

FAMILY ASSOCIATIONS IN COMMUNALLY ROOSTING BLACK VULTURES

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ABSTRACT.—Observations of marked individuals in a partially marked population of Black Vultures (*Coragyps atratus*) show that immediate family members maintain close contact throughout the year. Associations between mates and between parents and offspring are primarily responsible for this. Mutual allopreening, feedings, and intercessions in fights occur almost exclusively within families. Adults known to breed within the study area (neighbors) associate more strongly than nonneighbors, although not as strongly as mates. Certain families associate preferentially with certain other families. Strength of interfamily associations is not related to distance between nest sites within the study area. I argue, therefore, that birds actively seek particular individuals as associates. Further knowledge of breeding dispersal of young of known parentage will provide clues to relatedness of highly associated neighbors. Strong associations among related individuals can help explain the use of avian communal roosts as information centers. *Received 27 April 1984, accepted 10 June 1985.*

COMMUNAL roosts and breeding colonies could serve as "information centers" to which unsuccessful foragers return and follow successful individuals to a known food source (Ward and Zahavi 1973). Explaining the apparent aid-giving of successful foragers remains a difficulty of this hypothesis. Some workers emphasize the probability of high levels of relatedness within colonies (e.g. Erwin 1978, Waltz 1982) to help explain why successful foragers might tolerate any costs of being followed. By sharing food with closely related individuals, successful foragers could increase their inclusive fitness (Hamilton 1964). If mechanisms exist that allow preferential sharing with close relatives, inclusive fitness gains could outweigh costs of sharing.

Black Vultures (*Coragyps atratus*) form large communal roosts each night throughout the year, although they nest in pairs in isolated, well-protected locations. Indirect evidence suggests that Black Vulture roosts may serve as food-finding information centers. For instance, morning roost departures are significantly clumped both in time and in direction, and these clumped departures cannot be explained by weather conditions (Rabenold 1983).

A successful forager might return to the roost to recruit particular individuals with whom to

share or cooperatively defend its find. If these associations of individuals are stable over time, it should be possible to detect relative differences in the strengths of associations between different individuals in communal roosting and feeding situations. There is evidence suggesting that parent-offspring ties persist for several months past fledging in Black Vultures (Jackson 1975, McHargue 1977, this study). This behavior would help explain the use of roosts as information centers. Preferential association and preferential behavioral interactions among individuals in a population could structure the distribution of benefits accruing from shared information at communal roosts. The maintenance of family associations outside the breeding season is the subject of this paper.

To examine associations of individuals within Black Vulture communal groups, I ask specifically (1) whether mated pairs and individuals of known relatedness (parents and offspring or siblings) are seen together more often than predicted by chance; (2) whether these intrafamilial associations differ from associations of the same individuals with birds not known to be related (extrafamilial associations); (3) whether pairs nesting in an area associate more than expected by chance with other pairs nesting in the same area, and whether these neighborhood associations differ in degree from associations within families or between nonneighbors; and (4) whether strength of associations between neighbors is dependent on the distance between their nest sites.

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METHODS

Study area and population.—The study area, situated in farmlands of Chatham County in central North Carolina and covering approximately 250 km², is composed of 60% agricultural land and 40% woodland; it contains no towns (Reeves et al. 1970). The main farm products of this area are poultry, swine, dairy and beef cattle, and tobacco produced by many small farms. I have studied the population of Black Vultures there since autumn 1976, and I began a trapping and marking program in 1977. Birds were captured primarily in a walk-in funnel trap baited with carrion. By summer 1981, 344 Black Vultures had been marked with individually numbered vinyl wing tags (Wallace et al. 1980) legible at close range with 10× binoculars and at greater distance with a 15–60× zoom telescope.

Based on the proportion of birds marked at roosts and feeding areas and an estimated annual mortality of 12.5% (the annual mortality of breeding adults during this study), approximately 1,200 Black Vultures regularly use the area year-round. Not all of these birds roost in the study area on any given night, as there is considerable movement in and out. Seasonal estimates of the number of birds present range from 358/night during winter (mean size of winter roosting groups multiplied by mean number of active roosts/night) to 242/night in summer. The range over which these birds forage is unknown, although some movement of marked birds outside the study area suggests very large ranges for some individuals. Of the 344 marked Black Vultures, over 100 are seen regularly within the study area, 2 have been seen at a distance of 95 km (and have since returned), and 1 was seen repeatedly at a communal roost 170 km away. Daily ranges are not likely to include such long movements.

The study area contains seven roost sites used by the local population. Roosts are all in mixed conifer-hardwood forest near small creeks. Roost sites are traditional in the sense that each is regularly attended when birds are feeding nearby, and local residents report that the same sites have been occupied sporadically for many years, although no roost site is occupied every night. My observations of marked birds indicate that within a certain area individuals use a number of roosts over the course of a year, but often use a single roost for several days in a row.

Censuses of feeding and roosting groups.—Each roost was censused regularly through the course of the study. If a roost was occupied, I counted the number of Black Vultures present and identified tagged birds. Censuses were usually complete, except in summer when foliage sometimes partially obscured the roost. Measures of association, therefore, represent minimum estimates of actual associations between individuals. When scanning groups for tags, I recorded all social interactions involving at least one marked

bird, including mutual allopreening, fights (initiator, if seen, type of fight, and outcome), and begging by young birds (adults to whom begging was directed and whether the young bird was ignored, rebuffed, or fed by regurgitation). I performed 318 roost censuses during the study.

Feeding groups were located by following birds out of the roost to their morning feeding sites, or by driving a prescribed circuit through the study area during midmorning while watching for groups of vultures circling or descending. At all feedings, I counted the number of Black Vultures present, identified tagged birds, and recorded social interactions involving marked birds. I performed 86 feeding censuses during this study.

Ascertaining family membership.—In North Carolina, breeding Black Vulture pairs nest in isolated locations usually deep in woods. Between 1977 and 1981 I located 14 such nest sites within the study area. At 8 of these the same adults returned each year to breed. All adults at these 8 nests were marked with patagial tags. Each pair produced 1 clutch of 2 eggs each year (although 2 early failures resulted in later relaying), and all fledged young have been tagged at each nest in every year since its discovery. In all, 46 young birds of known parentage have been tagged in the 8 families, and different-age sibs (produced by the same parents in different years) are known for all sites.

Association measures.—I used only observations of feeding or roosting groups of birds to test the significance of associations between individuals in the groups. Sightings of birds at nest sites were not included. I also excluded observations made during the early breeding months of March, April, and May, when movement of breeding adults is restricted owing to incubation and brooding duties. Only the first sighting of an individual at a particular site on any day was used. To test associations within the group of birds regularly using the area, I attempted to omit transients and irregular visitors by considering only those animals sighted on at least 10 different days. If observations of two birds did not overlap completely as a result of different marking dates or disappearance of either one, the measurement of association was limited to the period of potential overlap.

Of the 344 marked Black Vultures, 102 (50 adults, 52 young) were resighted at least 10 times (maximum number of sightings for any individual in groups = 61), and these birds are considered the core group of vultures regularly using the study area. These 102 individuals were considered by pairs in three measures: the Chi-square test of independence within pairs; the point correlation coefficient V (Pielou 1976); and Dice's (1945) "association index." The point correlation coefficient, an index ranging from -1 to $+1$, was used as a comparative measure between subclasses of the population (e.g. between related pairs and unrelated pairs) and as a means of assigning direction to results of the Chi-square test (the Chi-square

TABLE 1. Association of 8 mated pairs of Black Vultures outside of incubation and brooding periods.

Pair	Number of censuses including:				Measures of association ^a	
	A and B (a)	A only (b)	B only (c)	Neither A nor B	χ^2	Dice's index
1	15	13	8	158	49.93	0.588
2	20	14	13	132	42.28	0.597
3	9	3	3	57	30.42	0.750
4	10	2	4	52	30.58	0.769
5	9	1	15	140	42.51	0.529
6	10	6	3	151	66.92	0.690
7	8	6	16	104	13.52	0.421
8	15	10	5	109	47.07	0.667

^a $P < 0.001$ for all Chi-square values. Dice's index = $2a/(2a + b + c)$.

test is two-tailed and will not differentiate between significantly positive and significantly negative associations). Dice's index was also used to make comparisons and to validate results based on the other two measures.

RESULTS

Associations in feeding and roosting contexts.—Individual vultures usually were resighted more often at roosts than at food for two reasons: (1) I made many more censuses at roosts than at food (318 vs. 86), and (2) roosting groups were much larger than feeding groups (means = 82 and 22). While 102 birds were resighted 10 or more times, only 53 of these had at least 10 resightings at roosts and only 11 had at least 10 resightings at feeding sites. The small feeding sample makes full comparisons of association rules between the two contexts impossible. However, 7 of the 11 birds resighted 10 or more times at food were local breeders comprising 4 mated pairs. These 4 pairs did not differ between roosting and feeding contexts; all were positively associated in both situations ($P < 0.05$, χ^2 test). If a larger subsample of the 102 is examined, using birds with as few as 2, but on average 6, feeding sightings, sufficient pairs exist to compare within-family associations at roosts (68 pairs) against those at food (37 pairs). Although feeding groups are smaller and random mixture would produce many fewer positive associations at food than at roosts, the proportion of positive associations did not differ between roosts and food for mates, parent-offspring pairs, or siblings. Pooled intrafamilial associations included 32% positive asso-

ciations at food, significantly more than the random expectation of 5% (χ^2 , $P < 0.01$). No age-paired category (e.g. adult-adult, adult-young, young-young) composed of known family members paired with extrafamilial birds, differed significantly from 0.05 in the proportion of positive associations at feeding sites. Because association rules among family members apparently do not differ between roosting and feeding, I pooled roosting and feeding observations for the remainder of the analysis.

Associations between mates.—Mated adults alternate nest shifts of approximately 24 h during the 55 days of incubation and brooding. I have 62 observations of an off-duty bird attending a communal roost, and in 27 visits to nests at dawn I never found more than 1 adult present. Except during March, April, and May, when they were incubating and brooding, members of the 8 mated pairs with known nest sites were seen together more often than expected by chance (Table 1, χ^2 , $P < 0.001$ for all). However, none showed complete overlap, as all 16 marked adults of known nest site occasionally were seen without their mates. Of the associations of these 16 individuals with all other adults that were not family members, only 18% were positive, significantly fewer than between mates (Fig. 1). Adults clearly associate with their mates more than with other adults outside the breeding season, but they also regularly associate with some adults that are not their mates.

Associations between parents and offspring.—Among parent-offspring pairs, 23 of 36 (64%) showed positive association through the course of this study (Fig. 1). I have insufficient yearly resightings of almost all pairs to test the decline of parent-offspring associations as the young birds mature, so for this analysis I pooled all parent-offspring pairs regardless of offspring age. In general, resighting rates of young birds decreased as the birds aged so that 3- or 4-yr-old offspring are resighted less frequently than either their parents or their younger siblings. However, when in the study area, subadults occurred with their parents with the same probability as did younger sibs. Associations of the 16 breeding adults of known nest site with all young known not to be their offspring yielded only 14% positive associations. Parent-offspring associations included significantly more positive associations than did parent-nonoffspring associations. The converse re-

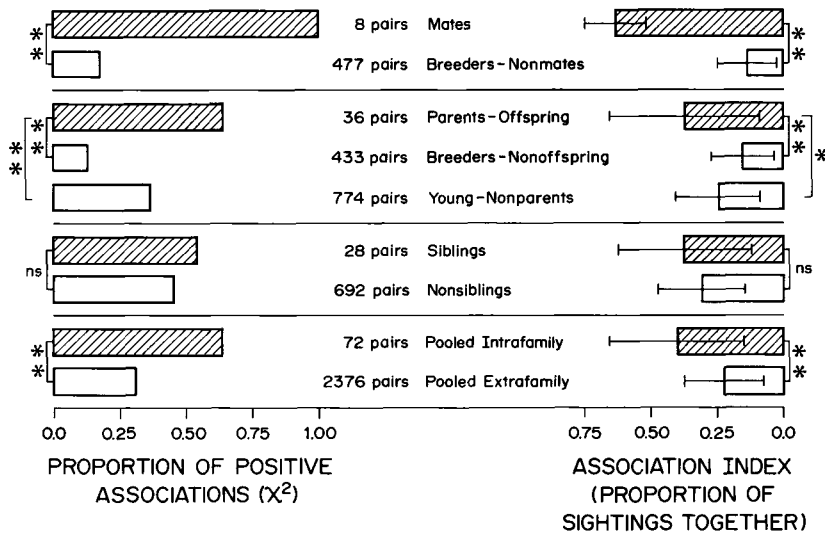


Fig. 1. Left histogram: proportion of significant positive associations (χ^2 , $P < 0.05$) within families (shaded bars) and between presumed unrelated (extrafamilial) birds (open bars), by age/status class. ** indicates significant difference in proportions at $P < 0.001$, using test of equality of 2 percentages (Sokal and Rohlf 1969). Right histogram: mean association-index values (\pm SD) within families (shaded bars) and between presumed unrelated (extrafamilial) birds (open bars), by age/status class. ** indicates significant differences in distributions at $P < 0.001$, * indicates $P < 0.01$ using Kolmogorov-Smirnov 2-sample test (Siegel 1956). ns = not significant.

relationship between offspring and all adults known not to be their parents was similar although not as pronounced (Fig. 1). Associations of young of known nest site with all nonparent adults included 37% positive associations, significantly lower than the comparable parent-offspring proportion. Young birds were found with their parents more often than with other adults.

Parent-offspring associations varied widely among families but were fairly consistent within families (Table 2). Within two families identified as TB and AH, no significantly positive associations were found in 9 pairings of parents with surviving offspring. To the extent that associations between parents and volant young represent the degree of postfledging parental care, these two breeding pairs invested little if anything in their young after fledging. Their overall reproductive success perhaps reflects the cost of not maintaining contact with offspring; 13 young fledged at these two nests over 4 yr, but only 6 (46%) were known to have survived more than 2 months after fledging. The remaining families showed positive associations in 23 of 27 (85%) parent-surviving offspring pairings during all postfledging appearances in

groups (Table 2). They also had significantly greater postfledging survival (26 of 28, or 93%, were known to have survived more than 2 months past fledging) when compared with the two families with low parent-offspring association (χ^2 , $P < 0.01$). I know little about the associations of parents with young that disappeared within 2 months of fledging because I do not have the requisite 10 resightings for these offspring. These calculations are based only on associations of parents with surviving offspring. For the two families with low associations between parents and surviving offspring, I assume these parents treated their nonsurviving offspring similarly.

Associations between siblings.—The proportion of positive associations among sib pairs (same- and different-age pairs pooled) was 55%, not significantly different from the 46% positive associations found when known-nest young were paired with all other nonsibling young (Fig. 1). This seemingly low proportion of positive associations among sibs (when compared with other intrafamilial categories) was not affected by separating sibs of different ages. Positive associations occurred in 7 of 12 (58%) same-age sib sets and 8 of 16 (50%) different-age sib sets.

TABLE 2. Fledgling survivorship and strength of parent-offspring association.

Family code	Proportion of fledglings surviving	Association measures ^a				
		No. of χ^2 values that were:			Dice's index	
		Significantly positive	Positive	Negative	Mean	SD
LA	6/6	6	2	0	0.329	0.182
DC	4/6	1	1	0	0.331	0.063
ML	6/6	6	0	0	0.550	0.275
LE	7/7	6	0	0	0.664	0.149
SA	3/3	4	1	0	0.422	0.274
TB	2/5	0	2	1	0.116	0.102
AH	4/8	0	0	6	0.000	0.000

^a Parents with surviving offspring.

In fact, young birds showed strong positive associations regardless of relatedness. Young apparently make no active attempt to follow or remain with their siblings as long as they are with a group of young vultures.

Pooled intrafamilial associations contained a higher proportion of positive associations than did pooled extrafamilial associations (Fig. 1). Overall, immediate family members occurred with each other in communal roosts and feeding groups outside the breeding season more often than they occurred with other presumably unrelated individuals. High intrafamilial associations, however, resulted primarily from parent-offspring and mated pair associations, rather than sibling associations.

Associations between neighbors.—All marked breeding adults of known nest site were tested in pairs with all other nonmate breeding adults of known nest site for association, excluding the months of March, April, and May. Of 82 pairs, 28 (34%) had positive associations, more

than the 18% positive associations between breeding adults and all extrafamilial adults (Table 3). However, the proportion of positive associations among neighbors was less than among mates (Table 3). Closer inspection reveals that some breeding pairs associated strongly with certain other pairs. Furthermore, because parents and offspring showed significant levels of association, entire family groups from different nest sites were positively associated. Levels of associations between neighboring breeding pairs could be a function of distance between nest sites. This would imply passive co-occurrence due to degree of home-range overlap in animals restricting their movements to the vicinity of their nest sites. There was no correlation between degree of associations and distance between nest sites within the study area (Fig. 2). A linear regression of mean V values for each distance against distance between nest was not significant ($r = -0.105$, $P \gg 0.05$).

TABLE 3. Comparison of associations between breeding adult Black Vultures and other adults.

Type of association	Measures of association				
	χ^2 tests ^a		Dice's index		
	n	p	n	\bar{x}	SD
Breeding adults with all nonmate adults	477	0.182 ($P < 0.01$) ^b	478	0.135 ($D = 0.275$, $P < 0.001$) ^c	0.115
Breeding adults with neighboring breeders	82	0.341 ($P < 0.001$) ^b	86	0.273 ($D = 0.520$, $P < 0.05$) ^c	0.210
Within mated pairs	8	1.000	8	0.628	0.115

^a n = number of dyads, p = proportion of associations that were significantly positive ($P < 0.05$).

^b Test of equality of two percentages (Sokal and Rohlf 1969).

^c Kolmogorov-Smirnov two-sample test (Siegel 1956); D = greatest interval difference between two cumulative frequency distributions.

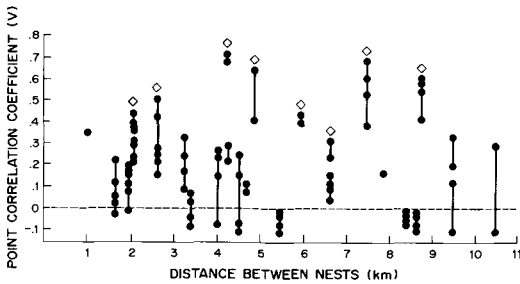


Fig. 2. Point correlation coefficient (V) for all breeding adults paired with nonmate locally breeding adults by distance between nests. V values for each nest-nest comparison (nest A adults paired with nest B adults) are connected by vertical lines. Diamonds indicate nest-nest comparisons in which all pairs are significantly positively associated (χ^2 , $P < 0.05$).

Comparisons of association measures.—All results from Dice's association index agreed with results of Chi-square tests (Fig. 1). Association-index values were greater among mates than unmated adults, and among parent-offspring pairs than among both parent-nonoffspring young and offspring-nonparent adults. Index values did not differ significantly between pairs of sibs and pairs of nonsibling young. Pooled intrafamilial association-index values exceeded extrafamilial values. Association indices between neighboring breeding adults (extrafamilial neighbors) were less than between mates (Table 3), but greater than between breeding adults and all nonmate adults (extrafamilial adult population) (Table 3).

Behavioral correlates of family associations.—Behavioral correlates of family associations include allopreening, feeding, and defending family members against attacks by unrelated birds. Of 70 mutual allopreening interactions involving at least one known family member in communally roosting or feeding groups, 61 were between family members (Table 4). Of the 9 instances of extrafamilial allopreening, 7 involved young birds with other unrelated young (with whom they were positively associated), and 2 involved breeding adults mutually allopreening with adults from neighboring nest sites (with their mates present in both cases). Although most extrafamilial observations were of young allopreening unrelated young, young apparently do not allopreen other young indiscriminately with regard to relatedness. Allopreening between sibs was more common

TABLE 4. Occurrences of behavioral interactions between different classes of Black Vultures.

Type of behavior	No. of cases involving:			
	Mates	Par- ents/ off- spring	Sib- lings	Extra- family
Mutual allopreening	27	26	8	9
Postfledging feedings	0	41	0	0
Interference at roost	2	2	2	0
Interference at food	3	7	0	0

than expected, based simply on the representation of sibs in the population of young birds ($\chi^2 = 66.87$, $P < 0.001$).

Forty-one postfledging feedings involving known parent-offspring pairings were observed. These feedings occurred as late as 8 months after fledging. Adults were never observed to feed young other than their own in spite of begging attempts by other young. Unrelated young attracted by conspicuous regurgitative feeding were always driven away by pecks from the feeding adult.

Central to the association of kin in Black Vultures is the fact that individuals will come to the aid of kin that are being actively displaced or physically attacked by unrelated birds. Although only 16 instances were observed, all involved intercession on behalf of known family members (Table 4).

Family gatherings at nest sites.—In addition to preferring the company of kin and behaving preferentially toward them in communal situations, Black Vultures rendezvous with family members at their unique nest sites. After fledging, young birds that become separated from their parents meet them back at their nest sites. Preening and feedings take place there before birds depart for the evening communal roost. In 188 midafternoon nest-site observations after August fledging through the end of December, at least one family member was present in 101 cases. Both adults and young (at least one of each) were present in 62 cases, and all four nuclear family members were present in 34 cases. In some of the meetings of an entire family, the four members arrived together from the same direction, whereas in other meetings some or all members arrived singly. Nest-site rendezvous of families probably occur daily for about 3 months after fledging and decline

slowly in frequency thereafter. By 5 months after fledging, young were no longer observed at the nest sites, and meetings of family members other than mates occurred at roosts and feeding sites.

Courtship and copulation.—Courtship and copulation did not occur in communal situations. Male Black Vultures have a characteristic courtship posture that immediately precedes copulation and is presented to the female at the nest site. I have witnessed 4 copulations; each was preceded by the courtship posture and occurred at the nest site. On only 7 occasions during hundreds of hours of roost and feeding observations during February and March (eggs are laid in mid-March) have I seen birds assume the male courtship posture. In these 7 instances, the posturing bird was approached quickly by several nearby birds of both sexes that began pecking and biting him violently until he fled the area.

DISCUSSION

In their lifetimes, Black Vultures may use many communal roosts. At any one roost the composition of individuals changes nightly, resulting in large-scale mixing of individuals. Nonetheless, family members maintain close contact outside the breeding season in communal feeding and roosting groups. A significantly greater proportion of positive associations involved mated pairs and parent-offspring pairs than their extrafamilial pairings, and pooled intrafamilial associations contained a greater proportion of positive associations than pooled extrafamilial associations.

Young birds, in general, have more positive extrafamilial associations than do their parents. This age difference in association patterns may be partially explained by differential movement rates and the relative site fidelity of young birds during the winter (Rabenold MS). Black Vultures form larger roosting groups during winter than summer. The winter roosting sites are stable within a winter, although smaller satellite roosts occasionally may be used. Turnover rates for adults are greater than turnover rates for young birds at the winter roost, and young birds are more likely to return after an absence. Young birds evidently tend to wait at the winter roost, whereas adults (including their parents) circulate among several roosts. This tendency for young birds to congregate

regularly at a single site leads to high association values among regular visitors to the roost, primarily young birds, and accounts for the high proportion of positive associations among unrelated young (Fig. 1) and the higher overall proportion of positive extrafamilial associations involving young from known nest sites (41%) compared with that of their parents (16%) (Fig. 1, $P < 0.05$).

Factors favoring maintenance of contact among family members.—High association between mates would be expected in animals that are highly gregarious immediately preceding and during courtship and egg-laying, when mate guarding might be necessary. However, in Black Vultures mates are highly associated year-round (except during incubation and brooding, when they take alternate nest shifts), with no marked increase immediately preceding reproduction. Although mate guarding could contribute to high association during the reproductive period, courtship and copulation do not occur in communal situations, but are confined to the nest site and isolated from other birds. Because birds adopting the courtship posture in groups are attacked by nearby birds, strict mate guarding by individual males is unnecessary.

Parent-offspring bonds persist in part because of extended postfledging dependence of young on direct parental feeding. Families with low parent-offspring association had lower fledgling survivorship than those with high parent-offspring association. Regurgitative feedings of offspring fledged in August occurred as late as the following April. During this period young birds will not compete for food at a carcass attended by many adults. They wait at the side for their parents to emerge, then beg loudly for regurgitative feedings. The postfledging nest-site rendezvous underscore the dependence of young on parents for feedings and feeding assistance in groups. Although family members, and especially young birds, often become separated in hectic morning roost departures, daily reassembly at nest sites assures that family members maintain contact during the period when young are dependent on parents for feeding and still unfamiliar with many parts of their ranges. During their first spring (almost 1 yr old) young birds begin to join large feeding groups, and their parents aid them by threatening other adults that attempt to drive these offspring away from food. This form of assistance has been docu-

mented in other species with long-lived associations between parents and young (Scott 1980). As juveniles mature and become more competitive feeders, the relationship with their parents may evolve into mutual aid-giving during competition within a large feeding group. That parent-offspring associations persist well beyond the age of strict dependence suggests that long-term associations continue to be mutually beneficial.

Aid in feeding may be the largest single factor favoring retention of strong ties among members of Black Vulture families. Associations of family members remained high when feeding observations alone were considered, while extrafamilial associations fell to the level expected from random assortment. Because their food supply is extremely patchy in space and time, an individual's chances of finding food while alone may be small, and competition at feeding sites can be fierce. Because a single source usually contains enough food for several birds, a finder should recruit his family members preferentially to share food with them, thereby increasing his inclusive fitness by fostering survival of genetically correlated individuals (Hamilton 1964). In addition, a coalition of individuals may better defend a small carcass or part of a large one. As a consequence, each may feed better than if competing alone.

Are associations based merely on range overlap?—If young birds cover large ranges centered on their natal nest sites until they become reproductive and adults center their ranges on their breeding sites, immediate family members would have extensive or complete range overlap. Although their ranges would overlap extensively with many other individuals' ranges, family members would have stronger associations with closely related birds than with others simply as a result of passive association from sharing an identical range, even if the birds moved independently of each other within this range. Extrafamilial association values should vary widely depending on the extent of range overlap, which may be correlated with the distance between nest sites. Mates would have the highest associations, followed by neighboring breeding adults, followed by nonmate adults, including all adults regardless of nest site. These predictions match my results (Table 3). However, within the neighbor-neighbor pairs, association values should decline with increasing distance between nest

sites; those nesting closer together might have more extensive range overlap than those nesting farther apart. No such relationship was evident when the association values of breeding adults nesting within this study area were plotted against distance between nest sites (Fig. 2). It appears instead that some families have strong alliances with others and that this pattern of alliances between families is not a function of distance between nest sites.

It is possible, however, that the greatest internest distance considered (<11 km) is trivial to a vulture and that it is not surprising, therefore, that associations tend to be high with no significant decline over this distance. My observations of breeding adults suggest that their movements are heavily concentrated within 20 km of their nest sites throughout the year. Within this restricted range, internest distances approaching 11 km include a significant portion of the estimated range of breeding adults. Furthermore, the daily afternoon meetings at nest sites make it unlikely that families would travel great distances out of the study area. If greater internest distances were considered, a decline in associations might be found that would support the passive range-overlap hypothesis. Associations must decline with increasing internest distance. Despite its potentially large range, an individual bird covers a finite area, and associations must eventually fall to zero. It is therefore of interest to look not only for a decline in associations with distance, but at the range of association values within a reasonable distance from each family's nest site. The passive range-overlap hypothesis predicts a smooth decline from center of range to edge. Not only was no decline found, but association values at each internest distance varied widely (Fig. 2); negative association values were found at even very small internest distances. In fact, for only one family was the most closely associated family found at the next-nearest nest site.

The lack of correlation between associations and internest distances suggests that particular associations, both at family and neighborhood levels, are based on some attribute of the birds other than wide overlap of ranges. The active nature of intrafamilial associations is also supported by conspicuous allopreening and intercessions in fights. Because intrafamilial association is so marked, it may be that breeding adults of highly associated families are also closely related. Although no birds marked as

nestlings have bred in the study area, 3- and 4-yr-old birds are still in the area and use local roosts. Age of first breeding is not known for this species. If many birds breed in their natal area and intrafamilial associations persist, it is likely that neighbors may include parent-offspring or sibling relationships.

Roosts as information centers.—Perhaps the chief theoretical criticisms of Ward and Zahavi's (1973) information-center hypothesis is that it relies on reciprocation between finders and followers. Unless reciprocation is assured, the participation of successful foragers appears paradoxical. Why should they return, only to be followed by competitors, unless there is a yet stronger advantage in joining an aggregation, such as reduced risk of predation (Alexander 1974, Hoogland and Sherman 1976)? A common assumption is that food is sufficiently abundant within a patch that competition would be weak and attempts to dissuade followers would be pointless (Krebs 1978). However, there must be a maximum number of followers beyond which this would not be true. Furthermore, the field evidence in support of this hypothesis has to date been gathered on colonially breeding birds (Krebs 1974, Erwin 1978, Waltz 1981), in which successful foragers must eventually return to feed young. In these cases, predator defense or localized nesting sites become particularly plausible explanations for aggregation. Black Vultures have no known predators as adults and thus represent a fairly simple system for examining certain aspects of the information-center hypothesis. Because they are not colonial breeders, members of the population that are vulnerable to predation (nestlings) are not present in the aggregations. Also, successful foragers need not return to a specific aggregation site to feed nestlings and they could conceivably avoid competitors by sleeping alone, although I have no evidence that such "cheating" occurs. While a single bird roosting solitarily would be difficult to detect, I have many examples of birds seen at carcasses joining a roosting group the same evening (Rabenold MS).

The paradox of the returning successful forager is partially resolved if it returns to lead its family members to food. But why should families not maintain separate fixed aggregation centers (such as their nest sites) to which they return with foraging information to avoid sharing with nonrelatives? If the food supply

is sufficiently patchy, entire families could search without success, and they could then rely on the larger group for foraging information. Even if they are followers, cooperation of entire families in competitive groups may increase their chances of feeding. If families or larger alliances of families function as units competing for food, no one nest site would provide a suitable meeting place. Families could instead meet allies and relatives at neutral roost sites. Beyond the observations reported here of family members aiding each other in roosting and feeding interactions, detailed observations of feeding interactions are needed to verify the competitive advantage of individuals feeding in the presence of family members or allies.

The evidence reported here suggests that Black Vulture communal roosts serve as meeting places for family groups and allied families. Family members associate with each other preferentially and assist each other in competitive interactions in large roosting and feeding groups. The extent to which kin selection has shaped the evolution of communal roosts in Black Vultures cannot be estimated without greater knowledge of the relatedness of allied family groups. If young birds eventually breed near their natal areas and family bonds persist, allied neighbors may also be closely related. The possibility that large roosting groups consist of a few large extended family units or clans is intriguing in light of the information-center hypothesis. This study demonstrates positive associations and cooperative behavior among family members, and I show elsewhere (Rabenold MS) that following from the roost and continued participation in a roost might be discouraged in unrelated birds by aggressive interactions in the roost. While these results do not present direct evidence that foraging information is transferred at roosts, they suggest that potential recipients of information are often family members, a condition under which the evolution of information sharing is more likely than among birds assorted randomly with respect to relatedness.

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