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Foraging behavior of a guild of Neotropical vultures.—Coexistence of two ecologically similar species within a habitat is achieved by the evolution of some degree of difference in resource use. By feeding on different foods, at different sites, or with different foraging behaviors, species can avoid competitive exclusion. Avian scavengers, which feed upon an unpredictable and ephemeral resource, may finely divide their food resource along one or more resource axes in order to survive. Wallace and Temple (1987) demonstrated that scavengers presented with very large carcasses in open habitat showed interference competition by establishing a dominance hierarchy among species locating the resource. This guild of New World avian scavengers formed a dominance hierarchy with Andean Condors (*Vultur gryphus*) on top, followed by King Vultures (*Sarcoramphus papa*), Crested Caracaras (*Polyborus plancus*), Turkey Vultures (*Cathartes aura*), and Black Vultures (*Coragyps atratus*), in that order. These authors observed feeding at large carcasses in open areas that were frequented by all the species of scavengers in the guild. The largest carcasses were opened to make them available to small scavengers and larger scavengers at the same time. More than half of the carcasses provided were burros (*Equus asinus*). In the forested areas of the tropics, this type of resource is unavailable. Houston (1984a) showed that most of the biomass available to vultures on Barro Colorado Island, Panama, comes from animals with masses less than 3 kg. In addition, differences in foraging behavior and sensory physiology may make carrion in forest habitats less available to some species of scavengers than to others. Niche overlap may be quite different for avian scavengers feeding on small carcasses in a tropical forest than it is for those same scavengers feeding in a coastal desert. In a tropical rain forest, competition for a dispersed, ephemeral resource may depend upon differential exploitation rather than interference.

Here I describe the interactions among the species in a guild of Neotropical vultures in a complex, natural environment. The carcasses used were not large and they were presented to the vultures in a variety of habitats. This method was intended to approximate the distribution of carcasses that a vulture would normally encounter in the rain forest. It is my hypothesis that vultures feeding in the rain forest use differential exploitation to avoid competitive exclusion. In this paper, I will discuss niches separated in space and along a time axis. Cody (1974) stated that time is only important to competition and coexistence due to seasonal shifts in the species composition of communities. I will provide an example in which differences in resource use by Neotropical vultures at different times allow coexistence of closely related and ecologically similar species.

Study site and methods.—This study was conducted at Estacion Sirena in Parque Nacional Corcovado on the Osa Peninsula in southwestern Costa Rica (8°26′N, 83°35′W) from June to August 1987. Turkey Vultures, Black Vultures, King Vultures, and Lesser Yellow-headed Vultures (*Cathartes burrovianus*) are sympatric in the coastal regions of Corcovado (Stiles and Janzen 1983). Estacion Sirena is adjacent to the Pacific Ocean and is surrounded by a patchwork of primary tropical wet forest (Herwitz 1981, Hartshorn 1983), second growth forest of various ages, gaps in the forest, and beach. Historically, portions of the area have been the sites of intensive agricultural use, but since the establishment of the park in 1975, the vegetation has been allowed to recover. The primary forest is characterized by a continuous canopy more than 10 m from the ground and a sparse understory. Due to the historical land use of this area, most of the primary forest is located on rough terrain (hillsides, ridges, etc.), with the exception of one large patch of forest on flat terrain adjacent to the ocean. The second growth forest is characterized by dense stands of *Heliconia* spp. and *Calathea* spp. This dense growth is typically 2 to 5 m tall and fairly homogeneous. There are frequently tall, slender trees (i.e., *Cecropia* spp.) emerging from this dense growth, but

the canopy is far from complete. As a result, much sunlight reaches the understory which is nearly impenetrable. The gap habitat is an area of mown grass surrounding the station and on the airstrip southwest of the station. This area is constantly maintained and lacks all vegetation except for herbal growth less than 20 cm tall. For this study, the beach, which lacks all vegetation, and the airstrip will be called gap habitat.

Resource partitioning and habitat use were studied by observing the feeding locations and behavior of all four species of vulture at carrion placed at several locations in each of the three habitats. Carrion baits were 33 similarly sized (3–5 kg) fresh, whole fish carcasses (*Caranx* spp.). The carcass of a spinner dolphin (*Stenella longirostris*) which was found shortly after it had died was also included in the study. Carrion placed in primary forest was completely obscured from above by the forest canopy which was 20 to 50 m above the ground. Carrion placed in the secondary forest was completely obscured from above by the dense understory. Carrion in open habitat was not obscured at all. Carcasses were concealed until they were placed on the ground at mid-day when the vultures were typically roosting. No carcasses were placed near roosts and no vultures were in view when the carcasses were distributed.

Each carcass was observed each day until it was totally consumed. To avoid disturbing the birds, observers remained 50 m or more away from the carcasses and observed the vultures using 10× binoculars and a 25× spotting scope from a concealed position. Observers were located in positions that provided views of the carcass, surrounding ground and vegetation, and a large portion of the sky above the carcass. The time course of vulture arrival and carrion consumption was recorded in days from the time that the freshly caught fish was placed out for the vultures.

In this study the resources considered were habitat type (gap, secondary forest, and primary forest) and age of the carcass (days since first available). The data collected were not adequate to determine the number of individuals of each species feeding upon each carcass, but the species feeding upon each carcass were identified. Since individual birds arrived at carcasses at different times and left after short feeding bouts, birds would have had to have been individually marked in order to estimate numbers of each species present. The numbers in the data represent the occurrence of one or more individuals of that species feeding on a single carcass on that particular day. Each observation could represent one or more individuals of a single species.

Results.—The composition and behavior of feeding aggregations were different depending upon where the food was located. When carrion was placed in the open gap habitat, either Turkey Vultures or Black Vultures were the first species to arrive and feed. Feeding aggregations in the gap habitat could be very large with three or four species represented, but no interspecific aggression or even casual displacement was observed. Intraspecific aggression was common only among Black Vultures. In the secondary forest, perhaps due to limited visibility and open ground, Black Vultures and Turkey Vultures foraged and fed individually or in small single species and mixed species groups. No interspecific aggressive encounters or displacements were seen. Under the primary forest canopy, where carcasses were obscured from view of birds above the canopy, Turkey Vultures or King Vultures were the first species to arrive. King Vultures were frequently the first birds to locate a carcass and would feed upon it before Turkey Vultures arrived. On one occasion, Turkey Vultures located a carcass 15 m away from the edge of a gap in the primary rain forest. They approached the carcass from downwind, flying back and forth perpendicular to the wind direction. As they were approaching and descending toward the carcass, a large group of Black Vultures from a nearby roost tree joined them. The Turkey Vultures began feeding first, and the Black Vultures began feeding moments later.

Vultures fed upon 18 carcasses in three different habitats (Fig. 1). On many occasions, more than one species fed upon the same carcass, and in all cases more than one individual

bird fed on each carcass. Turkey Vulture feeding activity was widely distributed in all three habitat types. Black Vulture feeding activity was concentrated around the gap habitat and highly disturbed areas of the adjacent forests. In both cases where Black Vultures fed in the primary forest, they landed in the open habitat and walked under the canopy. Most of the carcasses fed upon by King Vultures were in the primary rain forest, except for the spinner dolphin on the beach. This was also the only site where Lesser Yellow-headed Vultures were seen feeding. All four species were seen feeding on the dolphin on the same day.

Most feeding occurred the day after the fresh carcasses were made available. Carcasses made available on Day 0 were seldom fed upon until Day 1. In subsequent days, the number of feeding vultures decreased steadily due to consumption of the carcass. Few carcasses were still present beyond Day 4, and any feeding that occurred during this time was included in Day 4. Black Vultures and Turkey Vultures were observed on every day while King Vultures were not seen feeding on very fresh carcasses or carcasses more than four days old.

The temporal distribution of feeding varied among the three habitats (Fig. 1). Every species fed in the open habitat, with Turkey Vultures present only on the first three days and Black Vultures present on all days. King Vultures fed only on Day 1 and Day 2. The temporal distribution of feeding in secondary forest was very different, with only two species represented. The temporal distribution of feeding in the primary forest indicates that no feeding occurred on Day 0 and that the feeding was dominated by two species, Turkey Vulture and King Vulture.

Discussion.—Vultures feed on an unpredictable and ephemeral resource. Most of their foraging energy is spent searching for carrion, and when they find carrion, they are observed by other vultures which quickly follow them to the food source. The carcasses they feed upon are usually not large enough to allow all vultures to feed without some intraspecific or interspecific competition. In addition, the carcasses decompose rapidly and are only available to the vultures during a brief time period. As a result, many vultures are forced to feed upon a limited resource at essentially the same time.

Cathartid vultures in the lowland tropical rain forest of Costa Rica partition their feeding behavior spatially and temporally. A similar guild structure has been seen in accipitrid vultures in East Africa (Kruuk 1967). There, as here, the character of the resource changed over time and species with the appropriate adaptations were able to use the various resource states as they occurred.

The method that vultures use to locate carrion also affects the temporal segregation of feeding. The species that feeds on a carcass first should be the species that detects it first. Turkey Vultures probably use olfactory cues to locate food while Black Vultures rely on vision (Stager 1964, Houston 1986, but see Smith and Paselk 1986). Stewart (1978) suggested that Black Vultures seem to follow Turkey Vultures to carrion. In this study, Black Vultures arrived first at carcasses in the open where they were highly visible, but arrived second at carcasses under the forest canopy where olfactory cues may have been more important. It appears that the species that was most proficient at detecting carrion in each habitat arrived first. The less proficient species had to rely on cues from the other species to provide information about the location of food. Carrion placed in the open gap habitat was located quickly because more species were proficient at detecting it. All cathartid vultures have acute eyesight and are able to find carcasses that are visible from above. Carcasses that were on the forest floor were harder to detect. Only those species that have the ability to detect carrion by using non-visual cues could locate it. As a result, feeding began later on carrion in primary and secondary rain forest than it did in the gap habitat.

Little is known about the foraging behavior or physiology of King Vultures and Lesser Yellow-headed Vultures. Houston (1984b) suggested that King Vultures were unable to detect carrion by the use of olfactory cues. In this study, King Vultures were able to locate

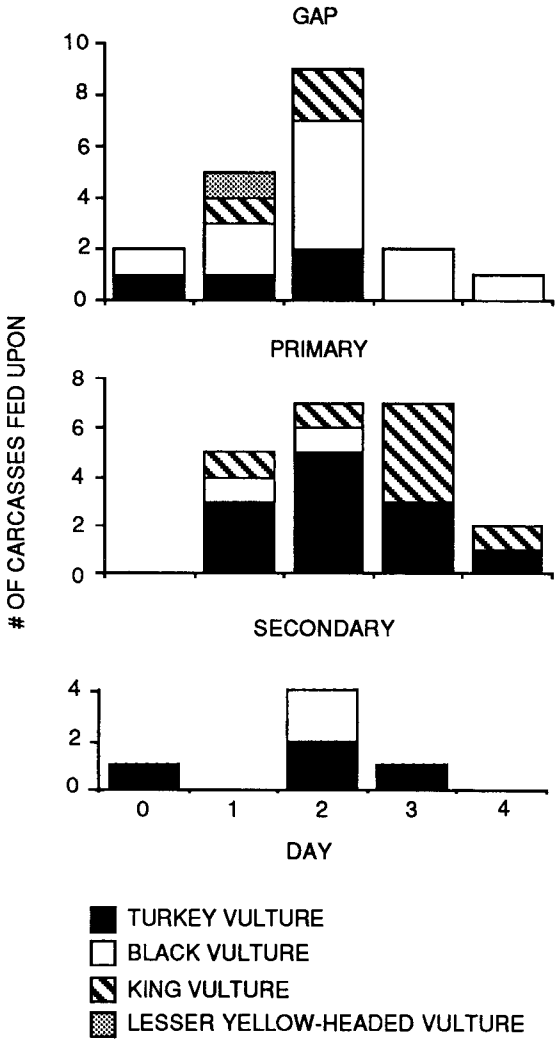

FIG. 1. The temporal distribution of vultures feeding in three habitats.

carrion beneath the closed primary forest canopy independent of Turkey Vultures. Although the physiological evidence that King Vultures use olfaction to locate food is not available, this study shows that King Vultures use cues other than visual cues, such as olfaction, to locate carrion in the forest. A more detailed study of the physiology and behavior of carrion detection by the King Vulture is needed.

In a relatively undisturbed tropical rain forest environment, cathartid vultures do not feed in the same habitats. Black Vultures specialize on carrion located in the open, while

King Vultures are forest specialists. Turkey Vultures are habitat generalists, feeding in the open and in the forest, but they separate their feeding from the other species temporally. Turkey Vultures specialize in carrion that is relatively fresh. In most cases, they locate it first and leave before individuals of other species arrive in great numbers. King Vultures feed on carrion that is slightly older, but they too leave while carrion is still available. Black Vultures are temporal generalists and will eat anything. They will commonly feed upon a carcass for two days after the last Turkey Vulture or King Vulture has departed.

The community structure of this guild of vultures closely parallels that of the accipitrid vultures in the open savannah of East Africa (Kruuk 1967). In that community the White-headed Vulture (*Trigonoceps occipitalis*) was typically first to arrive at a carcass and the White-backed Vulture (*Gyps africanus*) was a temporal generalist. Avian scavengers in the open agricultural land of Peru showed a similar temporal displacement pattern (Wallace and Temple 1987). The results reported here show that the temporal organization of a guild of avian scavengers was dependent upon the habitat in which they fed and upon the method used to detect carrion.

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