ORNITHOLOGICAL LITERATURE

THE ROLE OF OLFACTION IN FOOD LOCATION BY THE TURKEY VULTURE (*Cathartes aura*). By Kenneth E. Stager. Los Angeles County Museum Contributions in Science, Number 81, Los Angeles, 30 June 1964: 6 × 9⅛ in., 63 pp., 19 figs.

Because of their keen senses of sight and hearing, and the lack of any overt behavior in response to odors (except in the Kiwi, Turkey Vulture, and a few procellariiforms), birds have an olfactory sense that is usually dismissed as being poorly developed. The nasal cavities, however, serve the same functions as in mammals in conducting, cleansing, and warming the inspired air. It is the other function of the nasal cavities—smell—that has aroused the interest of ornithologists since 1826, when John James Audubon reported on his experiments to test the sense of smell in the Turkey Vulture, *Cathartes aura*.

Most ornithologists have, at one time or another, discussed and debated the question of olfaction in vultures. We need not do so any longer, at least in connection with the North American Cathartidae. Dr. Stager reviews the controversy that began with Audubon's experiments and discusses the olfaction experiments of other workers. From these earlier experiments a number of hypotheses were presented to explain the ability of the Turkey Vulture to find its food. The Turkey Vulture was believed to respond to the sight and sound of hordes of flies, to the movements of carrion-eating mice and ground squirrels, or to the movements of domestic dogs in forested areas. One experimenter assumed the presence of a food-finding sense. And another, although admitting the presence of a well-developed olfactory tract, believed that it served to detect air currents, not food.

Stager briefly mentions cathartid taxonomy and reviews the paleontological record. Much of the controversy over the role of olfaction in food finding resulted from applying the observations of one vulture to all vultures, and from assuming a basic similarity and close relationship between Old and New World vultures.

Stager's personal observations and simple experiments that led to this study are convincing evidence favoring the existence of an olfactory sense in *Cathartes*. In arriving at his conclusion that *Cathartes* utilizes olfaction in locating its food, Stager conducted field experiments with noncaptive Turkey Vultures, studied the comparative behavior of the Cathartidae, and undertook comparative morphological studies of the olfactory tracts of cathartine vultures. The purpose of the author's research was "to obtain evidence to support the premise that the Turkey Vulture has a well-developed sense of smell and employs this sense to a high degree as an integral part of its food-locomotor mechanism."

The author conducted most of the observations and experiments in California. But he also gathered data in Mexico, Brazil, Bolivia, India, and Burma. In the field experiments (except the decoy–carcass tests) all visual clues relating to the bait were removed so that an olfactory stimulus was the only clue to which the Turkey Vulture could respond. If the odors, emanating from the test site on wind currents of known direction, attracted the Turkey Vultures, Stager concluded that the birds reacted to the olfactory stimulus. One series of experiments included a forced-air unit in which odors from bait placed in a chamber were forced by a powerful fan through a vertical 7-foot stack. In another series of tests carcasses were placed in portable bait chambers that were hidden in vegetation. A third series included the response of *Cathartes* to an odorous and highly volatile substance, ethyl mercaptan. In a fourth series of tests a mounted decoy deer and a fresh deer carcass were placed in an open field. All experiments were set up at night to prevent detection by vultures. During the tests the birds

were carefully observed with binoculars and spotting scope from selected sites as much as 275 yards from the bait. No controls in the usual sense were set up. The author considered that the experiments were controlled "in the sense that all visual stimuli concerned with bait material were eliminated." The odors originating from all experiments attracted Turkey Vultures.

The tests using the mounted decoy and the fresh deer carcass indicated that the sight of an animal form is not sufficient to bring the vulture down to it. A mule deer that was professionally mounted and realistically positioned to mimic a dead animal did not attract the Turkey Vultures that passed over the area on five successive days, although the decoy was placed in an open field. However, a fresh carcass brought a positive response after it was substituted for the mounted specimen. Both the decoy and freshly killed deer were placed in the same spot and in identical positions. Rather than circling directly above the dead animal, the vultures circled about 100 yards downwind, in a position to receive the wind-carried odors of the decomposing animal.

Dispelling the notion that flies are the signal that attracts *Cathartes*, Stager shows that the Turkey Vulture responds to an olfactory stimulus emanating from a site free of necrophagous insects. For 5 days flies were attracted to a sweetened concoction, but Turkey Vultures were not, although they flew over the area periodically on foraging flights.

Following the discussion and analysis of the various experiments, Stager discusses the comparative behavior of the Cathartidae in relation to food habits. That the Turkey Vulture finds its food in a different manner from the other cathartine vultures is reflected in its flight habits. In flight, *Cathartes* flaps more than the condors, less than the Black Vulture, *Coragyps*. Its flight is wobbly. It can soar in calm and light winds better than other vultures. It will feed upon smaller animals than other vultures will, but will not take live prey. Nor will it respond to the sight of a carcass alone, but must receive an olfactory stimulus before alighting. But the most important characteristic of its flight in relation to this study is that the Turkey Vulture usually forages close to the ground. *Coragyps*, on the other hand, is aggressive, soars at a higher altitude, is known to kill live animals, and will drop from a considerable height to investigate. The Andean Condor, *Vultur*, and the California Condor, *Gymnogyps*, are the best of the soaring vultures. *Vultur* frequently soars along cliffs. I have seen this type of soaring a number of times in the Argentine Andes. But once I saw a flock of 33 Andean Condors soaring several thousand feet *above* the top of the 7,500-foot ridge from which I was watching them. Few observations are available for the King Vulture, *Sarcoramphus papa*. Stager suggests that the King Vulture may also use olfaction in finding its food. It is always seen in or over forest; it frequently skims low over the forest canopy; and its olfactory chambers, conchae, and olfactory epithelium are highly developed. In British Honduras I saw King Vultures on several occasions soaring just over the trees. But more often I saw them circling singly or in pairs high in the sky, so high that without field glasses they appeared only as unidentifiable specks.

Stager's morphological studies included an examination of the gross and microscopic anatomy of the olfactory chamber, and the comparative size of the olfactory bulbs. The results show that (1) the absolute size of the external nares is greater in *Cathartes* than in the other Carthartidae, although the Turkey Vulture is smaller than all others except *Coragyps*; (2) the anterior respiratory conchae in each genus of Carthartidae is different, markedly so in *Cathartes* and *Sarcoramphus* where it assumes a nearly vertical position instead of a horizontal one; (3) the olfactory chamber is more highly developed in *Cathartes* than in the other vultures examined (no example of *Vultur*);

(4) the olfactory chamber and its concha or tubercle are lined with a thicker layer of columnar epithelium that contains more gland cells than is found in *Coragyps* and in the Old World vulture, *Sarcogyps* (*Sarcoramphus* showed a high degree of development of the nasal epithelium similar to that in *Cathartes; Vultur* and *Gymnogyps* were not examined); (5) the olfactory bulb is larger in the Turkey Vulture than in any other cathartine vulture or several Old World vultures examined.

One question that occurred to me, as I perused this paper, concerned the distance at which the Turkey Vulture detects the odor of a decomposing animal. Olfaction undoubtedly operates at short range. There is nothing in the report to indicate otherwise. Obviously, many variables enter into this problem, such as the size of the animal, how long it has been dead, and the strength of the air currents. Stager does not mention the distance between the test site and the point at which the Turkey Vultures turned into the odorous air current and glided toward the bait. His only references to distance were when he walked "several hundred yards" and 200 yards downwind, and easily detected the odor of the bait or ethyl mercaptan.

The publication contains few typographical errors. But two of these may confuse the reader. Thus the captions for Figures 16, 17, 18, and 19 should be on the right-hand margin instead of the bottom of the page. On page 20, precaution Number 2 should read: "All baits were placed in the blower at night to rule out any possibility of detection by turkey vultures. Baits were placed in the blower at 4:00 a.m. to prevent molestation by carnivores." The date of the Koford reference on page 38 should read 1953.

This publication represents an important contribution to ornithological knowledge. For well over 100 years the question of olfaction in vultures with regard to food finding has remained an open one. Although much has been written on the subject of olfaction in vultures, no previous study was as thorough. Earlier studies were performed for the most part only with captive birds, or were one-shot field tests. Probably the most convincing field tests prior to this report were those conducted by Chapman (1938. "Life in an Air Castle"). Not only has Stager conducted a convincing series of field experiments, but has supplemented these with morphological studies that provide new knowlege on the olfactory sense of vultures. The development of the rubber latex technique provides a useful tool for the study of external form and size of major divisions of the brain in the absence of the brain itself. This study seems to show rather conclusively that *Cathartes aura* has a well-developed sense of olfaction used in locating food at short range. The other cathartine vultures, with the possible exception of the King Vulture, lack the degree of olfactory development and the flight behavior that enable the Turkey Vulture to locate its food by smell.—DOUGLAS A. LANCASTER.