

## FOOD FINDING AND THE INFLUENCE OF INFORMATION, LOCAL ENHANCEMENT, AND COMMUNAL ROOSTING ON FORAGING SUCCESS OF NORTH AMERICAN VULTURES

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**ABSTRACT.**—I investigated foraging behavior and competition for food between Turkey Vultures (*Cathartes aura*) and Black Vultures (*Coragyps atratus*) in southern Texas. Turkey Vultures usually located carcasses first, but often were displaced by later-arriving Black Vultures, which used local enhancement to locate the carcasses. Turkey Vultures occurred equally frequently at carcasses of all sizes, but Black Vultures were more likely to visit large carcasses (>5 kg) than small ones. In addition, at very large carcasses (>100 kg), Black Vultures outnumbered Turkey Vultures. Turkey Vultures apparently depend primarily on small items, which they can consume quickly before Black Vultures usurp them. Both vulture species roost communally and it has been suggested that their roosts may function as information centers. However, because recent research indicates that the information-center hypothesis is unlikely to be a sufficient explanation for communal roosting in vultures, I explored other possible foraging benefits of communal roosting. Specifically, I incorporated field data collected on the foraging behavior of vultures into two simulation models designed to evaluate the possibility that communal roosting facilitates the use of local enhancement by roost members, either by promoting the formation of foraging groups (the assembly-point hypothesis) or by concentrating birds in space (the spatial-concentration hypothesis). I conclude that birds depending on spatial-concentration effects occasionally may forage more successfully than noncommunally roosting individuals, but those that form foraging groups do best. Thus, communal roosting may be advantageous because it facilitates the formation of foraging groups. Received 29 September 1995, accepted 10 December 1995.

THE TWO COMMON SPECIES of North American vultures, the Turkey Vulture (*Cathartes aura*) and the Black Vulture (*Coragyps atratus*), feed almost entirely on carrion (Palmer 1988). Both are well adapted to their scavenging lifestyle by virtue of their hooked bills, acute vision, and ability to search large areas effectively using energy-efficient soaring flight (Pennycuick 1976, 1983). The Turkey Vulture, in addition, possesses an acute sense of smell, which enables it to locate carrion hidden from view (Chapman 1938, Stager 1964). The Black Vulture's olfactory bulbs are less well developed (Bang 1964), and this species appears to depend entirely on vision to locate carcasses.

Both vulture species roost communally in aggregations that may contain more than 1,000 individuals (Prather et al. 1976), although most roosts in southern Texas contain fewer than 100 birds (unpubl. data). In southern Texas, roosts often include individuals of both species, but

one species usually greatly outnumbers the other with the less numerous species in a roost rarely making up more than 10% of the membership (Buckley 1994). Many possible advantages have been proposed to explain the phenomenon of communal roosting, the most widely cited of which is the information-center hypothesis (Ward and Zahavi 1973). They suggested that roosts (and colonies) function as information centers, sites where unsuccessful foragers can learn the whereabouts of food patches by following successful roost mates to food patches the successful birds located earlier. For birds that feed on sparsely distributed but locally abundant and ephemeral foods (such as carrion), Ward and Zahavi (1973) suggested communal roosting would be favored because information about the location of difficult-to-find food patches would be valuable to foragers, and large patches would minimize the costs of sharing information.

Because carrion frequently fulfills the above food-source requirements (i.e. large size, spatial unpredictability, and temporary availability), vulture roosts are strong candidates to function

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as information centers. Recent studies (Rabenold 1983, 1987, Buckley 1994) have indicated that the communal roosts of Black Vultures do, at times, function as information centers. In southern Texas, however, relatively few Black Vultures (<10%) appear to locate carcasses by following roost mates (Buckley 1994). In addition, tests of the information-center hypothesis with Turkey Vultures (Prior and Weatherhead 1991a, Buckley 1994) indicate that the communal roosts of this species probably do not function importantly as information centers. Thus, advantages of communal roosting other than the possible information-center function need to be considered. The same characteristics of carrion that make vulture roosts candidate information centers might also favor other forms of social foraging and information exchange. One potentially important form of information exchange is local enhancement (Turner 1964, Pöysä 1992), the attraction of searching individuals to groups of already-feeding birds. Feeding vultures (or even vultures descending, as if to a carcass) often are visible from afar, so their presence at a carcass can make the food detectable from a much greater distance than would be the case if no other birds were present. In most cases, local enhancement is presumed to be an involuntary but unavoidable signalling of patch location through which the food's location is revealed to other foragers by the behavior necessary to harvest it (i.e. descending to carcass and feeding on it).

To employ local enhancement, it is obvious that a vulture must forage when and where other vultures are present. Thus, an individual trying to maximize its foraging success should search in areas where other foragers are present so long as the benefits from the increased likelihood of locating carcasses through local enhancement exceed the costs of subsequently sharing the food with other foragers (Kirk and Houston 1995).

Communal roosting might facilitate the use of local enhancement by foraging vultures in two ways. First, communal roosting may make it easier for vultures to purposely form foraging groups: the assembly-point hypothesis (Evans 1982). Second, by concentrating foragers in space, communal roosting may result in passively-forming aggregations of vultures that lead to more efficient use of local enhancement than if birds roosted separately. This results because when birds leave a roost, they take some time

to disperse over the foraging area. Thus, for a period the birds are more spatially clumped than if they had roosted separately, randomly or uniformly spaced throughout the foraging area. Spatial clumping would be enhanced further if birds tended, for any reason, not to disperse evenly in all directions, but instead departed in one or a few directions, or at the same time (Rabenold 1983). Such directional or temporal clumping, if favored by selection, might represent a potential intermediate step between randomly or uniformly distributed departures and active group formation. The group-formation and spatial-clumping hypotheses are related in that the selective advantages of both depend on having other foragers in view. However, group formation is an active process since groups are formed and maintained, whereas the spatial-concentration effects result as a relatively passive consequence of communal roosting.

It is difficult, if not impossible, to address with field experiments the costs and benefits of foraging strategies, such as those outlined above, because the variables of interest (i.e. foraging group size, roosting behavior) are not experimentally manipulable. However, costs and benefits can be addressed using appropriate simulation models in which ecological conditions are held constant and only the variable of interest is allowed to change. If such simulations are to be meaningful, however, they must be grounded in the biology of the subject species and incorporate biologically realistic assumptions. Therefore, I decided to use a two-step approach in evaluating the group-formation and spatial-concentration hypotheses. First, to gain a better understanding of the foraging ecology of vultures in the wild, I used a combination of field experiments and observations to gather a wide variety of data on the kinds and sizes of carcasses the vultures consumed, how they searched for food, and how they interacted with competitors at carcasses. I then used this information to develop the simulation models, incorporating relevant field observations into their structure and basing parameter values on data gathered in the field.

#### METHODS

*Study area.*—Fieldwork was conducted from 1988 through 1992 in southern Texas on and around the 3,160-ha Rob and Bessie Welder Wildlife Refuge near Sinton, San Patricio County, Texas (28°06'N, 97°22'W;

for description of refuge, see Box et al. 1978, Buckley 1994). Both vulture species were common on the refuge and used several roosts located either on electrical pylons or in large trees along the Aransas River.

*Spatial distributions.*—To assess spatial distributions of foraging vultures and to determine temporal patterns of activity, I drove a 12.8-km transect through the refuge on 50 occasions, between 0900 and 1800 CST (March–August 1989, May–June 1990). All vultures seen were recorded, and the estimated altitudes of flying birds were assigned to one of three categories ( $\leq 30$  m, 31–60 m, and  $> 60$  m). Birds within about 400 m of each other and heading in the same direction, or those that were circling together were considered to be members of the same foraging group. Vultures observed circling together over roosts were judged not to be seeking food and, hence, were excluded from the foraging analyses.

To assess whether foragers were spatially clumped, I analyzed data from 28 transects driven between 1000 and 1800 (when most birds seen were foraging) for which I had recorded the positions of all birds (estimated from readings of my vehicle's odometer). I divided the transect route into eight equal 1.6-km (1-mile) segments and determined the number of birds seen along each segment. I then combined data from all surveys and compared the resulting cumulative distribution for each species with expected values for a Poisson distribution of the birds.

*Carcass use.*—To locate carcasses, I watched for vultures feeding on or descending to carcasses. Whenever I located a food item, I identified it (to species if possible), assigned it to one of four size categories ( $< 1$  kg, 1–5 kg, 5.1–100 kg, or  $> 100$  kg), and recorded the species and numbers of birds present. Data were collected on 76 items located in this way.

I also recorded the number and species of birds that visited carcasses of large animals (mostly white-tailed deer [*Odocoileus virginianus*], feral hogs [*Sus scrofa*], and coyotes [*Canis latrans*]) that I kept under continuous observation as part of experiments designed to evaluate the information-center hypothesis (Buckley 1994). During these observations, I recorded data on feeding behavior, numbers of birds visiting carcasses, and aggressive interactions among foragers. In addition, I documented temporal patterns of occurrence and the amount of time individuals spent at bait sites based on observations of those of 247 Black Vultures and 107 Turkey Vultures wing tagged with numbered Allflex cattle ear tags (Wallace et al. 1980, Sweeney et al. 1985) that visited experimental carcasses (Buckley 1994).

To assess the use made by vultures of smaller food items, I provided 75 artificial patches of food, each consisting of a 0.5-kg piece of cattle lung or liver. At dawn on 15 days over a two-month period, I scattered five pieces at arbitrarily-chosen sites on the refuge. Of the 75 pieces of bait, 40 were left uncovered and 35 covered with vegetation so that they were com-

pletely hidden from view. All five baits provided on a given day were treated the same way, and the order of treatments among days was randomly assigned. All such bait sites were within 100 m of the road, an arrangement that allowed me to check baits roughly every 2 h for two days without disturbing birds that were feeding on them. All birds seen were recorded. In cases where the bait had been fed upon, but no birds were observed, I used footprints, beak marks on the bait, and feathers to determine whether vultures had eaten the bait. In 20 instances where I did not see birds at a bait site, I was able, using the above clues, to determine that vultures had been present at the food.

*Local enhancement and attraction of foragers to food patches.*—I used data gathered during observations at large carcasses to explore the importance of local enhancement in attracting birds to these carcasses and to evaluate whether the number of birds present at a patch influenced the likelihood of other birds finding the food. To address these questions, I used randomly selected times from my data. For each time chosen, I first determined if a particular number of birds (0, 1, 2, 3–5, 6–10, 11+) had been present at the bait site in the preceding 15 min and if no birds had arrived or departed during that time. If this was the case, I then determined whether other vultures arrived at the carcass in the following 15-min period. If vultures did arrive, I recorded how many. When all relevant data were tabulated, I determined for each group size the probability that at least one bird would arrive, as well as the number of birds expected to arrive in a 15-min period.

#### THE SIMULATION MODELS

Two simulation models were used to assess the potential importance of group foraging and spatial-concentration effects on the foraging success of communally roosting vultures. Both programs (copies available from author) were written in Think Pascal for the Macintosh and simulated vulture foraging behavior under the ecological conditions prevailing in southern Texas.

#### GROUP-FORAGING SIMULATION

In the group-foraging simulation, computer-vultures foraged in preset groups of one to eight (a range chosen to reflect the common range of foraging groups in the study area) with the probability of a group detecting a carcass being an increasing function of group size. Because the areas searched by individuals in a foraging group overlap, I considered that the probability of locating a patch would be an increasing, but decelerating function of the number of birds in the group. Because I was uncertain of the pre-

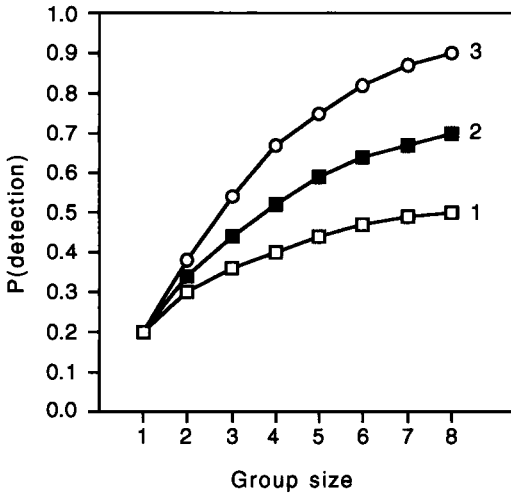


Fig. 1. Patch-detection curves used in computer simulations to determine probability ( $P$ ) that various-sized groups will detect food patches. Patch-detection curves refer to flocks that are (1) ineffective, (2) moderately effective, and (3) very effective at detecting carcasses (see text).

cise shape of the function I used three different decelerating food-detection curves (Fig. 1) to simulate the effects of group size on the probability of carcass detection. For each curve, the probability of detection increased with group size, but the rate of increase differed across curves, being least for curve 1 (flocks ineffective at detecting carcasses) and greatest for curve 3 (flocks very effective at detecting carcasses). These were drawn by setting one endpoint at 0.2 and the other, respectively, at 0.5, 0.7 and 0.9, then drawing the smooth curves in Figure 1.

In the simulation, a trial lasted 40 turns, each of which approximated 15 min of real time (thus, a total of 10 h); 2,000 trials were completed for each set of parameters. During each turn, foragers were considered to be searching an area that had some probability  $P$  of containing food ( $0 \leq P \leq 1$ ). Based on movement rates of vultures in the field, I considered that vultures would search an approximately 2.5-km<sup>2</sup> area in one turn. Therefore, I estimated (based on information on population densities and mortality rates of prey species in the area [D. L. Drawe, S. Gehrt, M. Hellickson, C. McDonagh pers. comm.]) the probability  $P$  that this area would contain an item of carrion as roughly 0.2. To

simulate day-to-day variation in food availability,  $P$  (which was a constant for a particular trial) could assume any value between 0.14 and 0.26. Across trials  $P$  was normally distributed around 0.20. For most simulations the mean  $P$ -value of 0.2 was used, but in some sensitivity analyses (described below) higher and lower mean values of  $P$  were used. For each turn during which birds were searching, a random number was generated from a uniform distribution to determine whether a carcass was present. If the random number drawn indicated that the area contained a carcass, a second random number was used to determine if the carcass were detected. The probability that a carcass was located by a vulture was a function of group size and depended on the food-detection curve in use. When a carcass was located, foragers were considered to land and begin feeding. For most simulations, the size of the carcass located was assigned randomly based on the size distribution observed in the field. However, for a series of simulations in which I evaluated the importance of the carcass-size distribution in determining optimal strategies, the distribution was varied between sets of trials. Because Turkey Vultures virtually always locate carcasses first, I made no corrections to the observed carcass size distribution. However, for Black Vultures, the effects of tissue removal by early-arriving Turkey Vultures was simulated by reducing the size of <1-kg carcasses by 60% and 1- to 5-kg carcasses by 40%. These estimates of the effects of Turkey Vulture feeding earlier were based on observations of the frequency of occurrence of Black Vultures at such carcasses and of the rate at which Turkey Vultures remove meat from carcasses.

Each individual was limited to consuming one unit of food per day, where one unit represented a carcass of less than 1 kg. Because feeding birds take approximately 30 min to become satiated (pers. obs.), I set the rate at which food could be removed from a carcass at 0.5 units per turn for Turkey Vultures (as only one bird feeds at a time) and at 1.0 unit per turn for Black Vultures (since more than one individual may feed at once). The food removed was then distributed equally among the birds present at the carcass. Foragers remained at a patch until the carcass was consumed or until each forager had acquired one unit of food.

To simulate the build-up of foragers at a car-

cass as a result of local enhancement, I used probability-of-arrival data (Fig. 2A) derived from field observations at carcasses to generate the probability of other foragers arriving at the patch. At the beginning of each turn, a random number was generated and used to determine whether additional foragers arrived (based on the number of birds at patch). If the program concluded that additional foragers had arrived, then the number of birds at the carcass was increased by two foragers (if fewer than six foragers had been present at patch at beginning of turn) or by three foragers (if more than six foragers originally had been present). These values of two or three foragers that accumulated per 15-min period are slightly lower than the observed number of arrivals per 15-min period (Fig. 2B), a feature intended to reflect the fact that a few birds depart after visiting carcasses only briefly (i.e. net accumulation of foragers was lower than observed arrival rate). In Turkey Vulture simulations, once 10 foragers were present at a carcass, I assumed that Black Vultures immediately discovered and usurped it, after which the Turkey Vultures departed and resumed searching. Black Vultures did not abandon a carcass until 20 birds were present, at which time I assumed that the average rate of food intake would be so low that individual foragers would do better by seeking other food patches than by remaining to feed. At the end of each set of trials, mean food intake was calculated and, as an indicator of the likelihood of starvation, the number of days on which the bird failed to obtain at least 0.5 units of food was determined.

Because of the difficulty in accurately assessing the available food supply for vultures in the field and the possibility that the estimates used in simulations might generate results that hold only for these parameter values, I conducted sensitivity analyses in which I varied both the food-size distribution and the amount of food available. To assess the influence of different food distributions on foraging strategies, I ran simulations in which the food-size distribution observed in the field was varied, while holding food detection constant (by using only intermediate food-detection curve; i.e. curve 2 in Fig. 1). Trials were run with either an excess of small carcasses ( $\leq 5$  kg) or an excess of large carcasses ( $> 5$  kg) available. The observed distribution of carcasses in the field was 70% small and 30%

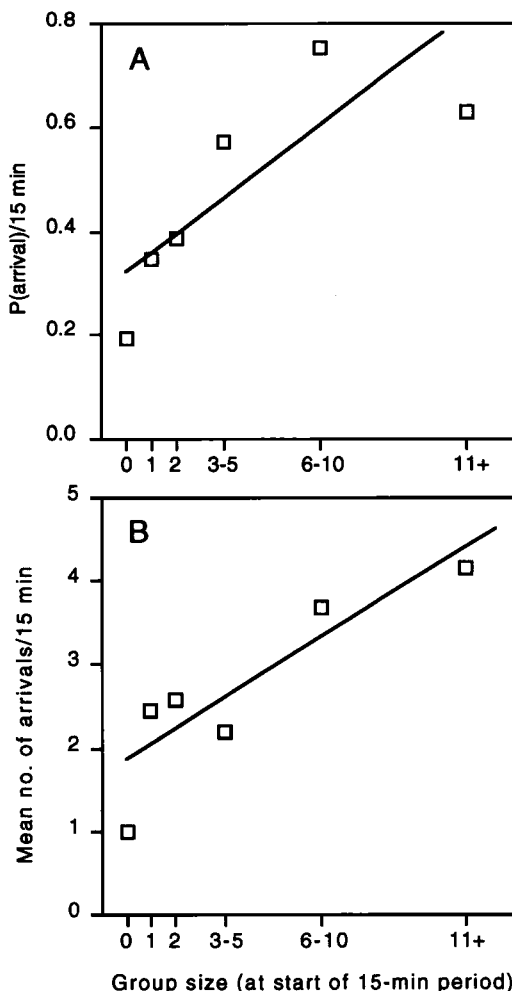


Fig. 2. Relationship of number of vultures (of both species) present at a carcass to (A) probability that at least one forager arrives within a 15-min period, and (B) mean number of foragers arriving in a 15-min period.

large (by this 5-kg cutoff): for small-carcass trials, 90% of available carcasses were small and 10% large; for large-carcass trials, 50% were small and 50% large.

To evaluate the effect of varying the amount of available food on food intake, I ran simulations in which I varied the probability  $P$  that an area being searched contained food. In most trials  $P$  was normally distributed around 0.2, but for the sensitivity analyses I used values of  $P$  normally distributed around 0.1 and 0.4, in effect halving or doubling the available food

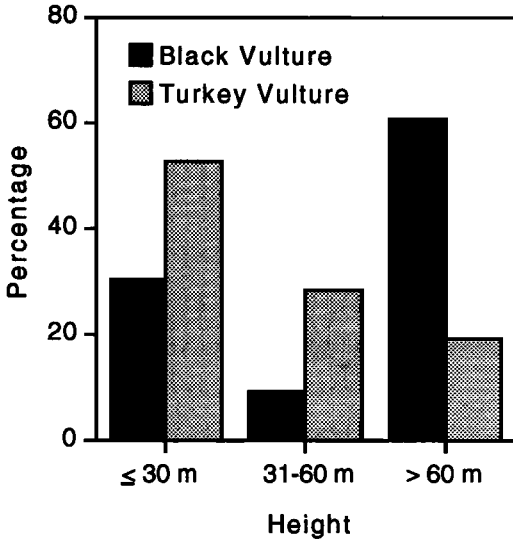


Fig. 3. Foraging heights of Black Vultures and Turkey Vultures observed during road surveys.

supply. Simulations were run for both vulture species using the observed carcass distribution and the intermediate food-detection curve (i.e. curve 2).

#### RANDOM-DISPERSAL SIMULATION

In the random-dispersal simulation I assumed that birds departed from their roost and searched for food over a surrounding circular area with a radius of 12 km. This area approximates that likely to be ranged over by foraging vultures based on the radio-tracking results of Coleman and Fraser (1989) and on my field observations of vultures. The probability of a carcass being located by foragers was determined based on the number of birds calculated to occur within an area of 8 km<sup>2</sup>. This estimate assumes foraging vultures can detect other vultures descending to a carcass from a distance of up to 1.6 km. It took eight time units for birds to distribute themselves randomly over the foraging habitat. The distribution of food available, recruitment of other foragers to carcasses, rate of food removal from carcasses, number of turns per trial, and number of trials per simulation were as described for the group-foraging simulation.

Directional clumping of departures from roosts could result in birds not dispersing randomly throughout the entire foraging area, but

instead searching only a portion of it. To simulate the effects of such directional clumping, I also ran simulations in which birds were artificially restricted to only one-half or one-quarter of the total area. The results for foragers dispersing over the whole, one-half, or one-quarter of the entire foraging area were compared with those obtained from the group-foraging simulation for one or two foragers (which would represent the mean density of birds expected if all foragers roosted independently, dispersed across the landscape, or if foragers roosted alone at random locations within the foraging area of a roost).

## RESULTS

### SPATIAL DISTRIBUTION

On 50 road surveys (driven between 0900 and 1800) I recorded 547 Turkey Vultures and 113 Black Vultures. The disparity in numbers of the two species seen contrasted with the ratio of these species at large experimental carcasses, where Black Vultures usually outnumbered Turkey Vultures. This difference may be due to Turkey Vultures spending more time in flight than Black Vultures and, hence, being more likely to be noted during road surveys. Additionally, Black Vultures may be more difficult to detect because they fly at greater altitudes than Turkey Vultures. Most Black Vultures were recorded at heights in excess of 61 m, while the majority of Turkey Vultures were flying less than 30 m above the ground (Fig. 3;  $X^2 = 87.6$ ,  $P < 0.001$ ,  $df = 4$ ).

The spatial distribution of foragers on road surveys differed significantly from that predicted by a Poisson distribution (Fig. 4). Both species were more clumped in distribution than expected (Turkey Vulture, data from 28 transects,  $X^2 = 22.79$ ,  $P < 0.001$ ,  $df = 4$ ; Black Vulture, data from 10 transects,  $X^2 = 10.53$ ,  $P < 0.01$ ,  $df = 2$ ).

Both vulture species frequently occurred in same-species groups (Turkey Vulture group size,  $\bar{x} = 1.64 \pm SE$  of 0.07, range 1-13,  $n = 333$  groups; Black Vulture,  $\bar{x} = 2.51 \pm 0.45$ , range 1-15,  $n = 45$  groups). However, the distribution of group sizes differed between the two species, with groups of Black Vultures tending to be larger than those of Turkey Vultures (Fig. 5; Kolmogorov-Smirnov,  $P < 0.001$ ). The mean Turkey Vulture group size obtained from road surveys

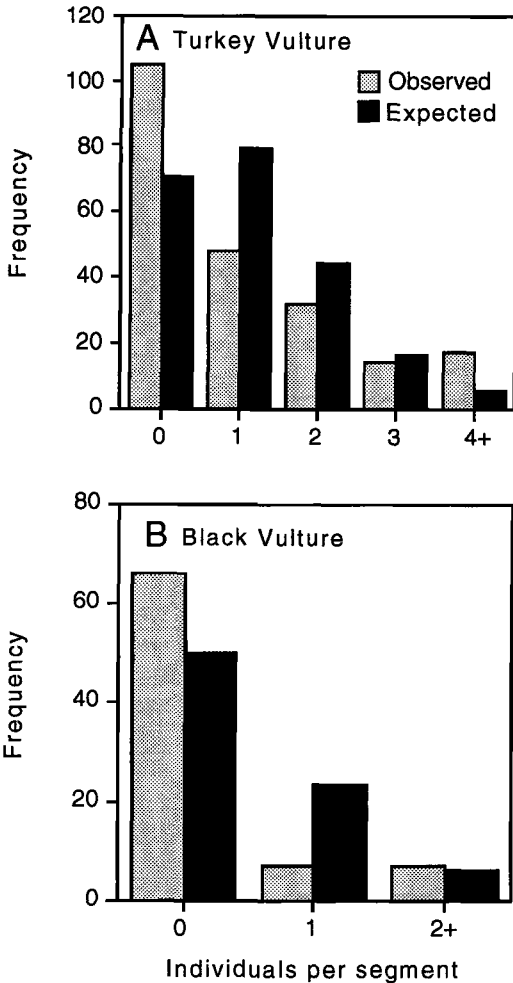


Fig. 4. Spatial distribution of (A) Turkey Vultures and (B) Black Vultures recorded during road surveys. Frequency denotes total number of times indicated number of individuals was recorded per 1.6-km segment of survey route. Expected values derived from a Poisson distribution.

was virtually identical to the mean size of first groups arriving at experimental bait sites ( $\bar{x} = 1.66 \pm 0.29$ ,  $n = 21$  groups; Buckley 1994). For Black Vultures, however, the mean group size of aerial foragers obtained on road surveys was somewhat smaller than the  $4.08 \pm 1.13$  ( $n = 13$  groups) recorded for first groups arriving at experimental bait sites.

CARCASS USE

*Nonexperimental food items.*—I recorded vultures feeding on 76 food items that included a

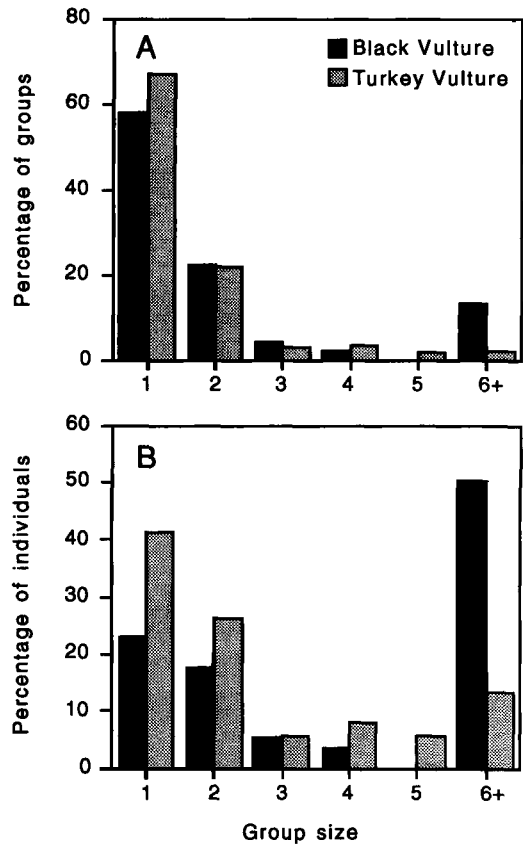


Fig. 5. Distribution of group sizes of Turkey Vultures ( $n = 333$  groups) and Black Vultures ( $n = 45$  groups) observed during road surveys. Data represented as (A) percentage of total number of groups and (B) percentage of total number of individuals.

wide variety of domestic and wild animals. Items ranged in size from cattle to mice (Table 1). Turkey Vultures were seen at 84.2% (64) and Black Vultures at 44.7% (34) of these items. The two species differed in their frequency of occurrence as a function of carcass size (Table 2). Black Vultures were significantly more likely to be recorded at carcasses larger than 5 kg than at smaller ones ( $X^2$  with Yates' correction = 18.4,  $P < 0.001$ ,  $df = 1$ ), but Turkey Vultures were not ( $X^2$  with Yates' correction = 0.2,  $P > 0.05$ ,  $df = 1$ ). Conversely, Turkey Vultures were present at a significantly greater proportion of items of less than 1 kg ( $X^2 = 36.5$ ,  $P < 0.001$ ,  $df = 1$ ) and those of intermediate size (1.1 to 5 kg;  $X^2 = 4.6$ ,  $P < 0.05$ ,  $df = 1$ ) than were Black Vultures (Table 2), but both species were recorded equally frequently at those larger than 5 kg.

TABLE 1. Food items on which Black Vultures and Turkey Vultures were recorded feeding. Items listed in decreasing order of size.

Item <sup>a</sup>	Black Vulture	Turkey Vulture	Total
Cattle	6	5	6
Donkey	1	1	1
Feral pig	1	1	1
White-tailed deer	4	2	4
Javelina	1	1	1
Coyote	3	2	3
Bobcat	0	1	1
Adult raccoon	4	6	7
White-tailed deer fawn	1	1	1
Nine-banded armadillo	4	7	9
Young coyote	1	1	1
Gray fox	0	2	2
Opossum	2	2	3
Domestic cat	0	1	1
Juvenile raccoon	1	1	2
White-tailed deer pieces	1	0	1
Bobcat pieces	0	1	1
Snow Goose	0	1	1
Striped skunk	1	1	1
Young nine-banded armadillo	2	3	4
Snake (unidentified)	0	3	3
Rat snake	0	1	1
Western diamondback rattlesnake	0	2	2
Eastern cottontail	0	2	2
Western box turtle	0	1	1
Northern Bobwhite	0	1	1
Common Pauraque	0	1	1
Frog ( <i>Rana</i> sp.)	0	2	2
Coyote dung	1	5	6
Mouse ( <i>Peromyscus</i> sp.)	0	1	1
Shrimp <sup>b</sup>	0	1	1
Snail <sup>c</sup>	0	1	1
Unidentified small mammal	0	3	3

<sup>a</sup>Scientific names of species: cattle, *Bos taurus*; donkey, *Equus asinus*; feral pig, *Sus scrofa*; white-tailed deer, *Odocoileus virginianus*; javelina, *Pecari angulatus*; coyote, *Canis latrans*; bobcat, *Lynx rufus*; raccoon, *Procyon lotor*; nine-banded armadillo, *Dasypus novemcinctus*; gray fox, *Urocyon cinereoargenteus*; opossum, *Didelphis marsupialis*; domestic cat, *Felis catus*; Snow Goose, *Chen caerulescens*; striped skunk, *Mephitis mephitis*; rat snake, *Elaphe guttata*; western diamondback rattlesnake, *Crotalus atrox*; eastern cottontail, *Sylvilagus floridanus*; western box turtle, *Terrapene ornata*; Northern Bobwhite, *Colinus virginianus*; Common Pauraque, *Nyctidromus albigollis*.

Although both species were recorded at most carcasses larger than 100 kg, Black Vultures occurred in significantly greater numbers than did Turkey Vultures (Table 2; Mann-Whitney  $U = 41$ ,  $P < 0.05$ ). Mean numbers of Turkey Vultures and Black Vultures recorded at carcasses of 1 to 5.0 kg and 5.1 to 100 kg did not differ significantly (Mann-Whitney  $U$ -tests, ns), but significantly more Turkey Vultures than

Black Vultures were recorded at carcasses of less than 1 kg (Mann-Whitney  $U = 751$ ,  $P < 0.001$ ), which Black Vultures rarely visited.

*Small experimental carcasses.*—In all, 49 of the 75 pieces of bait I provided were discovered by vultures. Turkey Vultures were seen at 26 patches (53.1%) and Black Vultures at only 3 (6.1%;  $X^2 = 23.7$ ,  $P < 0.001$ ,  $df = 1$ ). At the other 20 patches the species of vulture that occurred was undetermined, being based on cues such as beak marks on the bait. Of 40 uncovered baits, 35 were located on the first day, and 2 of the remaining 5 were discovered on the second day, for an overall discovery rate of 92.5%. In contrast, only 12 of 35 covered baits were located (34.2%) within two days of being provided. Uncovered baits were significantly more likely to be found by vultures ( $X^2$  with Yates' correction = 20.38,  $P < 0.01$ ,  $df = 1$ ). Only 1 of 35 (2.8%) covered baits was discovered the first day it was available, but 11 of 34 (32.3%) were found on the second day ( $X^2$  with Yates' correction = 8.49,  $P < 0.01$ ,  $df = 1$ ). This difference between days in detectability of baits suggests that the age of a piece of bait (and presumably its increased odor) significantly increases the likelihood it will be located by vultures.

*Large experimental carcasses.*—Of the 31 experimentally provided carcasses (all larger than 15 kg) discovered by vultures, Turkey Vultures arrived first at 30. Black Vulture numbers typically built up quickly as birds apparently located the bait site by local enhancement. Usually, within a few hours of discovery, Black Vultures greatly outnumbered Turkey Vultures at carcasses, and this pattern was maintained over the two to four days each carcass lasted (Buckley 1994). Typically, 15 to 25 Black Vultures were recorded simultaneously at carcasses, while usually fewer than 5 Turkey Vultures were present at once (for details of occurrence patterns, see Buckley 1994).

*Importance of local enhancement in attracting foragers to carcasses.*—There was a clear relationship between the presence of birds (of both species) at experimental carcasses and the likelihood that other foragers would arrive in the next 15-min period (Fig. 2A; Pearson's  $r = 0.848$ ,  $P < 0.05$ ). The probability of other foragers arriving generally increased with the number of foragers present, but declined slightly when very large numbers were present at the bait site. In addition, a positive relationship was detected between the mean number of vultures initially



TABLE 2. Frequency of occurrence and mean numbers of Black Vultures and Turkey Vultures recorded at nonexperimental food items.

Size of food item (kg)	No. carcasses	Black Vulture		Turkey Vulture	
		Frequency	Mean no. birds ( $\pm$ SE)	Frequency	Mean no. birds ( $\pm$ SE)
<1.0	29	3	0.24 $\pm$ 0.14	27	1.83 $\pm$ 0.29
1-5	23	11	1.83 $\pm$ 0.56	18	2.35 $\pm$ 0.61
5.1-100	17	13	8.88 $\pm$ 2.48	13	4.59 $\pm$ 1.24
>100	7	7	32.57 $\pm$ 8.39	6	4.71 $\pm$ 1.22

present at a carcass, and the number of vultures that arrived in the subsequent 15-min period (Fig. 2B; Pearson's  $r = 0.875$ ,  $P < 0.05$ ).

#### INTERACTIONS AT CARCASSES

*Vulture interactions at carcasses.*—In 72 of 129 encounters (55.8%), adult Turkey Vultures displaced adult Black Vultures from feeding sites at carcasses ( $X^2 = 0.38$ , ns). Although Turkey Vultures won more interactions with Black Vultures than they lost, Turkey Vultures stayed less time at bait sites where Black Vultures were present ( $\bar{x} = 21.3 \pm 2.38$  min,  $n = 45$ ), than where Black Vultures were absent ( $\bar{x} = 32.4 \pm 5.39$  min,  $n = 14$ ;  $t$ -test,  $t = 2.13$ ,  $P < 0.05$ ,  $df = 57$ ). The reverse comparison, mean time spent at bait sites by Black Vultures with and without Turkey Vultures present could not be made because there rarely were long periods during which Turkey Vultures were absent from bait sites. However, Black Vultures stayed significantly longer at bait sites ( $121.4 \pm 10.02$  min) than did Turkey Vultures ( $23.9 \pm 2.28$  min; Mann-Whitney  $U = 6210$ ,  $P < 0.001$ ; Buckley 1994). The disparity between the observed outcomes of aggressive interactions and time spent at carcasses may be due to only a small subset of (especially aggressive) Turkey Vultures becoming involved in interactions with Black Vultures.

The presence of Black Vultures not only reduced the duration of Turkey Vulture visits, but also reduced feeding opportunities for Turkey Vultures. The mean number of Turkey Vultures recorded feeding was  $0.63 \pm 0.06$  when Black Vultures were present ( $n = 102$  scan samples) versus  $0.98 \pm 0.02$  when they were absent ( $n = 47$ ; Mann-Whitney  $U = 3243$ ,  $P < 0.001$ ). Also, most Turkey Vultures were intolerant of conspecifics feeding close to them. No more than

two Turkey Vultures were ever seen feeding together at the same carcass and usually only a single bird fed. Nonfeeding Turkey Vultures awaiting an opportunity to feed stood or perched nearby until the feeding bird was satiated. Occasionally, a newly arrived (apparently dominant individual) displaced the feeding bird but, in general, birds waited for their chance to feed. Such queuing behavior has also been described for Turkey Vultures in Canada (Prior and Weatherhead 1991b). When Black Vultures were absent, single Turkey Vultures were recorded feeding in 46 of 47 scan samples. When Black Vultures were present, single Turkey Vultures were recorded feeding in only 48 of 102 scan samples, and two Turkey Vultures were recorded feeding together in 8 of 102 scan samples. In contrast to Turkey Vultures, Black Vultures often fed in close proximity with conspecifics (number feeding simultaneously,  $\bar{x} = 3.49 \pm 0.19$ ,  $n = 151$ ). Significantly greater numbers of Black Vultures fed together than Turkey Vultures (Mann-Whitney  $U = 6101$ ,  $P < 0.001$ ).

*Vulture interactions with other scavengers.*—The only other commonly recorded avian scavenger seen was the Crested Caracara (*Polyborus planicus*). Caracaras were recorded at 10 carcasses and on 18 of a possible 59 days. As many as six individuals were seen simultaneously and up to seven separate individuals were recorded in a day, but usually, only one or two were present. Both adult and immature caracaras were dominant over vultures of all age classes. A single Harris' Hawk (*Parabuteo unicinctus*) visited one carcass, but remained for less than 10 min after driving a mixed group of vultures away from the bait. Although a variety of other hawks were present on the refuge—including Red-tailed Hawks (*Buteo jamaicensis*), Red-shouldered Hawks (*B. lineatus*), and White-tailed Hawks (*B. albicaudatus*)—none was seen to visit carcasses.

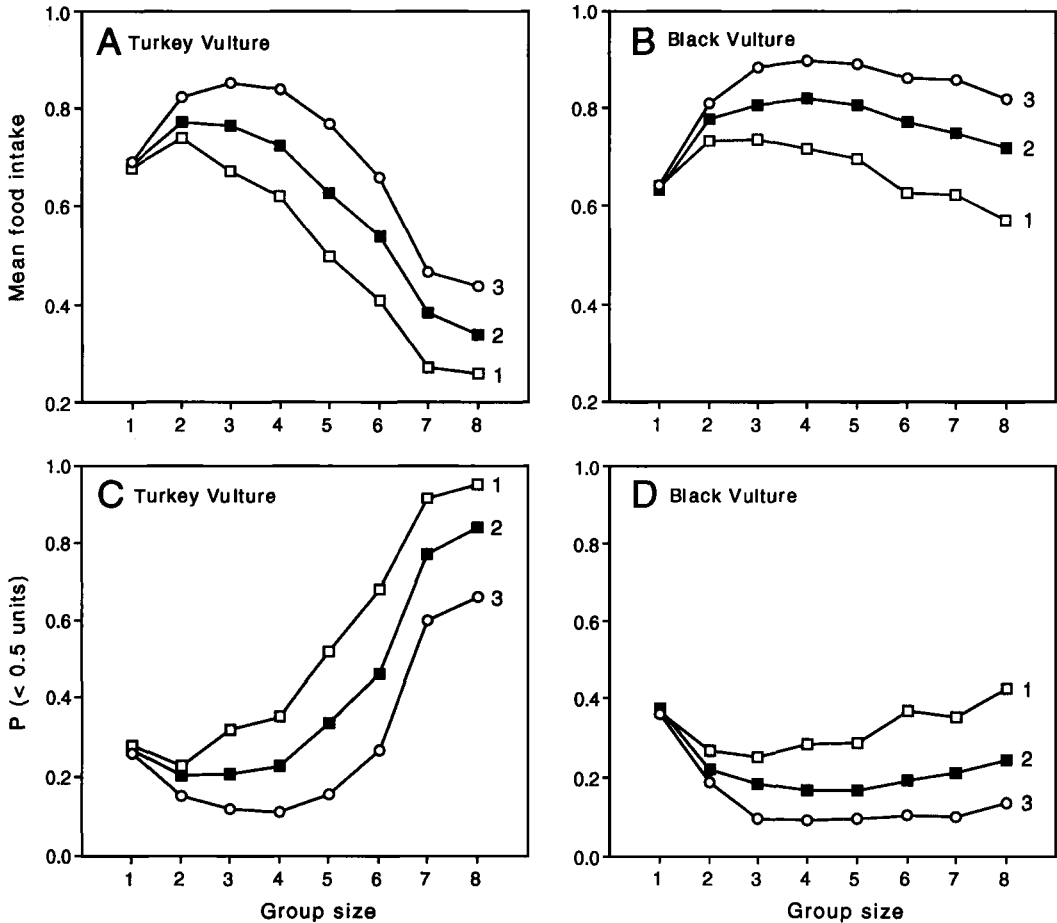


Fig. 6. Effect of foraging-group size on mean food intake per individual and probability of an individual obtaining less than 0.5 units of food in a day for (A, C) Turkey Vultures and (B, D) Black Vultures. Numbers to right of curves indicate patch-detection curves used in simulation (see Fig. 1).

Coyotes fed at 6 of 31 large carcasses. When coyotes visited bait sites, vultures moved away and waited on the ground or perched nearby. Coyotes made only brief visits, but sometimes ate large amounts of meat and ripped open the carcasses, making them easier for vultures to feed on. On one occasion coyotes dragged away a 20-kg javelina that was not adequately anchored.

#### SIMULATIONS

##### GROUP-FORAGING SIMULATION

*Turkey Vultures.*—For Turkey Vultures, simulated mean food intake peaked at group sizes of two or three foragers depending on the food-

detection curve being used. For detection curves 1 and 2 (Fig. 1), mean food intake per individual peaked at a group size of two. For detection curve 3 (in which food detection increases most rapidly with group size), mean food intake per individual was highest for groups of three foragers (Fig. 6A). For groups larger than these optima, mean intake rates decreased rapidly; specifically, for individuals in groups larger than four to six foragers (depending on food-detection curve used), mean intake was actually lower than for solo foragers. The pattern of starvation risk relative to group size (i.e. proportion of days on which less than 0.5 units of food obtained per vulture; Fig. 6C) was, as expected, the opposite of that observed for mean food intake (Fig. 6A). Individuals minimized their

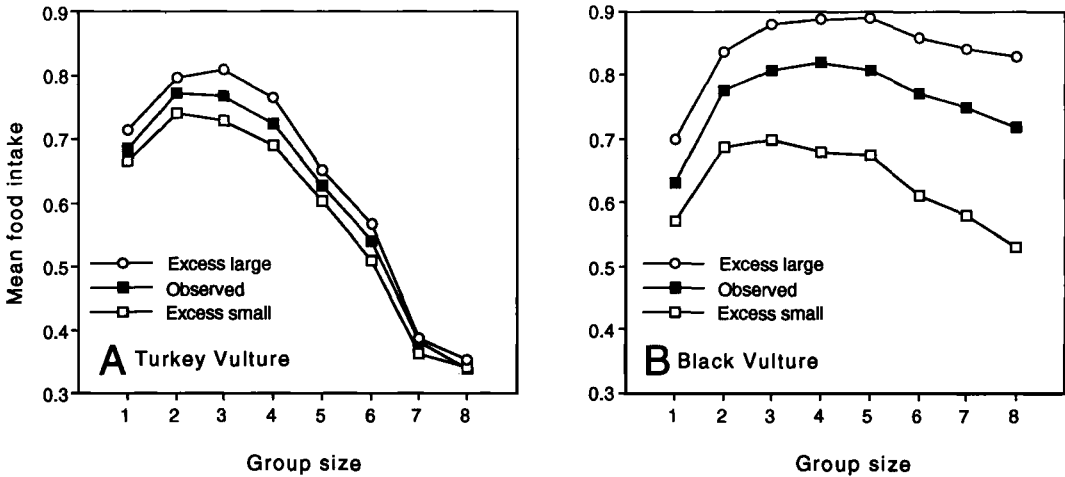


Fig. 7. Effects of different size distributions of carcasses on mean daily foraging success of individual (A) Turkey Vultures and (B) Black Vultures. Size distributions were: excess of large carcasses relative to observed distribution of carcasses; observed distribution of carcasses; and excess of small carcasses relative to observed distribution. All simulations run using intermediate food-detection curve (i.e. curve 2 in Fig. 1).

risk by foraging in groups of two when detection curves 1 and 2 were used, and by foraging in groups of four when detection curve 3 was used. Risk increased sharply for individuals in larger groups.

The choice of detection curve had a strong effect on foraging success in that, as expected, higher detection rates resulted in higher rates of food intake and reduced risk of starvation. However, the mean per-individual food-intake curves and starvation-risk curves generated using the three functions produced similar patterns with members of intermediately-sized groups being most successful.

*Black Vultures.*—As for Turkey Vultures, mean individual food intake rates peaked for Black Vultures at group sizes of three or four individuals depending on the detection curve employed (Fig. 6B). However, after the optimal point, intake curves declined less rapidly than in the Turkey Vulture simulations; for detection curves 2 and 3, individuals in foraging groups of two to eight birds had higher mean intake rates than solo foragers. Risk of starvation was minimized for members of groups of three to five foragers, and risk of starvation in nearly all circumstances was higher for solo foragers than for individuals in groups of up to eight foragers (Fig. 6D).

*Effects of carcass-size distributions and food availability on simulation results.*—For Turkey Vultures, the size distribution of available carcasses

affected foraging success (Fig. 7A), but differences in food-intake rate were relatively small and the resulting curves were similar in shape. The optimal group size was two individuals when either the observed distribution of carcasses or an excess of small carcasses was available, but increased to three individuals when an excess of large carcasses was available. For each carcass distribution, groups of two to four Turkey Vultures had higher intake rates than solitary foraging individuals, but the foraging success of individuals in groups of more than four foragers declined rapidly below that of solitary foragers. Changing the amount of available food (by adjusting  $P$ , the probability that an area contained food) changed mean food-intake rates correspondingly, but the resulting food-intake curves were similar in shape (Fig. 8A). Optimal group size increased from two to three individuals when  $P$  was increased from 0.2 to 0.4, but when  $P$  was reduced to 0.1, the optimal group size remained at two individuals. Increasing  $P$  to 0.4 raised from four to five the maximum group size for which mean food intake exceeded that of a solo forager (Fig. 8A), but lowering  $P$  to 0.1 did not correspondingly reduce it.

For Black Vultures, differences in food intake achieved under each carcass-size distribution were greater than for Turkey Vultures (Fig. 7B). Biasing the carcass distribution toward large carcasses substantially raised food-intake rates

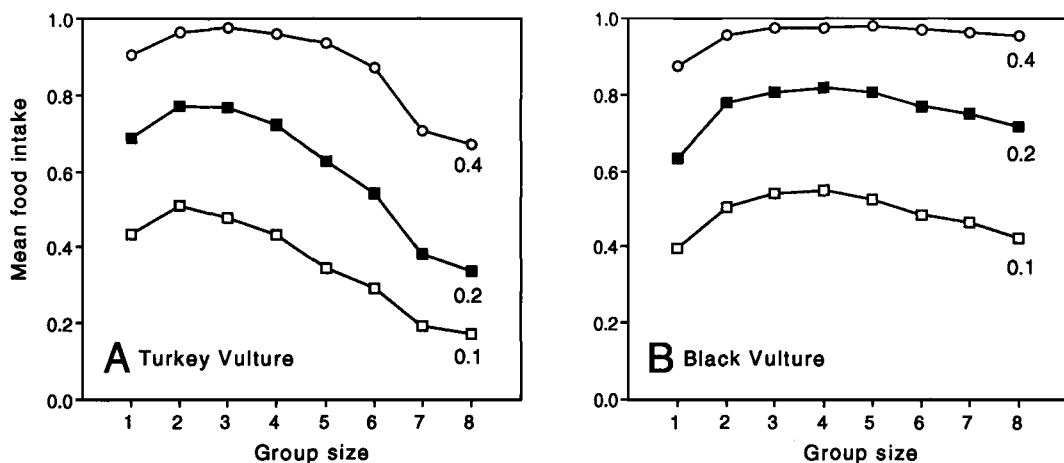


Fig. 8. Effects of level of carcass abundance on mean daily food intake of individual (A) Turkey Vultures and (B) Black Vultures. Carcass abundance expressed as mean probability (0.1, 0.2 or 0.4) that area searched contained food. All simulations run using intermediate food-detection curve (i.e. curve 2 in Fig. 1).

for individual Black Vultures, and optimal group size increased from three to five foragers as the proportion of large carcasses available was increased from an excess of small carcasses to an excess of large. Except for groups of eight foragers when an excess of small carcasses were available, food-intake rates of groups of foragers always exceeded those of solitary birds.

Varying  $P$  shifted the food-intake curves of Black Vultures up or down, but had less effect on their shape (Fig. 8B). Increasing  $P$  from 0.2 to 0.4 produced a general flattening of the curve and an increase in the optimal group size from four to five, but the overall shape was similar to that obtained with  $P$  values of 0.1 or 0.2. Birds in intermediate group sizes attained the highest intake rates, but all group sizes achieved higher food-intake rates than solo foragers.

#### RANDOM-DISPERSAL SIMULATION

*Turkey Vultures.*—Mean food intake per individual Turkey Vulture under the random-dispersal model never exceeded that for individuals in pairs of foragers, and most intake rates were at or below that of solo foragers (Fig. 9A). The optimal dispersal area for each roost size resulted in a food intake greater than that for a solo forager, but dispersal over other areas resulted in food intake falling below that of a solo forager. The dispersal-area effect was most obvious for individuals in roosts of 100 birds, whose mean food intake declined from 0.7 units

to less than 0.4 units when confined to only one quarter of the foraging area rather than being allowed to disperse over the whole area.

*Black Vultures.*—As was the case for Turkey Vultures, mean food-intake rates of Black Vultures in the random-dispersal simulations never exceeded that of a pair of foragers, but equalled or exceeded that of solo foragers (Fig. 9B). For roosts containing 100 individuals, the highest levels of food intake were obtained when foragers were dispersed over the whole foraging area or one-half of it, but intake fell when foragers were dispersed over only one-quarter of it. In contrast, intake rates for individuals in roosts containing 25 or 50 foragers were relatively low when they were dispersed over the whole foraging area, but increased when they searched over only one-half or one-quarter of it.

#### OVERALL SIMULATION RESULTS

Under some circumstances, random dispersal of foragers (especially Black Vultures) from communal roosts did result in enhanced foraging success relative to that of independently roosting solo foragers. However, the foraging benefits obtained from randomly dispersing from a communal roost were much less than those accruing to individuals foraging in optimal-sized groups and frequently less than those of individuals in nonoptimal-sized groups. Overall, Turkey Vultures were most successful

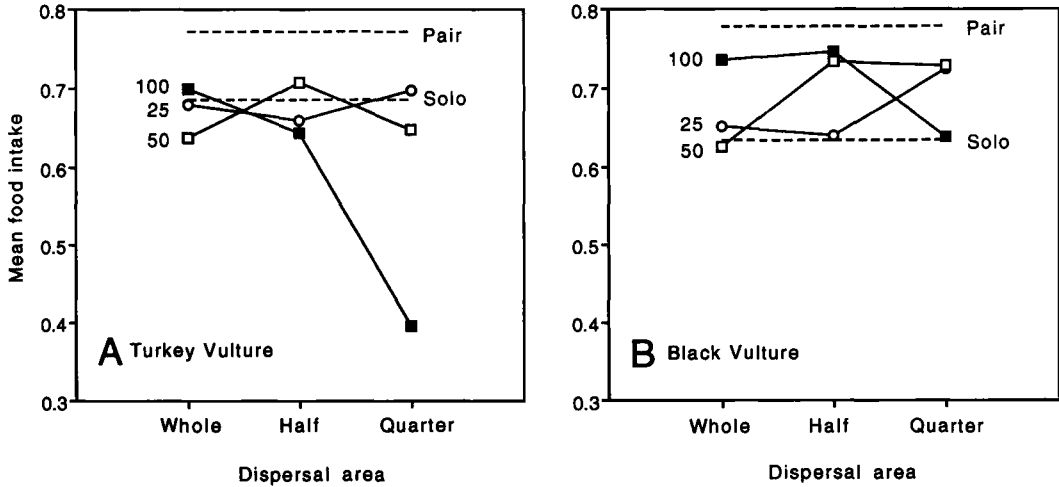


Fig. 9. Simulation results showing relationship between degree of dispersal of foragers (i.e. whether foragers dispersed over whole, one-half, or one-quarter of foraging area) and roost size (indicated by numbers to right of curves) on foraging success of (A) Turkey Vultures and (B) Black Vultures relative to foraging success of individuals searching alone (solo) or in pairs (pair).

when foraging in small groups of two or three individuals and did poorly relative to solo foragers when searching as members of large groups. In contrast, Black Vultures were most successful when searching as members of groups of three to five individuals, and under most circumstances achieved higher food-intake rates even as members of nonoptimal-sized groups than they would have by searching alone. The results of sensitivity analyses suggest that the above general conclusions are robust and not due to the use in simulations of a restrictive set of ecological parameters.

DISCUSSION

Turkey Vultures and Black Vultures appear to be the major vertebrate consumers of carrion in southern Texas. Although Crested Caracaras and coyotes are socially dominant over vultures, vultures are more abundant at carcasses than either caracaras or coyotes. Hence, the most intense competition for carrion among vertebrates appears to be within and between the two vulture species.

The effects of this competition are reflected in the relative importance of small and large carcasses in the diets of the two species. Turkey Vultures with their superior sense of smell have an advantage in locating carrion and are almost always the first vultures to arrive at carcasses

(Stewart 1978, Houston 1986, Wallace and Temple 1987, Kirk and Houston 1995). However, despite their superior ability to detect food, Turkey Vultures have limited opportunities to consume the carcasses they discover because Black Vultures frequently usurp the food. The need to feed quickly—before Black Vultures arrive—forces Turkey Vultures to depend largely on small, easily consumed food items, occasionally supplemented by meals obtained from larger carcasses (Stewart 1978, Coleman and Fraser 1987). The different foraging strategies of the two species are clearly reflected in the heights at which they fly. Turkey Vultures fly close to the ground where olfactory cues are strongest and their chances of spotting small carcasses are greatest, whereas Black Vultures soar much higher looking for feeding or descending birds that signal the location of a carcass.

Turkey Vultures in southern Texas forage in smaller groups than do Black Vultures. The group-foraging simulation results suggest that they forage in such small groups because the increased carcass-detection benefits of foraging in larger groups cannot compensate for the increased costs of intraspecific competition, and because of the increased likelihood of Black Vultures detecting the carcasses through local enhancement. In contrast, simulation results for Black Vultures indicate that in this species foraging-group size is limited not by the need to

avoid interspecific competition, but by the effectiveness with which different-sized groups can locate carcasses and by the size distribution of available carcasses. Thus, Black Vultures can be expected to often search for food in large groups and field observations confirm this expectation.

I conclude from the results of the group-foraging simulations that for both Turkey Vultures and Black Vultures foraging in groups can be a profitable strategy, but the costs and benefits differ for the two species, with optimal group size for Black Vultures being larger than that for Turkey Vultures. Because the simulation results show that searching in groups is better than searching alone, and the data from field observations indicate that foragers are spatially and temporally clumped, I suggest that an assembly-point function (i.e. communal roosts facilitate formation of foraging groups; Evans 1982) is a plausible selective advantage of communal roosting in vultures.

The results obtained from the random-dispersal simulations indicate that (at least for Black Vultures) local-enhancement benefits accruing from concentrating in roosts and randomly dispersing from there to search for food (instead of roosting separately, randomly spread throughout the foraging area) could provide a selective advantage for roosting communally. Possible spatial-concentration benefits, however, depend on foragers tailoring their dispersal pattern from the roost so as to achieve an optimal spatial distribution (perhaps by departing in only a few directions, as both Turkey Vultures and Black Vultures often do; Rabenold 1983, Buckley 1994). While the likely benefits of spatial-concentration effects achieved through random dispersal from roosts may be small relative to those obtainable by foraging in more organized groups, such spatial clumping of departures might represent an intermediate step between completely random dispersal from roosts and active group formation.

Given the disparity for both species between the observed size of foraging groups and the number of birds found in roosts, it is clear that far more birds aggregate in roosts than are necessary to form the observed foraging groups. It is possible that large numbers of individuals occur in roosts because of some advantage in associating with a large number of birds per se. For example, joining a large roost may increase the likelihood that there will be other foragers

willing to depart with an individual when it is ready to go foraging. Alternatively, however, the large number of individuals in roosts simply may be the outcome of a runaway process that occurs because joining a roost is a better decision for each individual than the alternative of roosting alone (Sibly 1983). As a result of a series of optimal individual decisions, roosts grow to contain more birds than are needed to form optimal-sized foraging groups.

Information-center following appears to contribute to the foraging success of Black Vultures (Rabenold 1987, Buckley 1994). However, there also are other potential advantages of communal roosting. For example, a variety of nonforaging benefits of communal roosting have been proposed. These include improved thermoregulation (Brenner 1965, DuPlessis and Williams 1994) and increased protection from predators (Lack 1968). Such benefits, however, are unlikely to be important to vultures because they do not huddle together in roosts to conserve heat and rarely are attacked by predators. Alternatively, communal roosting may be advantageous because it offers kin-selection benefits. Black Vultures sharing communal roosts in North Carolina frequently are closely related (Rabenold 1986, Parker et al. 1995), and aggressive interactions between Black Vultures at carcasses and roosts appear to be a negative function of the degree of relatedness (Rabenold 1986). Therefore, Black Vultures may derive kin-selection benefits from communal roosting by cooperating with kin when searching for food or sharing food with relatives.

Recent work has demonstrated that many birds show extreme flexibility in their foraging behavior. For example, nonterritorial Common Ravens (*Corvus corax*) commonly search for food singly or in pairs, but when they locate large carcasses controlled by pairs of territorial birds, recruit followers from communal roosts (Heinrich 1988, 1989) or call loudly to attract conspecifics (Heinrich and Marzluff 1991, Heinrich et al. 1993) who then aid them in gaining access to the food. Similarly, depending on prevailing conditions, colonially breeding Cliff Swallows (*Hirundo pyrrhonota*) forage singly or in groups, follow conspecifics to food patches, or make use of local enhancement to locate insect swarms (Brown 1986, 1988). Furthermore, when it benefits them to do so, individual Cliff Swallows actively recruit conspecifics to mobile insect swarms, apparently because this behavior in-

creases the probability that when the original calling bird returns from feeding chicks it will be able to relocate the patch (Brown et al. 1991).

In the context of this demonstrated flexibility in avian foraging behavior, it seems likely that, even if one ignores possible nonforaging and kin-selection benefits, communal roosting may benefit individual foragers simply because it provides them with an array of foraging options and allows each individual to tailor its foraging strategy to fit its particular circumstances. Thus, an individual may choose (a) a low-risk strategy by joining a group of searchers or by departing in the same direction as other foragers, or (b) a more risk-prone strategy by noting the departures of other birds from its roost and departing to search in the opposite direction, where there are likely to be fewer competitors. Such simple strategies represent a potentially valuable use of information by foragers that is more subtle than the simple following to food patches envisioned by Ward and Zahavi (1973). As Rabenold (1987) has pointed out, information is anything that reduces uncertainty. Thus, roosting communally may be advantageous because by doing so foragers are able to make the most informed decisions possible when deciding when, where, and with whom to forage.

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