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**FORAGING ECOLOGY OF TURKEY VULTURES:
A TEST OF INFORMATION TRANSFER**

by

Kent A. Prior

A thesis submitted to
Faculty of Graduate Studies and Research
in partial fulfillment of
the degree of
Master of Science

Department of Biology
Carleton University

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in partial fulfillment of the requirements
for the degree of
Master of Science

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Chair, Department of Biology

A handwritten signature in black ink, appearing to read 'P. J. Jett', written over a horizontal dotted line.

Supervisor

roosting or nesting solitarily. While this is unlikely, the problems of acquiring data on predation rates among natural populations make it a difficult hypothesis to test.

The "information centre hypothesis" (Ward and Zahavi 1973) suggests that communal roosts and breeding colonies function primarily as centres of information exchange between participants about the location of randomly dispersed and ephemeral food resources. Perhaps the simplest way in which such food information could take place would be for relatively unsuccessful foragers to follow their more successful roostmates to a food patch, thereby increasing their foraging efficiency. There is evidence both for (Brown 1986, 1988, Gori 1988) and against (Andersson et al. 1981, Gotmark 1988) breeding colonies operating as information centres. Communal roosts can be considered as distinct from breeding colonies since they do not contain any defendable resource (e.g., eggs or young), need not remain in the same location, and usually are visited by the birds only once each day. Some evidence in support of communal roosts operating as information centres has been detected (Loman and Tamm 1981, Rabenold 1987a).

Weatherhead (1983) suggested that both food information-transfer and anti-predation benefits operating together have promoted the evolution of communal roosts. The "two principal strategies hypothesis" (Weatherhead 1983) is distinguished from the information centre

and spatial clumping of departing groups, environmental variables (e.g., temperature, windspeed, topography) also play significant roles.

These results indicate that Turkey Vulture roosts in Ontario do not operate as centres for food information transfer. Intraspecific competition, preferential selection of small-sized carrion, and a low degree of kin association make the proposed benefits of information transfer much less applicable to Turkey Vultures than has been found for other scavenging species.

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GENERAL INTRODUCTION

Turkey Vultures (Cathartes aura) are currently expanding their breeding range northward into Ontario (Goodwin 1978, Wilbur 1983, Cadman 1987). Suggested reasons for this expansion include a long-term warming trend in the northeast, increased availability of carrion resulting from changes in land-use practices, and a deterioration of habitat in the southern part of the Turkey Vulture's range (Bagg and Parker 1951, 1953, Wilbur 1983, Cadman 1987). Irrespective of the ultimate causes, the effects of this range expansion have been two-fold. First, Turkey Vultures have now become regular seasonal members of the scavenging guild of southern Ontario. While their numbers in the province appear to increase each year, the ecological impact of vultures in the region has remained largely unexplored.

Second, Turkey Vultures breeding in Ontario do so in the absence of Black Vultures (Coragyps atratus), arguably their principal food competitors in other parts of their range. In areas where the two species are sympatric, Turkey Vultures are usually dominated by the larger and more aggressive Black Vultures in competitive interactions at feeding sites (Stewart 1978, Coleman 1985, Wallace and Temple 1987). Both Stewart (1978) and Coleman (1985) have suggested that, in areas of sympatry, competitive pressure from Black Vultures has constrained the feeding niche of

Turkey Vultures. An investigation of the foraging ecology of Turkey Vultures in Ontario may help determine the evolutionary importance of competition in shaping the feeding niche of Turkey Vultures.

Food-Information Transfer

Turkey Vultures roost communally (i.e., several to several hundred individuals congregate every evening and spend the night together). Several ideas have been proposed to explain the possible advantages to communal roosting. While some of these theories have been extant for over 20 years, the adaptive basis for avian communal roosting remains poorly understood. Exploration of these theories is the central theme of this thesis.

Lack (1968) first proposed that communal roosts and breeding colonies provided reduced predation risk for members. However, predation can be quite high at large, conspicuous, and predictable gatherings of birds simply because predators are readily attracted to them (Ashmole 1963, Kruuk 1964, Rodgers 1987). Any anti-predator benefits associated with roosting or nesting socially (more eyes, dilution effect) are secondary advantages due to the relatively higher predation pressures experienced. For Lack's predation avoidance hypothesis to be considered viable, the predation risk for all individuals within a communal group would have to be lower than for those

roosting or nesting solitarily. While this is unlikely, the problems of acquiring data on predation rates among natural populations make it a difficult hypothesis to test.

The "information centre hypothesis" (Ward and Zahavi 1973) suggests that communal roosts and breeding colonies function primarily as centres of information exchange between participants about the location of randomly dispersed and ephemeral food resources. Perhaps the simplest way in which such food information could take place would be for relatively unsuccessful foragers to follow their more successful roostmates to a food patch, thereby increasing their foraging efficiency. There is evidence both for (Brown 1986, 1988, Gori 1988) and against (Andersson et al. 1981, Gotmark 1988) breeding colonies operating as information centres. Communal roosts can be considered as distinct from breeding colonies since they do not contain any defensible resource (e.g., eggs or young), need not remain in the same location, and usually are visited by the birds only once each day. Some evidence in support of communal roosts operating as information centres has been detected (Loman and Tamm 1981, Rabenold 1987a).

Weatherhead (1983) suggested that both food information-transfer and anti-predation benefits operating together have promoted the evolution of communal roosts. The "two principal strategies hypothesis" (Weatherhead 1983) is distinguished from the information centre

hypothesis (Ward and Zahavi 1973) in that it assumes that two classes of individuals receive different benefits from roost participation. The first class consists of socially dominant, superior foragers who are able to secure preferential sites within the roost. At these sites dominants are buffered from predation by their subordinate roostmates. The second class are inferior foragers, those in need of food information. Roosting structure based on dominance hierarchies has been observed in a number of species (Nauman 1965, Sigfried 1971, Burger et al. 1977, Swingland 1977, Weatherhead and Hoysak 1984, Still et al. 1986, Rabenold 1987b, Summers et al. 1987). Foraging abilities or skill levels are known to develop with age in several groups of birds (Norton-Griffiths 1968, Orians 1969, Recher and Recher 1969, Dunn 1972, Houston 1976, Weatherhead and Greenwood 1981, Rabenold 1987b, Wallace and Temple 1987), supporting the premises that roost participants are not equally successful foragers, and that not all roost participants are in equal need of food-information.

Regardless of the emphasis, both the information centre hypothesis and the two strategies hypothesis predict the occurrence of information transfer in communally roosting species which forage for randomly dispersed, ephemeral foods. Turkey Vultures are appropriate models with which to test for evidence of information transfer

since they roost communally throughout the year and they rely on carrion, which is a spatially and temporally unpredictable food resource. In addition, age-related social dominance appears to be important in determining the social organization of roosts (Nauman 1965) and access to carcasses in feeding groups (Wallace and Temple 1987).

Field experiments are probably the best approach for detecting information transfer (Rabenold 1987a, Weatherhead 1987, Mock et al. 1988). Positive recruitment to especially rich patches of food provides indirect support for the occurrence of information transfer. Obviously, mechanisms other than information transfer may operate in the attraction of birds to food sources. Initially, at least one bird must locate a new food source independently. Following this, any birds acting upon either the sight of others descending to, or directly feeding at, a food patch would be taking advantage of a type of socially-facilitated searching referred to as local enhancement (Krebs et al. 1972). Providing that one can distinguish the relative contributions of independent discovery/local enhancement and roost-centered food information exchange in attracting individuals to a feeding site, then data on bird arrivals at novel food patches across several days can be used to test for evidence of information transfer. If information transfer is operating within a particular roost, one would expect to find that the total number of birds using a food

patch on the day following its discovery is greater than the number expected to arrive if all "knowledgable" birds (i.e., those that discovered the patch on day 1) return and all others arrive simply by means of independent discovery or local enhancement alone. Some evidence supporting this prediction has been found in Hooded Crows (Corvus corix) and Ravens (C. corax) (Loman and Tamm 1980).

If a food patch is of sufficient quality, knowledgable birds should return on the day following its discovery, thus providing an opportunity for information exchange to occur. Given this, one would predict that returning individuals should be among the first to arrive on day 2. If "naive" birds obtain information from the departures of dominants, the temporal distribution of all birds arriving at the patch on day 2 should be skewed towards the earlier part of the day. Because of following, group size on day 2 might also be expected to be larger. Strong evidence along all these lines has been presented by Rabenold (1987a) for Black Vultures. The similarities between Black Vultures and Turkey Vultures in ecology (i.e., both are scavengers) and in forming mixed roosts (Prather et al. 1976, Rabenold 1983, Yahner et al. 1986) suggest that the above findings may also apply to Turkey Vultures.

Roost departures, as opposed to recruitment to food, have also been analyzed for evidence of information transfer. If naive birds are following successful foragers

from the roost to known food sources, then departures should be temporally and spatially clumped. While non-random departures have been cited as indirect support for information transfer within a roost, non-social variables (e.g., wind, thermals, topography) and alternative foraging tactics can also generate temporally and spatially clumped distributions (Mock et al. 1988). Thus, temporal and spatial clumping of departures alone are insufficient evidence for information transfer. Departure data need to be coupled with data on recruitment to food, as discussed above.

Aims of the Study

The aims of this study are to describe the foraging ecology of Turkey Vultures in southern Ontario and test for roost-centered food information transfer in Turkey Vultures.

In Chapter 1, I describe the use of carrion by large vertebrate scavengers in southern Ontario and quantify the level of intra- and interspecific competition for food that Turkey Vultures experience. This is important because the temporal persistence of food patches and competition at those food patches can directly affect the opportunity for and utility of food information exchange.

In Chapter 2, the results of field experiments testing for information transfer are presented.

In Chapter 3, I detail the arrival and departure patterns of Turkey Vultures to and from the communal roost. Analyses of these temporal and spatial distributions will constitute additional tests of information transfer, and allow for the assessment of alternative foraging tactics potentially used by Turkey Vultures.

In the final section, I summarize my conclusions and briefly discuss the importance of information transfer in the evolution of Turkey Vulture communal roosting behaviour and roosting theory in general.

GENERAL METHODS

Study Area

Fieldwork was conducted near the town of Milton in the Halton Region of southern Ontario (Fig. 1). The Niagara Escarpment, the major geological feature of the area, bisects the region's 984 sq km area from north to south. Approximately two-thirds of the land consists of farmland and wooded areas, the rest being urban.

Marking Turkey Vultures

Between 23 April and 4 June 1988, 25 adult (i.e., > 1 yr, P. Rabenold pers. comm.) Turkey Vultures were captured and marked for individual recognition with patagial tags (Wallace et al. 1980, Sweeney et al 1986). A single vulture was captured and tagged on 29 May 1989.

All 26 vultures were captured with modified Woodstream "Soft Catch" (no.3) leghold traps at sites baited with carrion (primarily chicken (Gallus gallus) carcasses obtained from local producers). All vultures captured were checked for brood patches (to determine breeding status), and tagged on both wings with yellow patagial tags bearing black numerals (1-26).

The Communal Roost

The principal communal roost⁺ used by Turkey Vultures in the study area was located in a mixed species forest

tract managed by the Ontario Ministry of Natural Resources approximately 10 km north-west of Milton (Fig. 2). The roost was directly adjacent to an open area of approximately 5 ha. Toward the north end of the open area was a single mature Red Oak (Quercus rubra). Shortly after sunrise the vultures habitually flew from the roosting trees to this oak and the open ground at its base to preen, sun, and rest for several hours prior to departing to forage. This process was repeated in reverse when the vultures returned from foraging in the late afternoon, entering the communal roost just after sunset. This habit of pre- and post-roost assembly in the open area afforded me a clear view of all arriving and departing vultures and an opportunity to accurately count all roost participants.

Experimental Feeding Trials

Thirty-five experimental feeding trials were conducted in open agricultural fields between 14 June and 20 August 1988 and between 22 April and 13 August 1989. Trial sites (Fig. 2) were located a minimum of 2 km from the communal roost to avoid easy detection by commuting vultures, and were generally selected on the basis of suitability (e.g., unobstructed view, minimal disturbance) and landowner permission. Baits consisted of road-killed mammals and chicken carcasses and were generally placed at trial sites before sunrise at the start of a trial. Observations were

made from a concealed location (in a blind or vehicle) at least 250 m away from the bait. I recorded the arrival and departure times of all mammalian and avian scavengers that used baits and the outcome of all inter- and intraspecific interactions. For vultures, I recorded the duration of feeding bouts for focal individuals and the identity of all "marked" birds. "Marked" birds include those with wing-tags or those with recognizable physical characteristics (e.g., diagnostic facial warts, wing and/or tail feather molt patterns).

CHAPTER 1 : COMPETITION AT THE CARCASS

INTRODUCTION

Turkey Vultures are obligate scavengers that specialize in locating and feeding on small carcasses (Stewart 1973, Houston 1986, Coleman and Fraser 1987, Prior in press). While many of the types of carrion identified in the diets of Turkey Vultures are small enough to be easily consumed during one feeding bout by a single bird (e.g., shrew [Soricidae], mole [Talpidae]), others are potentially large enough to provide a number of meals for several vultures over two or more days (e.g., large Woodchucks, Marmota monax or piles of poultry carcasses discarded by farmers).

The persistence of carrion food patches in the environment is important since only patches lasting two or more days have the potential to attract naive birds via roost-centered food information transfer. Turkey Vultures visit communal roosts once each day. Therefore, the opportunity for roost-centered information exchange is limited to this single period of roost participation every 24 hours. Food patches that are entirely consumed on the day of discovery will obviously be unavailable for use the

following day. "Knowledgeable" birds that return to patches lasting several days may be followed by "naive" birds allowing them to gain food information.

Rich food patches may or may not last several days, depending upon the amount removed by vultures on the day of discovery, the level of exploitation competition from other scavengers (both vertebrate and invertebrate), and the rate of carcass decay. Thus, my general aim was to determine if carrion food patches persisted long enough to allow for the possibility of roost-centered information transfer.

Depending upon the carcass type, size, and the time of year, invertebrate scavengers and carcass decay rates may be responsible for significant loss of tissue otherwise available for vultures. Large mammalian carcasses may be more susceptible to the establishment of invertebrate colonies (Houston 1988) whereas hot summer weather may accelerate decay of the carcasses beyond edibility within 24 hours (Rabenold 1987b). Vultures can consume the vast majority of tissue available on a given carcass. Houston (1988) estimated that vultures consumed 87% of the weight of chicken carcasses provided them in neotropical regions. Therefore even medium sized carcasses may be virtually depleted on the day of discovery by vultures alone.

Other avian and mammalian scavengers can also compete directly with vultures for carrion. While Turkey Vultures are usually the first vertebrate scavengers to detect

carcasses, they are often outcompeted at the food patch by later arriving avian species (e.g., other Cathartid vultures, Wallace and Temple 1987, Houston 1988). It is also conceivable that mammalian scavengers may compete for carrion to the detriment of vultures. For instance, while Old World vultures (Aegypiinae) often benefit from the remains of kills made by predators they must also compete with mammalian scavengers (e.g. Jackals, Canis mesomelas Kruuk 1967). Therefore, my first specific aims were to determine the causes of carrion food patch depletion and the level of interspecific competition experienced by Turkey Vultures. These factors could be critical in determining whether or not roost-centered information transfer is a viable foraging tactic for Turkey Vultures.

If a food patch does last several days, the potential benefits of information transfer for naive birds (i.e., those in need of food information) depend on their ability to share in the food patch. Wallace and Temple (1987) have documented the existence of age dominance hierarchies within feeding groups of Turkey Vultures (Turkey Vultures cannot be sexed by fieldmarks). Dominant individuals may therefore be able to control access to carcasses, limiting the use by subordinate birds. As Mock et al. (1988) have pointed out, naive birds must be tolerated by knowledgeable birds at the feeding site (i.e., allowed to feed), if they are to benefit from the information gained on food

location. For these reasons it is important to have some understanding of the competitive relationships between vultures at a food patch.

Food patch size may also be critical in determining the number of birds that are able to share in a carcass(es). Single carcass food patches offer few sites to feed, while multiple carcass patches potentially provide many more feeding sites (especially if the carcasses are scattered) and therefore may accomodate many more individuals. Similarly, feeding group size may impact upon the division of a food patch(es) among individuals and the amount of time allocated to resource defense and time spent feeding.

In summary, this chapter will describe food competition between Turkey Vultures and other scavengers at carrion food patches in southern Ontario. An understanding of the level and type of competition experienced by Turkey Vultures will enable me to better assess the benefits they might gain, and thus, the potential evolutionary importance of roost-centered food information transfer for the species.

METHODS

Behavioural Observations at Feeding Sites

I observed the feeding behaviour of Turkey Vultures and other scavengers from a concealed position at bait sites during daylight hours on 52 days. Baits consisted of single carcasses (road-killed mammals) and multiple carcasses (chickens) placed in open fields before sunrise (see **GENERAL METHODS** for location of bait sites). I purposely made the baits "rich" with the intention that they should last several days. However, baits provided were of a type (species and quantity) naturally encountered and fed on by Turkey Vultures in the study area (Prior, in press). I normally observed bait sites for all daylight hours on two consecutive days, although some trials lasted up to four days and several were terminated early due to interference, inclement weather, or bait depletion. At the end of each observation period, I recorded the number of intact carcasses and then counted the number remaining early the next morning in order to estimate the amount of removal due to nocturnal scavengers. Occasionally overnight removal of carcasses required that I supplement baits early the next day before observations began.

The time of arrival and departure, and outcome of social interactions were recorded for all mammalian and avian scavengers at baits. Focal observations of individual Turkey Vultures were made opportunistically

(e.g., dependent upon visibility or level of activity). During such sample periods I monitored the duration of individual feeding bouts, the number of birds in the feeding group, and the number and outcome of agonistic interactions. Agonistic interactions included pecking displacements, protracted fights, and "beak-toss threats" (after Rabenold 1987b). (Beak-toss threats involved a quick forward extension of the head and open beak, toward a conspecific. These movements were often accompanied by a sharp, hissing vocalization). Subsequent behaviour enabled me to easily determine the "winners" and "losers" of such agonistic contests. Individuals were assigned a relative dominance status (dominant or subordinate) within their feeding groups on the basis of their ability to monopolize or defend carcasses from conspecifics. Feeding groups as a whole were also sampled for agonistic interactions during one minute sample periods ($N = 63$).

When I was able to, I also recorded the impetus for departure of focal individuals or groups from food patches. Vultures that had fed to satiation exhibited distended crops (Davis 1983), walked away from the carcass unhurriedly, and often gaped their beaks and wiped them on the ground before flying from the feeding site. Disturbed individuals or groups suddenly flew up directly from the carcass(es). Such interruptions in feeding were often the result of individuals being startled by the departure of

conspecifics. Those marked individuals (e.g., tagged or with unique physical characteristics) that made multiple visits to a food patch were recorded as "returning birds".

Statistical Analyses

Sample distributions of behavioural data were tested for normality and homogeneity of variance. Following arcsine transformation, distributions of percentage of time spent feeding (individual feeding bout length/total time on the ground at a feeding site) remained negatively skewed. However, variance among groups was stabilized. Analysis of variance was used to test for differences in the percentage of time spent feeding between individuals of different dominance status, at two food patch types, and in feeding groups of various sizes. The same type of analysis was used to look for differences in actual time spent feeding between the various contexts. Within group differences were compared using t -tests. Departure impetus from bait sites (e.g., satiation, disturbance) as it relates to status, order of arrival, and group size was compared by Chi-squared tests. Finally, the relationship between feeding group size, duration of time spent on the ground and the mean number of agonistic interactions was investigated by simple linear regression (S.L.R.). All analyses were performed using the Statistical Package for the Social Sciences (Nie 1988). Statistical significance

was accepted at the 0.05 level. All means are presented $\pm$ 1 standard deviation.

RESULTS

Interspecific Competitors of Turkey Vultures

In addition to Turkey Vultures, eight species of vertebrate scavengers used carrion baits during daylight hours. Mammalian scavengers included Raccoon (Procyon lotor), Red fox (Vulpes fulva), Coyote (Canis latrans), dogs (Canis familiaris), and domestic cats (Felis domesticus). All of the mammalian scavengers I observed were attracted only to piles of chicken carcasses. None made use of road-killed mammal carcasses. Raccoons, fox, dogs, and cats made fewer than four visits to bait sites. Collectively this accounted for only thirteen percent of the 52 sample days. Raccoons and cats fed upon single carcasses at bait sites while fox and dogs removed single carcasses to locations beyond my field of vision. All of these mammals arrived after Turkey Vultures had discovered the food patch. On separate occasions all four of these species either flushed feeding Turkey Vultures when they approached bait sites or appeared to impede Turkey Vultures from alighting because of their presence at the bait site. However, I did observe one instance of a Turkey Vulture defending a carcass against an approaching cat by means of a vocal beak-toss threat.

Coyotes were attracted to bait sites on 11 (21%) of the sample days and usually made only one visit, removing single chicken carcasses from view. On three occasions

single coyotes made multiple visits (range = 4-11) during daylight hours, removing several carcasses ($\bar{X} = 0.45 \pm 0.18$ chickens per 5 min), consequently disturbing feeding vultures repeatedly. Coyotes never visited food patches before they were discovered by Turkey Vultures. On 11 nights a mean of 9.10 ± 2.87 whole chickens (range = 2-25) were removed, resulting in complete exhaustion of the food patch on two occasions. Coyotes seem the most likely suspects responsible for the disappearance of chicken carcasses from bait sites overnight since they are known to be active at night (Bekoff and Wells 1980).

Three avian scavengers other than Turkey Vultures were observed feeding at carrion baits. These included Herring Gulls (Larus argentatus), Red-tailed Hawks (Buteo jamaicensis), and American Crows (Corvus brachyrhynchos). Single gulls landed at chicken carcasses on four (8%) occasions but only fed during two of these visits (mean duration of feeding bout = 3.0 ± 3.08 min). The only observed encounter between Turkey Vultures and Herring Gulls involved a gull landing briefly (4 min) about 20 m away from a feeding and apparently unconcerned vulture.

Red-tailed Hawks (singles and pairs) were present at bait sites on 21 of 52 (40%) observation days. Only once did hawks appear to discover the food patch prior to Turkey Vultures. Hawks fed on both mammalian and chicken carcasses for an average of 21 ± 3.16 min ($N = 13$).

Although I did not quantify carrion consumption by Red-tailed Hawks, my observations indicate that they are probably more efficient at tearing apart fresh whole carcasses and likely consume larger amounts of tissue per unit time than do Turkey Vultures. Hawks dove directly towards and flushed feeding vultures 11 times. Startled vultures usually left the vicinity immediately but on four occasions they rejoined the hawk on the ground after several seconds. Following initial displacement of Turkey Vultures, hawks never had to reassert their dominance over vultures that relanded. Single carcasses were completely monopolized by hawks. Vultures always maintained a "safe distance" of several metres from feeding hawks. I observed three instances of vultures and a hawk feeding simultaneously upon separate carcasses. In all cases, vultures assumed a "relaxed" feeding posture only after having dragged a chicken carcass approximately 3 m away from the feeding hawk. Red-tailed Hawks flew away from bait sites with scraps of chicken carcasses in their talons on three occasions.

Next to vultures, crows were the most commonly occurring of all vertebrate scavengers at bait sites, being present on 39 of 52 (75%) sample days. Crows were frequently (50% of the time) the first scavengers to land and feed at newly established bait sites and regularly made several visits to both mammalian and chicken baits on a

given day. The relatively early discovery of baits by crows was likely a function of their attraction to my activities since they were often (heard or seen) in the area of bait sites while I placed out carcasses at sunrise. Crows most often fed alone or in pairs although family groups (2 adults, 3 young) and large flocks (range = 30-50+) were also attracted. Vultures were always dominant to crows when they fed together. Vultures routinely displaced crows passively (i.e., no beak-toss threats) from carcasses and at large gatherings of vultures, crows generally walked about the periphery of the bait site picking at scraps of food. On only one occasion did I observe an agonistic interaction between a crow and a vulture. In this instance a pair of crows were feeding together on a raccoon carcass when a vulture arrived and supplanted them. Following this, one of the crows grabbed and pulled on the tips of the vulture's tail and primary feathers with its beak. In response the vulture turned and directed a beak-toss threat toward the crow, then resumed feeding. These two birds continuously repeated essentially the same behaviour pattern for 8 min, at which time the two crows departed together and the vulture continued feeding alone.

Invertebrate larvae (Diptera) infested both mammalian and chicken carcasses only after they had been in place at bait sites for about two days. Most carcasses were partly frozen when first placed out and this may have inhibited

early invertebrate infestation. Tissue removal by invertebrates appeared to be minimal and vultures did not appear to find older carcasses inedible because they continued to feed at carcasses for up to 4 days.

In summary, food patches established for vultures persisted for two days on most occasions (66%). Coyotes were by far the most significant cause of patch reduction. Thirty-one percent of the food patches were virtually depleted by coyotes within 24 hours.

Intraspecific Interaction :

In my analysis of Turkey Vulture feeding activity I distinguished between an individual's opportunity to feed while at a food patch (i.e., percent time spent feeding) and the actual time spent feeding when given an opportunity (i.e., duration of feeding bout). Such an analysis may be important in characterizing advantaged and disadvantaged individuals or classes of birds within foraging groups.

Percentage of time spent feeding

The relative dominance of an individual vulture within its feeding group and the type of food patch (i.e., single or multiple carcass(es)) played significant roles in determining the percentage of time a vulture spent feeding while on the ground (Tables 1 and 2). The size of the

feeding group, however, was not important. The results of an analysis of variance (Table 2) on the percentages of time spent feeding show that group size did not explain a significant amount of variation. Dominant birds spent a greater percentage of time feeding than did subordinates, regardless of food patch type. However, within social status groups, the percentage of time spent feeding differed between food patch types. Dominant birds fed for a greater percentage of time at single patches ($t = 2.09$, $d.f. = 71$, $p = 0.04$), as opposed to multiple patches, while subordinates spent a greater proportion of time feeding while at multiple patch sites ($t = -4.77$, $d.f. = 59$, $p < 0.001$) (Table 3). Together dominance status and food patch type explain 27% of the variation in percentage of time spent feeding.

Vultures that were members of groups initially discovering new food patches (discoverers) spent a significantly higher percentage of time on the ground not feeding than did those that arrived later ($t = -2.11$, $d.f. = 225$, $p = 0.036$) (Table 1). Birds that were the first to discover new food patches took a great deal of time assessing the carcass(es) once they had landed, before they began to feed. Those that arrived later appeared to be less hesitant in approaching the carcass and proceeding to feed. It is likely that the sight of a partially consumed carcass or others feeding indicated that it was a safe

place to feed. This interpretation is supported by the fact that birds with prior experience at a particular food patch (i.e., returning birds) spent proportionately more time feeding than discoverers. Recognizable individuals (marked birds) that returned to food patches on the day following its discovery (i.e., day 2) spent a greater proportion of their time on the ground actually feeding than did discoverers ($t = -2.70$, $d.f. = 57$, $p = 0.009$) (Table 1).

Duration of feeding bouts

The mean duration of feeding bouts was significantly affected by an individual's dominance status and the food patch type (Tables 1 and 4). Feeding group size was also important. An analysis of variance of feeding bout durations revealed that it correlated significantly with group size ($r = 0.47$, $N = 134$, $p = 0.008$) (Table 4). Therefore, while one's opportunity to feed (i.e., percent time spent feeding) appears to remain constant regardless of foraging group size, feeding bout duration apparently increases along with group size. Whether longer feeding bouts in large groups actually translate into more food consumed remains to be seen.

When the effects of patch type are controlled for, socially dominant birds fed for longer periods of time than subordinates. Both dominants and subordinates had longer

feeding bouts at multiple carcass patches than they did at single carcass sites ($t = -3.60$, $d.f. = 71$, $p = 0.001$ and $t = -3.88$, $d.f. = 59$, $p < 0.001$, respectively) (Table 3). Dominance status and food patch type combined explain 22% of the variation in feeding bout duration.

Dominant birds departed food patches satiated more often (67%) than did subordinates (41%) ($\chi^2 = 8.16$, $d.f. = 1$, $p = 0.004$). Individuals that discovered food patches did not on average feed longer ($t = -0.05$, $d.f. = 225$, $p = 0.962$) (Table 1) nor depart food patches satiated (61%) any more frequently ($\chi^2 = 0.057$, $d.f. = 1$, $p = 0.8106$) than non-discovering birds. However, returning birds fed for longer periods of time ($t = 3.77$, $d.f. = 225$, $p < 0.001$) (Table 1) and departed food patches satiated more often (77%) ($\chi^2 = 5.2708$, $d.f. = 1$, $p = 0.0217$) than all others. In fact, returning birds always had longer feeding bouts, upon returning to the same food patch, on the day following discovery ($z = -2.52$, $p = 0.011$). Thus, socially dominant birds are advantaged at feeding sites and birds making multiple visits to food patches improve their feeding success by returning.

Agonistic interactions

Virtually all of the agonistic interactions I observed between vultures were clearly related to food access. Carcass sharing among Turkey Vultures is extremely rare.

Vultures never shared carcasses at multiple carcass food patches and were even reluctant to feed in close proximity (<2 m) to others. Piles of chicken carcasses were pulled apart and vultures fed upon them individually several metres from one another. On two occasions I saw vultures feeding simultaneously on road-killed mammal baits. In both instances three vultures fed amicably (i.e., no threats) from the same carcass for no more than 15 seconds. All three fed at different sections of the carcass and the dominant individual had secure access to the largest opening in the carcass.

The longer an individual spent on the ground at a food patch the more likely it was to engage in agonistic interactions (e.g., carcass defense or takeover) (S.L.R. $r^2 = 0.181$, $N = 167$, $p < 0.001$) (Fig. 3). Group size also determined to a significant extent the number of agonistic interactions that occurred within feeding groups. Large feeding groups had far more aggressive encounters per minute than did small groups (S.L.R. $r^2 = 0.569$, $N = 63$, $p < 0.001$) (Fig. 4). The slope of the regression line that describes this relationship is less than 1 ($\beta = 0.634$), suggesting that the number of agonistic interactions **per individual** may actually be lower in large groups. However, while individuals may have a lower probability of being directly involved in an aggressive encounter in larger groups the overall increase in interactions surrounding

them may be sufficient to disturb their feeding. Perhaps as a result, the time required by an individual to reach satiation increased positively as a function of group size (S.L.R. $\underline{r^2} = 0.039$, $\underline{N} = 129$, $\underline{p} = 0.023$).

DISCUSSION

Interspecific Competitors

Turkey Vultures in Ontario experience varying degrees of both exploitation and interference competition for food resources from other vertebrate scavengers. The level of competition appears to be dependent upon the relative importance of carrion in the diet of competitors, their ability to locate food patches, and the relative dominance of vultures. Intraspecifically, an individual's relative dominance and feeding group size clearly affected foraging efficiency. Therefore, direct interference competition between Turkey Vultures may be a more important factor with respect to any potential benefits of roost-centered information transfer.

Competition from Herring Gulls, raccoons, fox, dogs, and cats appears to be minimal since these species were observed very few times at bait sites during the day. The importance of raccoon, fox, dogs, and cats in reducing the size of food patches overnight remains unclear but seems likely to be of less significance than that of coyotes. Coyotes removed chickens from bait sites during the day and night. My observations indicate that the exploitation of carrion food patches by coyotes can be so extreme that even rich patches (e.g., 25 carcasses) can be entirely depleted overnight. Carrion (including chicken) is a major food source of coyotes and they usually return to rich food

patches until they are completely consumed (Berg and Chesness 1978). Under natural conditions, coyotes probably do inhibit Turkey Vultures from using specific food patches over several days. If I had not experimentally supplemented food patches on 11 occasions (i.e., 31% of food patches), vultures returning to the food patch would have found very little or no food remaining. Repeated disturbance of vultures at feeding sites by coyotes during the day may also make an otherwise appealing food patch somewhat less attractive to vultures.

The use of carrion by Red-tailed Hawks is well known (Errington 1933, Orians and Kuhlman 1956). Palmer (1988) considers their habit of scavenging to "converge somewhat with vultures". Red-tailed Hawks, by virtue of their social dominance over Turkey Vultures and greater feeding efficiency, can be important competitors at food patches. At single carcass food patches they are able to completely monopolize the carcass and remove considerable amounts of tissue, thereby limiting the amount available for vultures. However, since Red-tailed Hawks are less abundant than Turkey Vultures in the study area and are not carrion specialists, they probably are of minor importance as food competitors.

Territorial behaviour by pairs of hawks may also limit access to food patches in particular locales. Hawks, presumably breeding in the area, often flushed feeding

vultures without making any use of the food patch themselves.

Crows are largely opportunistic foragers and consequently carrion makes up a considerable portion of their diet (Bent 1946, Heinrich 1988c). They exploited carrion used by vultures and regularly made many more visits to food patches during the day than any other scavengers. However, the small feeding groups of crows (2-3) and their lower individual daily food requirements make their depletion of food patches minimal. Once vultures had arrived at a food patch any crows on site would remain at the periphery of the feeding group or leave the area altogether. Crows may also inadvertently aid vultures in locating carrion by means of local enhancement since they were often the first (50%) scavengers to discover newly established food patches and were often on the ground feeding when vultures arrived.

In spite of the diversity of species that make use of carrion in the study area, the combined impact upon vultures appears to be negligible. The effects of direct or indirect competitors are not sufficient to deter vultures from returning to food patches and feeding (at least) a second time. In general the experimental food patches that I established lasted two or more days from the day of discovery by vultures. Sixty-six percent of the food patches persisted two days, without supplementation.

Two days is the minimum duration period for food patches necessary if roost-centered food information transfer is to operate.

Intraspecific Competition

A carcass as a food patch for Turkey Vultures is discrete and can be monopolized by single dominant individuals. Multiple carcass sites are effectively many food patches and can therefore accomodate more birds, although dominants try to retain exclusive access to as many as possible. The relatively high percentage of time spent standing around at feeding sites by subordinate individuals reflects the time they are willing to wait in order to gain access to a food patch in the presence of dominant birds. Subordinates would often stand by throughout the whole feeding bout of one dominant bird, begin feeding once the dominant had walked off satiated, only to be supplanted a short time later by a newly arrived bird. Even at multiple food patch sites subordinates were often reluctant to approach unoccupied carcasses because dominants regularly tried to defend more than one carcass. In a similar fashion subordinate gulls refrain from approaching dominants at refuse dumps (Greig et al. 1984, 1986).

The "economic defendability" of single and multiple carcass food patches differ for single vultures because of

the greater dispersion of multiple carcasses. The percentage of time spent feeding by subordinates was higher at multiple carcass patches than at single patches since even dominants could not successfully control access to all of the many more feeding sites available. In their effort to defend more than one carcass dominant birds spent a lower percentage of time feeding at multiple food patches than they did at single carcasses. Presumably the benefits of priority of access to several carcasses outweigh the increased energy expenditure and reduction in the percentage of time spent feeding for dominant birds, at least to a certain level. Monopolization of a single carcass requires less effort on the part of dominants and therefore a greater percentage of time can be spent feeding.

Longer feeding bouts by dominant birds do not necessarily mean that they are consuming any more food than are subordinates. Slower feeding rates (i.e., fewer bites per unit time) could result in dominants having to spend longer periods feeding than do subordinates in order to acquire the same amount of food. Kirk (1988) found that the subordinate subspecies of Turkey Vultures (C. aura ruficollis) in central Venezuela fed faster for shorter periods than did the dominant subspecies (C. aura meridionalis). A similar relationship may hold for subordinate and dominant individuals within the same

subspecific group. Subordinates may have to feed faster because of their lower competitive abilities. It also seems reasonable to assume that subordinates have a higher hunger-state than dominants. If so, then subordinates should require relatively more food during a given feeding bout in order to achieve satiation. That subordinates are not able to completely compensate for their lower social status and reduced time spent at the carcass by feeding faster is demonstrated by the fact that they depart food patches satiated less often than do dominants.

All birds had longer feeding bouts at multiple patch sites, presumably because of the greater availability of feeding sites and the lower overall competition for access to carcasses within feeding groups of a given size. The positive correlation between group size and feeding bout duration likely reflects a parallel increase in the number of agonistic interactions. Nearby foragers may interfere with the foraging efficiency of others (Goss-Custard 1976). Feeding in large groups requires that birds defend their food patch from conspecifics more often. Bald Eagles (Haliaeetus leucocephalus) feeding on fish carcasses increase their vigilance against conspecific "pirates" while feeding in large groups, consequently limiting the time spent actually feeding (Knight and Knight 1986). If vultures are more frequently disturbed by conspecifics while feeding in large groups, they must necessarily spend

a greater amount of time on the ground feeding than do those in smaller groups in order to consume the same amount of food. In support of this interpretation, Kirk (1988) observed a drop in the feeding rates of Turkey Vultures with increasing group size. Feeding in larger groups seems to be less efficient for Turkey Vultures.

The pattern of reduced feeding efficiency as group size increases may be in contrast to the organization of Black Vulture feeding groups. Black Vultures often feed in large groups (e.g., 50 birds; Wallace and Temple 1987) and are apparently much more tolerant than are Turkey Vultures of conspecifics feeding in close proximity. In fact, Rabenold (1983) has suggested that the frenzied pulling at the carcass commonly seen in Black Vulture feeding groups may provide a mechanical benefit of tearing apart carcasses that might otherwise be difficult to consume. Turkey Vultures appear to defend a minimum distance from one another at feeding sites. Individual distances may be maintained through passive, mutual recognition of dominance status, asserting dominance by beak toss threats, or, rarely, through escalated fights. Such aggressive acts or displays can interfere with the feeding of the aggressor as well as the target of this aggression (Pearson 1989).

If interference from group members detracts from feeding such that birds must feed longer in order to consume the same amount of food, then this may explain why

individuals achieve satiation sooner in small groups. Turkey Vultures feeding alone do not achieve satiation any sooner than do birds feeding in larger groups but they may be constrained from feeding by the need to scan for potential predators or arriving conspecifics that may supplant them from the carcass. Knight and Knight (1986) found that Bald Eagles that were looking up at the time of a pirating attempt were more successful in keeping their food than eagles with their heads down. I was often alerted to the arrival of vultures at the food patch by the skyward glances of birds on the carcass(es), suggesting that vultures too may be concerned about early detection of incoming conspecifics. Individuals feeding in pairs achieved satiation an average of 8 min sooner than those in larger groups, perhaps because they can afford to reduce their scanning effort, benefitting from mutual scanning with their feeding partner while incurring a minimal cost of competition from a single feeding partner. This suggests that small groups of 2 birds may be an optimal foraging unit for Turkey Vultures.

Birds who made food patch discoveries spent a relatively high proportion of time standing around before approaching a carcass to feed. Presumably this time is spent assessing the safety of a potential feeding site (e.g., predator concealment, whether the "carcass" is living). Heinrich (1988a) discusses a "fear" of novel food

sources in Common Ravens (Corvus corax), another carrion specialist. In spite of this time investment, discovering birds fed on average for just as long and departed food patches satiated just as often as those birds which arrived later. Returning to a previously discovered carcass seems a most profitable strategy. Returning birds were highly efficient feeders and left food patches sated more often than other classes of birds. Possibly because they often returned early in the morning, after a full night of food deprivation, they feed for considerably longer periods of time.

In summary, subordinates are at a disadvantage within feeding groups because of their social status. They suffer reduced access to carcasses as a direct consequence of their lower competitive abilities and depart food patches hungry more often than do dominants. The result is that subordinates likely spend relatively more time overall simply foraging for new food patches. The "costs" associated with such expenditures are difficult to assess but presumably such time could be spent engaged in other important activities such as care for young or maintenance behaviour (e.g., preening). At the very least, the ability of dominant individuals to control access to food patches and thereby limit sharing of carcasses seriously restricts the advantages subordinates may gain from following others to food patches from the roost. This does not of course

prevent individuals (subordinate or otherwise) from returning "unguided" to food patches they've observed, but perhaps not fed at. The apparent gains returning birds receive by revisiting a known food patch early in the morning (before others have begun to forage) make this a more profitable tactic than following from the roost, especially for subordinate birds. Based upon the degree of intraspecific competition that takes place at feeding sites it is unlikely that roost-centered information transfer provides any substantial benefits for Turkey Vultures in southern Ontario.

CHAPTER 2 : EXPERIMENTAL FEEDING TRIALS

INTRODUCTION

The evolution of roost-centered information transfer requires not only the sufficient duration of food patches within the environment and a toleration of conspecifics by socially dominant members of feeding groups but also that successful foragers habitually return to rich food patches they have discovered. In doing so they would provide an opportunity for less successful foragers (naive birds) to follow them from the roost to the food patch, the simplest process by which food information exchange might occur. If this criterion is met within a species or population and assuming that successful (i.e., returning) individuals can be recognized by their roostmates, a number of predictions can be made with respect to the arrival patterns of birds at the food patch. These arrival patterns can be interpreted as indirect evidence for or against the occurrence of roost-centered information transfer. An experimental approach has proved useful in this regard (see Weatherhead 1987, Mock et al. 1988 for reviews).

The simple experimental design involves the establishment of rich yet ephemeral food patches. The

patches should be located distant from the roost such that not all members of the roosting population are likely to discover it by chance on the first few days. In the case of Turkey Vultures, any individuals finding the food patch on the day that it is first discovered (day 1) could only have located it by either independent discovery or local enhancement. Independent discovery implies that an individual encountered the food patch on its own while foraging (i.e., without the aid of any conspecifics or ecologically similar species e.g., crows).

Local enhancement (Krebs et al. 1972) is a type of socially facilitated foraging tactic whereby individuals are attracted to a food patch by the sight of others descending to or feeding at the patch. In this case, while food information is gained by the foraging individual (i.e., the location of food patches) the site of information transfer is at or near the food patch itself rather than at the roost, as proposed by the information centre hypothesis (Ward and Zahavi 1973) and the two strategies hypothesis (Weatherhead 1983). Local enhancement has been demonstrated as an important foraging tactic employed both within and between species (Kushlan 1977, Andersson et al. 1981, Caldwell 1981, Barnard and Thompson 1985, Houston 1988, Senar and Metcalfe 1988).

Roost-centered food information transfer is not a potential mechanism responsible for attracting vultures to

food patches on the day of discovery since they visit the communal roost only once each day at the end of their foraging period. Only on the second day, following roost participation, does roost-centered information transfer become possible. Therefore, if a food patch is rich enough to last at least two days, information transfer in addition to independent discovery and local enhancement may contribute to the attraction of vultures to the patch on days following the day of initial discovery. By monitoring the arrival patterns of birds at food patches over several days, one should be able to detect any effect attributable to roost-centered information transfer.

In terms of the null hypothesis, no more birds should arrive at the food patch on day 2 than expected if only local enhancement and independent discovery were operating to attract them. The number of birds expected on day 2 is equal to the number that found the patch on day 1, plus the number that find the food on day 2 without following (i.e., by local enhancement and/or independent discovery alone). This assumes that all knowledgeable birds return to the food patch. Thus, an estimation of the number of birds expected to arrive at the food patch on day 2, without the aid of information transfer, can be calculated (see **METHODS** for formal calculations). If the number of birds arriving on day 2 exceeds this expectation then the null hypothesis will have been falsified, suggesting that roost-centered

information transfer was responsible for the increase in the number of birds attracted to the food.

In addition to specific differences in the number of vultures occurring at a food patch over several days, certain patterns in their temporal distribution of arrival are also predicted by the information transfer hypotheses. Aside from the high return rate by knowledgeable birds necessary for the possibility of roost-centered information transfer, such individuals are also expected to return early in the foraging period on day 2. The ephemeral nature of carrion requires expedient use of the food patch since it will otherwise be lost. Therefore, returning birds should make use of known food patches as soon as possible after roost departure. Their arrival should in general precede those of their "naive" roostmates since they are able to fly directly from the roost to the food patch. Any birds making use of food information gained at the roost will arrive at about the same time by virtue of the fact that they are using returning birds to lead them to the food patch. Those that discover the food patch independently or by local enhancement that day will be somewhat delayed in their arrivals since they must spend time actively foraging. If returning birds are acting as leaders, voluntarily or otherwise, and others are following them from the roost, then the whole temporal distribution for day 2 should be skewed towards an earlier part of the

day, relative to day 1, since those gaining food information should make use of it as soon as possible.

The size of groups arriving at food patches on day 2 is also be expected to be larger than those observed on day 1 if following from the roost occurs because returning birds should be followed closely by conspecifics. In this chapter I present the results of experiments designed to test the above predictions and evaluate the information transfer hypotheses from the perspective of recruitment to food patches.

METHODS

Thirty-five experimental food patches consisting of multiple chicken or single road-killed mammal carcasses were established during the spring and summer field seasons of 1988-89 in order to test for evidence of roost-centered food information transfer in a population of Turkey Vultures in southern Ontario (see **GENERAL METHODS** for location of experimental bait sites). Throughout the duration of the feeding trials I recorded the arrival times of all vultures landing and/or feeding at the food patch on the day that the patch was discovered (day 1) and on the subsequent day (day 2). Not all food patches were discovered on the day they were established. I made particular note of the time of arrival of any "marked" and "returning" vultures. For the purposes of analysis I considered all birds arriving within the same 5-min period to be members of the same foraging group (after Rabenold 1987a). Turkey Vultures typically forage by flying at low elevations (30 m), at slow speeds (20 km/hr), closely inspecting the ground, and regularly retracing their flightpath. Therefore it is not improbable that birds passing the same point within 5-min of one another are members of the same loose foraging flock.

Statistical analyses

The temporal distributions of the time of arrival (per

5-min interval) at food patches were pooled across all trials for both day 1 and day 2. These two distributions were tested independently against random (Poisson) distributions by means of a Kolmogorov-Smirnov two-tailed test (K-S test). The mean time of arrival on day 1 and day 2 were compared by a Mann-Whitney U-test. Arrival times for returning birds on day 1 and day 2 were tested using a Wilcoxon Matched-pairs test.

The number of vultures expected to arrive at food patches on second days, in the absence of roost-centered information transfer, was calculated based upon the number of birds visiting the patch on day 1 and the estimated number participating in the communal roost at that time (see **RESULTS, CHAPTER 3** for roost population estimates). Estimates of expected values for each trial were calculated using a formula developed by Loman and Tamm (1980).

$$N2_{exp} = N1 + (R-N1) (N1/R)$$

where;

N1 = the number arriving at the food patch on day 1

R = the estimated roost population

R-N1 = the number of birds in the roost after day 1 who remain naive as to the location of the food patch

N1/R = the proportion of birds that discovered the food patch independently or by local enhancement on day 1

$N2_{exp}$ = the number expected to arrive at the food patch
on day 2 in the absence of roost-centered
information transfer

Therefore, if information transfer were operating
within the roost I would expect:

$$N2_{exp} < N2_{obs}$$

where;

$N2_{obs}$ = the number arriving at the food patch on day 2

I compared the number of birds expected on day 2 with
the number observed on day 2 by means of a Wilcoxon
Matched-pairs test. I only considered those trials in
which day 2 > day 1 as successful experiments, as opposed
to evidence against information transfer, since variables
such as low patch quality could have been responsible for
not all birds returning on day 2 (Weatherhead 1987).

RESULTS

Returning birds

For roost-centered information transfer to occur, it is necessary for knowledgeable birds to return directly to the food from the roost. Out of 51 marked birds that visited food patches on day 1, 43 (84%) made return visits to the same patch on the following day. In order to assess whether the temporal distribution of returning birds could be considered early, I compared their arrival at food patches with those of others. Over the 35 second days, 198 vultures arrived at the food patches. The first groups to arrive (i.e., earliest) on each day totalled 33 birds (17% of total) over the 35 days. The number of returning birds expected to arrive among the first groups on day 2, had they been distributed proportionately across all potential arrival intervals was just over seven. In fact, 12 actually arrived among the first groups, making up 36% of the total. Returning birds came back to food patches much earlier on second days than they did on the day of discovery (Wilcoxon Matched-pairs test, $z = -3.77$, d.f. = 38, $p = 0.0002$) (Table 5). These knowledgeable individuals were able to fly directly from the roost to the food patches, in many instances arriving before the mean roost departure by several hours.

The high return percentage I calculated is probably an under-estimate of the actual number of birds making

multiple visits to experimental food patches across days (and thus the potential sources of food information available at the roost), since it is based upon my ability to recognize individuals between days. Several birds which arrived at food patches extremely early on day 2, and thus obviously had prior knowledge of its existence, were not scored as "returning birds" simply because I was unable to verify their having visited the site on the previous day.

Temporal pattern of arrivals at baits

Of the 35 experimental feeding trials, 24 (69%) attracted Turkey Vultures for two or more days. Ninety-two groups arrived on first days and 138 arrived on second days totalling 343 birds overall. Pooling data across all trials, the temporal distribution of birds arriving per 5-min interval at food patches differed from random (Poisson) on both the first ($\chi^2 = 6.34$, $p < 0.001$) and second days ($\chi^2 = 6.23$, $p < 0.001$) (Fig. 5), suggesting that individuals were not arriving independently of one another. However, the mean foraging group size on day 1 was no different from that of day 2 ($U = 5967.0$, $p = 0.3447$) (Table 5). Arrivals on second days were skewed towards earlier arrivals ($U = 11256$, $p < 0.001$) (Fig. 6). The mean time of arrival on day 2 was over an hour and a half earlier than it was on day 1 (Table 5). When I excluded returning birds from the analysis the mean time of arrival of vultures

remained significantly earlier on day 2 ($U = 9908$, $p = 0.001$). However, the difference between days was less than 1 hour. This disparity could be attributable to enriched local enhancement on second days and not necessarily roost-centered information transfer.

Second day recruitment to food patches

During 16 of 24 (67%) feeding trials the total number of vultures arriving on day 2 exceeded those visiting the food patch on the day of its discovery. The remaining 8 trials were considered failed experiments since not all the birds that found the food patch on day 1 returned on day 2, perhaps because of low patch quality. In only eight of the successful trials did more birds arrive on day 2 than would be expected if only independent discovery and local enhancement served in attracting them (Wilcoxon Matched-pairs test, $z = -0.57$, $d.f. = 15$, $p = 0.57$) (Table 6). The model I used in this test is biased in favor of confirming existence of food information transfer. By extending the count of birds on day 2 until the end of the day a higher proportion of birds should discover the patch by independent discovery and local enhancement than on day 1, since there are more vultures at the food patch for a longer time (see Fig. 6). This disproportionately contributes to the observed value for day 2, and thus improves the probability that it will exceed the expected

number. A more stringent test of information transfer would limit the count of birds arriving at the food patch on day 2 only until shortly after the time of arrival of the last returning bird, since any birds using information transfer should follow close behind.

The results of trial 8911 appear, at first, to be positive evidence for roost-centered food information transfer. However, the temporal pattern of arrival of vultures at this site clearly indicate that local enhancement was responsible for attracting birds to the food patch. The only bird to discover this patch on day 1 returned at 0814 E.D.T. on day 2. The second bird did not arrive until after 1600 E.D.T. Between then and 1733 E.D.T., 9 more vultures discovered the patch. Obviously, no birds followed the returning, knowledgeable individual from the roost in the morning, and therefore roost centered information transfer was not responsible for attracting birds that day. Similarly, the large numbers of vultures attracted to trial sites 8804 and 8914 were likely due to local enhancement. These sites were situated close to the Niagara Escarpment (see Fig. 2). Vultures regularly use the escarpment as a dispersal corridor from the roost, therefore it is not surprising that so many individuals discovered these food patches.

Considered together, these findings suggest that information transfer was not operating within the roost.

Recruitment to food patches was not enhanced above that expected by independent discovery and/or local enhancement alone.

DISCUSSION

Second-day recruitment to experimental food patches was not significantly enhanced over the day on which food patches were first discovered. The size of foraging groups arriving at food patches did not differ between the two days as would be expected were naive birds following knowledgeable individuals from the roost. The pattern of arrival of Turkey Vulture foraging groups at food patches on both the day of discovery and subsequent days is indicative of local enhancement. If the majority of vultures discovered food patches independently of one another, then one would expect to see a random arrival of groups. Earlier arrivals by naive birds on day 2 (i.e., on average 1 hr earlier than on day 1) may simply be a function of "enriched" local enhancement, due to the presence of returning birds at the food patches, and not necessarily roost-centered information transfer. Small groups (≤ 2) of vultures independently searching for carrion are not precluded from investigating and potentially capitalizing on food patches discovered by others.

Knowledgeable birds meet the essential prerequisite of a high return rate to previously-visited food patches necessary for the possibility of roost-centered information transfer. They also returned to food patches at the earliest possible opportunity on second days. From the perspective of unsuccessful foragers (naive birds),

returning birds, at least in principle, appear to be "reliable informants" worth following from the roost.

The possibility of following from the roost, and indeed the level of recruitment expected via roost-centered information transfer, is predicated on knowledgeable birds actually attending the communal roost. Several pieces of evidence indicate that this assumption was not violated. First, the communal roost to which I assume most vultures in the study area return each evening appears to be the principal roost in the region. It has had a growing attendance for the past 15 years and is the only major gathering (>5 birds) I have been able to locate within approximately 80 km of the study area.

Second, 78% percent of those birds captured during the study had brood patches. This suggests that a relatively high proportion of the roosting population breed in the area and are therefore unlikely to wander far from the region to use other roosts. More direct evidence of attendance at the roost by knowledgeable (returning) individuals comes from observations of their direction of arrival at food patches on second days. All returning birds, for which I was able to ascertain direction of arrival, approached experimental food patches along flight paths expected had they spent the previous night at the roost. The flight paths of vultures early in the morning (e.g., returning birds) are particularly direct, in

contrast to those flying later in the day. Therefore, the point of arrival at food patches is a reliable indication of the flight course taken by early returning birds.

Resighting of knowledgeable birds at the roost, on the day they discover food, obviously constitutes the best evidence of roost participation by this class of birds. Such data would fulfill the assumption that knowledgeable individuals are at least available to be followed to food patches. I was able to confirm the presence of 4 knowledgeable birds at the roost on the evening of the day they were observed at experimental food patches. Fifteen others were seen attending the roost within 2 days of food patch use. This record of roost attendance by knowledgeable birds in no way estimates the level of roost participation by this class of birds since I did not regularly monitor pre- or post-roost assemblies during experimental feeding trials nor were all "marked birds" (e.g., knowledgeable birds) equally recognizable among the many birds attending the roost (i.e., wingtags were often hidden from view under feathers). I simply present these observations as evidence that successful foragers do continue to participate in communal roosts. Given that birds with knowledge of an existing food patch do attend communal roosts, the question remains why naive individuals apparently do not follow them from the roost?

Returning birds arrive at food patches significantly

earlier than others. Consequently, they must also depart the roost earlier. If returning birds are recognizable, unsuccessful foragers may be constrained by the energy costs associated with premature roost departure.

Individuals that depart the roost early do not benefit from the favorable wind conditions that develop later in the morning and are forced to engage in laborious wing-flapping flight as opposed to the more energetically efficient thermal and slope soaring typical of Turkey Vultures (Pennycuick and Scholey 1984, Obrecht 1988). Returning birds may be willing to bear the energetic costs of such flight only because of their knowledge of the "guaranteed" food patch they will be rewarded with at their destination. During the breeding season unsuccessful foragers run the risk of following a bird that is simply flying to a nest site and not to a known food patch. Naive birds may be tactically better off waiting to join a loose foraging flock later in the morning when the energy demands of flight are reduced and there are many more conspecifics in the sky contributing to any local enhancement foraging network from which they may benefit.

Alternatively, many knowledgeable birds may not be recognized as such by their roostmates. A large proportion of early returning birds may not be regularly or currently "successful" foragers per se, but simply have knowledge of the location of a rich patch of food. In support of this

is the fact that such individuals feed for significantly longer periods on the days following food patch discovery. With no particular cue with which to identify these returning birds (e.g., proven foraging skill or full crop), individuals that are in need of food information may be reluctant to follow them from the roost at such an early hour.

Perhaps a more important restraint on relatively unsuccessful foragers (e.g., subordinates) is the ability of socially dominant individuals to effectively control access to food patches. The fact that Turkey Vultures have a low tolerance for conspecifics obviously limits the benefits subordinates can gain from following knowledgeable birds. An apparent preference for small sized carrion (Coleman and Fraser 1987, Prior in press) and a lack of food sharing among Turkey Vultures may make roost-centered information transfer a largely unprofitable foraging tactic.

My observations indicate that roost-centered information transfer is almost certainly not important for Turkey Vultures in the study region. This does not necessarily mean that Turkey Vultures cannot benefit from roost-centered information transfer under different environmental conditions.

In similar tests on Black Vultures in North Carolina, Rabenold (1987a) was only able to detect significant

second-day recruitment to food patches during the winter, a season when carrion is relatively scarce in her study area. A high availability of carrion in southern Ontario during the spring and summer months may mean that few Turkey Vultures are seriously deprived of food. Under such conditions the need for food information within the roosting population is relatively low. In their winter range subordinate individuals may be more food stressed because of decreased carrion availability and the consequent higher levels of intraspecific competition. If foragers become more risk prone with increasing food deprivation (Stephens and Charnov 1982, Ekman and Rosander 1987) then following from the roost may occur only during the winter months (Rabenold 1987b). Unsuccessful foragers may then shift toward the apparently energetically expensive tactic of following returning birds to food patches early in the morning. The possibility that the food patch has already been depleted and that they will have missed the opportunity to join a foraging flock departing from the roost constitute the risk incurred by followers. If the "leader" returns to a rich food patch followers may receive a worthwhile payoff early in the day.

However, there does appear to be a hunger gradient within the study population. Subordinate birds do not often feed to satiation. On several occasions I saw individuals feeding in a rapid or apparently desperate

fashion and many birds fed until very late in the day, well past the time of mean roost assembly. The food demands of breeding birds are also probably quite high. In spite of this, relatively unsuccessful foragers do not appear to benefit from roost-centered information transfer during the summer. If this is the case then there must be some other advantage(s) associated with communal roosting. The extent to which Turkey Vulture roosts operate as assembly points for the establishment of small foraging flocks and a loose foraging network (Evans 1982a, Evans and Welham 1985, Wittenberger and Hunt 1985), to the benefit of all participants, is discussed in the following chapter.

CHAPTER 3: COMMUNAL ROOST DEPARTURES AND ARRIVALS

INTRODUCTION

The departure patterns from communal roosts (and colonies) are probably the most easily acquired, and thus frequently described, type of observation relating to tests of food information transfer (Krebs 1974, Andersson et al. 1981, Bayer 1981, Rabenold 1983, Waltz 1987, Gori 1988). Temporal synchrony and spatial clumping of departures from communal roosts are predicted by information transfer hypotheses, assuming that simple following of knowledgeable individuals by naive birds is the mechanism of information exchange.

Some degree of departure synchrony would appear to be necessary for communally roosting species if information transfer is operating since "followers" must be able to track the flight paths taken by knowledgeable "leaders". Prolonged delay of departure by a follower (i.e., less synchronous) may cause it to lose track of the individual or group it is pursuing, especially if leaders do not maintain a straight-line course.

However, as Mock et al. (1988) have pointed out, there are problems associated with interpreting this kind of

data. For instance, non-random temporal and spatial patterns of roost departure (and arrival) can be a product of non-social factors including, hours of sunlight, wind, thermals, tidal fluctuations, and prey activity periods (Rabenold 1983, Barnard and Thompson 1985, Evans and Welham 1985, Kiis and Moller 1986, Reebbs 1986, Warkentin 1986). The contribution of environmental variables to temporal clumping and/or spatial clustering of departures does not rule out the possibility of socially-facilitated roost departure patterns and following from the roost, but simply makes such data more difficult to interpret.

In this chapter I describe the patterns of communal roost departure (and arrival) by Turkey Vultures. I also critically evaluate the possibility that vultures are following one another from the roost, by testing the departure and arrival patterns against several social and non-social factors.

METHODS

The Turkey Vultures using the principal communal roost in the study area habitually assembled in an open area adjacent to the roost trees both before they entered the roost in the evening and prior to departure each morning. I observed the departure and arrival of vultures from a central position in the open area on 48 mornings and 34 evenings (4-31 July 1988 and 15 May-24 August 1989).

During morning sample periods I began recording departures when the first bird(s) left the roost. I watched departing groups and assigned them a departure time and direction when they were lost from view over the horizon. I summed the number of birds departing per 5-min interval and recorded the directional bearing taken by departing groups when they were last observed. Directional sectors consisted of 16, 22.5° arcs encompassing 360° (i.e., North = 0°). Departing vultures would typically fly up from the pre-roost and circle individually or in "kettles" of up to 50 birds, in order to gain elevation. After several minutes, loose flocks would break off and soar quickly away from the roost along relatively straight headings, until they were lost from my view. For this reason I believe that a 5-min interval is a reasonable period to define individuals departing within the same group. Beyond 5 min individuals are too strung-out or discontinuous to be considered a part of the same loose

flock. In the evening I scanned the horizon for incoming birds and recorded group size, direction of arrival, and arrival time in the same manner as during roost departures.

I estimated the number of birds attending the roost each evening by counting vultures as they flew individually from the pre-roost to the roost trees. Weekly averages of the roosting population were calculated to monitor any changes through the study period. I also used these values to estimate the number of vultures expected to be recruited to experimental food patches in the event of roost-centered information transfer (see Chapt. 2).

Statistical Analyses

The degree to which vultures left the roost in synchrony with one another was tested by means of a Kolmogorov-Smirnov test. I compared the pooled distribution of departures per 5-min interval throughout the evacuation period to a random (Poisson) distribution. The same procedure was used in testing for temporal synchrony of late afternoon arrivals at the roost.

To test for any directional bias by vultures departing the roost within departure periods, I applied a Rayleigh test (Batschelet 1981) to the spatial departure distributions. The Rayleigh test also allowed me to calculate the orientation (angle) of the mean departure vector or the mean departure direction. The mean vector is

the average of all departure headings for the sample period. Rayleigh tests were also used to test for directional clustering of vultures arriving at the roost in the late afternoon.

Between-day differences in the directions taken by departing groups over 8 days (out of a 10-day sequence) were assessed by collapsing the 16 directional categories into 4 quadrants (i.e., 90° arcs centered on the compass points N.E., S.E., S.W., and N.W.) and applying a Chi-square test to the data. Similarly, I tested for changes in the orientation of arrivals at the roost over an 8-day period.

The potential variables (social and non-social) that may lead to temporal and/or spatial clumping of roost departures, as predicted by information transfer, were investigated in several ways. For those dates on which I monitored morning roost departures immediately following experimental feeding trials, I was able to look for alignment between departing birds and the direction of bait sites. Specifically, I compared the orientation of 7 previously used bait sites around the roost with that of the mean departure vector ($\pm 33.75^\circ$) for vultures on the day following use of the food patch. I chose an arc of only 67.5° (i.e., $2 \times 33.75^\circ$), to assess orientation to food patches, since returning (knowledgable) birds should be expected to take a fairly direct heading toward such

patches from the roost.

I also looked at the importance of environmental variables as factors influencing roost departures. I compared the departure headings of those birds departing within a 112.5° arc, centered on the mean departure vector for each day with that of the prevailing wind at the time. I selected 112.5° (i.e., $5 \times 22.5^\circ$ sectors) to make my results comparable with Rabenold's (1983). The same procedure was used to test the influence of wind direction on roost arrivals. I also tested the degree of spatial clumping during morning departures as a function of wind speed by simple linear regression analysis (S.L.R.). In addition, I investigated the relationship between wind velocity, air temperature, and the synchrony of vultures arriving and departing from the roost each day by multiple regression analysis (M.R.). I used the coefficient of variation of the mean arrival or departure interval as a relative measure of assembly or evacuation synchrony within each day. Data on environmental conditions were recorded at a weather station 30 km east of the roost.

By comparing the size of groups departing the roost, the size of groups observed foraging, and the size of groups returning to the roost I tested the expectation that group size should be larger during roost departures, if following occurs. I made this comparison by performing two-sample Kolmogorov-Smirnov tests on group size

distributions for the three time periods or contexts.

RESULTS

Communal roost population changes

Weekly means of the Turkey Vulture attendance at the principal communal roost increased from 50-60 during the second week in June, to 80-90 in the second week of July (Fig. 7). I believe this increase in the population is associated with the mean first-chick-date of 25 June for the study area (Jackson 1983). Since both parents incubate eggs, and nest shifts usually last 24 hrs., only the "off-duty" parent is able to attend the evening communal roost during the period of incubation and the first few days after hatch. Once the young achieve thermal independence (approx. 5 days), nest attendance by parents decreases rapidly. By the time the chicks are about 14 days old, the parents are making only brief, infrequent visits to the nest (Davis 1983). At this point, both parents are free to participate in the roost, thereby nearly doubling the roost population. In terms of information transfer, the increase in the roosting population through the season implies that the relative level of potentially available food "information" for naive individuals should increase as well.

Communal roost departures

Turkey Vultures departed the communal roost in a non-random, synchronous fashion ($\chi^2 = 15.15$, $N = 1333$, $p <$

0.001). The pattern of roost departures per 5-min interval on 39 mornings, for which I was present at the initiation of departures, suggests that they leave in discrete groups across the period of evacuation (Fig. 8). While following from the roost can produce such a pattern, non-social variables may also contribute to temporal clumping of departures. Together, air temperature and wind velocity explained 15% of the variation in departure synchrony across the mornings sampled (M.R. $r^2 = 0.15$, $N = 39$, $p = 0.049$). Roost departures were relatively more synchronous on cooler mornings (S.L.R. $r^2 = 0.10$, $N = 39$, $p = 0.045$) or when the wind blew the strongest (S.L.R. $r^2 = 0.09$, $N = 39$, $p = 0.057$).

Within days, vultures also tended to leave the roost in the same direction on the majority of mornings. The headings taken by departing groups were significantly clustered during 24 of 29 (62%) sample periods. Seven of those sample mornings immediately followed successful experimental feeding trials (i.e., vultures discovered and used baits). Since bait still remained at these sites, knowledgeable birds (and any followers) might be expected to return directly to them, thereby causing a concentration of departures in the direction of the food patches. On only two such mornings did the groups departing along the mean vector, plus all those within 33.75° on either side, align with the direction of known bait sites. However, some

birds (28%) did fly directly toward the bait sites on all 7 days, and were likely those observed feeding there later in the morning. This suggests that some individuals, if followed, could be reliable indicators of the locations of food patches.

The orientation of the mean departure vector over 8 days shifted significantly, in accordance with my assumption that the vultures were using a changing (i.e., ephemeral) food supply ($\chi^2 = 105.92$, d.f. = 21, $p < 0.000$) (see Figs. 9a,b,c). The sample circular histograms illustrate that vultures departed differently on different days and that no single food source was responsible for the concentration of departure directions. There were always several flocks leaving in several directions.

The general pattern of roost departures fits the prediction of following from the roost. However, just as temporal clumping can be partially attributable to environmental variables so too can the spatial distributions of departing birds. Wind speed and direction are the most obvious non-social factors potentially affecting the orientation of departing groups. However, wind speed does not appear to influence the spatial clumping of departures. Vulture groups were equally clustered about the mean departure vector whether the wind blew strong or weak (S.L.R. $r^2 = 0.04$, $N = 39$, $p = 0.191$). Of all the birds flying out of the roost within the "mean

departure arc" (i.e., mean departure vector $\pm 56.25^\circ$) on each of 39 mornings, 53% departed cross-wind, 37% down-wind, and 11% headed into the wind. The mean wind speed for mornings when most vultures departed into the wind was significantly lower (4.0 ± 4.5 km, $N = 4$) than it was when most groups flew either across-wind (11.26 ± 5.18 km, $N = 20$), or down-wind (11.0 ± 3.65 km, $N = 14$) ($t = 2.88$ and 5.58 respectively, both p 's < 0.01). Given that the prevailing wind during the study came from the northwest, any birds departing either cross-wind or down-wind (approx. 90%) were therefore, also heading in the direction of the Niagara Escarpment. The east-facing escarpment receives sunlight early in the morning and is therefore likely to be where the first thermals occur in the area. Turkey Vultures habitually soar along the escarpment edge, perhaps making use of "thermal streets" (Pennycuick 1972), so it is not unreasonable to assume that they might head for such areas early in the day. Rabenold (1983) noted far fewer (<10%) vultures flying cross-wind out of the roost, the majority (55%) moving down-wind. Thus, spatial clumping of departures from the roost may be largely a function of local environmental conditions and/or topography.

Group size and communal roost arrivals

If Turkey Vultures are following one another out of the roost, then groups departing the roost in the morning

might be expected to be larger than those observed later in the day, unless birds follow one another throughout the day. Contrary to this expectation, I found no size differences between groups leaving the roost ($\bar{X} = 2.15 \pm 2.07$, $N = 1333$) and those foraging away from the roost during the late morning and early afternoon ($\bar{X} = 1.90 \pm 1.59$, $N = 121$) ($d.f. = 2$, $p = 0.809$, Fig. 10). However, foraging groups do not apparently remain intact throughout the day, since groups arriving at the roost in late afternoon were statistically smaller than those observed departing the roost ($\bar{X} = 1.53 \pm 0.97$, $d.f. = 2$, $p < 0.000$). Rabenold (1983) found Turkey Vulture groups departing from a roost in North Carolina to be larger than those observed foraging. Considered together, these results suggest that Turkey Vultures in my study area are departing the roost to forage in small, discrete flocks, which may represent basic social units and not any further clumping as a result of having roosted together.

Despite the fact that returning groups were relatively small, their assembly at the roost in the late afternoon differed significantly from what would be expected, had they been arriving independently ($N = 1397$, $p < 0.000$) (Fig. 11). However, vultures arrived at the roost less synchronously than they departed in the morning. The mean coefficient of variation for departures ($\bar{X} = 0.43 \pm 0.17$) was significantly lower than that for arrivals ($\bar{X} = 0.62 \pm$

0.13, $p < 0.000$). In addition, the temporal synchrony of arrivals at the roost is not explainable by any environmental factors that I tested. Neither wind speed or air temperature appear to be responsible for the variation in synchrony of vultures assembling at the roost across days (M.R. $r^2 = 0.006$, $N = 33$, $p = 0.65$ and $r^2 = 0.007$, $N = 33$, $p = 0.63$; respectively).

Vultures arriving at the roost were spatially clumped. Twenty-three of 33 (70%) circular distributions of arrival data significantly differed from random (Poisson). Late afternoon soaring by vultures along the Niagara Escarpment likely causes a degree of clustering of groups assembling at the roost. However, the most popular quadrant of arrival (i.e., N.E., S.E., etc.) differed across an 8-day period ($\chi^2 = 58.35$, $d.f. = 18$, $p < 0.001$). Forty-eight percent of the birds returning to the roost along the "mean arrival arc" (112.5°) on 33 days arrived flying against the wind. Of the remainder, 21% flew with the wind, and 30% arrived at the roost flying across wind. Thus, wind direction does not appear to be as important a factor in determining the direction of arrival of vultures as it is in influencing orientation of morning departures. The location of late afternoon feeding sites is probably a more critical factor in determining which direction vultures come from when returning to the roost.

DISCUSSION

Turkey Vultures at the principal communal roost I studied departed in the morning in a somewhat predictable manner. They appear to leave in discrete flocks heading out in several directions from the roost, with a shifting concentration of groups moving off in different directions on a daily basis.

Environmental factors appear to play a role in the timing and orientation of group departures. Turkey Vultures are particularly sensitive to changing wind conditions. With their low wing-loading they are able to maintain a low altitude, almost flapless flight by taking advantage of thermal and slope air currents (Pennycuik and Scholey 1984, Ehrlich et al. 1988).

The preponderance of groups moving out along the Niagara Escarpment, either down-wind or in a cross-wind orientation from the roost, also suggests that vultures are gaining an advantage from the prevailing winds and rising air currents associated with this topographic feature in the landscape. Similarly, Davis (1974) commonly observed Turkey Vultures circling over high ridges after they had left the roost in her Oregon study area. That my findings differ from those of Rabenold's (1983), with respect to wind orientation, may point to the importance of local topography in determining the departure heading of flocks. Those birds unaware of any long-lasting food patches

probably seek favorable soaring conditions before heading out to forage.

Departures were not regularly clumped in the direction of known bait sites, in spite of the fact that several, apparently knowledgeable, individuals flew directly to them. This further supports my experimental finding that recruitment to food patches via roost-centered information transfer is not occurring, though the opportunity to do so appears available.

The reason vultures depart the roost in greater synchrony on cooler mornings may be simply related to a significant negative correlation between temperature and wind speed (corr. = -0.32, $p < 0.05$). If cool temperatures and relatively strong winds co-occur (e.g., storm fronts) then high departure synchrony under such conditions may be a function of more favorable soaring conditions. Regardless of the importance of the environmental factors I tested, there remains a degree of unexplained variation (85%) in the departure synchrony of Turkey Vultures leaving the roost. Social facilitation is likely responsible, in part, for the formation of circling kettles of vultures prior to roost departure. One or two vultures that had obviously located a favourable thermal were often quickly joined by several others from the pre-roost area. While rising kettles might regularly be composed of up to 50 vultures, smaller groups would break-off intermittently

heading out in several directions, apparently "following" one another.

The interpretation that these small groups (2 birds), heading out from the roost, are basic foraging/social units is supported by the fact that they do not differ in size from groups clearly observed foraging during midday. The significantly larger size of departing groups of Turkey Vultures in North Carolina (Rabenold 1983) could be a function of recently fledged young joining foraging groups or simply different departure patterns due to some peculiarity of the roost in which she worked (e.g., topography, mixed species roost composition). Departing Black Vulture groups are much larger than those found foraging (Rabenold 1983). Black Vulture foraging groups also appear to be composed largely of related individuals, as they exhibit strong extended family association year round (Rabenold 1986). In contrast, there is no evidence of Turkey Vulture mates socializing outside of the breeding season, and young appear to be virtually independent of their parents upon fledging (Coleman 1985, Rabenold and Decker 1989). Therefore, membership of Turkey Vulture foraging groups is unlikely to be particularly consistent.

Foraging groups of Turkey Vultures appear to be organized on the basis of social dominance. Dominant members of such groups achieve priority of access to carcasses, because of their superior competitive abilities

and therefore, reach satiation sooner (see **CHAPT. 1, RESULTS**). I do not have sufficient data to test whether those members of foraging groups who make food patch discoveries (i.e., superior foragers), are in fact dominant over their later arriving (within 5 min) flockmates. However, out of 8 observations in which I was able to clearly assess the relative dominance of both members of a foraging group, the bird making the discovery of the food patch was dominant over the later arriving bird in 5 instances.

Subordinates (likely younger birds) usually wait around to feed once the dominant birds have departed, thus breaking up foraging groups. Vultures that arrived together at food patches rarely departed together. The mean delay in departure by the second bird after it's satiated flockmate had flown off was 11.10 ± 13.90 min ($N = 38$). This, in effect, probably causes groups to be smaller upon arrival at the evening roost. If displaced by later arriving birds, subordinates still retain the knowledge of the location of the food patch and can return later that day or even early the next morning. (Returning birds do not have to be well fed but simply "knowledgable"). For these reasons it is unlikely that foraging group memberships are long lasting or stable.

Synchrony of arrival of groups at the roost in the late afternoon may be explained by the fact that vultures

commute along the Niagara Escarpment in the vicinity of the roost in the late afternoon. The sight of others cruising in the area of the roost may attract others, leading to a temporal clumping of birds entering the roost. The significantly lower degree of temporal clustering of arrivals of vultures at the roost, relative to their morning departure synchrony, is also probably related to differential foraging success throughout the day, and the break-up of foraging groups. The ephemeral nature of carrion is reflected in the changing orientation of the mean arrival vector for vultures across several days. Turkey Vultures in my study area do not appear to be reliant upon any particularly long-lasting, or predictable food supplies (e.g., large carcasses or multiple carcass piles).

In summary, the patterns of departure and arrival of vultures from their communal roost are influenced to a significant degree by environmental conditions and topographic features. Social facilitation also appears to contribute to the temporal synchrony of departures (and arrivals), and the formation of small foraging groups leaving the roost in several directions each day. However, my results do not suggest that departing groups of vultures are composed of knowledgeable birds, returning to specific food patches and individuals following them to share food, as predicted by roost-centered information transfer.

Rather, departing, groups may simply be opportunistic foraging associations between dominant and subordinate individuals (usually 2 birds).

Subordinates may indeed capitalize on food discoveries made by other foraging group members, while dominants may receive benefits from the simple presence of subordinates at food patches (e.g., shared vigilance effort). Temporal synchrony of departures, and thus communal roosting in general, may help promote the formation of such foraging groups. Several groups departing the roost simultaneously could lead to the establishment of a loose "foraging network" across which local food information would be relayed via local enhancement. Recruitment by such a system would result in non-random arrivals at food patches. However, the number of birds attracted would be fewer than expected by roost-centered information transfer, thereby keeping intraspecific competition to a minimum.

Alternatively, being followed by a subordinate bird while foraging may be an unavoidable "cost" incurred by dominant birds as a result of having roosted communally. Dominant birds may be willing to tolerate such a cost only because they benefit by having subordinate birds surrounding them, and shielding them from potential predators while roosting at night (Weatherhead 1983).

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depart satiated more frequently than others.

Chapter 2

1. Birds that discovered rich experimental food patches on the day they were established often returned (84%) the next day. They also arrived at a much earlier hour than they did on the day of food patch discovery.
2. Vultures arrived at experimental food patches non-randomly, on first and second days, indicating that they were not discovering the patches independently of one another. Arrivals at food patches were earlier on second days, suggesting a different (e.g., roost-centered information transfer) or simply enriched (e.g., local enhancement) food-finding mechanism was operating.
3. Fewer birds used experimental food patches on second days than was expected if roost-centered information transfer had contributed to their attraction.

Chapter 3

1. Communal roost attendance increased sharply during mid-summer in accordance with the decline of nest attendance by breeding adults.
2. Morning roost departures by vulture groups were non-random temporally and spatially. The level of temporal synchrony was highest on cool, windy

mornings. However, 85% of variation in temporal synchrony remained unexplained by abiotic factors measured. Departing groups often flew towards the Niagara Escarpment and/or in the direction of the prevailing wind.

3. While some birds flew directly toward known food patches, the majority of departing groups did not orient toward them on 7 sample days. Mean departure vectors varied across days suggesting changing food sources or environmental conditions.
4. Group size did not differ between those departing the roost and those observed foraging. Therefore, departing group size was not a function of following from the communal roost. Groups arriving at the roost in the afternoon were relatively smaller because of group fragmentation during foraging. Differential foraging success and therefore group break-up was the likely cause of a lower roost arrival synchrony.

Considered together, these results do not support the hypothesis that the primary advantage of communal roosting for Turkey Vultures in the study area is roost-centered food information transfer. This does not mean that under different environmental conditions (e.g., low carrion availability) Turkey Vultures cannot benefit from this food-finding mechanism. However, because Turkey Vultures

are intolerant of conspecifics, prefer small-sized carrion, and do not form long-term associations with kin, the potential advantages, and therefore, the importance of information transfer in the evolution of communal roosting behaviour in this species appears limited.

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Table 1. Percentage of time spent feeding and mean feeding bout duration (min) with respect to social status, food patch type, and arrival sequence.

	% Time spent feeding	Feeding bout duration	S.D.	N
Social status:				
Dominant	94	21.56	12.39	73
Subordinate	74	17.64	10.46	61
Patch type:				
Single	79	15.67	11.69	61
Multiple	87	21.28	11.87	166
Arrival sequence:				
Discoverer	78	19.67	11.16	28
Returning	91	27.16	12.16	31

Table 2. Analysis of variance of the percentage of time spent feeding.

Source	F	d.f.	p
Covariate:			
Group size	1.68	1	0.197
Factors:			
Status (dominant/subordinate)	51.52	1	0.000
Patch type (single/multiple)	6.58	1	0.011
Factor interactions:			
Status x Patch type	28.95	1	0.000

Table 3. Percentage of time spent feeding and mean feeding bout duration (min) within social status groups.

	Patch type	% Time spent feeding	Feeding bout duration	S.D.	N
Dominants	Single	97.1	14.43	8.29	23
	Multiple	92.5	24.84	12.65	50
Subordinates	Single	47.7	10.12	9.21	17
	Multiple	84.1	20.55	9.49	44

Table 4. Analysis of variance of the duration of feeding bouts.

Source	F	d.f.	p
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Covariate:			
Group size	7.18	1	0.008
Factors:			
Status (dominant/subordinate)	3.85	1	0.052
Patch type (single/multiple)	25.78	1	0.000
Factor interactions:			
Status x Patch type	0.023	1	0.880
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Table 5. Mean ($\pm$ S.D.) time of arrival (hrs) at experimental food patches and foraging group size on the day of discovery and the following day.

	Day 1	Day 2	Significance
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All birds:			
Arrival time	1318 $\pm$ 2.65	1145 $\pm$ 3.25	0.001
Group size	1.58 $\pm$ 1.16	1.43 $\pm$ 0.87	N.S.
Returning birds:			
Arrival time	1344 $\pm$ 3.41	1010 $\pm$ 2.96	0.001

Table 6. First- and second-day arrivals at
experimental food patches; estimated
totals for roost-centered information
transfer.

Trial	Arrivals		No. expected day 2*	Observed arrivals day 2
	first day	Proportion of mean roost population		
8803	3	0.052	5.83	11
8804	15	0.209	26.85	16
8805	6	0.083	11.49	10
8806	5	0.069	9.64	7
8809	2	0.027	3.94	3
8810	4	0.055	7.77	9
8811	2	0.027	3.94	6
8901	3	0.053	6.02	5
8902	2	0.033	3.91	5
8903	4	0.066	7.69	11
8904	3	0.061	5.80	5
8909	6	0.122	11.24	16
8911	1	0.017	1.98	11
8912	2	0.035	3.92	6
8914	17	0.298	28.92	27
8918	8	0.080	15.31	11

* See text for explanation

Figure 1. Location of Halton Region study area in southern Ontario.

Figure 2. Detail of study area within Halton Region.
Location of principal communal roost
indicated by triangle, and experimental
feeding sites represented by filled circles.

Figure 3. Relationship between the time spent on the ground at food patches and the number of agonistic interactions engaged in by individuals in feeding groups of two or more birds.

Figure 4. Relationship between feeding group size and the number of agonistic interactions per minute occurring within the group.

Figure 5. Temporal pattern of arrivals at experimental food patches on first and second days, beginning with the first arrival on each day and summing across the 24 trials when vultures returned to the food patches on the second day.

Figure 6. Temporal pattern of arrival at experimental food patches on first and second days summing across 24 trials when vultures returned to the food patches on the second day.

Figure 7. Mean weekly roost attendance through two seasons; shaded bars represent 1988, unshaded represent 1989. The mean first-chick-date is indicated by *.

Figure 8. Morning roost departures per 5-min interval across 39 days (i.e., first departure(s) on each day occur in first interval).

Figure 9a,b,c. Number and orientation of vulture
groups departing the roost on 3
consecutive mornings: 1, 2, 3, June 1989.
Circle represents 8 birds.

Figure 10. Group size distribution of vultures departing the roost; shaded bars, and foraging away from the roost; unshaded bars.

Figure 11. Late afternoon roost arrivals per 5-min interval across 33 days (i.e., first arrival(s) on each day occur in first interval).

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