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SCAVENGING EFFICIENCY OF TURKEY VULTURES IN TROPICAL FOREST[1]

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Abstract. A series of baits was used to study the scavenging efficiency of Turkey Vultures (*Cathartes aura*) in tropical forest. These birds were found to rely almost entirely on their sense of smell to locate food. They could not easily find animals that had died recently, were efficient at locating one-day-old carcasses, and tended to reject meat that was rotten. Estimates of the amount of food taken from the baits showed that Turkey and Black vultures removed about 90% of the provided food supply.

Key words: *Turkey Vultures;* Cathartes aura; *Panama; scavenging.*

INTRODUCTION

Cathartid and accipitridine vultures are important members of many tropical communities (Houston 1979). The vultures of the Old and New Worlds differ markedly, however, in the range of habitats they occupy. Forested areas of Africa or Asia do not support scavenging birds, while neotropical forest is the center of distribution for the cathartid vultures. This contrast implies a difference in the scavenger food chains of these regions (Houston 1985), but I know of almost no published information on the role of various scavenging animals in tropical forest. The present study examines the importance of the Turkey Vulture (*Cathartes aura*) as a consumer of carrion in the forest and considers two main questions: how do vultures find carcasses, and how much of the available carrion is consumed by Turkey Vultures?

Turkey Vultures have a well-developed olfactory lobe (Bang 1964) and sense of smell (Stager 1964) which is used for finding food in forested areas (Chapman 1929, 1938). This species and the closely related Greater Yellow-headed Vulture (*C. melambrotus*) are the commonest vultures of neotropical forests.

Chapman (1929, 1938) described the foraging behavior of Turkey Vultures over forest. The birds soar at low altitude immediately above the tree canopy and rarely flap their wings, gaining lift chiefly from the rising air on the windward side of tall trees that emerge through the canopy. They do not descend below the canopy unless they have detected food, but once inside the forest they can maneuver well at low flight speed, even in congested vegetation, and fly from branch to branch or walk along the ground until they locate food.

I made this study by placing out carcasses in different situations in a forest. I assumed that birds would depend on both vision and olfaction to locate food in such a dense habitat. I investigated the relative importance of these two senses in several ways. First, I placed carcasses in sites that were of varying visibility from above the tree canopy, to see if baits in open positions were located most rapidly. Secondly, I compared the time taken for birds to find uncovered and hidden carcasses. If smell were an important cue for locating food I assumed that the age of a carcass, and hence its smell, might influence whether vultures could find it. I therefore provided a series of carcasses of different ages to compare how quickly they were located. I also investigated whether the birds preferred fresh or decayed meat by offering a choice of carcasses and recording which they selected to eat.

Vultures are not the only animals in forest that feed from carcasses. Several mammal species will scavenge, and many insect larvae develop in carrion. The effectiveness of vultures as scavengers will depend on how quickly they can locate and consume the food compared with these other scavengers. I therefore recorded the time taken for vultures and other scavengers to find carcasses and the amount they ate.

METHODS

Observations were made during November and December 1982 in secondary forest at the Smithsonian Tropical Research Institute on Barro Colorado Island, Panama (area 15 km^2); see Leigh et al. (1982) for habitat details. I used chicken carcasses as baits because natural carcasses are difficult to find in forest. Chickens weigh approximately the same as the commonest food items for vultures, such as dead sloths, small monkeys, and opossums (Houston 1985). I bought chickens early in the morning at the market in Panama City, where the birds were killed but were not eviscerated. I chose brown feathered birds, but when this

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supply was not available I had to use some carcasses that had been plucked but were otherwise intact. I took the chickens straight to the island and either placed them directly in the forest or kept them in wire cages in the forest until they were needed. My observations from a canopy tower on the island over eight days showed that Turkey Vultures never flew over the forest before 0700 or after 1730. Unless otherwise stated, all carcasses were placed in the forest at times when birds were not flying; this was to prevent birds from watching me and following above the tree canopy as I distributed the baits. I mostly used areas of the island rarely visited by other scientists (Fairchild, Gross, Miller, and Barbour trails) to avoid disturbance. In order to obtain a reasonable number of observations in a short study, I set out a number of carcasses at each trial, positioning them in a line along a trail. To prevent birds from concentrating where bait was being offered, trails were reused only after an interval of at least two weeks. Carcasses were placed 200 m or 400 m apart, unless otherwise stated. I took each bait 50 paces from the path and laid it directly on the ground, trying to cause minimal disturbance to the surroundings to prevent visual cues at the bait site. Any notable characteristics of the bait site (hill ridge, valley bottom, etc.) were recorded. I did not take account of wind direction in these trials. There is no easy way to detect wind direction above the canopy from the still air on the forest floor, and observations I have made from a canopy tower show wind direction often changes during the day. It was not possible to standardize the time interval between my visits to the carcasses. I tried to use baiting sites where the same route could be followed each time, so that time intervals were roughly similar. But on trails along a peninsula I had to reverse direction for successive checks of baiting stations, and intervals between checks varied as a result. I tried to visit each carcass at least every 3 hr through the day, and I varied the number of baits used to make this possible. On most trails I monitored six to eight separate bait sites. Earlier observations over a 5-day period from a blind had shown that Turkey Vultures usually took more than an hour to descend from the canopy to a carcass and feed slowly, so I could usually estimate an arrival time within 1 to 2 hr according to the feeding stage the bird had reached. But all times given here are intended as rough estimates only and not as precise figures. I found that the birds were not alarmed by my presence, provided that I approached the bait sites carefully. If birds were present, I withdrew as soon as I saw them and continued on to the other bait sites. Carcasses were examined only after birds had finished feeding and had left the sites. Birds were recorded as having located a bait if they were seen either feeding from it or perched below the canopy nearby. All times are given in hours from when the bait was placed in the forest. For those carcasses not located until the next day, I have subtracted the 12 hr of darkness, and results are given as "daylight hours." The first visit each day was made before vultures were airborne, to record if nocturnal mammalian scavengers had fed. The final visit was made before dusk, when vultures were no longer flying, to record the food available for nocturnal scavengers.

All other animals seen feeding at a bait were recorded at each visit. Carcasses were weighed on a spring balance before being set out, and again at each visit if any meat had been removed. I sometimes estimated weight because vultures dismembered carcasses and flew away with bones, making an accurate measure of meat consumption impossible. Weight loss through dehydration was not accounted for, nor weight gain due to light rain, because these were found to be slight. Partly eaten baits were left in position, and subsequent scavengers were also recorded. Baits were monitored until they had been entirely consumed.

To investigate the use of vision by the birds, I estimated the proportion of clear sky above some baiting sites to indicate the visibility of the carcass to a bird flying above the canopy. To do this I used a 35-mm camera with a 35-mm lens to take a photograph from eye level looking vertically above the site where each bait was placed. These photographs were printed onto high contrast paper, and I used a computer program for plotting area to measure the proportion of sky visible in each photograph. To investigate the use of olfaction, I covered some carcasses with dried leaves until they were invisible to me.

RESULTS

HOW VULTURES FIND CARCASSES

The effect of overhead cover above a carcass. These results were obtained from uncovered carcasses that were one day old when placed in the forest. I found that there was no clear correlation between the percentage of open sky above a carcass, as measured from photographs of the canopy, and the time taken in daylight hours for vultures to find the food ($r = -0.24$; $P > 0.5$; $n = 24$). There was no difference ($t = 0.35$; df = 15; $P > 0.5$) in the time taken to locate carcasses sited on hill ridges (mean daylight hours 7.9 ± 1.2; $n = 12$) or valley bottoms (8.8 ± 2.5; $n = 5$).

The effect of carcass visibility on the ground. These results were obtained from carcasses that were one day old when placed in the forest. There was no significant difference ($t = 0.54$; df = 34; $P > 0.5$) in the time taken for carcasses that were covered by dried leaves to be located (mean daylight hours 8.25 ± 0.8, $n = 12$) compared with those left uncovered (9.02 ± 0.92, $n = 24$). The method used here for when birds located a carcass, however, often recorded only the time when birds reached the general area in which the carcass was sited; many birds had not yet found the exact position of the carcass. Vultures may have landed at and started to feed more quickly on visible baits than on hidden ones, but this cannot have been a difference of more than a few hours because there was also no significant difference in the time recorded when vultures had finished feeding from covered and uncovered carcasses (mean daylight hours 10.5 ± 1.1 and 11.6 ± 0.9 respectively: $t = 0.69$; df = 34, $P > 0.5$). Turkey Vultures were also regularly attracted to the wire cages at the Research Institute where the carcasses were stored but were not visible.

Age of carcass. I compared the proportion of fresh, one-day-old, and four-day-old carcasses which were located. Unfortunately it was not possible to place all these out at the same time of day because of problems in getting carcasses to the island: the chickens killed at dawn had to be placed at midday, while the older carcasses were placed soon after dawn. I can therefore compare only the number of carcasses located by vultures during the afternoon. This may have given an advantage to carcasses which had been placed at dawn, some of which might have been detected during the morning by birds I did not see above the canopy. During the 4-hr period between 1400 and 1800, 1 out of 16 fresh carcasses, 11 out of 24 one-day-old carcasses, and 2 out of 7 four-day-old carcasses were located. Thus, vultures were much less efficient at locating fresh bait than at locating one-day-old carcasses ($\chi^2 = 7.16$; $P \leq 0.01$), probably because the fresh bait was not yet releasing a strong odor. However, both the one-day-old and four-day-old carcasses had a powerful scent, by human standards, and yet vultures did not locate four-day-old baits significantly more than fresh carcasses ($\chi^2 = 2.14$; $P \geq 0.1$), and they were less efficient, but not significantly so ($\chi^2 = 1.53$; $P > 0.1$), at finding four-day-old carcasses than those one day old.

There could be two reasons why it was the older of these two strongly smelling baits that seemed not to attract Turkey Vultures quite so effectively: either the older carcasses produced a different odor that the vultures could not detect so well, or the vultures did detect them but on some occasions chose not to respond because they preferred meat that was not so badly decayed. To consider this second alternative, I baited nine sites with two carcasses each, one 24 hr old and one 120 hr old, placing these carcasses 5 m apart at each site. The mean amount of meat consumed by the first group of vultures to locate the bait was 64% ± 9.5 from the 24-hr carcasses and 19% ± 7.9 from the 120-hr carcasses, four of which remained untouched. This shows that where vultures were given a direct choice they preferred to eat a younger carcass ($P < 0.01$, Mann-Whitney U-test).

EFFICIENCY OF VULTURES AS SCAVENGERS AT CARCASSES

Efficiency of Turkey Vultures at locating carcasses. I was extremely surprised at the speed and efficiency with which carcasses were located. Of 24 uncovered carcasses which were one-day-old when placed in the forest, 80% were located within 12 hr; the remainder were all located the following day. Of a total of 74 baits used in this study, Turkey Vultures found 71 within three days of their becoming available; the only baits that did not attract birds were all badly decayed when provided.

It is possible that birds were locating these baits so rapidly because they were placed out in a line. If Turkey Vultures could smell carcasses over distances of several hundred meters, then having located one bait in the series they might be attracted to the others in the trial. Or, vultures circling over one carcass may attract birds to the general area, who would then be more likely to find adjacent carcasses. To investigate these possibilities, I compared the time interval between the location of the first carcass in each trial and the two nearest adjacent baits with the time interval to the most distant two baits; there was no difference (mean daylight hours 4.6 ± 0.8 and 4.1 ± 0.8, respectively, $t = 0.40$, df = 22, $P > 0.5$). On 10 separate occasions I also placed an isolated chicken carcass, which was not one of a series, on the island during this study and on an earlier visit in March 1972. They were all located by Turkey Vultures within two days. This further suggests that the baiting method used in this study did not distort the normal searching efficiency of the vultures.

Amount of carrion consumed by vultures and other scavengers. Vultures were the major scavengers and removed a total of about 90% of the original weight of the chicken baits (Table 1). For these data I did not include any baits that were more than 24 hr old when placed in the forest. Because some of the baits were placed out as fresh carcasses and some as one-

TABLE 1. Proportion of available carcasses located by vultures and scavenging mammals and estimates of the food consumed.

	Time interval since carcass was placed								
	1st day	1st night	2nd day	2nd night	3rd day	3rd night	4th day	4th night	Total
Number of carcasses available	28	28	61	17	17	4	3		
Weight of carcasses available (kg)	49.0	48.1	108.4	30.2	28.0	9.4	7.9		110.7
Number located by vultures	1		52		16		3		
Weight of food eaten by vultures (kg)	0.9		78.2		18.6		2.0		99.7
Number located by mammalian scavengers		3		3		1		1	
Weight of food eaten by mammalian scavengers (kg)		1.4		2.2		1.5		0.2	5.3

day-old carcasses, the sample size changes between Days 1 and 2. The sample size on subsequent days depended on how many of the carcasses from previous days still had meat available. Large bones, representing about 5% of carcass weight, were usually not swallowed by vultures, but smaller bones were. If the large bones are considered as inedible, the vultures were taking about 95% of the available tissues. It was not possible to distinguish the food consumption of Turkey Vultures from that of Black Vultures (*Coragyps atratus*). Details of the interactions between these species will be published elsewhere, but is was unusual to see more than two or three Turkey Vultures at a carcass. Black Vultures were present at only 17% of carcasses, and they sometimes arrived long after Turkey Vultures had been feeding. Black Vultures were dominant over Turkey Vultures at food sites and were also present in much larger groups; 14 birds were seen at one bait. But overall, their food consumption cannot have been substantial. Mammalian scavengers did not locate any of the carcasses during the first day and then subsequently found only a few carcasses at night. It is not known which mammals had fed, but an opossum (*Didelphis marsupialis*) and a coati (*Coati coati*) were seen feeding on carcasses placed near the research station. Mammals accounted for about 5% of the total food taken by scavengers.

Carrion flies and hymenoptera were recorded on all carcasses, but no baits remained intact long enough for invertebrate scavengers to consume a substantial proportion of the carrion. In some cases small pieces of skin and tissue remained on bones after the vultures had left, and these supported a few dipteran larvae. Their overall food consumption was too small to record.

DISCUSSION

Neotropical forests may provide a large food supply for scavenging animals. Estimates based on mammalian biomass data from Eisenberg and Thorington (1973) suggest that the forests on Barro Colorado Island may have about 750 kg of animals dying per year per km^2, providing an average food supply in the form of one animal weighing 4.1 kg dying every two days per km^2 (Houston 1985). The density of carcasses provided during this study was therefore somewhat greater than, and in addition to, the normal supply of carcasses, but probably no more than natural seasonal variation and not sufficient to distort seriously the normal food supply.

This study used unnatural carcasses, but there is no evidence that scavengers treated them differently from natural food items. The results show smell to be the major sense used by Turkey Vultures to locate carrion and puts vision in a minor role, for completely hidden food was found as quickly as visible bait. The vultures found few carcasses until these were about a day old, and had begun to putrefy. Olfaction in Turkey Vultures is so highly developed that it is surprising how contentious a subject this has been (see review by Stager 1964). Audubon's first publication (1826) was on trials which suggested that these birds could not smell. Many such early experiments probably gave conflicting results because they were based on the assumption that the more putrid, stinking, and rancid the food being offered, the more likely the vultures were to seek it out. The reverse is probably the case. This study showed that wild birds, if given the choice, preferred meat that was comparatively fresh. Janzen (1977) has suggested that many bacteria produce toxins and unpalatable compounds whose main function is to deter larger scavengers. Vultures undoubtedly have a resistance to some of these compounds, but it is reasonable to assume that the birds would not ingest toxins if this were unnecessary. The chemicals given off by rotting meat vary with time, and insect scavengers use these cues to determine whether a carcass is suitable for egg laying (Lindstedt 1971). Even the human

nose—with experience—can tell from the smell approximately how old a chicken carcass is. Doubtless vultures can do the same and may sometimes detect carrion but not bother to descend to feed on it if they know it to be rotting.

It was not possible to separate the food consumption of Turkey Vultures from that of Black Vultures. Black Vultures do not have a sense of smell (Stager 1964), and my observations in other study areas have shown that they are not found in undisturbed forest and cannot locate food in forest conditions unless led there by Turkey Vultures. The Turkey Vulture is the only species to be commonly found inside the forest on Barro Colorado Island, while some other areas of the neotropics have other vulture species coexisting and competing for the food supply.

I find it surprising that the mammalian carnivores were so inefficient at locating carcasses. The common opossum alone has a density of 45 animals per km^2 on Barro Colorado Island (Glanz 1983). However, the daily foraging area of mammals is limited by the energy they expend in food searching and by their slow walking speed. Vultures use little energy in soaring (Pennycuick 1976) and can quickly cover large areas of forest. Most mammalian carnivores will probably consume carrion whenever they have the chance. But the greater foraging efficiency of the vultures enables them to locate and consume most carcasses first. In this study vultures found almost all carcasses long before carrion insects had been able to consume the food; invertebrates may be more important in the breakdown of small carcasses (Cornaby 1974).

Barro Colorado Island supports a high density of Turkey Vultures. Chapman (1929, 1938) concluded that the island usually contained about 12 foraging birds at any one time. My own observations on the island and counts of birds from boats suggest that this figure is still a reasonable estimate, giving a density of about one bird per 1.25 km^2. This is similar to the density of *Cathartes* vultures along the Rio Negro in Amazonia in Brazil (Houston 1984). On Barro Colorado Island the birds are not resident and are regularly seen crossing to the mainland. Chapman (1938) reported that in a banding study 37 birds were caught over a two-month period, and at the end of this time there were five times as many unmarked birds being caught as marked ones. Birds therefore forage widely and do not patrol a fixed feeding range.

There is no reason to believe that Turkey Vulture activity on Barro Colorado Island was abnormal or was unrepresentative of neotropical forests in general. Vulture migrations were taking place over Panama at the time of this study (Smith 1981), but there is no indication that this caused an increase in the density of foraging birds in the study area. This study was undertaken during the dry season, however, which probably provides the optimum conditions for soaring, and it is likely that foraging efficiency would be lower during the rainy season.

These trials suggest that Turkey Vultures are the major scavengers in neotropical forest and depend on their sense of smell to locate food. None of the Old World vulture species have a sense of smell, which may account for their absence from all forested areas of Africa and Asia. The scavenger food chains there must be quite different from those of neotropical forest.

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