# COMPETITIVE INTERACTIONS WITHIN AND BETWEEN SPECIES IN A GUILD OF AVIAN SCAVENGERS

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ABSTRACT.—We observed Andean Condors (*Vultur gryphus*), King Vultures (*Sarcoramphus papa*), Black Vultures (*Coragyps atratus*), Turkey Vultures (*Cathartes aura*), and Crested Caracaras (*Polyborus plancus*) interacting at 217 animal carcasses at two sites in northern Peru. At 53 carcasses for which we knew order of arrival, Turkey Vultures usually arrived first, Black Vultures second, and condors third. On the basis of our observations of 8,066 aggressive encounters between birds, we constructed dominance hierarchies by calculating the proportion of encounters won by an individual of one species, sex, or age during encounters with an individual of another species, sex, or age. Within each species there was a positive relationship between a bird's dominance and its age. In condors, males dominated females of the same age. Interspecific dominance was correlated positively with body mass. There are convergent similarities between the organizations of guilds of Old and New World vultures.
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WHEN limited resources are found in widely dispersed, rich patches that are ephemeral and unpredictable in spatial and temporal occurrence, competition between consumers could involve either differential exploitation or interference. Differential exploitation in such situations is often based on the differential ability of individuals to locate the resource, and interference usually is achieved through the establishment of dominance hierarchies among individuals that have found the resource (Maurer 1984). Avian scavengers that feed on carcasses of large animals compete for just such a limited, dispersed, rich, ephemeral, and unpredictable food source, and differences in order of arrival at carcasses and dominance hierarchies when birds are feeding together have been reported among members of scavenging guilds (Kruuk 1967, Houston 1975).

The most detailed studies of competitive interactions between avian scavengers have taken place in Africa where large guilds of Old World vultures (Accipitridae) feed on ungulate carcasses (Petrides 1959; Attwell 1963; Kruuk 1967; Houston 1974, 1975). In contrast, there have been few descriptions, most of them anecdotal accounts (e.g. Koford 1953, Stuart 1978), of competitive interactions in guilds of New World vultures (Cathartidae).

We observed patterns of differential exploitation and interference within and between 5 species that are competing members of a guild of avian scavengers in northern Peru: Andean Condors (*Vultur gryphus*), King Vultures (*Sarcoramphus papa*), Black Vultures (*Coragyps atratus*), Turkey Vultures (*Cathartes aura*), and Crested Caracaras (*Polyborus plancus*). We have shown previously that during our study several of these species were being limited by the availability of carrion during a prolonged pre-El Niño drought (Wallace and Temple 1987).

## STUDY AREA AND METHODS

The field observations took place between 1980 and 1984 in northern Peru in the Cerro Illescas region and in the vicinity of Ñaupe. The Cerro Illescas is an isolated mountain range of the Sechura Peninsula (6.0°S, 81.0°W). Avian scavengers in this study area fed almost exclusively on the carcasses of either marine birds and mammals that washed ashore on the peninsula's beaches or feral ungulates that died in the surrounding desert. The Ñaupe area is about 150 km east of the Cerro Illescas in the western foothills of the Andes (5.35°S, 79.4°W). Avian scavengers in this study area fed primarily on carcasses of domestic livestock that died on the area's desert grasslands.

In both areas we observed birds interacting at 217 carcasses of large animals at as many sites: 129 burros (*Equus asinus*), 57 dogs (*Canis domesticus*), 12 sea lions (*Otaria byronia*), 10 goats (*Capra hircus*), 4 horses (*Equus caballus*), 4 pigs (*Sus scrofa*), and 1 green sea turtle (*Chelonia mydas*). Each of these carcasses was sufficiently large to be highly attractive to all members of the guild. We opened the largest carcasses so that they could be consumed by all guild members. If we had not done this, smaller vultures would have been forced to wait until larger birds had first ripped the thick-skinned carcasses open. We watched these carcasses for a total of 4,071 h from blinds positioned

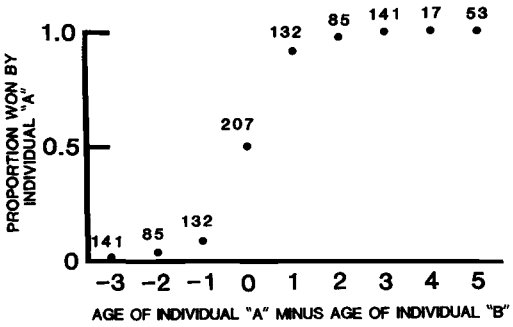


Fig. 1. Proportion of encounters won by a King Vulture of a certain age (individual A) when interacting with a King Vulture of another age (individual B). Number above each point is sample size. Age differences are in years.

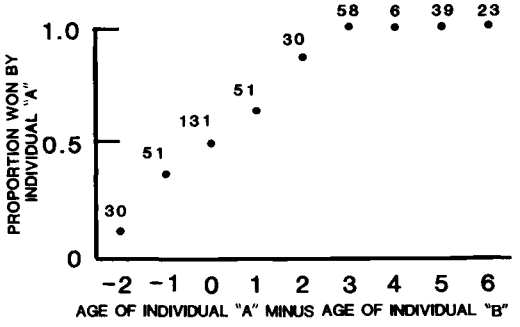


Fig. 2. Proportion of encounters won by a male Andean Condor of a certain age (individual A) when interacting with a male condor of another age (individual B). Number above each point is sample size. Age differences are in years.

nearby or, by using telescopes, from vantage points up to 0.75 km away. The number of scavengers observed at these carcasses ranged up to 240 individuals at a time.

We identified all species that visited the carcasses, and when possible we noted individual sex and age. Andean Condors are sexually dimorphic and undergo sequential changes in plumage, beak, and eye coloration until they are 6–7 yr old (K. C. Lint pers. comm., J. W. Carpenter pers. comm.). This allowed us to distinguish 7 age classes of condors as well as their sex. King Vultures are sexually monomorphic, but undergo sequential changes in plumage and skin coloration with age that allowed us to distinguish 6 age classes (Heck 1968, C. Benevidies pers. comm.). Turkey Vultures, Black Vultures, and Crested Caracaras are also sexually monomorphic, but birds less than 1 yr old were distinguished from older birds on the basis of plumage, skin, and beak color (Brown and Amadon 1968).

We recorded the outcomes of 8,066 direct aggressive encounters between individuals that fed actively at carcasses. The winner was the bird that supplanted the other individual, regardless of whether the supplanting involved physical contact or mere intimidation. Because of the large number of Turkey and Black vultures that often interacted at the carcasses at the same time, only about 50% of their interactions were recorded. Condors and King Vultures, because of their size and lower numbers at feeding sites, were easier to track, and 95–100% of their interactions were recorded. From these data the frequencies of interactions between different species, sexes, and age classes were calculated. Not all of the potential categories of interactions were observed, but for those observed we calculated the proportion of encounters won by an individual of one species, sex, or age during encounters with an individual of a different species, sex, or age. On the basis of these probabilities we constructed dominance hierarchies.

During our observations we also had opportunities to record the sequence of arrival of Turkey Vultures, Black Vultures, and Andean Condors at 53 carcasses we knew had not been visited previously by scavengers. We positioned these 53 carcasses in open areas frequented by all three species so that all birds had chances of encountering them.

## Results

*Use of carcasses by scavengers.*—We observed carcasses on 239 days. Turkey Vultures visited the carcasses on 199 (83%) days, Black Vultures on 149 (62%) days, Andean Condors on 124 (52%) days, King Vultures on 15 (16%) days, and caracaras on 6 (3%) days. When Turkey Vultures were present, they were accompanied by Black Vultures on 73% of the days, by condors on 58% of the days, by King Vultures on 8% of the days, and by caracaras on 3% of the days. When Black Vultures were present, they were accompanied by Turkey Vultures on 95% of the days, by condors on 75% of the days, by King Vultures on 10% of the days, and by caracaras on 4% of the days. Caracaras were accompanied by Turkey and Black vultures on 100% of the days and by King Vultures and condors on 66% of the days. On days when King Vultures were present both Turkey and Black vultures were always there; caracaras were present on 47% of the days, and condors on 36% of the days. When Andean Condors were present, Turkey Vultures accompanied them on 95% of the days, Black Vultures on 90% of the days, King Vultures on 9% of the days, and caracaras on 6% of the days.

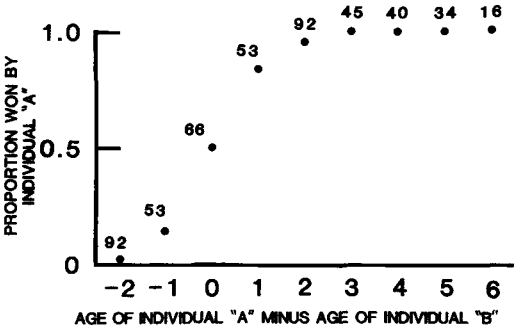


Fig. 3. Proportion of encounters won by a female Andean Condor of a certain age (individual A) when interacting with a female condor of another age (individual B). Number above each point is sample size. Age differences are in years.


Fig. 4. Proportion of encounters won by a male Andean Condor of a certain age when interacting with a female condor of another age. Number above each point is sample size. Age differences are in years.

*Order of arrival.*—Usually, Turkey Vultures arrived first at the carcasses, Black Vultures second, and Andean Condors last. Turkey Vultures arrived first at 92% of the 53 fresh carcasses for which we knew the sequence of arrival. Black Vultures arrived second at 72% of the carcasses, and Andean Condors arrived third at 70% of the carcasses. The order of arrival was not determined solely by the relative abundance of the three species; Black Vultures outnumbered Turkey Vultures by at least a 2-to-1 ratio on the study area. The condor was the least common of the three species.

*Interactions within each species.*—During aggressive encounters between juvenile and adult Turkey Vultures, 231 (68%) of 339 interactions were won by adults; the remaining encounters were won by juveniles. In contrast, juvenile Black Vultures were much more submissive to adult Black Vultures; adults won 528 (93%) of 567 interactions with juveniles. We never saw more than 3 caracaras feed at a carcass at one time, and the threesomes behaved as if they were mated pairs accompanied by their offspring. We never saw aggression between adults and juveniles, even though they were often in close proximity.

King Vultures usually arrived in pairs or in what appeared to be family groups of 3, and landed in trees near the carcass. Although occasionally as many as 8 King Vultures perched in surrounding trees, we never saw more than 5 birds at a carcass at the same time during 17 days on which King Vultures were present. The proportion of encounters won by an individual King Vulture varied with the magnitude of the difference in ages of the birds (Fig. 1). This produced an intraspecific hierarchy based on age.

Because Andean Condors are sexually dimorphic, we were able to record the outcome of interactions on the basis of sex as well as age. The proportion of encounters won by individuals of a certain age in encounters with individuals of the same sex but a different age increased linearly and leveled off when the difference between their ages was greater than 3 yr (Figs. 2 and 3). Both among males and females there was a dominance hierarchy based on age.

We also observed aggressive interactions between condors of different sexes (Fig. 4). Males

TABLE 1. Number of interactions observed between species of avian scavengers in Peru and the proportion of interactions won by each species. Sample sizes are given in parentheses.

| | Percentage of interactions won by species A when interacting with: | | | | |
|---|---|---|---|---|---|
| Species A | *Vultur gryphus* | *Sarcoramphus papa* | *Coragyps atratus* | *Polyborus plancus* | *Cathartes aura* |
| *Vultur gryphus* | — | 100% (185) | 94% (818) | — (0) | 100% (682) |
| *Sarcoramphus papa* | 0% (185) | — | 99% (2,142) | — (0) | 100% (148) |
| *Coragyps atratus* | 6% (818) | 1% (2,142) | — | 17% (196) | 44% (863) |
| *Polyborus plancus* | — (0) | — (0) | 83% (196) | — | 91% (114) |
| *Cathartes aura* | 0% (682) | 0% (148) | 56% (863) | 9% (114) | — |

generally dominated females, unless the female was more than 1 yr older than the male.

*Interactions between species.*—Juvenile and adult caracaras were generally dominant during interactions with either Black Vultures or Turkey Vultures (Table 1). Adult caracaras won more encounters with Black Vultures than did juvenile caracaras (85% vs. 72%), but both adult and juvenile caracaras had high proportions of wins during encounters with Turkey Vultures (91% and 90%, respectively).

In one-on-one situations, Turkey Vultures won only slightly over half of their aggressive encounters with Black Vultures, demonstrating very little dominance over Black Vultures (Table 1). However, when Black Vultures outnumbered either Turkey Vultures or caracaras at a carcass, individuals of the latter two species were always intimidated by the Black Vulture groups.

King Vultures, which weighed about twice as much as Turkey and Black vultures (Table 2), held a nearly complete dominance over both these vultures (Table 1). We never saw King Vultures and caracaras interact, although there were opportunities. At no time did we see a King Vulture initiate an encounter with a condor. Condors won all 185 aggressive encounters with King Vultures (Table 1). Condors were also dominant over the smaller vultures.

*Dominance hierarchy within the guild.*—Within each species there was a positive relationship between a bird's rank and its age (Table 2). Male condors were generally dominant over females of the same age. Between species, a bird's rank was correlated positively with its body mass (Spearman's rank correlation test, $r_s = 0.823$; $P < 0.001$).

TABLE 2. Ranks and body mass of members of an avian scavenging guild in Peru.

| Species and class of individual | Rank in guild hierarchy[a] | Average body mass and range (kg)[b] |
|---|---|---|
| *Vultur gryphus* | | |
| Adult males | 1 | 12.5 (10.9–13.6) |
| Older juvenile males | 2 | 12.3 (10.9–13.6) |
| Adult females | 3 | 10.1 (9.6–11.4) |
| Older juvenile females | 4 | 10.2 (8.6–10.9) |
| Younger juvenile males | 5 | 11.3 (10.9–11.6) |
| Younger juvenile females | 6 | 9.5 (9.1–10.2) |
| *Sarcoramphus papa* | | |
| Adults | 7 | 3.4 (3.1–3.7) |
| Older juveniles | 8 | 3.4 (3.0–3.6) |
| Younger juveniles | 9 | 3.1 (3.0–3.6) |
| *Polyborus plancus* | | |
| Adults | 10 | 1.6 (1.4–1.7) |
| Juveniles | 11 | 1.6 (1.6) |
| *Cathartes aura* | | |
| Adults | 12 | 1.4 (0.9–1.8) |
| Juveniles | 13 | 1.3 (1.0–1.5) |
| *Coragyps atratus* | | |
| Adults | 12 | 1.5 (1.2–1.8) |
| Juveniles | 13 | 1.3 (1.1–1.5) |

[a] Based on the win/loss data presented in the text, Table 1, and Figs. 1–4. For groups given the same ranking, there were insufficient observations to determine the precise relation of closely ranked birds.

[b] Based on measurements of trapped individuals of each species.

## DISCUSSION

*Organization of the guild.*—Turkey Vultures have a well-developed olfactory sense that permits them to use odor as an aid in finding food (Bang 1964, Stager 1964, Houston 1984). There is no evidence that the other members of the scavenging guild possess this ability. Furthermore, Turkey Vultures have lighter wing-loading than the other avian scavengers in the study area (Poole 1938, Brown and Amadon 1968). This facilitates slow flight close to the ground, where the Turkey Vulture's olfactory abilities are most effective. Turkey Vultures can rip open small- to medium-size, but not large, carcasses by themselves. If they could get to smaller carcasses before the other species arrived, they could acquire a meal without interacting with the more dominant guild members that arrive later.

Caracaras arrived at a carcass only after it had been visited by other vultures. They usually fed on carcasses only when no other birds were present, often at daybreak before vultures had begun flying. When other scavengers were present, caracaras usually stayed one to several meters away and picked up insects or small scraps of meat. Most aggressive interactions between caracaras and other species occurred when Black Vultures or Turkey Vultures attempted to supplant a caracara from a scrap of meat.

Although individual caracaras and, to a lesser extent, individual Turkey Vultures were dominant over individual Black Vultures, they were completely intimidated by Black Vulture

TABLE 3. Number of interactions observed between species of African scavengers and the proportion of interactions won by each species (based on Kruuk 1967, Anderson and Horwitz 1979). Sample sizes are given in parentheses.

| Species A | Percentage of interactions won by species A when interacting with: | | | | | |
|---|---|---|---|---|---|---|
| | *Neophron* | *Necrosyrtes* | *Pseudogyps* | *Gyps* | *Trigonoceps* | *Torgos* |
| *Neophron* | — | 0% (4) | — (0) | — (0) | 0% (1) | — (0) |
| *Necrosyrtes* | 100% (4) | — | 0% (6) | 0% (4) | 0% (1) | — (0) |
| *Pseudogyps* | — (0) | 100% (6) | — | 71% (80) | 0% (1) | 6% (50) |
| *Gyps* | — (0) | 100% (4) | 29% (80) | — | 0% (2) | 16% (18) |
| *Trigonoceps* | 100% (1) | 100% (1) | 100% (1) | 100% (2) | — | 0% (15) |
| *Torgos* | — (0) | — (0) | 94% (50) | 84% (18) | 100% (15) | — |

groups, which often included over 50 birds. The largest Black Vulture group we saw included 230–240 birds that arrived in less than 1 h.

Intact carcasses of large animals had such thick hides that the smaller scavengers could gain access only through the anal and buccal areas or places where lesions broke the skin. When smaller birds congregated at a large intact carcass, this access problem permitted only 5 or 6 to feed simultaneously; subordinate individuals had to wait for dominant birds to be sated. The waiting birds became noticeably excited when the later-arriving King Vultures and Andean Condors approached the carcass. With their heavier beaks and greater strength, the larger birds opened the carcass at several points. This often caused Black Vultures to swarm on the carcass in a "feeding frenzy." Normally subordinate birds apparently associated the presence of condors at a carcass with greater access to the food and became too excited to be dominated by higher-ranking conspecifics. When a large number of subordinate individuals attacked the carcass at once, the resource temporarily became impossible to defend. Within minutes, generally, the easily accessible food was consumed, and the carcass could again be defended by dominant individuals. Black Vultures frequently fed close to King Vultures and condors, but were pecked constantly and displaced by the larger scavengers.

TABLE 4. Rank and body mass of species of an African scavenger guild.

| Species | Rank in guild hierarchy[a] | Body mass (kg)[b] |
|---|---|---|
| *Torgos tracheliotus* | 1 | 7.5 |
| *Trigonoceps occipitalis* | 2 | 5.9 |
| *Gyps ruppellii* | 3 | 6.4 |
| *Pseudogyps africanus* | 4 | 5.7 |
| *Necrosyrtes monachus* | 5 | 1.9 |
| *Neophron percnopterus* | 6 | 1.9 |

[a] Based on Kruuk (1967) and Anderson and Horwitz (1979).
[b] From Brown (1971).

King Vultures generally arrived in pairs or what appeared to be family groups. Aggressive interactions were initiated by adults when juveniles were present, but the young apparently were not their dependent offspring. When an aggressor supplanted its victim from a feeding spot, the displaced King Vulture usually relocated and resumed feeding promptly, but occasionally a victim counterattacked. We observed four such fights between King Vultures; each lasted only a few seconds before the ultimate loser was chased from the carcass area.

Condors were usually last to arrive at a carcass. Marked individuals waited hours or even days after they discovered a carcass before they landed and approached it. Their hesitancy may have been due to several factors. Condors can easily go for several days between feedings, unlike smaller vultures that feed more frequently (Calder 1984). Because it was difficult for the larger condors to regain flight when they were on the ground, particularly after a large meal, they possibly were cautious about landing until confident they would not be disturbed. Once condors approached the carcass, their size and strength allowed them to easily displace other members of the guild. When condors interacted, males generally dominated females, probably because they weighed more (Fig. 4, Table 2). However, young male condors were generally subordinate to females that were more than 1 yr older, even though a young male could weigh as much as a third more than a female. Apparently there is a learned, social component to dominance in addition to the advantage of greater size.

*Comparisons with other scavenger guilds.* — Among Old World vultures, Kruuk (1967) and Houston (1975) found that sympatric avian scavengers on the African plains showed a high degree of ecological segregation. Competition for food at carcasses was reduced by the differential arrival of species at carcasses, the utilization of different parts of the carcass, and the maintenance of a dominance hierarchy between species when they were together at carcasses.

We compared the interspecific dominance hierarchies among Old and New World scavengers. Combining species-interaction data from Kruuk (1967) and Anderson and Horwitz (1979), we calculated the proportion of encounters won by one species in encounters with another species (Table 3). Comparison of the African data (Table 4) with that from Peru (Table 2) revealed that in both guilds of avian scavengers the interspecific dominance hierarchy is based primarily on body size. There was a strong correlation between rank and body mass of African scavengers (Spearman's rank correlation test, $r_s = 0.900$; $P < 0.05$), as there was among Peruvian scavengers.

There is remarkable convergence in the organization of the guilds of avian scavengers in Africa (members of the family Accipitridae) and South America (mostly members of the family Cathartidae). Within both guilds there is differential exploitation based on the order of arrival at carcasses and interference based on intra- and interspecific dominance hierarchies determined by size, sex, and age.

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