulture once more landed on the ground, some thirty feet from the bait, but on this occasion the landing was made directly down-wind of the bush. After a short inspection of the area, the vulture walked directly up-wind toward the bait and, with its beak, pulled the paper-wrapped carcass from the center of the creosote bush. The paper was torn from the carcass with little effort and feeding on the badger commenced. This experiment was only partially controlled, in that the package was partially visible from a point above and to the side of the bush. Visual stimulus cannot, therefore, be ruled out completely, but the actions of the vulture appeared to be based on an olfactory cue.

The second opportunity to observe the food-locator mechanism of turkey vultures was afforded me during the winter of 1946-47. During this period I was engaged in field activities in the tropical hill country of southern Sinaloa, Mexico. Base of operations was the small village of Copala, situated approximately sixty miles east of the seaport city of Mazatlan, on the Mazatlan-Durango highway. The town of Copala harbored a population of domestic pigs which more or less roamed at large. During my stay in Copala, I witnessed the outbreak of a devastating epizootic among the pig population that killed approximately 90 percent of all the pigs in the village. The putrifying carcasses of pigs were encountered everywhere in the vicinity of Copala and the stench was most unpleasant.

Black vultures (*Coragyps atratus*) and turkey vultures (*Cathartes aura*) were always to be found in the area in normal numbers, but with the outbreak of the epizootic among the pigs, the concentration of vultures increased to several hundred. The ratio of black vultures to turkey vultures was approximately ten to one.

During this period of vulture concentration in the Copala area I had occasion to set a number of steel traps for the collection of small carnivores. The first set was made in a dark cavity under a debris-covered log in the bottom of a dry stream course. The bait, consisting of several skinned bird bodies, was placed far back in the dark cavity, completely out of sight when viewed from any angle. On the morning of the second day an adult turkey vulture was found caught in the steel trap which had been set in the entrance to the bait cavity. Even though caught in the trap, the bird had devoured the bait. To explain this behavior on the grounds that it was vision that had led the vulture to the bait is far too simple an approach. While it is true that no conclusions could be made on the basis of this one incident, the behavior of other turkey vultures on subsequent days gave ample evidence that a sense other than vision was being utilized in food location.

A supply of fresh fish was obtained from the seacoast and ground into a thick, oily paste for use as bait for further carnivore trapping. The fish paste was allowed to age for a period of days and during that time blow flies managed to get to it to deposit eggs, with a subsequent hatching of larvae. As a result the fish paste became putrified and developed an odor so foul that it was difficult to work near it. The decomposed mass took on the consistency of cream with a grayish-brown color.

A number of steel traps were baited with this foul-smelling paste. This was accomplished by smearing a small amount on the rock surface at the back of a cairn of rocks, piled so as to compel the animal to step into the steel trap at the entrance before it could reach the bait. The paste was of ground color and invisible when viewed from directly in front of the rock cavity. Although invisible, the fish paste gave off a decidedly putrid odor that could be detected even by the human nose at a distance of several yards. In an attempt to prevent the traps from being sprung by turkey vultures, all sets were made at night.

During the following days, fourteen turkey vultures were captured in steel traps as they attempted to reach the hidden bait. Although the black vulture (*Coragyps*) outnumbered the turkey vultures approximately ten to one in the trapping area, not one specimen of *Coragyps* was caught by the steel trap sets. Black vultures would be found congregated around the trapped turkey vulture, but were apparently attracted to the site by the flapping of the turkey vulture in its attempt to free itself from the steel trap.

On one occasion a trap set was made in a heavily shaded ravine filled with tropical plant growth. A complete canopy of tree branches shielded the trap area, making it difficult to see even close by at the ground level. The putrid fish paste was smeared at the back of a dark rock cavity as in previous sets. On the following day an adult turkey vulture was found securely caught by the foot. The vegetation was so dense that the vulture could only reach the bait by walking to it from several yards down the ravine. Nothing was visible from above; the set was made at night, and yet the bird had had no difficulty finding the bait even though it could not fly to the site. From these observations it became evident that the subject of olfaction in cathartine vultures would be worthy of further investigation, at least with regard to the turkey vulture *Cathartes*.

My early observations on the food-locating behavior of the turkey vulture, supported by a detailed survey of the literature pertaining to food location by vultures, indicated the need for a careful re-examination of this interesting problem. The paths of investigation I followed and the techniques I used are set forth in the following pages.

E. METHODS

1. *Study Area*

The study area for this research includes both the Old World and the New. The major portion of the controlled field experimentation has been conducted in Ventura County, California, but additional experimentation and extensive comparative ethology of vultures has been conducted in southeastern California; the States of Sonora and Sinaloa of western Mexico; central Goias, Brazil; the Bolivian Chaco of eastern Bolivia; central India in the State of Madhya Pradesh; and the Myitkyina area of northern Burma.

The major study area in Ventura County, California, was the 1200-acre Cerro Viejo ranch located five miles north of Santa Susana. Cerro Viejo ranch consisted of varied terrain–small open valleys flanked by gently rolling grass covered hills in some portions, which were in contrast to the steep canyons and broken ridges of the higher elevations. The south slopes of the higher hills were covered with *Artemesia*. Dense chaparral (primarily *Sumac* and *Ceonothus*) covered the north exposures. The canyon bottoms were filled with scattered stands of live oak (*Quercus*) and cottonwood (*Populus*). One high pasture area, known as Eagle Nest, was covered with grass and scattered groves of black walnut (*Juglans*).

From April until October the entire area was patrolled by a small population of turkey vultures, estimated at fourteen. The varied terrain of Cerro Viejo ranch proved ideal for experimentation with the forced air unit, the concealed bait chambers and the decoy replacement techniques which are described in detail in this section.

The second major study area in Ventura County was located on the property of the Rancho Sespe in the bottom lands of the Santa Clara river, three miles east of the town of Santa Paula, and approximately nineteen miles west of the Cerro Viejo study area. In this latter area the river bottom land consisted of pasture with stands of cottonwood (*Populus*) and willow (*Salix*) with scattered windbreak rows of *Eucalyptus*. Ethyl mercaptan tests were conducted in this area. The river bottom land of this study area was the feeding area of a colony of turkey vultures numbering approximately thirty, with a known nocturnal roost two miles to the northwest of the test site.

2. *Forced Air Unit* (Fig. 5)

A four-bladed exhaust fan with a 20-inch diameter was mounted in a horizontal position atop an enclosed frame 30 inches by 30 inches by 45 inches. The fan was driven by a quarter horse-power motor attached directly below. Fitted to the circular lip of the exhaust fan housing was a 7-foot circular stack 18 inches in diameter. A baffle placed in the top portion of the circular stack aided in the upward draft of air above the top of the tower. On one side of the base frame, and near the bottom, there was a hinged door 18 inches high and 24 inches wide. The door consisted of a frame covered with fine mesh window screen and equipped with a spring catch. The door also served as the main air

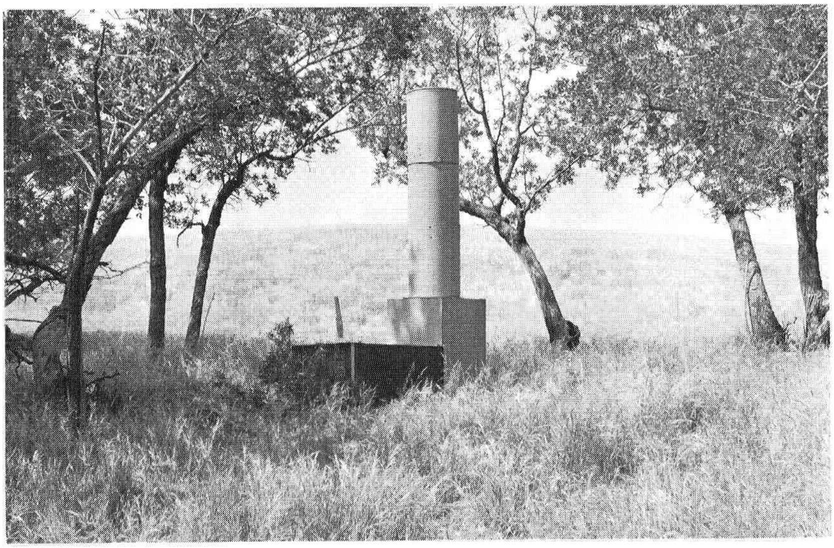

Figure 5. Forced air unit, showing auxiliary bait chamber attached.

intake vent of the unit. Canisters of odorous baits were placed in the bottom of the chamber and the odors sucked upwards through the powerful fan. Electric power was supplied to the unit from a portable gasoline-driven 1500-watt generator. This unit was generally placed at least 100 yards from the fan unit and connected to it by a heavy-duty rubber insulated cord. The fan unit was completely portable, breaking down into three sub-units. In order to accommodate large baits the size of small deer (*Odocoileus*), bobcats (*Lynx*), dogs and cats, a supplementary chamber 30 inches wide by 48 inches long by 22 inches tall was adapted for attachment to the air-intake door side of the base frame. An air-intake screen the same dimensions as those of the hinged door described above was fitted to the end of the bait chamber at the end opposite the base frame door. The entire chamber was collapsible by means of slotted joints. The top of the chamber overhung the walls 3 inches on all sides.

3. *Portable Hidden Bait Chambers*

A number of chambers of several sizes were used. The largest and most used unit consisted of a breakdown chamber 5 feet long by 3 feet wide by 10 inches high. The sides and ends were made of perforated pressed fiber board ⅜ inch thick with perforations one inch apart. The chamber was bottomless with a folding top of unperforated fiber board 6 feet wide and 7 feet long, thus allowing a 6-inch overhang all around. The sides and ends were connected by tongue and groove joints with retaining pins to permit breakdown for easy transport.

A large number of smaller chambers consisting of heavy cardboard packing boxes with perforations on their sides were also used. These small units averaged approximately 2 cubic feet and were used for hidden baits placed in tree foliage, hollow cavities of tree trunks and large, dense-foliaged bushes.

4. *Mounted Decoy Deer—Fresh Deer Carcass Replacement*

A mounted specimen of a yearling female mule deer (*Odocoileus hemonius*) was employed as a visual decoy in conjunction with substituted fresh carcasses of road-killed yearling female deer supplied by the California Department of Fish and Game.

5. *Ethyl Mercaptan—Compressed Air Unit*

A dispensing device for ethyl mercaptan (Fig. 6) consisted of using a high pressure compressed air cylinder with a capacity of 90 cubic feet, or 2,000 pounds pressure. The cylinder contained dry (SCUBA type) air and was placed on its side in a wooden cradle for support. A standard oxygen pressure regulator was attached to the cylinder outlet so that the flow of air could be held to a minimum amount. To cut the flow of air to a still smaller quantity, a low pressure gas petcock was attached to the outlet of the regulator. A two-foot length of quarter-inch polyethylene tubing led from the petcock to a two-

Figure 6. Ethyl mercaptan dispensing device, showing compressed air tank attached.

hole rubber stopper in the mouth of a one-gallon canister of ethyl mercaptan. An outlet tube from the second hole of the stopper allowed the highly volatile mercaptan to be dispensed on predetermined wind currents. The air pressure applied to the mercaptan canister helped to force the mercaptan fumes onto the prevailing wind. The unit was compact, completely portable, and could be set up and concealed in vegetation with little effort. It was readily put into operation by attaching the two-way rubber stopper unit to the mercaptan canister and regulating the air flow through the system.

Ethyl mercaptan (CH_3CH_2SH), a thioalcohol, is one of a large group of highly volatile organosulfur compounds. It is used as a fuel gas odorant, especially for liquefied petroleum gases. Because of the highly volatile quality and dangerously low flash point (below 0°F.) of ethyl mercaptan, it was thought unwise to dispense it by means of the forced air unit. The gas would have had to pass the electric motor and this would probably have resulted in an explosion within the unit.

6. *Hidden Baits–Central India*

Tests were conducted with aegypiine vultures in the State of Madhya Pradesh, central India. Baits consisting of large quantities of fresh animal meat were placed on an elevated wooden platform and concealed with thick layers of thatch straw.

7. *Anatomical Studies*

In order to obtain comparative reproductions of avian brains for illustrating the size of their respective olfactory bulbs, a technique was developed for taking latex rubber casts of cranial cavities. The process consisted of flowing successive coats of liquid latex into the clean cranial cavity. An average of six coats of latex was laid down within the cavity and care was taken to insure that the latex filled all areas in the anterior portion of the brain chamber. Prior to introduction of the latex, care was taken to block off all small foramina with lacquer cement. The cavity was then coated with a wash of medical green soap to prevent bonding of the latex with the walls of the cavity. After the final coat of rubber had dried, the cast was allowed to cure for several days before removal. The thin cast was then collapsed from the walls and withdrawn through the foramen magnum. Powdered talc was dusted into the hollow cast and worked between the exterior surface of the cast and the cranial walls during the removal operation to prevent binding. Once removed, the cast immediately resumed its original shape, thus showing the conformation of the brain and the presence and size of the olfactory bulbs. The thin latex casts were then carefully filled with plaster of Paris, so as to preserve their shape and facilitate handling.

Latex casts were made of all the recent genera of cathartine vultures, namely *Cathartes, Coragyps, Sarcoramphus, Gymnogyps* and *Vultur,* as well as fossil forms from the Pleistocene deposits of Rancho La Brea. Pleistocene species included are: *Cathartes aura, Coragyps occidentalis, Gymnogyps amplus, Breagyps clarki* and the giant vulture *Teratornis merriami.* Similar casts were obtained of Old World vultures of the following genera: *Sarcogyps, Neophron, Pseudogyps, Torgos, Aegypius, Trigonoceps, Gyps, Necrosyrtes, Gypohierax* and *Gypaëtus.*

Dissections of the olfactory tracts of *Cathartes aura, Coragyps atratus, Sarcoramphus papa,* and *Gymnogyps californianus* (partial) were made from material preserved in 70 per cent ethyl alcohol.

Complete olfactory tracts of a number of species of cathartine and aegypiine vultures were obtained fresh and fixed for sectioning in Heidenhains "Susa" solution. Fixed material was stored in 70 per cent ethyl alcohol. After decalcifying, sectioning and mounting, the serial sections of the olfactory tracts were alternately stained with silver nitrate and Masson's Trichrome (Foote-Goldner modification). Species whose olfactory tracts were fixed, sectioned and stained were: *Cathartes aura, Coragyps atratus, Sarcoramphus papa, Gymnogyps californianus, Sarcogyps calvus* and *Columba livia.*

FIELD EXPERIMENTATION TO DETERMINE THE ROLE OF OLFACTION IN FOOD LOCATION BY THE TURKEY VULTURE (*Cathartes aura*)

There has been relatively little serious experimentation on the olfactory acuity of birds in general. Aside from the work already commented upon involving both cathartine and eagypiine vultures, it is of interest to note that many of the bird species selected for use in olfactory experimentation by physiologists have been those species known to show little or no development of olfactory epithelium. This has been particularly true in the use of the domestic pigeon (*Columba livia*). Numerous physiologists (Banjandarow and Larin, 1935; Walter, 1943; Calvin, 1957; and Michelsen, 1959) have conducted laboratory experiments directed towards eliciting a conditioned reflex on an olfactory stimulus in the domestic pigeon, yet a histological examination of the upper respiratory tract of this species shows it to be quite devoid of any well developed olfactory epithelia. Walter (1943:1) states:

> . . . it is of no importance to physiologists to deal with anatomical data. If the olfactory organ were not developed at all, we could hardly expect a sense of smell to exist. But on the other hand the occurrence of the anatomical substratum does not in the least ensure the presence of sensory perception.

The findings in the present study indicate strongly that the sensory physiologist in particular will do well to consider neuroanatomical and neurohistological evidence in choosing his experimental species.

The reason that pigeons have figured so predominantly in physiological experiments is probably attributable to the fact that the species is readily obtainable. Pigeons are available for the taking, while more suitable species such as the turkey vulture (*Cathartes aura*), the kiwi (*Apertyx*) and procellariiform birds such as the albatross, shearwater and petrel require more effort to obtain and maintain.

The purpose of my research was to obtain evidence to support the premise that the turkey vulture (*Cathartes aura*) has a well-developed sense of smell and employs this sense to a high degree as an integral part of its food-locator mechanism. The possession of such a mechanism would help account for the species being the most successful of all cathartine vultures in the New World today. To obtain this evidence I followed three paths: (1) experimentation with non-captive turkey vultures; (2) comparative morphological studies of cathartine vulture olfactory tracts; and (3) comparative behavior studies of cathartine vultures.

Field experimentation by earlier workers with non-captive turkey vultures has been justly criticized for the poor manner in which the tests were contrived. Because of lack of proper controls, the possibility of a visual stimulus was not ruled out in tests that were designed to test olfaction alone.

A. FORCED AIR UNIT

In order to avoid the mistakes made by these earlier workers, it was considered necessary to develop a device capable of dispensing the odors of fresh and decomposing animal tissue, yet one completely eliminating all visual clues. The forced air unit (see "Methods" for description of unit) was designed to fill this need. The experiments set forth here were considered controlled experiments in the sense that all visual stimuli concerned with the bait material were eliminated. The machine itself was visible to the turkey vultures and it was not operated without bait for any definite period of time.

Considerable care and study were given to the problem of proper terrain selection, in order that the device could be employed under optimum conditions. The basic idea underlying these experiments was to place animal tissue odors upon air currents of known direction and dependability. If these requirements could be met and a subsequent pattern of attraction of *Cathartes* to the dispensing site could be established, it would be safe to conclude that the stimulus that brought the vultures to the site was olfactory rather than visual.

Precautions employed to rule out all visual stimuli were as follows:

1. The forced air unit was set up at test sites under cover of total darkness.

2. All baits were placed in the blower at night to rule out any possibility of molestation by nocturnal carnivores.

3. The power generator was fueled and tested at time of bait placement in order to limit to a minimum servicing activity after daylight.

4. The unit was placed in operation by 8 A.M. each day, although the first vultures were often not observed on the wing until approximately 10 A.M. Preflight operation of the unit insured the dispersal of all insects, due to the very strong exhaust force of the fan unit.

5. At the end of each day's run, all baits were removed from the unit to prevent disturbance by carnivores.

6. The observation point was located at least 200 yards from the generator unit and 275 yards from the blower unit proper. Check of proper functioning of both units was visual with the aid of a tripod-mounted 25-power spotting scope. A small cloth streamer opposite the exhaust of the gasoline engine generator indicated operation of this unit, while a small piece of paper placed on the intake screen of the forced air unit indicated suction. If the fan unit ceased operating, the paper would immediately fall off.

The Cerro Viejo ranch area (see "Study Area,") was selected for the forced air tests because of ideal terrain to be found there. A maze of deep canyons and sharp ridges on the north portion of the ranch made it possible to select canyons where wind direction was steady up-canyon as the south ridges warmed and thermal up-draft caused the air masses to move in a definite pattern.

Air dispersal patterns from the forced air unit were checked at a number of canyon sites prior to actual tests by placement of small fumigating smoke bombs in the unit and observing the smoke pattern from the circular tower. Burning, oil-soaked rags and leaves were also employed. Continuous check on wind direction during actual odor dispersal tests was made with the aid of a simple hand-made weather vane located at the site and visible from the observation point.

Turkey vultures were not abundant on the Cerro Viejo ranch, but this condition proved to be an advantage rather than a detriment. The study area was regularly patrolled by an estimated four vultures, although as many as fourteen were observed in the immediate vicinity on one occasion. The few birds that worked up into the canyon country where the test sites were located were solitary birds that consistently cruised the ridge lines at low elevations or swept down through the maze of canyons, often only a few feet above the ground. Vultures flying in this manner were the targets of the experiment, for it was thought that knowing the directional dispersal of the odors from the forced air unit it would be possible to predict the exact direction of approach of a vulture if it were receiving an olfactory stimulus from the unit. Conversely, any vulture passing up-wind of the unit would not be influenced in any manner and would cruise on out of the area.

When all was in readiness, the unit was set up in a deep canyon, fifty yards below the confluence of two smaller canyons. All controls previously described were observed and the unit was baited at 4 A.M. on June 1. The bait consisted of the bodies of nine ground squirrels (*Citellus beecheyi*) collected the previous day.

The unit was put in operation at 8 A.M., with the wind freshening and blowing steadily up-canyon by 9:30 A.M. No vultures were observed in any sector throughout the morning. The unit was shut down for refueling at 12 noon and began operating again at 12:15 P.M. A vulture sighting was made at 1:48 P.M. when a single individual crossed the canyon a quarter of a mile below the unit (up-wind).

At 4:30 P.M. a lone vulture was observed coming down the right-hand canyon within fifty feet of the canyon floor and directly towards the unit. The bird was quartering back and forth on a one hundred foot front. It passed over the unit at an elevation of approximately fifty feet, wheeled sharply and began to circle tightly, directly above the tower. The vulture made seven complete circles above the unit and then began to swing in wider circles, completing a total of three. At this point it once again closed the diameter of its circles, decreased its altitude and swept around the unit for five complete circles at an elevation approximately five feet above the top of the tower. On the sixth circle it swooped low below the level of the top of the tower to a point where it had to resort to wing beats, with the tips of its wings almost touching the ground. It appeared as though it was about to land, but instead continued to circle at tower level for an additional four complete circles. The vulture then increased its elevation and widened the diameter of its circles. After a total of six more passes above the tower it sailed over the ridge line to the southeast and was gone. The bird had approached the unit on one of the two specifically predicted olfactory routes available to it and had evidenced a very positive interest in the test site proper. The behavior of this vulture indicated that it was responding solely to an olfactory response, as all visual stimuli related to baits were absent.

The unit was moved that night to a new location in a large canyon approximately one mile to the southeast of the first site. Installation was made in a small grove of pepper trees (*Schinus*) and the unit was baited at 4 A.M. the following day with the same bait used the previous day, plus the body of a bobcat (*Lynx felis*).

The unit was set in operation at 8 A.M. on June 2, although a dense ground fog masked the entire area until 9 A.M. The first vulture in the area was not sighted until 10:10 A.M. The bird was crossing the ridge lines at right angles and as it crossed the head of the canyon occupied by the forced air unit it swung into a circling flight, executing three rising spirals and then continued off across the higher ridges to the north. At 10:40 A.M. a vulture was noted in the same area at the head of the canyon but at a lower elevation and moving directly down-canyon towards the unit. The bird held a steady course towards the pepper tree grove and did not quarter to the right or left as the vulture had done on the previous day. It passed directly over the unit at an elevation of approximately fifty feet, pulled into a steep climb and turned back on its course in a tight circle of approximately one hundred feet in diameter. This action was followed by a series of eight slow circles directly over the unit. On the ninth turn it set a course to the southwest and glided on out over the large valley below. As on the previous day, the response had been from the exact predicted route of approach. No additional vultures were observed in the area during the remainder of the day. The unit was shut down at 5 P.M., the bait boxed up and removed by truck to the headquarters area of the ranch. On June 3, 1960, the same bait was placed in the unit at the pepper tree site at 4 A.M. and the unit operated throughout the day, with no vulture activity observed in the entire Cerro Viejo area.

Under cover of darkness on June 3, 1960, the forced air unit was disassembled and moved to the high meadow area known as Eagle Nest on the upper slopes of the Santa Susana Mountains. Installation was made in a scattering of black walnut trees (*Juglans*). The large lateral bait chamber (see "Methods") was attached.

At 4:30 A.M. on June 4, 1960, one half of a mule deer (*Odocoileus*) carcass was placed in the large lateral bait chamber along with the bodies of twelve ground squirrels. A densely-leaved branch of black walnut was cut and placed in front of the intake vent of the lateral bait chamber to further safeguard against any visual stimuli. A dense fog cover began dissipating by 7:45 A.M.

No vultures were observed in the area until 2:10 P.M. when a solitary bird was noted 200 yards to the northwest approaching directly towards the unit from down-wind in the predetermined approach zone. The vulture circled the blower eight consecutive times and then drifted back on the down-wind corridor. Facing up-wind it rode the air current slowly for approximately three minutes and then closed slowly on the blower once again at an elevation of approximately 75 feet. Another series of five 50-foot wide circles were completed directly above the unit, after which the bird drifted down the slopes toward the main valley to the south. The vulture had circled directly above the stack for a total of twelve minutes.

During the period of July 18 to 24, 1960, inclusive, the experiments were repeated at all three of the previously-used test sites, with results similar to those described for the first series being obtained at all three sites. A total of nine approaches were made during this period.

B. PORTABLE HIDDEN BAIT CHAMBERS

A number of experiments employing the use of various types of animal baits concealed in perforated cardboard cartons (see "Methods") were carried out at selected sites at Cerro Viejo ranch between August 24 and 30, 1959, as well as at other selected localities. Baits consisting of decomposing fish, shellfish (*Haliotus*), ground squirrels (*Citellus*), kangaroo rats (*Dipodomys*), domestic cat, and snakes (*Pituophis*) were used. The same control procedures for placement of baits were employed in these tests as had been used with the forced air unit.

Prior to daylight on August 24, 1959, a perforated box containing approximately thirty-five decomposing fish was placed on a horizontal limb of a large oak tree, well within the dense canopy of foliage. The tree was situated at the base of the west slope of a large north-south canyon. Immediately behind the tree the hillside was cut by a small but steep ravine which led to the top of the slope. No vulture activity was noted in the immediate area of the baited oak tree until 3:30 P.M. At this time five turkey vultures were observed circling at the head of the small ravine directly to the west of the oak tree site. The birds were repeatedly observed to swoop down the ravine directly toward the oak tree, then pull out in a steep climb directly above the tree and return to their original position above the head of the ravine. This activity was continued for thirty-five minutes, during which time the number of vultures increased to a total of nine birds. A fence line with wooden posts ran along the top of the ridge at right angles to the ravine in question. The three fence posts opposite the head of the ravine were occupied by resting vultures, while the remainder executed the swooping action over the bait-laden tree. None of the nine vultures made any attempt to enter the dark interior of the tree, and after the lapse of thirty-five minutes the birds sailed off towards the large valley to the south. Following the departure of the vultures I made an examination of the immediate area of the baited tree. I could smell the bait while standing under the canopy of the tree, but it was barely discernible a few feet from the edge of the tree. I then climbed to the head of the ravine behind the tree to a point next to the fence posts previously occupied by the vultures. From this point the odor of the decomposing fish was extremely strong, although the bait site was 200 yards below. A steady current of air could be felt blowing up the ravine from the direction of the tree to the fence line on the ridge. A smoke bomb ignited at the bottom of the ravine in close proximity to the bait site sent a column of smoke directly up the ravine past the fence posts at the ridge. From the pattern of the smoke column it was evident why the vultures had concentrated at this point.

The large hidden bait chamber (see "Methods") was utilized at various sites at Cerro Viejo ranch. The first trial was made in a small stand of live oak trees (*Quercus agrifolia*) in a pasture to the south of the ranch headquarters. The chamber was set up several days prior to the introduction of bait. The same control procedures were followed as previously described, with bait placed in the unit prior to daylight. Bait consisted of a domestic cat and five ground squirrels (*Citellus*). The bait was completely invisible inside the chamber, which stood in the deep shade of the oak grove. The pasture was bordered on the south side by a very steep hillside densely covered with chaparral. The hillside with a north exposure was masked in shadow in the late afternoon, and consequently was subjected to an up-draft on its slopes toward the warm exposed ridge. The grove of oak trees was situated close to the foot of this slope.

At 4 P.M. of the day following the introduction of the bait to the chamber a single turkey vulture was observed circling above the group of trees. Its circling pattern carried it to the ridge of the steep hill, directly to the south of the oak trees harboring the bait chamber. As the vulture neared the ridge line, it turned sharply and swooped down towards the oak trees. When directly above the trees it rose in a steep climb and circled back to the ridge line with a behavior much resembling that of the vultures previously commented upon in connection with the box of fish in the oak tree. This circling and diving pattern was executed for approximately ten minutes, at which time the lone vulture changed to a series of close-to-the-ground circles about the grove of oak trees. The circles were approximately ten feet off the ground and the bird had to resort frequently to wing flapping to maintain air speed. From this low angle of flight it was possible for the vulture to see the bait chamber under the oaks. The bird did not land, however, and after four complete turns around the bait chamber, it sailed out over the pasture to the north and was lost to view.

The large bait chamber was next set up in the pepper tree grove mentioned in earlier experiments (see "Forced Air Unit"). All control procedures were observed and the chamber was baited with a hind quarter of fresh mule deer and several freshly killed ground squirrels. No vulture activity about the bait site was observed until approximately 2 P.M. of the first day. At this time a lone vulture came down the canyon towards the pepper tree grove on a down-wind course. It circled the clump of pepper trees for three turns and then landed in an open portion of the canyon bottom, down-wind from the bait chamber concealed in a dense portion of the pepper tree grove. The bird stood motionless for several minutes facing directly up-wind towards the bait chamber, located some 75 yards distant. After five minutes the bird gave a few quick wing beats, lifted itself into the air, and sailed over the pepper trees and on down the canyon, up-wind of the test site.

Various other baits were used in the small-sized bait chambers (see "Methods") with varying success. A perforated box, containing a number of decomposing abalone (*Haliotus*) and the bodies of approximately two dozen kangaroo rats (*Dipodomys*), was securely hidden in a dense growth of thorn-apple (*Datura*), but it attracted no vultures. A single four-foot long gopher snake (*Pituophis*), found dead on the highway and placed in the hollow cavity of a tree, attracted two turkey vultures. The dead snake had in this instance been placed in a burlap sack and dropped into the dark cavity of a large half-dead cottonwood tree (*Populus*). The two vultures were observed to circle the tree repeatedly before landing in the dead branches of the tree top. From here they again took flight and continued circling the tree. The two birds next landed on the ground, down-wind from the tree, and walked to within fifty feet of the hollow trunk. Taking wing once again, they resumed their circling of this tree and landed in the upper branches a second time. After perching in the top of the tree for several moments they, again, took wing and left the area.

C. MOUNTED DECOY DEER—FRESH DEER CARCASS REPLACEMENT

The mounted decoy mule deer (see "Methods") was placed in a pasture overgrown with wild mustard (*Brassica campestris*). Placement was made before dawn and care was taken to make the decoy resemble as closely as possible the carcass of a dead deer. Mule deer (*Odocoileus hemonius*) were abundant at Cerro Viejo ranch and, therefore, a normal source of food for the turkey vulture. The decoy was not a crudely prepared specimen, but had been mounted by modern taxidermy methods and therefore resembled the actual animal in every detail. Care was taken not to disturb the vegetation about the decoy, and although it lay on its side among the mustard as though dead, it was plainly visible to any vulture passing over the pasture. A central observation point 50 yards to the west afforded a full view of the pasture as well as the low hills on both sides and the entire sky above. During the next five days (August 25 to 29, 1959), repeated sightings of vultures were made over the pasture area. The vultures were obviously aware of the decoy as they frequently passed over it at a normal hunting elevation of 100 to 200 feet. Observation of the site by me and by assistants was continuous throughout the daylight hours of the five-day period. We employed ordinary vision, 6-power binoculars and a 25-power spotting telescope. At no time during this period were any vultures observed closer to the decoy than in the normal searching passes over the pasture as previously described. At the end of the five-day period the decoy was removed and the test was terminated.

On July 18, 1960, the following season, the experiment was repeated, but with modifications. On this date the same mounted decoy was placed at the head of a pasture adjacent to the one used as the test site in 1959. Placement of the decoy was again made before daylight and all precautions were taken not to disturb the vegetation about the decoy. During the subsequent three days, turkey vultures were repeatedly seen to pass over the decoy (which was in plain view from the air above). Observation of the site was made from the same location used in 1959. On no occasion, however, did a single vulture descend to the decoy during the three-day period. Both the 1959 and 1960 sites were in the open and sufficiently far from any object or animal that might have deterred the relatively shy turkey vulture from investigating the decoy. During the pre-dawn hours of the fourth day, the mounted decoy was carefully removed and the fresh carcass of a road-killed mule deer, furnished by the California Department of Fish and Game, was substituted at the exact spot previously occupied by the mounted decoy. The carcass had been selected as to size and sex, so as to resemble very closely that of the mounted decoy. Considerable care was taken to insure that the head of the fresh specimen was turned downward in the same manner as that of the decoy. To the human observer the two decoys appeared to be one and the same. Several vultures passed over the pasture during the day, but none descended to the fresh deer. The bait was left in place during the night and was examined before dawn to insure that it was still in the same position and had not been disturbed by carnivores during the night.

At 10:55 A.M. a vulture was observed circling above the decoy site, and by 11:05 A.M. the first vulture had been joined by two others. The circling, however, was not directly above the carcass, but was some 100 yards to the north at a point where the pasture pinched off into a small canyon. At 11:20 A.M. the three circling vultures were joined by a fourth bird. The offset circling continued much in the same manner as before, but was closer to the ground (35 feet). At 11:25 one vulture left the circle and drifted directly towards the carcass. When directly above the decoy the vulture turned sharply upward and back on its course toward the other circling birds 100 yards away. A second bird repeated the flight pattern and soon all four vultures were making the direct pass over the carcass, turning sharply upward and back to the circling area. At 11:36 one of the four vultures made directly for the carcass as before, but instead of turning back on its course it circled close above the carcass and on the second turn landed beside the deer. Within two minutes all four vultures were on the ground and pulling at the decomposing deer carcass. An immediate check of wind direction at the decoy site verified the fact that the offset circling area in the mouth of the small ravine at the head of the pasture was in the down-wind zone of the decoy. A similar experiment was repeated during the 1960 season at a different site, with the same results. The turkey vultures did not land and examine the mounted decoy, but readily came to the fresh carcass after flying a verification pattern in the down-wind zone (Fig. 7).

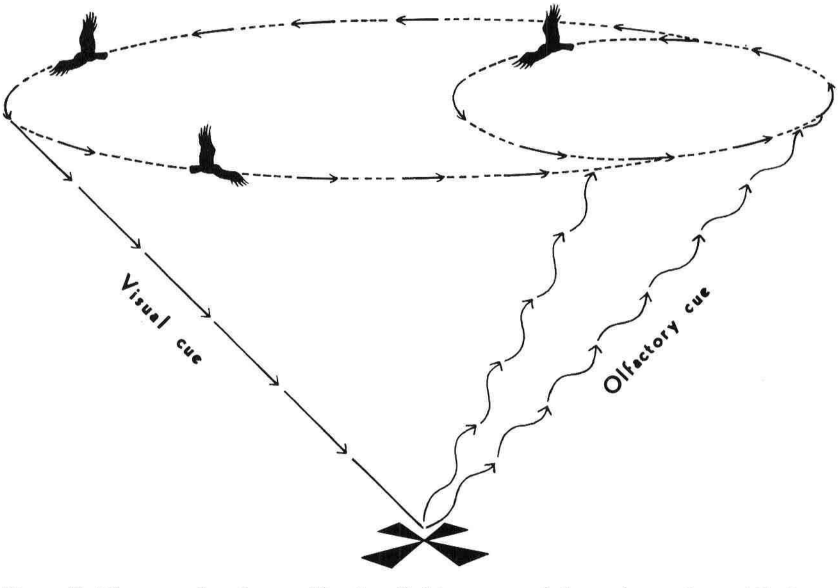

Figure 7. Diagram showing verification flight pattern of the turkey vulture (*Cathartes aura*).

D. ETHYL MERCAPTAN—COMPRESSED AIR UNIT

The decision to conduct field tests with ethyl mercaptan (CH_3CH_2SH) as an olfactory attractant for turkey vultures came as a result of conversations with field engineers of the Union Oil Company of California.

According to Mr. Ralph Openshaw, a retired engineer of the company, his organization had used turkey vultures to aid in locating leaks in large natural gas lines. During the period of 1938-1939, the company was troubled by a number of hard-to-find leaks in a 12-inch natural gas line that extended from Orcutt Hill, California, northward for 42 miles to the town of Avila, California. It was suggested to them by a company engineer in Texas that an effective way of locating line leaks in rough terrain was to introduce a heavy concentration of ethyl mercaptan into the line and then patrol the route and observe the concentrations of turkey vultures circling or sitting on the ground at definite points along the line. According to Mr. Openshaw, this procedure was most successful. A high concentration of ethyl mercaptan was introduced into the forty-two miles of gas line and a traverse of the route was made. At several points along the line, turkey vultures were observed either circling or sitting on the ground. At those locations the odor of the ethyl mercaptan was very pronounced and examination of the line revealed the leaks. As a result of using this procedure, the field engineers of the Union Oil Company have long ago recognized the turkey vulture as possessing a well-developed sense of smell.

The first trials using ethyl mercaptan as an attractant for turkey vultures were made at the head of the Gulf of California in Sonora, Mexico, between January 10 and 14, 1961. The test area was just north of the gulf town of Puerto Peñasco. Careful observation just before the tests had shown that a winter population of approximately twenty turkey vultures roosted in a lone tree on the desert floor some ten miles due north of the town. The birds daily took flight at approximately 9:30 A.M. and flew due south to the town and the beaches of the Gulf of California. The prevailing wind on the desert flat north of the town was from west to east and blew steadily each day from approximately 9 A.M. on. Three test sites were selected at varying distances north of the town. All were to the west (up-wind) of the flight line of the vultures from their roost to feeding grounds in and around the town.

On January 10, 1961 at 9:30 A.M. an 8-ounce container of ethyl mercaptan was uncapped and placed in a bush some 500 yards west of the established flight line. The fresh morning breeze carried the volatile fumes due east so that they intersected the line of flight at a right angle. A 25-power spotting scope was set up 200 yards to the west of the mercaptan site and on the same east-west line. The bush containing the mercaptan was visible in the foreground and any vulture passing the point of intersection with the fumes was visible in the field of the scope. The first vultures (three birds) flying south to Puerto Peñasco were noted at 9:48 A.M. Two minutes later their line of flight brought them abreast of the mercaptan-laden wind and they swung abruptly into a circling flight approximately 200 feet above the ground. The three birds circled tightly at this point for five minutes before one of the three began quartering up-wind towards the mercaptan site. Decreasing its elevation to approximately 100 feet, the vulture passed directly over the bush containing the mercaptan. From this point it continued on to the west and was lost to view. Attention was then directed back to the intersection point where the remaining two vultures had been circling. Five vultures were observed circling tightly at approximately 200 feet elevation, but it was impossible to determine whether the original two birds were among these five. After approximately six minutes the birds spiraled upwards and then flex-glided on southward toward Puerto Peñasco. At 11:15 A.M., a single vulture was observed moving on the south-bound line toward Puerto Peñasco, and as it passed into the field of the focused spotting scope, it also swung in a tight circle at the point of intersection with the mercaptan fumes. Directly behind it came two more birds that joined the circling flight of the first vulture. The three vultures were joined by an additional four birds and the group of seven soared slowly up-wind toward the mercaptan site. When a short distance down-wind of the mercaptan, the vultures again began their circling action for a period of three minutes. The circling was within 100 feet of the ground at this point. At the end of the three-minute period the group of vultures drifted on southward toward Puerto Peñasco.

On January 11, 1961, a similar site was established six miles north of Puerto Peñasco and the mercaptan was uncapped at 9 A.M. The first vulture sighting was made at 10 A.M. when four vultures were noted heading south on the same line as the previous day. As the lead vulture sailed into the field of the spotting scope, it wheeled sharply and began a tight circling action down-wind of the mercaptan fumes. The three other birds immediately joined the lead bird and all four circled tightly within the telescope field for approximately eight minutes, gradually working up-wind toward the mercaptan site. When directly over the bush holding the mercaptan, the birds began to fly in widening circles and then moved out of the area in three directions. At 10:30 A.M., three additional south-bound vultures crossed the fume-dispersal line and again all three birds began a tight circle in the area covered by the spotting scope. The vultures circled steadily at point of intersection for ten minutes and then moved on south toward Puerto Peñasco without closing on the mercaptan site as the previous group of vultures had done.

A third test site, five miles north of Puerto Peñasco, was used on January 14, 1961. In contrast to the previous two tests, the mercaptan was poured into an open pan rather than being retained in an uncapped bottle. The pan was placed in a dense bush at 9:45 A.M. but no vultures were observed moving south until approximately 10:30 A.M. At this time, six vultures, strung out in an irregular column, were observed moving south along the north-south tract to Puerto Peñasco. At a considerable distance behind the group of the first six came an additional three birds. As the first of the six birds came into the down-wind zone of the mercaptan, it swung into a tight circle as on the previous test days. The remaining five birds individually took up the tight circling as they arrived opposite the mercaptan. A short time later the second group of three birds also joined those already circling, making a total of nine birds circling close together approximately 150 feet above the ground and directly down-wind of the mercaptan. The group of nine turkey vultures continued to circle the same spot for a period of approximately five minutes. All were visible in the field of the prefocused spotting scope. At the end of five minutes two of the vultures landed on the ground and stood motionless and facing up-wind toward the mercaptan site while the seventh bird moved on south toward Puerto Peñasco. The six other birds passed directly over the mercaptan and then drifted off slowly toward the south. The two vultures continued to stand motionless on the open ground down-wind of the mercaptan for a full six minutes. They then rose into the air once more with several rapid flaps of their wings. Several more tight circles were executed and the two birds then moved south toward the beach without closing on the mercaptan. The experiments in the Puerto Peñasco area were terminated at this time.

It was of interest to note that flies, especially green blow flies (Family *Calliphoridae*), were attracted to the mercaptan containers as long as they were closed and giving off only a limited amount of odor. However, as soon as the containers were uncapped or the mercaptan was poured into an open pan, all flies disappeared. The mercaptan apparently acted as an attractant in low concentrations, but became a repellant in heavy concentration.

Following the field trials with ethyl mercaptan in Sonora, a more sophisticated mercaptan-dispensing unit was devised (see "Methods").

On September 6, 1961, the compressed air unit described above was put into action on the upper brush-covered slopes on the north side of the Santa Clara River Valley, directly to the north of the Rancho Sespe site (see "Study Area"). Ground fog enveloped the entire area at the time of installation. The compressed air flow through the mercaptan canister was initiated at 8 A.M. The fog dissipated from the valley at approximately 9 A.M. A steady breeze was blowing up the slopes from the valley floor, thus carrying the mercaptan fumes toward the ridges to the north. Any vulture receiving an olfactory stimulus from the mercaptan would have to be foraging along the ridges to the north. At 9:15, eight turkey vultures were sighted foraging over the floor of the valley to the south and up-wind of the unit. No response was expected or received from these birds. The unit operated throughout the morning and continued observation of the ridges to the north disclosed no vultures in the down-wind area. In the valley below, however, numerous vultures were observed throughout the morning. The compressed air unit was securely hidden in a dense stand of live oak, but the mercaptan fumes were easily detected by the human nose in the down-wind zone several hundred yards from the site. By mid-afternoon it was obvious that the concentration of vulture activity was on the valley floor and up-wind of the dispensing site. The unit was shut down and dismantled at 3:30 P.M.

On September 7, 1961, the unit was installed on the floor of the Santa Clara River valley in the area where the vulture activity had been noted the previous day and directly below the previous dispensing site on the slope to the north. The unit was placed under a small willow tree (*Salix*) and further camouflaged with several large tumbleweeds (*Salsola*). The mercaptan flow was initiated at 8:30 A.M., although the entire valley was enveloped in a dense ground fog. By 9:20 A.M. the fog had begun to lift and visibility was approximately one-half mile. A steady breeze began to blow up the valley from the west. At 9:45 the fog had completely disappeared, leaving the entire valley in sunlight. At 10:25 twenty-four turkey vultures were observed spiraling up from their known roosting trees (see "Study Area") two miles to the northwest. After gaining altitude the flock of vultures scattered in several directions with many of the group moving up the valley toward the mercaptan site. At 11:08 A.M. two vultures were observed circling directly down-wind of the unit at an elevation of 200 feet. These vultures were joined by a third at 11:10 and all three birds continued to circle in the down-wind zone. The circling was frequently interrupted by the birds facing into the wind and gliding slowly up-wind towards the dispensing site, only to swing about upon reaching the willow bush containing the dispenser and return to the down-wind circling area, approximately 200 yards from the dispenser. From 11:30 on throughout the remainder of the day there was a continuous circling and quartering with from two to twelve vultures in the pattern. At 11:46, one bird from a circling group of seven glided slowly up-wind towards the willow bush. The bird was cruising at ten feet above the ground, and upon reaching the dispenser site went into a tight, low-level circling flight, frequently resorting to wing flapping in order to maintain air speed. After two minutes of circling the bird returned down-wind to the circling group of vultures that now numbered nine birds. At 12:40 P.M., vultures began landing on an earthen dike 150 yards from the dispenser, but exactly in line with the flow of mercaptan fumes. The birds stood motionless on the dike, but all were facing directly into the wind. The wind held steady from the west and numbers of vultures continued to circle or face into the wind, quartering back and forth on a 50-yard front. The number of birds on the ground varied from two to five, with arrivals and departures from the circling group in the air above. Vultures remained continuously in the down-wind air zone and on the ground until the experiment was terminated at 4 P.M.

On September 9, 1961, the unit was operated as on the previous day. Dispensing of mercaptan began at 8:15 A.M., with the fog burning off at 9:10 A.M. Vultures began circling directly down-wind of the unit at 9:30 A.M., and behavior was similar to that of the previous day. The largest number circling and on the ground down-wind of the dispenser at any one time was fourteen. At 1:30 P.M., the number of birds had dropped to two and examination of the unit showed that the tank of air had been exhausted. A fresh tank of air was quickly substituted and by 2:15 the number of circling birds was back to ten. Frequent sorties would be made towards the dispenser site as on the previous day, but the most used air position appeared to be 150 to 200 yards down-wind. Immediately down-wind of the dispenser the mercaptan fumes were overpowering to the human nose to the point of being nauseating. Two hundred yards down-wind, however, the fumes were very strong, but not so overwhelming and with a different odor. This difference of odor of the same substance at varying distances is in accord with the observations of Kinross (1930:116) who states:

> . . . the odors of many substances change so much with dilution that a strong solution and a weak solution seem to have nothing in common; indole, which in strength smells like a sewer, when very dilute had the fragrance of narcissus.

The attractant quality of the ethyl mercaptan kept vultures circling and standing on the ground down-wind of the dispenser the remainder of the afternoon until the experiment was terminated at 4:30 P.M.

Operation of the compressed air unit was resumed on September 10, 1961, but a change in weather resulted in a cloud overcast with strong, gusty and erratic winds in the valley. Fewer vultures were noted in the air and these birds showed little interest in the mercaptan, as the fumes were swirled in all directions. The limited supply of mercaptan was exhausted by midday and the experiment was terminated. The two previous days, however, had provided adequate data, coupled with the observations already described from the Puerto Peñasco area, to show a definite olfactory response by the turkey vulture to an ethyl mercaptan stimulus.

E. HIDDEN BAIT TESTS—CENTRAL INDIA

During the period of February through March of 1959, while participating in a Los Angeles County Museum expedition to central India, I was afforded an excellent opportunity to observe the habits of a number of species of aegypiine vultures. Opportunities were also afforded to conduct field experiments on the olfactory acuity of this subfamily of birds.

The main base camp of the expedition, located in the Balaghat Forest District of the state of Madhya Pradesh, was the scene of considerable skinning and preparation of large specimens of mammals, such as tigers, leopards, and large ruminants. Activity of this nature in India soon draws a large concentration of vultures, ready to feed on any discarded carcasses. Because carcasses were continually present, the concentration of vultures remained in the immediate vicinity of the camp, ever alert to swarm upon a carcass when the latter was dragged into an open area for them. During the waiting periods, the giant Sal trees about the camp were heavy with them, both day and night. The vulture population about the camp area numbered approximately 150 individuals of three species. The Indian white-backed vulture (*Pseudogyps benghalensis*) made up approximately 95 per cent of the group, with 3 per cent being *Neophron percnopterus* and the remaining 2 per cent, *Sarcogyps calvus*. The latter two species did not roost in the immediate camp area, but were always on the periphery of activity during daylight hours.

In order to perform a controlled test designed to detect possible olfactory acuity, the skinners were requested to set aside over 200 pounds of muscle during the fleshing out of a large tiger specimen. A site was selected in a nearby open, dry paddy field. An elevated platform in the center of the paddy field enabled the bait to be placed off the ground out of reach of jackals and pariah dogs.

At 10:00 P.M. that night, with the help of two assistants, I placed the mass of muscle atop the platform and security covered it with a thick, ten-inch layer of thatching straw. By putting the bait in place under the cover of darkness, there was no possibility of observation by the diurnal vultures.

During the subsequent days the large concealed bait developed an overpowering odor, discernible at a considerable distance–even by the relatively weak olfactory equipment of man. Each night the thatch straw cover was checked to insure that it had not become dislodged to disclose the bait to the keen-eyed vultures. Vultures swarmed the area during the daylight hours of each day, but never once did any of the three species show the slightest indication that they had detected the location of such a desirable food item. On the night preceding the twelfth day the thatch was removed so as to disclose the bait. The following morning a large king vulture (*Sarcogyps calvus*) immediately located the remains of the bait, alighted on the platform and began to devour the remains of the tiger meat.

F. FLY ATTRACTANT TESTS

During the course of field studies with turkey vultures at Cerro Viejo ranch it was thought advisable to devise an experiment that would attract large numbers of flies in order to test the hypothesis of Taber (1928) and Darlington (1930), both of whom believed that the turkey vulture locates hidden carrion by observing concentrations of necrophagous insects rather than by a sense of smell.

The hypothesis is an interesting one, but hardly tenable in the light of the findings presented in this report. Experimentation with hidden baits in Central India showed that, although the bait site was black with flies and other necrophagous insects, the vultures were unable to detect the presence of the carrion. It is reasonable to assume that the aegypiine vultures of the Old World, which are apparently completely dependent upon vision for the location of food, would be attracted readily to baits by the presence of necrophagous insects if these insects served as a visual indicator of food. I have also had considerable experience with kills made by tigers and leopards in India and Burma, and observation has shown that these large carnivores drag their prey under cover of brush or trees. Although the carcasses are covered with flies and the air above is thick with insects, the vultures seldom if ever detect the presence of the kill. Experimental use of the forced air unit in this study has shown that the turkey vulture readily responds to an olfactory stimulus from a site that is free of necrophagous insects. The absence of insects about the forced air unit during operation was due to the very strong exhaust qualities of the machine. There is no evidence to support the proposal of Darlington (1930) that the turkey vulture may possess an auditory sense attuned to the sound of buzzing insects.

For a fly attractant, a twenty-four-hour-old mixture of casein, brown sugar and water in equal parts, as suggested by Dethier (1947:2), proved effective for this purpose when placed in the mouth of an abandoned ground squirrel burrow. The baited burrow was located in the center of an open pasture and kept under observation for a period of five days. Large numbers of flies were attracted to the site, but no interest was indicated by turkey vultures, although the vultures periodically passed over the pasture on hunting flights during the five-day test period.

COMPARATIVE FOOD-LOCATION BEHAVIOR OF CATHARTINE VULTURES

As pointed out by Fisher (1944:272), the New World vultures of the family Cathartidae form a heterogeneous group of large birds limited in range to the Americas. In addition to morphological differences, they differ decidedly in their behavior. In order to understand the differences as well as the similarities among the five cathartine genera, I shall compare them on the basis of flight, food-locating habits, and agonistic and predatory behavior. This is pertinent to the present inquiry as these differences are reflected in food location behavior, and must, therefore, be properly evaluated.

A. FLIGHT

The detailed mechanics of cathartine flight were ably discussed by Fisher (1946:549-553). The flight of Old World vultures has been studied in detail by a number of persons, with the best general account being presented by Hankin (1913). On the other hand, the mannerisms of cathartine flight have been reported by relatively few persons. A recent publication by Cone (1962) presented a detailed study of soaring flight in land birds, especially vultures.

The giant condors *Vultur* and *Gymnogyps* are both excellent soaring vultures, and although they are relatively clumsy on the ground and often resort to considerable wing flapping at take-off, once airborne they soar and sail with a minimum of wing motion. A great many observations pertaining to the flight of *Gymnogyps* have been recorded by Koford (1953), but detailed accounts of the flight of *Vultur* are lacking. According to Koford (1953:41):

> The outstanding characteristic of the flight of condors is high stability in soaring. Frequently even an experienced observer mistakes a distant transport plane for a condor or a condor for a plane. It is probable that condors can soar for more than one hour at a time without flapping.

With regard to altitude, Koford (1953:46) stated that:

> In general, condors do not soar as high or as low over the ground as turkey vultures in the same locality. On days of light breezes condors rise higher than on days of strong winds. . . . Over high ridges and peaks near roosting areas it is rare to see a condor more than 500 feet above the ground. Over lower hills near feeding areas, where condors circle in rising columns of air in order to gain altitude for long glides, they rise to an estimated 3000 feet. . . . In areas where condors are actively searching for food they usually soar less than 500 feet above ground except when arriving and departing. Doubtless there is an optimum altitude for searching for food. Great height would not favor the detection of carcasses as small as those of ground squirrels.

For take-off on level ground, *Gymnogyps* must run into the wind for 25 to 40 feet, but if the wind is strong, take-off can be effected by merely extending the wings while facing into the wind. From the brief discussions of the flight of *Vultur* by other authors, Fisher (1946:553) obtained the impression that its flight is similar to that of *Gymnogyps.* Along the Peruvian coast, Murphy (1936:276) found that *Vultur* ". . . is given to soaring just above the brinks of sea cliffs and in the same relative position over seaward ridges of coastal hills." This type of flight is similar to that recorded by Grinnell (1933:164) for *Cathartes* along the coast of northern California.

The black vulture *Coragyps* is also a soaring vulture but much less so than the large condors. *Coragyps* circles more, alternately flapping and soaring. It possesses a broad soaring wing but, according to Fisher (1946:552), the shortness of the wing decreases the lifting surface, making frequent flapping necessary. Howell (1924:128) states that the black vulture is always distinguishable from the turkey vulture by its habit of alternately flapping and sailing. It is necessary for *Coragyps* to take two or three hops on the ground before springing into the air. Even so, it becomes air-borne more rapidly than *Cathartes.* Compared to the other four cathartine genera, *Coragyps* is a relatively sedentary vulture, spending most of its active hours around the habitation of man, ever ready to scavenge bits of food. It rarely resorts to long flights unless food is scarce.

Very little published information is available concerning the flight of *Sarcoramphus.* Dickey and van Rossem (1938:99-102) observed king vultures in El Salvador and reported that these vultures ". . . were seldom observed soaring overhead, but from the hilltops we could look down on them circling about and just skimming the tree tops of the jungle." They (p. 100) also observed that:

> King vultures may be fairly common in a locality and still not be particularly noticeable. Although occasionally to be seen soaring at high altitudes, they are essentially inhabitants of the forest and spend a great deal of time at rest in such cover.

My own experience with *Sarcoramphus* in Brazil agrees essentially with that of Dickey and van Rossem. I have frequently observed king vultures soaring in small circles high above dense forested areas, but my most frequent encounters with them have been in dense gallery or continuous primary forest (Stager, 1961:9). In attempting to get within shotgun range of *Sarcoramphus,* I have found that they will repeatedly fly with relative ease from the crown of one giant rain forest tree to another without going above the forest canopy. They descend to the floor of dense forest apparently with little effort, as I have flushed them from such locations on two occasions. Their flight through forested areas is rather labored and audible, however, as it requires continuous flapping of the wings. As far as I am able to determine, *Sarcoramphus* is the only cathartine vulture that can be described as a forest dweller. The king vulture apparently has no forest-dwelling counterpart among the aegypiine vultures of the Old World. The palm nut vulture *Gypohierax* of Africa frequents peripheral areas of forests along river courses (Chapin, 1932:521), but apparently does not penetrate deep within the forest as does *Sarcoramphus* in tropical America.

It is interesting to note that Slud (1960:89) did not observe *Sarcoramphus* within the forest on any occasion, but frequently saw it circling in the air above. His observations were made during a year-long stay in the heavy wet forest of northeastern Costa Rica.

The flight of *Cathartes* differs decidedly from that of the other four cathartine genera. Fisher (1946:552) stated: "Use of the wing in *Cathartes* in most respects holds an intermediate position between *Coragyps* and *Gymnogyps*. It flaps more than does the Condor but less than the black vulture." In a strong wind *Cathartes* can take off by extending the wings and facing into the wind. In the absence of wind, *Cathartes* is slower than *Coragyps* on take-off from level ground. Fisher (1946:553) noted that *Cathartes* needs a longer take-off run than *Coragyps* and flapping flight appears to be more difficult for it than for the latter species. Sprunt (1937:383) commented on the large numbers of turkey vultures killed by automobiles on the roads of the southeastern United States as the birds attempt to rise into the air from the carcasses of automobile-killed animals on the highways. Sprunt attributes the large number of casualties to the inability of *Cathartes* to make a rapid take-off in the path of the oncoming auto. It would be interesting to compare the ability of *Coragyps* to escape the oncoming car with that of *Cathartes*. Sprunt (1937) made no mention of *Coragyps,* however, so it must be assumed that this feeding on roads is confined mostly to *Cathartes* in his area.

Off the ground, however, *Cathartes* is a superb flyer. The soaring flight of the turkey vulture is not as stable as that of *Gymnogyps* and *Coragyps,* as it tends to wobble and tip from side to side. In calm weather it soars with greater facility than any of the other cathartines. It can spiral upward at a very rapid rate and often climbs to considerable heights. Observers often attribute too much importance to the circling soaring flight of turkey vultures in connection with feeding activities. This type of flight is primarily used in gaining altitude. The vulture catches a rising thermal, spirals rapidly upwards, and then flex-glides on a straight course for great distances.

Contrary to the popular opinion that *Cathartes* is a high-altitude hunter, it is basically a very low-level forager. In its searching flight it skims over crest lines of hills and sails down canyons, often only a few feet above the surface of the ground. It is frequently observed sailing swiftly below tree-top level through broken stands of vegetation, then banking sharply to swoop back on its course, apparently to reinforce an olfactory or visual cue. If it loses air speed close to the ground it will resort to wing flapping until speed is regained. *Cathartes* is highly adept at wind-facing and can remain within a relatively small area of air space for long periods of time. In wind-facing it does not hang motionless in one spot, but will quarter back and forth on a relatively small front with much tilting from side to side. Over level ground it commonly flies a low-level searching course, frequently resorting to upward swoops to regain altitude. With necessary altitude regained it will then side-slip downward with a rush, often skimming just above the surface of the ground. In this low-level type of flight it has no peer among the other cathartine vultures.

B. FOOD LOCATING HABITS

The California Condor feeds primarily on large animals that are generally in open areas, and therefore easily located by visual means. Koford (1953: 62), from his extensive observations, suggested that *Gymnogyps* may observe the actions of *Cathartes* and ravens (*Corvus corax*) and thereby learn the location of a carcass. Koford also noted that condors will readily join a circling condor group, indicating that each condor is aware of the activities of other condors as each goes about its own search for food. This action is in agreement with the observations made by Stewart (1959:56) on Old World vultures in Spain. In areas where condors feed on ground squirrels (*Citellus*), Koford (1953:62) frequently saw condors fly straight to a group of turkey vultures, either in the air or on the ground. Koford (1953:55) reported that a stuffed doe deer (*Odocoileus*) decoy placed near another carcass on two occasions failed to attract turkey vultures and ravens feeding nearby, or condors flying overhead. This action is in accord with my experimentation with *Cathartes*. Koford (1953:55) concluded that the favorite food species of *Gymnogyps* in order of preference were: cattle, sheep, deer, ground squirrels and horses. He also estimated that these five species provided 95 per cent of the condor's diet. With the exception of the ground squirrel, all of the above species are large and obvious and easily located by visual means. Koford (1953:56) points out that:

> . . . condors alight, walk, and take off in a laborious manner, but they excel in flying long distances. Their specializations fit them for eating carcasses which are large enough to feed them for a day or more at the expense of only one landing and one take-off. It would be wasteful from the standpoint of derivable energy, for a condor to descend to the ground in order to feed on a single small carcass.

Koford (1963:62) concluded that if *Gymnogyps* possesses a sense of smell, it is normally of little importance in finding food.

The food-locating habits of *Vultur* are essentially the same as those of *Gymnogyps,* but with certain notable exceptions. The Andean condor feeds on the large and obvious mammal carcasses occurring on the high wind-swept paramos of the Andes. It is also known to descend to sea level along the coasts of Peru and northern Chile where it feeds on the carcasses of fish, cetaceans, and pinnipeds. Unlike *Gymnogyps,* the Andean condor is known to attack and kill animals the size of a calf (Wiggins, 1945:168). According to Murphy (1936:908) the Andean condor feeds upon the fresh eggs of the guano cormorant (*Phalacrocorax bougainvillii*) on the rookery islands off the coast of Peru. As in the case of *Gymnogyps,* the Andean condor can only afford to expend energy feeding on small items of food if this type of food is present in sufficient quantity to justify a landing and take-off. In a large sea bird colony this condition would be amply met. Murphy (1925:189) presents conclusive evidence that *Vultur* also feeds upon live diving petrels (*Pelecanoides garnotii*) secured from the mouths of their nesting burrows.

The habits of *Sarcoramphus* are the least known of all the cathartine vultures. The king vulture finds a large portion of its food on the floor of tropical forests but is occasionally known to join the two smaller species, *Cathartes* and *Coragyps,* at a carcass at the margin of forested areas. Most observers of *Sarcoramphus* agree that this large vulture seldom if ever ventures out on the open savanna or upon denuded mountainsides to feed (Lehmann, 1940:459). The method employed by the king vulture to locate food has puzzled its observers for a long period of time. Pinto (1936:49) pointed out that the king vulture comes to food in the forest with rapidity and in a direct line, although he questions the ability of the bird to locate food by visual means because of the low-level approach it makes through the trees. Pinto was reluctant to attribute the food location to olfaction because of the distances from which it comes to food. Lehmann (1940:459) was of the opinion that the king vulture forages through the dense forest in search of kills made by jaguar (*Felis onca*). Dickey and van Rossem (1938:100) were of the belief that the king vulture arrives at a carcass after it has been discovered by *Cathartes* or *Coragyps.* They also noted that king vultures often showed up at the side of a carcass long after it had been reduced to only skin and a few bones by the smaller species of vultures. Wetmore (1957:22) found it watching *Cathartes* closely within secondary forest growth near the beach on Coiba Island, Panama.

The black vulture (*Coragyps*) obtains a large portion of its food by general scavenging around the habitations of man. In some areas, *Coragyps* forages out from communal roosts and resorts to soaring high above the countryside. Bent (1937:37) stated:

> When a black vulture flying and circling at great height becomes aware of a carcass lying far below it, the bird at first circles down but soon drops with great swiftness with legs hanging and,

> at times, wings flapping furiously. Such actions of descent from a height immediately attract the attention of other vultures on the ground or roosting in trees and they at once follow up the clue. One such action, even a mistaken one, can quickly collect a flock of vultures.

In August of 1953, I made extensive observations on the feeding habits of both *Coragyps* and *Cathartes* in southeastern Sonora, Mexico, and found that there appeared to be a definite food-finding relationship between the two genera. *Cathartes* was observed on the wing earlier in the day that *Coragyps,* but as the countryside warmed and thermals began to rise, the black vultures, by flapping and gliding, would spiral upwards to considerable heights. From these points of vantage they might easily watch the actions of the low-flying *Cathartes* as the latter quartered back and forth over the dense arid tropical forest below. If a turkey vulture turned back or began circling at a given point, the black vultures would come streaming to the site from all directions. My observations have frequently indicated that although *Cathartes* is the first to discover or arrive at a source of food, it is generally driven from the food by the hordes of black vultures. It is safe to assume that as the high circling *Coragyps* observe the movements of the low-flying *Cathartes,* they likewise would be quick to react to the stimulus of one of their own number dropping downward towards a turkey vulture or to a carcass that the plummeting bird had discovered on its own.

It is a well-established fact that *Coragyps* will attack and kill live animals as large as young pigs and lambs and remove the eyes of new-born calves and cows in a weakened condition (Bent, 1937:35). McIlhenny (1939:472) described in detail the mass attacks of *Coragyps* on skunks (*Mephitis*) and opossums (*Didelphis*) foraging in open fields during daylight hours. Figgins (1923: 666) found *Coragyps* taking live young herons from the nest. Live food of this type was in all the open and easily located by visual means. To date there is no evidence to indicate that *Coragyps* employs olfaction in food location.

Food location by the turkey vulture forms the basis of this research and detailed information found elsewhere in this paper will not be repeated here, except as a general comparison of behavior. *Cathartes* is the most widely distributed vulture in the Americas (Figs. 3 and 4) and forages over a great variety of terrain. For the most part it is solitary in its widespread and continuous search for food. Communal roosting is of common occurrence throughout its range, but numbers of individuals at the roost are fewer than is recorded for the roost of *Coragyps*. The turkey vulture is migratory in the northern portion of its range where the bulk of the population withdraws southward in October, to return in March. The wide-ranging *Cathartes* has been found foraging at 10,000 feet elevation in the Sierra Nevada mountains of California (Emlen, 1931:83).

Solitary individuals are to be found sailing over the remotest desert areas of the western United States and Mexico, as well as over the bleak wastes at the extreme tip of South America (Peters, 1931:190). The low-level searching flight of the turkey vulture allows the bird to take advantage of small items of food. The low-level traverse also places the vulture in a position to receive and respond to olfactory stimuli. *Cathartes* is known to have excellent eyesight, and vision may well be its most important sense; but, as demonstrated in the field experiment section of this paper, olfaction plays a most important role in the food-finding economy of the species. Even in the case of large and obvious items of food, the turkey vulture, under controlled field conditions, has repeatedly demonstrated the need for obtaining a reinforcing olfactory cue before alighting for final investigation and actual feeding. *Coragyps* will drop with great rapidity upon a large suspect item and investigate afterward. The final and sometimes lengthy, close circling flight of *Cathartes* about a large carcass prior to landing, has often been interpreted by observers as extreme caution and timidity on the part of the vulture (Bent, 1937:23). My own observations, however, indicate that olfactory cues are necessary releasing components for feeding behavior. The procedure is reversed when the primary cue is olfactory and the potential food source is hidden from view. The low-flying vulture closes on the odor source and locates the object of its search by the combined senses of olfaction and vision.

The turkey vulture will readily feed upon the large and obvious carcasses, but a large percentage of its diet consists of small items. Pearson (1942:87) stated: "The black vulture seems to pay but little attention to the small carcasses that form a large part of the food of the turkey vulture." Snakes, lizards, small mammals, birds and fish are readily taken as food. Bent (1937:20) mentioned that they will eat grasshoppers and even stranded tadpoles. Observations indicate that *Cathartes* shows a preference for food that is relatively fresh rather than putrid. If food is in short supply in a given area, the turkey vulture will feed on carrion that is well advanced in putrefaction. The tests of Owre and Northington (1961:204) indicated that their captive *Cathartes* showed a decided preference for recently-dead, newly hatched chicks, rather than for putrefied carrion.

My field observations have also shown that *Cathartes* will readily pass over choice items of food, both obvious and hidden. This action can be attributed to lack of hunger and is generally indicated by the vulture's mode of flight. When the vulture is not hungry, its flight is at higher elevations and on a set course. The low-level, quartering flight that carries the bird close over ridge lines and down through ravines or through broken stands of vegetation, indicates that the daily quota of food has not yet been attained. Various observers have suggested that for the most part the other four genera of cathartine vultures observe the food-locating actions of *Cathartes* and are directed to much of their food in this manner. My own observations in Sonora, Mexico, indicate a possible relationship of this sort between *Coragyps* and *Cathartes*. Schomburgk (1839:255) considered *Cathartes* to be a "scout" for *Sarcoramphus*. In areas where condors feed on ground squirrels, Koford (1953:62) has on many occasions observed *Gymnogyps* flying toward turkey vultures as they circled or sat on the ground. Although Murphy (1925) mentioned both *Vultur* and *Cathartes* as being common on the guano islands off the coast of Peru, he gives no indication that there is any relationship between these two genera of the sort mentioned for the other members of the family Cathartidae.

C. AGONISTIC AND PREDATORY BEHAVIOR

The five genera of cathartine vultures differ so decidedly in their agonistic and predatory behavior that a comparison of these types of relationships is important in achieving an understanding of the behavior of the family as a whole.

Although equally large in size, the two condors differ remarkably as to aggressive behavior. There appear to be no records of *Gymnogyps* attacking live animals, although *Vultur* is known to kill both mammals and birds. In captivity, the California condor is a docile species, but Lehmann (1940:458) reported that some captive Andean condors are savage and pugnacious.

Sarcoramphus is not known to be aggressive or to kill live prey, but *Coragyps* has a well-documented reputation for attacking live animals. The turkey vulture is a very timid species in its contacts with live animals. Reports of predation on live animals by *Cathartes* should be evaluated with extreme care, as it is quite likely that they are based on misidentification. Hamilton (1941:254) reported the killing of young pigs by *Cathartes,* but his information was hearsay and the description of the action of the birds involved fits that of *Coragyps.* Owre and Northington (1961:204) reported that when live chicks were released in the compartments occupied by captive turkey vultures, the latter immediately retreated, although they had had a great deal of experience in feeding on dead chicks. Owre and Northington (1961) also noted that on one occasion when a turkey vulture started to feed on a dying chick, it dropped it and moved away in haste when the chick suddenly moved. Bent (1937:20) commented on the wariness of *Cathartes* when preparing to feed on young pigs killed on the road by automobiles. The vulture would walk carefully about the dead pig, apparently ready to beat a hurried retreat if the pig should move. Murphy (1936:837) stated that the turkey vulture is the enemy of the blue-footed booby (*Sula nebouxii*) but presents no proof that the vulture actually preys on the species. Murphy (1936:907) implicated the turkey vulture in the destruction of cormorant eggs with the statement: ". . . great destruction of guanay eggs had been wrought by gulls, turkey vultures and condors." Referring to destruction of the eggs of the Inca tern (*Larosterna inca*), Murphy (1936:1145) stated: ". . . the vultures are inveterate nest-robbers and quickly gobble up eggs left within sight or within easy reach." It may be that the turkey vultures of the Peruvian guano islands have developed a taste for bird eggs, but from personal experience I would expect the species to be present in the guano islands mainly for the purpose of feeding on the dead birds that normally accumulate in sea bird colonies.

Further study might well show that the turkey vulture has been implicated in the descriptions of the depredations made by Andean condors, solely upon the basis of its being present in the area along with the condors.

Numerous observers have commented upon the agonistic behavior of Old World vultures. One of the best and most recent papers on the subject is that by Petrides (1959:104) concerning the competition for food between five species of African vultures.

Among the cathartine vultures, the smaller species (*Coragyps* and *Cathartes*) appear to give way to the larger species, but mostly in deference to their size rather than because of any aggressive behavior on the part of the larger vultures. Dickey and van Rossem (1938:101), reporting the relationship of *Coragyps* to *Sarcoramphus*, stated that ". . . once they do arrive there is no doubt that the smaller species keep their distance." Among the two smaller genera, *Cathartes* will readily give way to the aggressive *Coragyps*. Although the turkey vulture most frequently discovers or arrives at a food site ahead of the black vulture, the former will soon be crowded aside by the swarming masses of *Coragyps*. Bent (1937:36) stated: "The black vultures are often obliged to share their feasts with turkey vultures . . ." My observations, however, have repeatedly shown that the opposite is true and it is most frequently the turkey vulture that is forced to share its food with the black vulture.

A COMPARATIVE ANALYSIS OF THE OLFACTORY MORPHOLOGY OF CATHARTINE AND AEGYPIINE VULTURES

As early as 1837, Richard Owen (1837:35), the eminent British anatomist, called attention to the well-developed olfactory tract of the turkey vulture and concluded with the statement:

> The above notes show that the turkey vulture has a well-developed organ of smell, but whether he finds his prey by that sense alone or in what degree it assists, anatomy is not so well calculated to explain as experiment.

One hundred years later, Technau (1936:570), in his excellent paper on the nasal glands of birds, again called attention to the highly-developed olfactory tract of the turkey vulture and pointed out that it must, indeed, be functional and utilized by the bird.

Very recently, Bang (1960:547) stated the problem very clearly when she said:

> It seems curious that the large olfactory organs of certain species have so often been pointed out by anatomists, yet most olfactory learning studies have been done on feebly equipped birds such as pigeons and have tended to keep alive in textbooks the idea that the chemical sense in birds is minimal or lacking. The maze type and conditioned reflex studies on microsmatic forms and the succession of uncontrolled field-tests initiated by those of Audubon have kept dust from settling on the question, but have proved nothing about birds with superior receptors.

Portmann (1961:47), in reviewing the problem of olfaction in birds, pointed out the unsettled state of current knowledge on the subject and urges a re-examination of the whole problem. He indicates that the morphological facts are strong evidence against the simple conclusion that birds are anosmatic. He believes that the development of the olfactory part of the nasal cavity, and the well-marked variation in the proportion of the olfactory bulb of the brain support an opposite view.

In order to re-emphasize the high degree of development of the olfactory chambers of the turkey vulture and to draw comparisons between it and the other four genera of cathartine vultures, I have divided the comparison into four categories as follows: (1) External Nares, (2) Posterior or Olfactory Chamber, (3) Microanatomy of the Olfactory Chamber, and (4) Comparative Size of the Olfactory Bulbs.

A reference index as to the relative size of the cathartine vultures is as follows:

Gymnogyps and *Vultur*–very large, with a wing measurement of more than 760 mm.

Sarcoramphus–large and robust, with a wing measurement of 480 to 525 mm.

Coragyps–medium size and heavily built, with a wing measurement of 409 to 464 mm.

Cathartes–medium size to rather small, lightly built, with a wing measurement of 450 to 485 mm.

A. EXTERNAL NARES

The external nares are perforate in all five genera of cathartine vultures, but differ decidedly in their respective sizes (Fig. 8). Measurements made on museum specimens reveal that, in order of nostril size, *Cathartes* possesses the largest nostril (10.8 mm. x 3.8 mm.) which occupies the entire nasal fossa. The nostril of *Gymnogyps* is the next in size (9.5 mm. x 3.8 mm.). In relation to the size of the head, however, the nasal opening is quite small. In *Coragyps* the small opening (7.9 mm. x 2.3 mm.) occupies only the posterior half of the nasal fossa and is narrowly acuminate anteriorly. The nasal openings in *Sarcoramphus* (7.5 mm. x 2.7 mm.) are partially obstructed by the fleshy protuberances of the cere. Although *Vultur* is one of the two largest vultures, it possesses the smallest nostril openings of all (7.2 mm. x 3.2 mm.).

It is of interest that the largest nostril openings occur in *Cathartes*, the genus showing the highest degree of olfactory chamber development. To what degree the large nares assist in olfaction is not known. All five genera possess a wide secondary choana, and, as pointed out by Portmann (1961:47), ". . . choanal smell is probably a fact in many birds and particularly in groups where the external nasal openings are small or even closed."

The anterior respiratory conchae of the five genera of the family Cathar-

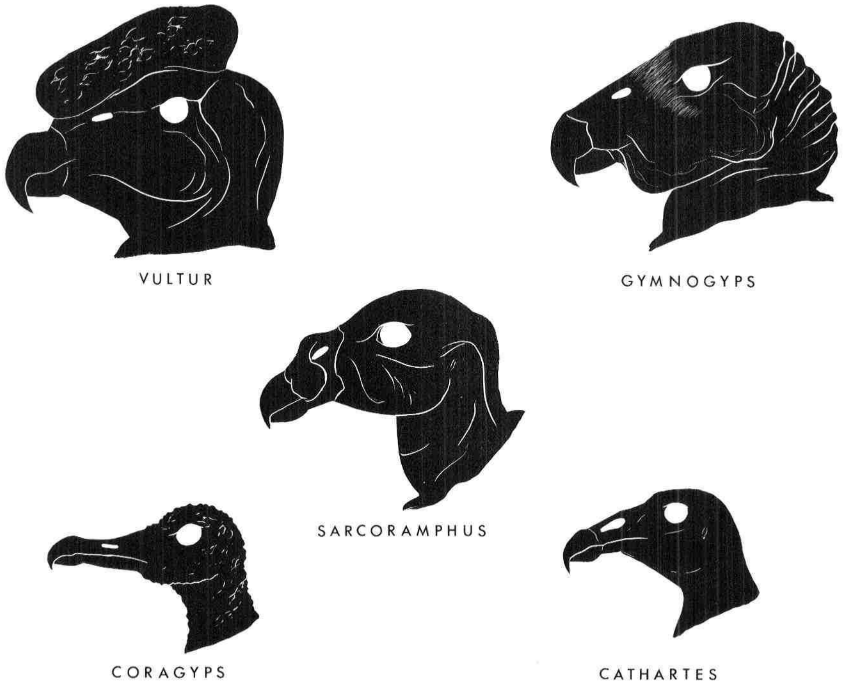

Figure 8. Lateral view of the heads of *Cathartes, Coragyps, Sarcoramphus, Gymnogyps,* and *Vultur,* showing the relative size of the external nares.

tidae appear to vary with each genus. In *Cathartes* and *Sarcoramphus,* the anterior concha is tilted from the horizontal to an almost vertical position. This condition is especially evident in *Sarcoramphus,* where the anterior end of the concha opens in a horizontal position towards the external nares, while the main axis of the structure turns directly downwards to open into the secondary choana (Fig. 9).

In *Coragyps,* the anterior concha is well developed and lies on a horizontal axis (Fig. 10). The area of anterior concha in the single specimen of *Gymnogyps* available was so damaged that I cannot present a proper description of the structure. I have not had an opportunity to examine the respiratory tract of the Andean condor (*Vultur*) so I am unable to make a statement regarding the structure in this genus.

B. POSTERIOR OR OLFACTORY CHAMBER

The paired olfactory chambers in cathartine vultures are cul-de-sacs enclosed on three sides, as pointed out by Bang (1960:549). The olfactory tubercle is situated on the latero-ventral side of each chamber and its degree of development varies according to the genus of vulture.

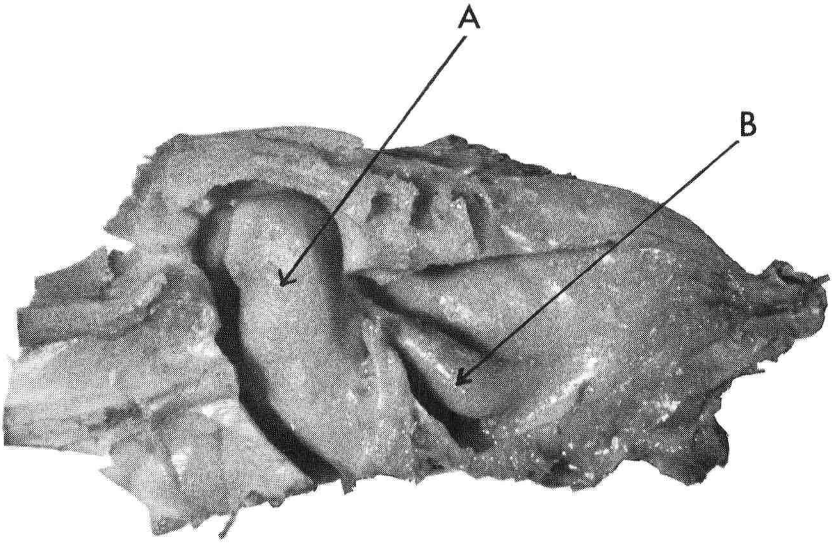

Figure 9. Dissection of olfactory chamber of the king vulture (*Sarcoramphus papa*), showing right anterior concha (a) and olfactory tubercle (b).

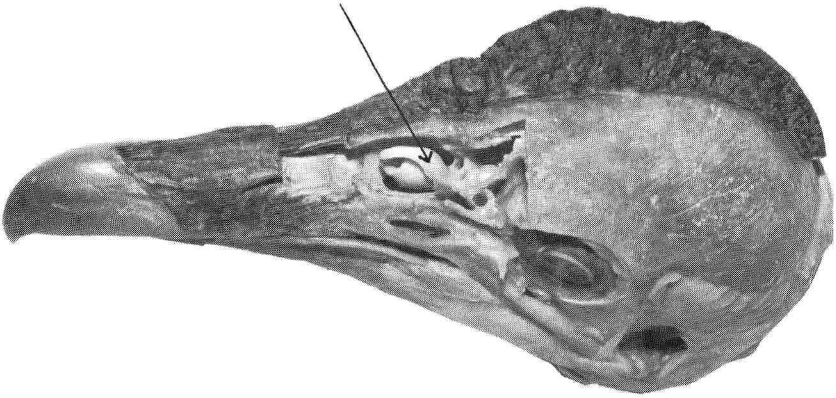

Figure 10. Dissection of anterior respiratory chamber of the black vulture (*Coragyps atratus*) showing left anterior concha.

Olfactory chambers of all genera of New World vultures were examined, with the exception of the genus *Vultur* for which no anatomical specimens were available. The highest degree of development within the family Cathartidae appears to occur in the genus *Cathartes*. In this vulture the tubercle is in the form of a large concha, scrolled two and one-half times (Fig. 11). The

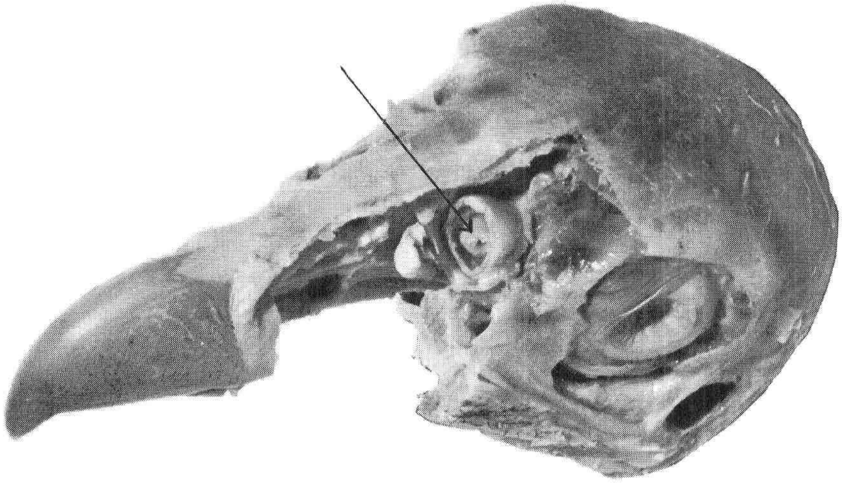

Figure 11. Dissection of olfactory chamber of the turkey vulture (*Cathartes aura*), showing a cross section through the left olfactory concha.

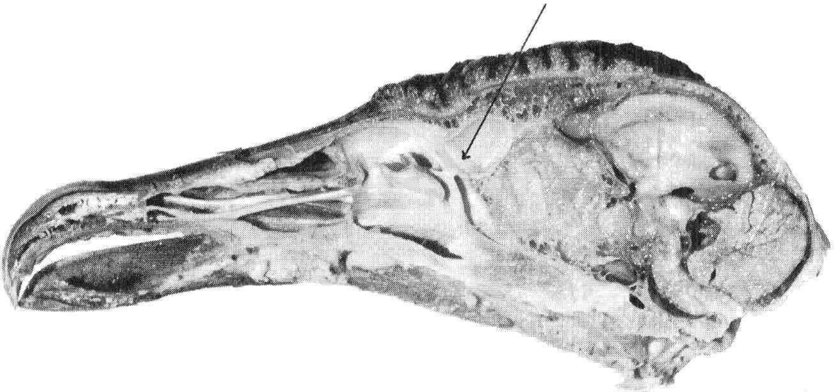

Figure 12. Dissection of olfactory chamber of the black vulture (*Coragyps atratus*), showing right olfactory tubercle (right median sagittal view).

concha fills the olfactory chamber and measures 14 mm. in length by 9 mm. high. In cross section the scrolled concha is 8 mm. in diameter.

In *Gymnogyps* there is evidence of a beginning of a concha, as the olfactory tubercle is in the form of a thin lip, 15 mm. long. The lip extends out from the lateral wall and is 4 mm. wide at its greatest width. In *Sarcoramphus* the tubercle is somewhat "S" shaped, with a length of 8 mm. (Fig. 12). There is no evidence of a lip formation as in *Gymnogyps.* The tubercle in *Coragyps* is the smallest of all the cathartine vultures examined. It is oval in shape, with a length of only 6 mm. (Fig. 12).

C. MICROANATOMY OF THE OLFACTORY CHAMBER

Portmann (1961:44) stated that the olfactory tubercle or concha is the only region of the nasal cavity that is covered with true olfactory epithelium, but Bang (1960:549) presented evidence to show that, not only is the tubercle or concha of the olfactory chamber of the turkey vulture innervated by branches of the olfactory nerve, but that strong branches of the olfactory nerve also lie along the roof, posterior and ventro-lateral walls and upper portion of the septum nasi of the olfactory chamber.

The olfactory chamber areas of four of the five genera of cathartine vultures were fixed and sectioned for microscopic examination (see "Methods"). The only genus for which material was not available was the Andean condor (*Vultur*).

Cross sections through the olfactory tubercle or concha area of *Cathartes* shows what appears to be a thick layer of olfactory epithelium on both surfaces of the large and much scrolled conchae (Fig. 13). The lining of the olfactory chamber appears to have a lining of epithelial cells identical in appearance to those of the conchae.

The surfaces of the concha appear to consist of an outer layer of epithelium comprised of olfactory and sustentacular cells. The sub-layer that I in-

Figure 13. Photomicrograph of olfactory epithelium of the turkey vulture (*Cathartes aura*).

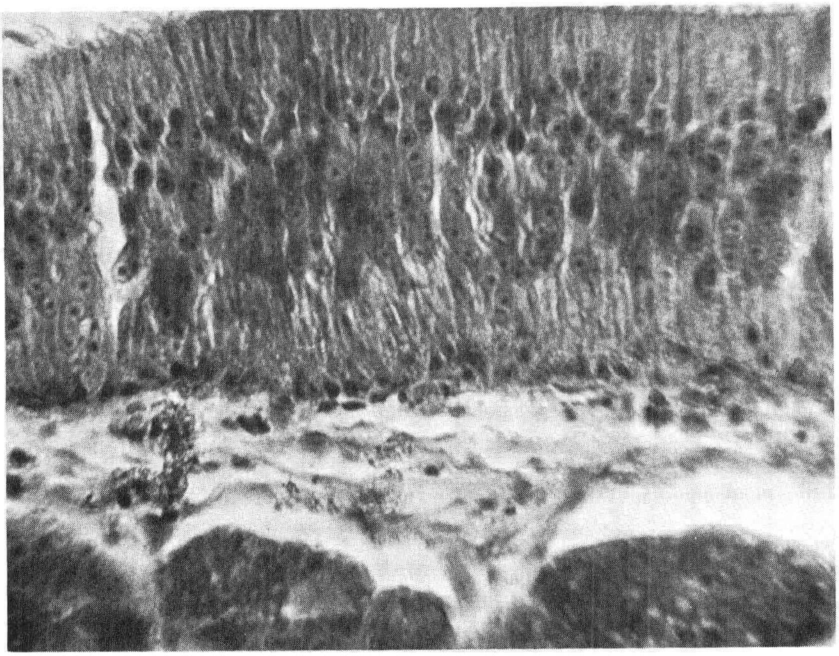

Figure 14. Photomicrograph of olfactory epithelium of the king vulture (*Sarcoramphus papa*).

terpret to be the tunica propria appears to contain a large concentration of Bowman's and mucous glands. The cell layers lining the walls of the olfactory chamber appear to be of a similar arrangement.

Examination of cross sections through a similar area in the olfactory tract of *Sarcoramphus* reveals a similar arrangement of cells on the surface of the olfactory tubercle as well as on the lining of the lateral wall of the chamber above the tubercle (Fig. 14). In *Sarcoramphus* there appears to be a great reduction in the number of Bowman's and mucous glands of the tunica propria, as compared to the large numbers of those glands present in *Cathartes.* It can be postulated that *Sarcoramphus,* living in the humid forests of the American tropics does not require the large number of glands to keep the olfactory epithelium moist as does *Cathartes* which ranges into extremely arid regions.

A cross section through the olfactory tubercle of *Coragyps* discloses an arrangement of cells somewhat resembling that described for *Sarcoramphus.* However, the layer of olfactory epithelium (Fig. 15) is not as thick as that observed in the preceding two genera, nor are the sustentacular cells as compact. The walls of the olfactory chamber show a lining of cells similar in appearance to those described for the olfactory tubercle.

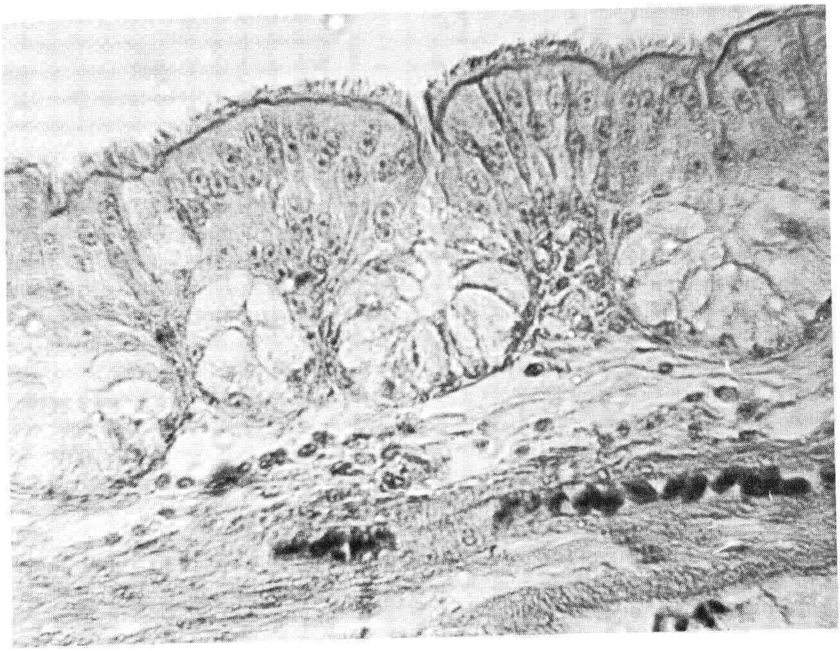

Figure 15. Photomicrograph of olfactory epithelium of the black vulture (*Coragyps atratus*).

The olfactory tract material obtained from the California condor (*Gymnogyps*) unfortunately had been frozen before I received it. The freezing of the specimen caused a general rupturing of the epithelial layer, due to formation of ice crystals within the cells. Consequently, it is not possible to make a statement with regard to the arrangement of the epithelial cells in this genus.

Examination of a cross section through the olfactory chamber of the Old World vulture *Sarcogyps* fails to show an epithelial development comparable to the cellular arrangement observed in the cathartine vultures. Sections through the olfactory tract of the domestic pigeon (*Columba livia*) likewise show no appreciable development of an olfactory epithelium.

D. OLFACTORY BULB

Latex rubber endocranial casts (see "Methods") of the five recent genera of cathartine vultures provide an excellent index to the size of the olfactory bulb. Although *Cathartes* is the smallest cathartine vulture, it possesses an olfactory bulb far surpassing in size that of any of the other New World vultures, including the large condors.

When viewed dorsally (Fig. 16), the general configuration of the brain of *Cathartes* differs from that of the other four genera in the reduction of mass in the latero-anterior area of the cerebral hemispheres. This reduction of mass

Figure 16. Endocranial casts of recent and Pleistocene cathartine vultures. Dorsal view, upper row, left to right (Recent): *Vultur, Gymnogyps, Sarcoramphus, Coragyps,* and *Cathartes.* Bottom row, left to right (Pleistocene): *Teratornis, Gymnogyps, Breagyps, Coragyps,* and *Cathartes.*

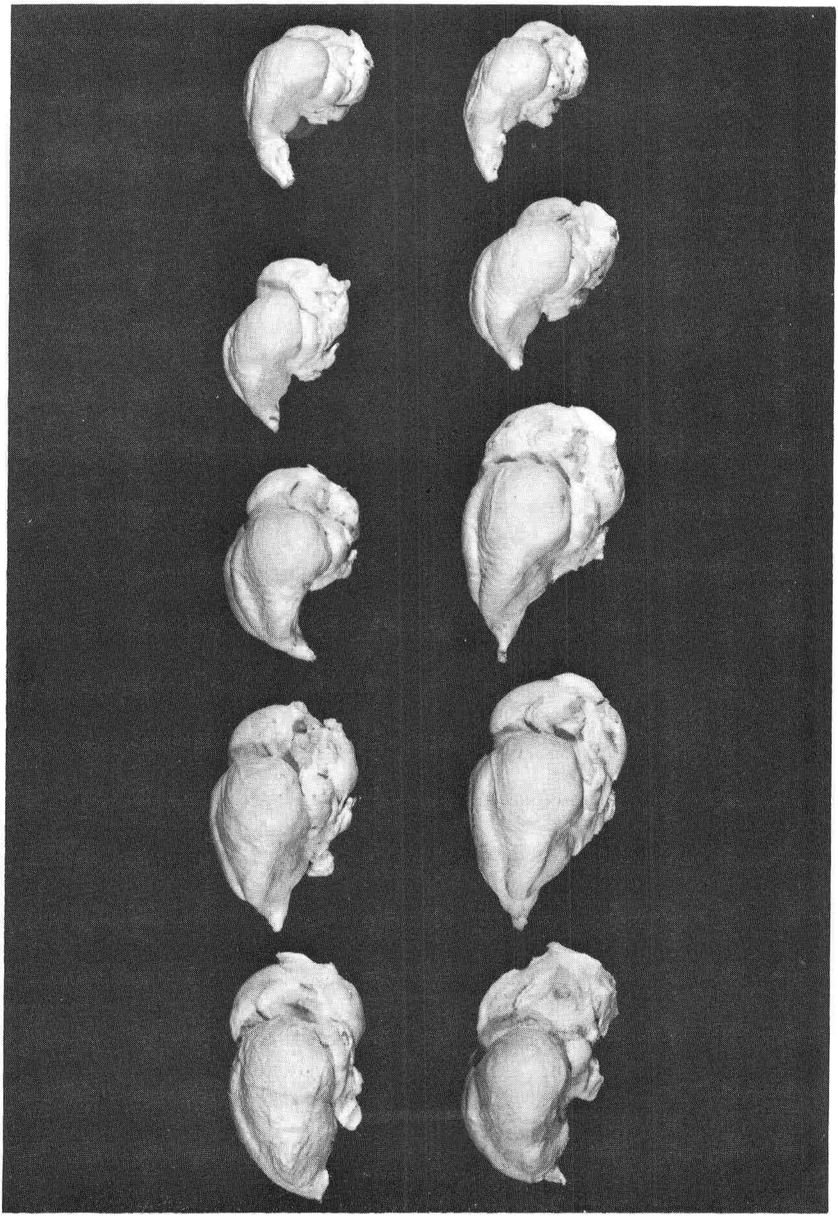

Figure 17. Endocranial casts of recent and Pleistocene cathartine vultures. Lateral view, upper row, left to right (Recent): *Vultur, Gymnogyps, Sarcoramphus, Coragyps,* and *Cathartes.* Bottom row, left to right (Pleistocene): *Teratornis, Gymnogyps, Breagyps, Coragyps,* and *Cathartes.*

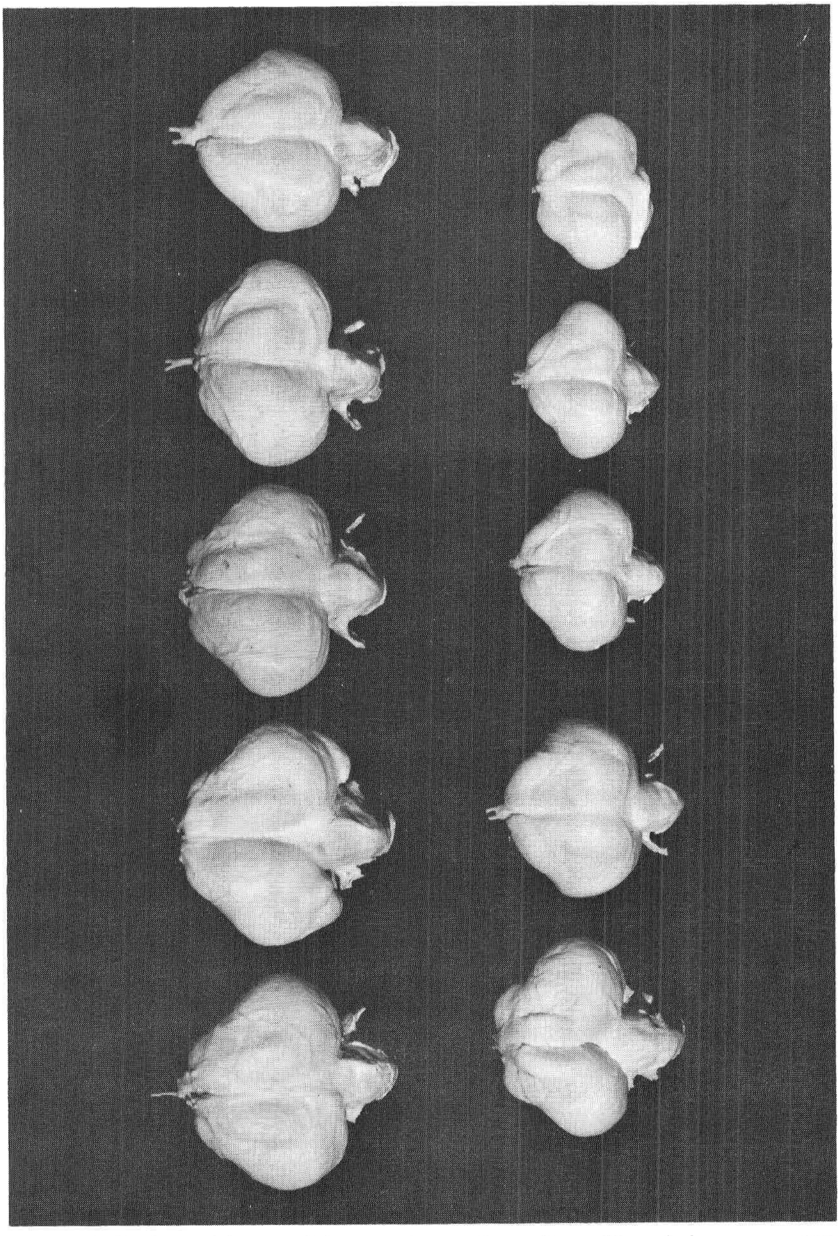

Figure 18. Endocranial casts of the recent aegypiine vultures. Dorsal view, upper row, left to right: *Torgos, Trigonoceps, Aegypius, Sarcogyps,* and *Gyps.* Bottom row, left to right: *Pseudogyps, Gypäetus, Necrosyrtes, Gypohierax,* and *Neophron.*

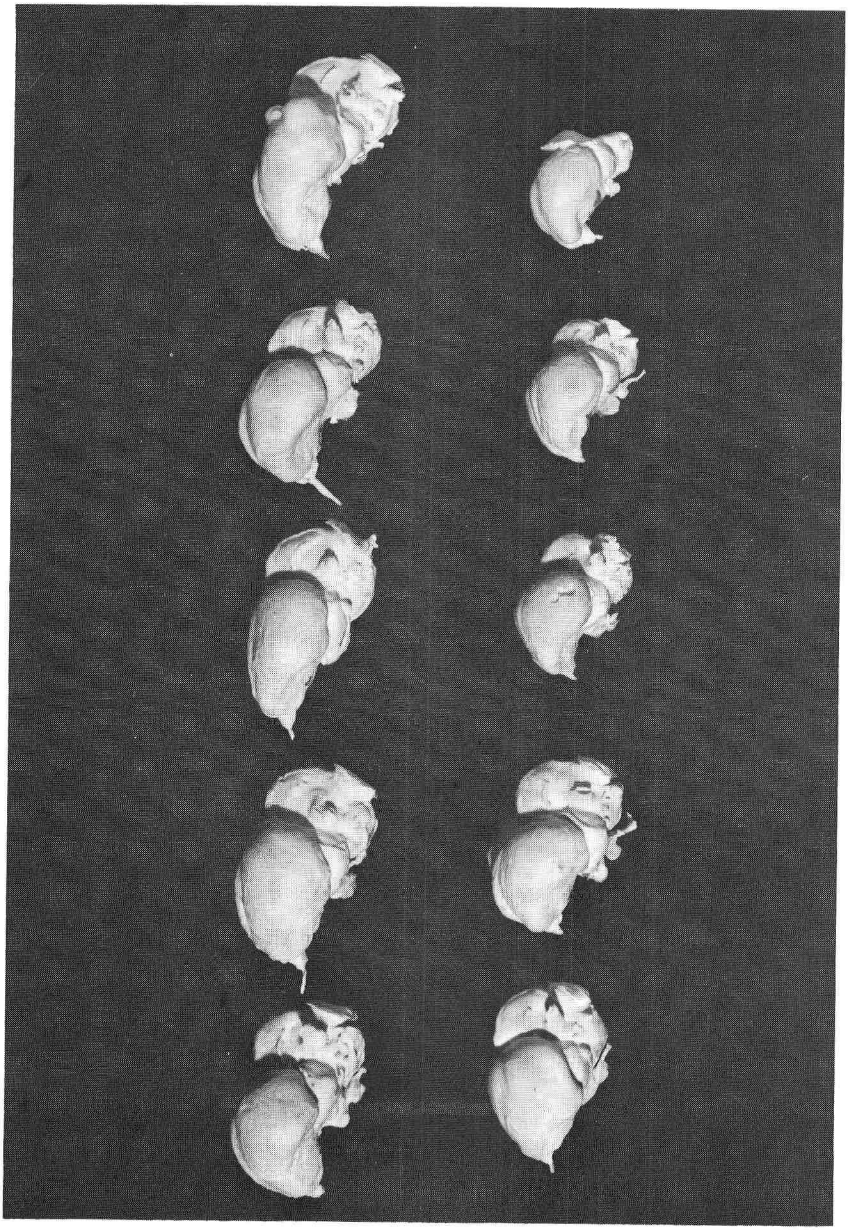

Figure 19. Endocranial casts of the recent aegypiine vultures. Lateral view, upper row, left to right: *Aegypius, Torgos, Gyps, Sarcogyps,* and *Trigonoceps.* Bottom row, left to right: *Gypäetus, Pseudogyps, Necrosyrtes, Gypohierax,* and *Neophron.*

in the forward area gives it a unique triangular shape, accentuated by the forward extension of the large olfactory bulbs.

The next largest olfactory bulb is found in the king vulture (*Sarcoramphus*). In gross size, the brain of *Sarcoramphus* is larger than that of the two smaller vultures *Cathartes* and *Coragyps*, but is smaller than the brain of either *Gymnogyps* or *Vultur*.

In lateral view (Fig. 17), the endocranial casts of *Vultur, Gymnogyps* and *Coragyps* bear a striking resemblance in general outline, while that of *Sarcoramphus* resembles the profile of *Cathartes* except for the greater size of the olfactory bulb in the latter genus.

It would appear to be of some significance that the largest olfactory bulb occurs in the genus *Cathartes*, the cathartine vulture demonstrating the greatest olfactory prowess in food-location.

Due to the unique mode of preservation of Pleistocene fossils in the asphalt deposits of Rancho La Brea, California, crania of all species of cathartine vultures entrapped there are available for use in the preparation of endocranial casts. Casts were prepared of *Breagyps clarki, Gymnogyps amplus, Coragyps occidentalis*, and *Cathartes aura* (Figs. 16 and 17). An endocranial cast was also obtained of the giant vulture-like *Teratornis merriami*.

Casts of the brains of the vultures of the Pleistocene period, when compared with casts of present-day forms, permit a postulation as to the possible olfactory abilities of these ancient birds.

The olfactory bulb of *Cathartes aura* of the Pleistocene equals in size that of the present-day *Cathartes*. There appear to be no appreciable morphological differences between the two birds. The cast of the Pleistocene *Cathartes* is slightly smaller than the brain of the present-day form, but this may well be individual variation. Based upon a comparison of size of the olfactory bulbs of the two forms, it can be stated with assurance that the turkey vulture of the Pleistocene probably had an olfactory acuity equalling that of the turkey vulture today. The species is sparsely represented in the Rancho La Brea deposits and this fact has been interpreted by some workers as indicating that the species was uncommon in the area during the Pleistocene. Viewed from an ethological standpoint, however, it may well be that the shy *Cathartes* did not join the other species of vultures at the great asphalt entrapment feasts, and thereby escaped the fate of the other species of vultures that are represented so abundantly at Rancho La Brea.

Coragyps occidentalis, the progenitor of *Coragyps atratus*, although somewhat larger than the latter, possessed an olfactory bulb equally small. The olfactory bulb of *Gymnogyps amplus* is similar in size to that of the present-day *Gymnogyps* (Fig. 16). The giant vulture *Teratornis merriami* was apparently dependent upon vision for food location, as the endocranial cast reveals a very small olfactory bulb (Fig. 16).

The endocranial casts of the ten aegypiine vulture genera (Figs. 18 and 19) have small olfactory bulbs as compared with those of the Cathartidae.

SUMMARY AND CONCLUSIONS

The historical background of the long-debated question of olfaction in birds, especially as it applies to New World vultures, is reviewed.

Field experiments, free of all visual food stimuli, conducted with the turkey vulture (*Cathartes aura*), are reported in detail.

Odors from fresh and decomposing animal tissue baits, placed on predetermined air currents by means of a forced air unit, elicited positive olfactory responses from turkey vultures. Turkey vultures were also able to detect the presence of concealed animal baits placed in bait chambers at various sites.

Experiments employing a visual decoy in the form of a mounted deer carcass failed to draw turkey vultures to the site. When the decoy was replaced with a fresh deer carcass of identical size and appearance, there was a rapid response from the turkey vultures in the area. Assembly at the carcass and feeding did not begin, however, until the vultures had obtained an olfactory cue from the potential food site. The dispensing of ethyl mercaptan on predetermined air currents elicited strong olfactory responses from large numbers of turkey vultures at test sites in Mexico and California. The hypothesis of Taber (1928) and Darlington (1930) which proposes that turkey vultures locate hidden food by observing the activities of necrophagous insects was found to be untenable as a result of the above-mentioned experiments, coupled with fly attractant tests in California and hidden bait experiments with aegypiine vultures in central India.

All previous references in the literature indicate a marked difference in behavior between the five genera of New World vultures, and an examination of these behavioral differences and similarities have contributed towards a clearer understanding of vulture food-locating behavior.

A comparative analysis of the mode of flight of the five genera of cathartine vultures shows that the turkey vulture (*Cathartes*) is capable of, and utilizes, a a low-level searching flight that brings it close to the ground and in range of low-lying olfactory cues. The high-altitude soaring and circling habits of *Coragyps* and *Gymnogyps* enable these genera to locate food by visual means and also to locate food indirectly by observing the actions of low-flying *Cathartes* below. The ability of the turkey vulture to locate food sources by olfaction enables it to forage over a greater variety of terrain types than permitted the other cathartine genera. *Coragyps* will readily drop upon a suspect item of food without prior inspection, but *Cathartes* circles the potential food source until an olfactory cue has been obtained, even though the carcass is large and obvious.

Although *Cathartes* is the smallest of the five cathartine genera, is possesses the largest external nares. The anterior respiratory conchae are similarly arranged as to the angle at which they tilt downward towards the secondary choana. Only *Cathartes* possesses a large, much scrolled olfactory conchae in the olfactory chamber. Microscopic examination of the sectioned material from the olfactory chamber of *Cathartes* shows what appears to be a highly developed olfactory epithelium, not only on both surfaces of the scrolled conchae, but on the walls of the chamber as well. Examination of sectioned material from the olfactory chamber of *Sarcoramphus* shows an arrangement of olfactory epithelium very similar in appearance to that found in *Cathartes*. The tunica propria of *Cathartes* contains large numbers of Bowman's and mucous glands in contrast to the small number present in the tunica propria of *Sarcoramphus*. It can be postulated that *Sarcoramphus*, living in the humid forests of tropical America, does not require the large number of glands to keep the olfactory epithelium moist as does *Cathartes* which ranges into extremely arid regions. The layer of olfactory epithelium present in *Coragyps* is not as thick as that observed in *Cathartes* or *Sarcoramphus*, nor are the sustentacular cells as compact. Examination of a cross section through the olfactory chamber of the Old World vulture *Sarcorgyps* fails to show an epithelial development comparable to the cellular arrangement present in cathartine vultures.

A comparison of endocranial casts of cathartine vultures shows that although the brain of *Cathartes* is the smallest of the five genera, it possesses the largest olfactory bulb. The second largest olfactory bulb occurs in *Sarcoramphus*. On the basis of the size of the olfactory bulbs of fossil vultures, as demonstrated by endrocranial casts, it can be postulated that among the cathartine genera of the Pleistocene period, *Cathartes* possessed olfactory equipment closely resembling that of the present-day turkey vulture, while *Coragyps, Breagyps,* and *Gymnogyps* of the Pleistocene lacked the needed morphological structures, as do their descendents today. Examination of endrocranial casts of all recent genera of aegypiine vultures reveals that all possess a very small olfactory bulb, smilar in size to the bulbs found in the other members of the suborder Falcones.

From the evidence at hand it can be concluded that among the cathartine vultures, the turkey vulture (*Cathartes aura*) possesses and utilizes a well-developed olfactory food-locating mechanism. The king vulture (*Sarcoramphus*) of tropical America, although its behavior is little known, appears on the basis of present ethological and morphological data, also to utilize olfaction in its location of food. The need for a detailed study of the food-locating habits of *Sarcoramphus* is thus indicated. There is no evidence, either ethological or morphological, to indicate that olfaction plays more than a minor, if any, role in food location by *Coragyps, Gymnogyps* and *Vultur*. There likewise were no data to indicate that the Old World vultures employ any sense other than vision in the location of food.

Finally, it can be said that the turkey vulture appears to be the most successful of all cathartine vultures in the New World today, and that this success can be attributed largely to its demonstrated olfactory acuity. Olfaction, assisted by a specialized type of foraging flight, enables the turkey vulture to seek and locate food in a greater variety of terrain types than are available to the other members of the family Cathartidae.

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