

COMPARISON OF ROOST USE BY THREE SPECIES OF COMMUNAL ROOSTMATES¹

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Abstract. Our previous studies of communally roosting European Starlings (*Sturnus vulgaris*) revealed that each bird fed daily for months on its own "diurnal activity center" (DAC) and commuted to a variety of nearby and distant roosts. Since these observations contrast sharply with the predictions of most foraging explanations for communal roosting, we wanted to determine if this DAC-centered roosting pattern occurred in other communally roosting species. In this study we used radiotelemetry to monitor feeding and roosting sites used by starlings, Common Grackles (*Quiscalus quiscula*), and American Robins (*Turdus migratorius*), three species that share communal roosts in central New Jersey. Our goals were to determine (a) whether avian species that roost together use the roosts in similar ways, and (b) when and why individuals change roosts. Foraging patterns were similar in all three species; individuals fed daily on their DACs for many weeks. Roosting patterns were similar for grackles and starlings; individuals switched among nearby and distant roosts. In contrast, robins always roosted near their DACs, changing both roosts and DACs at the end of the breeding season. Predation rates at roosts were extremely low and did not explain the use patterns of large and small roosts. We argue that (a) DACs and DAC-centered roosting are probably widespread among communally roosting species, and (b) DAC-based individuals select roosts primarily on the basis of their proximity to good sources of food.

Key words: *Communal roosting; foraging; diurnal activity center; predation; European Starling; Sturnus vulgaris; Common Grackle; Quiscalus quiscula; American Robin; Turdus migratorius.*

INTRODUCTION

Several investigators have hypothesized that communal roosting by birds evolved to facilitate foraging in various ways. For example, roosting in a central location can reduce average commuting costs when food patches are short-lived (Horn 1968). Communal roosts might also serve as "information centers" at which individuals can learn about new or better food sources by following successful roostmates (Ward and Zahavi 1973). These and other "roost-centered" models (e.g., Weatherhead 1983) are based on the assumption that the roost is a relatively stable base of operation from which individuals exploit less stable food sources.

A very different picture of communal roosting emerged when roostmates were individually marked (Morrison and Caccamise 1985). Radio-tracking studies of communally roosting European Starlings (*Sturnus vulgaris*) revealed that

individuals actually used a variety of roosts but returned to feed on their own "diurnal activity center" (DAC, an area of 1-2 km²) day after day for months. Contrary to the assumptions of earlier models, foraging and roosting were centered around a stable feeding area (DAC) rather than around a roost.

Foraging and roosting behaviors of starlings change in midsummer. During most of the year, starlings feed exclusively on their DACs and join small (50-500 bird) communal roosts nearby (<2 km away). During late summer and fall, starlings begin to commute to roosts that are much larger (5,000-50,000 birds) and more distant (4-12 km). These larger roosts do not form because of a shortage of acceptable roosting sites (Lyon and Caccamise 1981), and they are not premigratory aggregations, because they form months before migration (Caccamise et al. 1983).

When using distant roosts, starlings continue to feed primarily on their DACs, but also stop briefly at food sources near the distant roosts. By roosting overnight near food patches far from their DACs, starlings can reduce commuting costs

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to supplemental food patches by as much as 50% (Caccamise and Morrison 1986). Recent observations of individual starlings en route to and from roosts support this "patch sitting" aspect of communal roosting (Caccamise and Morrison 1988). Is the DAC-centered roosting pattern of starlings unique or do other communally roosting species have similar patterns?

To investigate the relationship of communal roosting to DACs, we undertook a comparative study of starlings, Common Grackles (*Quiscalus quiscula*), and American Robins (*Turdus migratorius*), three species that share communal roosts in central New Jersey (Caccamise and Fischl 1985). This is the first study to monitor both roosting and foraging behavior of heterospecific roostmates. By radio-tagging individuals captured from the same feeding area, we controlled for the effects of habitat heterogeneity. We found that DAC-based foraging behavior is not unique to European Starlings and may be widespread among communally roosting species. We argue that DAC-based birds select among suitable roosting sites primarily on the basis of their proximity to good feeding areas.

METHODS

We radio-tagged nine European Starlings, nine Common Grackles, and nine American Robins, all adults, in central New Jersey during the local roosting season (June–November) of 1987. All starlings and grackles were postbreeding individuals. Five of the robins were captured toward the end of their breeding season and may have been reproductively active for the first 10–20 days of the 46–102 days (\bar{x} = 77 days) that they were tracked (Bovitz 1990).

All birds were captured during the day in the horticultural display garden of Rutgers University, New Brunswick, New Jersey. Robins were mist-netted; starlings and grackles were captured using decoy traps and baited walk-in traps. Birds selected for radio-tagging appeared in good health, with well-maintained plumage and body weights above the mean for that species and sex. We tagged and released all birds at the site of capture ≤ 3 hr after they were trapped. The birds subsequently frequented an urban-suburban area that was primarily residential and commercial (81%) but contained a few agricultural fields (4%) and woodlots (2%) (Fischl and Caccamise 1985).

The transmitter package (<5 g) was attached to the back of the starling (71–85 g), grackle (95–131 g) or robin (73–84 g) with a "vest" made

from cotton shoelace (Morrison and Caccamise 1985). After an initial period of adjustment (6–48 hr), the bird's behavior was not noticeably affected by the transmitter; the radio-tagged birds flew and foraged normally for months. The range of the transmitters was greater than 1.0 km for birds roosting in trees and less than 0.5 km for birds foraging on the ground. Transmitter life averaged 90 (SD = 15) days.

To determine whether the birds had DACs (i.e., spatially clustered diurnal sightings), we used an automobile with a rooftop antenna to locate each bird during the day, 6 days a week, at randomly predetermined times between 06:00 and 18:00. Attempts to locate the birds were successful over 85% of the time for all three species. This success rate was somewhat lower than in previous studies (Morrison and Caccamise 1985) because of a lack of experienced field assistants in 1987.

For interspecific comparisons, spatial clustering was quantified as the mean distance from each diurnal sighting to the use-weighted center (i.e., mean x and y coordinates) of all diurnal sightings made on that bird. Separate DACs were recognized when all sightings in one cluster were > 2 km from all sightings in the other cluster. In practice, the few cases of multiple DACs involved separations of several kilometers.

We located the roost used by each radio-tagged bird six nights a week. Attempts to locate roosting sites were successful over 93% of the time. The birds could almost always be found by censusing after dark the many traditionally used roost sites in the study area. Distances from DACs to communal roosts were measured from the use-weighted center of the bird's DAC.

To describe long-term patterns of roost use, we restricted our analysis to the 17 birds for which we had greater than 40 days of observations: six starlings (four males, two females), four grackles (three males, one female), seven robins (four males, three females). Radio contact with the other 10 birds (\bar{x} = 20 days) was much shorter. Four had transmitters with defective batteries; after only 1–2 weeks in the field, their pulse rates increased almost two-fold, symptomatic of a voltage drop in lithium batteries. The other six transmitters lost their antennas, reducing their effective range to < 100 m.

Estimates of predation rates were based on the fates of 63 adult starlings tracked during four summer roosting seasons (1983–1986). Each bird was assigned to one of five categories: eaten, dead

but not eaten, battery expired, premature transmitter failure, and unknown. The eaten category may have overestimated predation rate because it may have included birds eaten after dying of other causes. The battery expired category was assigned only when the signal was lost (a) after the expiration date calculated on the basis of battery capacity and transmitter current drain, and/or (b) after a significant (1.5- to 2.0-fold) increase in transmitter pulse rate, indicating a voltage drop in lithium batteries. Premature transmitter failure was assigned only when the bird had been visually sighted with a nonworking transmitter. The unknown category includes unconfirmed transmitter failures and birds that moved out of the study area.

Interspecific comparisons were made using one-way ANOVAs (GLM procedure of PC-SAS). Duncan's multiple range test ($P < 0.05$) was used to compare species' means.

RESULTS

FIDELITY TO DIURNAL ACTIVITY CENTERS

Foraging grackles and robins showed starling-like fidelity to DACs. The diurnal sightings made on individuals of all three species were spatially clustered. The mean distance of diurnal sightings from the use-weighted center of the DAC (shown as circle radii in Fig. 1) were not significantly different for starlings (0.87 km), grackles (0.88 km), and robins (0.48 km; $F = 1.93$, $P = 0.18$).

Daily sightings suggested that starlings and grackles moved around more than robins, but the mean distance moved between sightings made on successive days was similar for starlings (0.54 km), grackles (0.55 km), and robins (0.36 km; $F = 1.16$, $P = 0.34$).

Most of the birds had a single DAC (e.g., Fig. 1A–C). All six starlings and three of the four grackles returned daily to a single DAC for the entire observation period. In contrast, four of the seven robins shifted to new DACs 7–9 km to the south at the end of the breeding season (e.g., Fig. 1E, F). The only other case of DAC shifting involved grackle female 207 (Fig. 1D); she used three distinct DACs in succession, separated by distances of 6.5 and 5.5 km, respectively.

USE OF ROOSTS

Although all 17 radio-tagged birds were captured in the same foraging area, they commuted to a variety of different roosts. During the June–November roosting season, the 17 birds joined com-

munal roosts at a total of 15 different sites. The three species were frequently found roosting together. The six starlings ($n = 487$ nocturnal sightings) and the four grackles ($n = 279$ nocturnal sightings) joined roosts known to include both starlings and grackles over 97% of the time. Robins ($n = 462$ nocturnal sightings) roosted with starlings and grackles at least 57% of the time.

Of the 15 roosts, 12 were minor roosts of <2,000 birds. One site (R-88) was occupied by an intermediate-sized flock that peaked at 3,000–5,000 in late August. Two sites (R-42 and R-97) were occupied by major roosting flocks of 10,000–35,000 birds. Major roosts have formed at the latter two sites every roosting season for many years (Caccamise et al. 1983). In past years, R-42 has peaked as high as 65,000–125,000.

The two major roosts (R-42 and R-97) were the only distant roosts to which our radio-tagged birds commuted; i.e., the only roosts used that were >4 km from their DACs. Therefore, in this study major roost and distant roost are synonymous.

Although all individuals used more than one roost, most birds (11 of 17) used only nearby roosts (e.g., Fig. 2E, F). All seven robins, one of four grackles and two of six starlings roosted within 3 km of their DACs 100% of the time. On average, robins used roosts that were significantly closer to their DACs (1.0 km) than did starlings (3.9 km) and grackles (3.6 km; $F = 10.94$, $P = 0.001$).

Six individuals (three starlings and three grackles) used distant roosts (>4 km from their DACs). Distant roosts were used for extended periods (50–90% of the time) by three starlings (e.g., Fig. 2A) and two grackles (e.g., Fig. 2C). One starling (Fig. 2B) used distant roosts on only five of 78 nights: one roost (R-42) 9 km west of its DAC and one roost (R-97) 8 km south of its DAC.

ROOST SWITCHING

In 1,228 bird nights of observation, we recorded 133 cases of roost switching in which the bird used a roost different from the roost it had used the previous night. The average distance moved from night to night was significantly greater for grackles (0.85 km) than for starlings (0.39 km) and robins (0.18 km; $F = 7.82$, $P = 0.005$). Grackles not only switched roosts frequently (15.1% of the time), but almost always (39 of 41 cases) switched to roosts >2 km from the previous night's roost ($\bar{x} = 5.74$ km). Robins switched

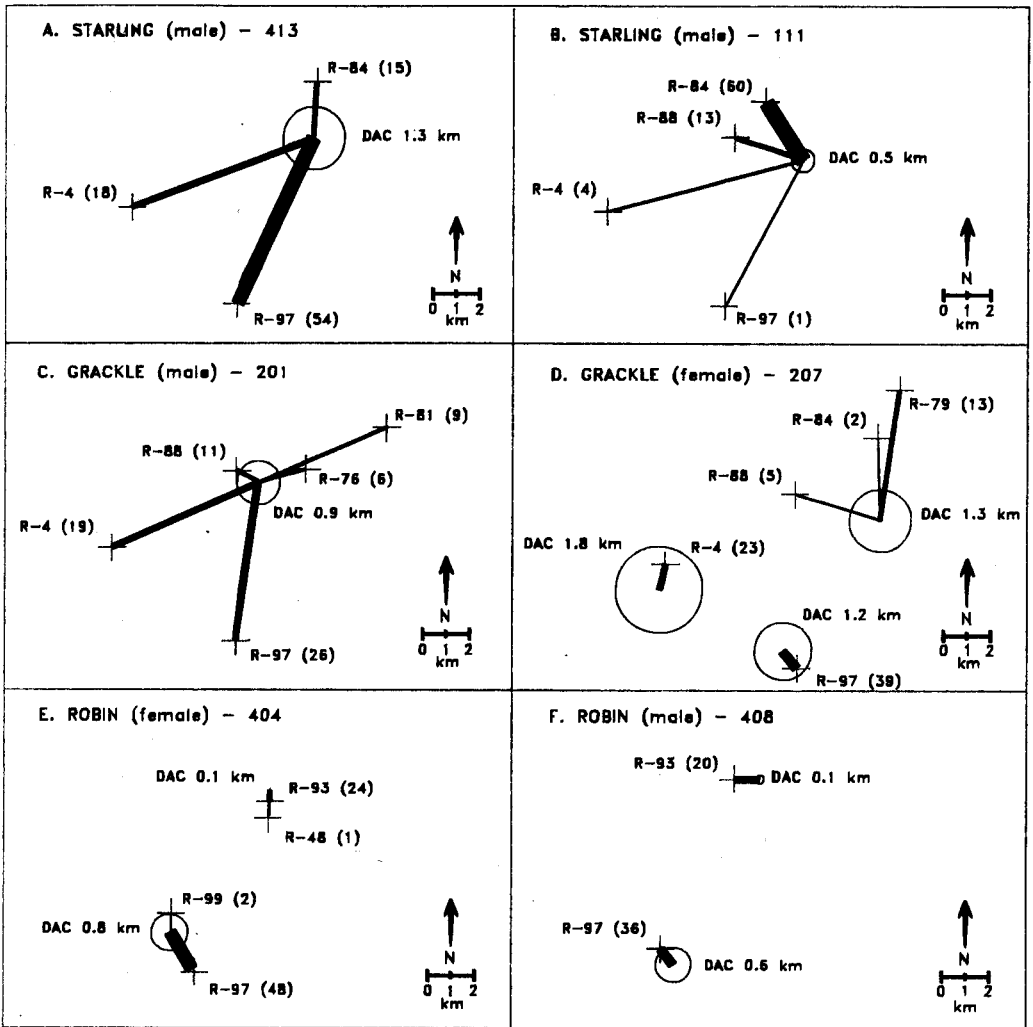


FIGURE 1. Maps showing relationship of communal roosts to diurnal activity centers (DAC, circles) used by starlings, grackles, and robins. The number by each DAC circle is the average distance (km) of all diurnal sightings from the use-weighted center of the DAC. R-numbers refer to roosts. Numbers in parentheses and width of lines indicate how many nights the bird was found at each roost. DAC-centered roosting is evident in all three species.

almost as frequently (12.3% of the time), but only rarely (four of 56 cases) did they switch to a roost >2 km away (\bar{x} = 1.44 km). Starlings switched less frequently (7.8%), but always (36 of 36 cases) to roosts greater than 2 km away from the previous night's roost (\bar{x} = 5.15 km).

In all three species, individuals switched roosts (n = 133 cases) much more frequently than they changed DACs (n = 5 cases). Accordingly, most roost switches could not be attributed to a change

in DAC location. Most birds (three grackles, seven starlings, and three robins) returned daily to a single DAC.

Of the five cases of DAC shifting (four robins and one grackle), all were accompanied by a major switch in roost. Prior to the change, the four robins foraged daily in the Rutgers Display Gardens and roosted together in a small (200-bird), all-robin roost <1 km away. Over a 1-week period in mid-July, at the end of the breeding sea-

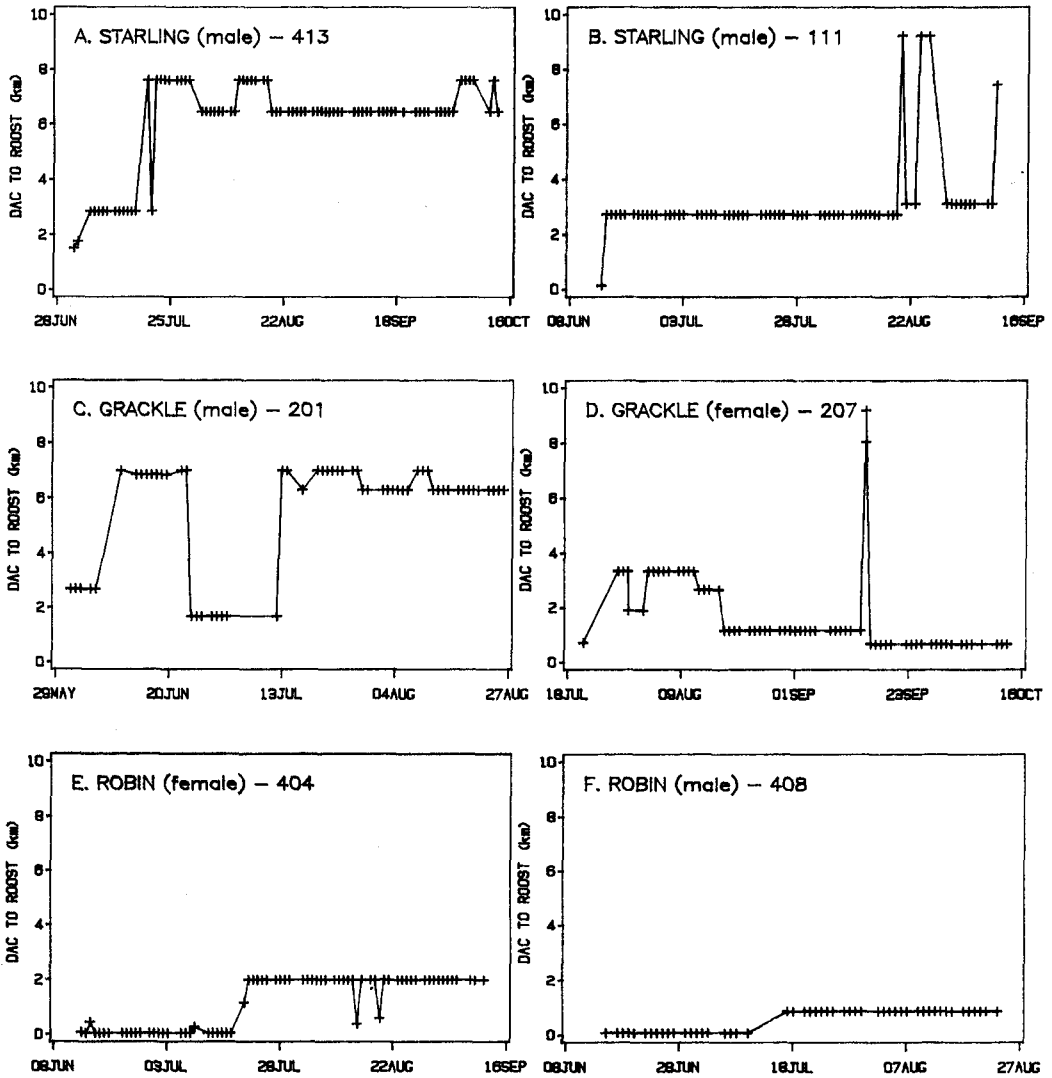


FIGURE 2. Seasonal patterns in the distance between diurnal activity center (DAC) and communal roosts used by individual starlings, grackles, and robins.

son, all four abandoned this roost. Two of them (females 404 and 412; Fig. 1E and 2E) moved 1.5 km south to a roost (R-48) of several hundred robins and starlings, but continued to feed in the Display Gardens. After two and five nights at R-48, they switched to R-97, a major roost of 30,000 starlings, grackles, and robins, 8 km to the south. The other two robins (males 407 and 408; Fig. 1F and 2F) also joined R-97 after using unknown roosts and foraging areas for 5 and 6 days. All four robins established new DACs with-

in 1-3 km of R-97. The only other bird that shifted its DAC was grackle female 207 (Fig. 1D). She twice moved her DAC and roost simultaneously, first 6 km S to a DAC near R-97 and then 5 km NW to a DAC near R-42 (Fig. 2D).

PREDATION RATES

During the roosting seasons of 1983-1986, 63 adult starlings were radio-tracked for a total of 4,665 bird days. Seven of these birds were found eaten or partially eaten; e.g., one bird found on

a tree branch was likely eaten by a bird of prey, and two were found with cat-like tooth marks in the transmitter coating. The eaten category may have overestimated predation because some of these birds could have been eaten after dying for other reasons. Relevant here is that none of the seven suspected predations occurred at roosts. All occurred during the day.

DISCUSSION

The overall pattern of foraging and roosting was similar for starlings, grackles, and robins. Individuals fed daily on their DACs and commuted to a variety of nocturnal roosts. These similarities may reflect the similar feeding habitats used by these species. During the spring and early summer, all three species forage primarily for soil invertebrates on commercial and residential lawns, habitats that have a relatively homogeneous distribution in our study area (Fischl and Caccamise 1985). During this period, the birds use only small roosts near their DACs. As the summer progresses, diet composition begins to change, becoming almost entirely plant material by autumn in starlings (Fischl and Caccamise 1987), grackles (Maccarone 1985), and robins (Wheelwright 1986). These foods are found in habitats that are more heterogeneously distributed, e.g., orchards and grain fields. The change to plant material coincides with the formation of larger roosts (Fischl and Caccamise 1987).

Interspecific differences in this DAC-centered pattern were primarily differences of scale. Starlings and grackles had similar-sized DACs and commuted to both nearby and distant roosts. Robins had somewhat smaller DACs and used only nearby roosts. These differences may reflect more subtle, unmeasured differences in the spatial and temporal distribution of food patches.

DIURNAL ACTIVITY CENTERS

In all three species, individuals returned to feed on their DACs day after day for many weeks. Fidelity to a DAC may bestow a number of selective advantages. Returning to a familiar area is known to increase foraging success in starlings (Tinbergen 1981). Frequenting a familiar feeding area might also decrease the risk of diurnal predation (Feare 1984, p. 216). Our observation that all predations on adult starlings occurred away from a roost suggests that diurnal predation is an important selective force.

We had speculated that DAC fidelity in starlings might improve the chances of securing a nest hole the next spring (Morrison and Caccamise 1985), because competition for nest holes begins in winter (Kessel 1957), and some starling DACs contained the bird's nesting site. However, a nesting site is not required for this behavior to manifest itself. Robins maintained DAC-centered foraging patterns even after shifting their DACs far from their breeding areas.

Four of seven robins changed the location of their DACs at the end of the breeding season. DAC-shifting also occurred in grackles and starlings, but less frequently. One grackle shifted her DAC twice. No starling shifted its DAC in this study, but we observed DAC shifting by five of 63 adult starlings tracked prior to 1987. One male and two females moved their DACs just after breeding, and two females shifted in late summer (Morrison and Caccamise 1985, unpubl. observ).

DAC shifting might be a response to a decline in food availability on the original DAC or may reflect the dietary change from invertebrates to fruits and grains. Robins may also move to more protective habitats (from lawns to forests) in preparation for their molt in August–September (Bovitz 1990).

Whatever its adaptive significance, fidelity to DACs may be found in many communally roosting species. Our studies of starlings, grackles, and robins are the first to quantify this behavior, but similar fidelity to feeding areas is suggested in the descriptions of foraging by wing-tagged starlings (Feare 1984), Red-winged Blackbirds *Agelaius phoeniceus* (Johnson 1979), Cattle Egrets *Bubulcus ibis* (Siegfried 1971), and Great Blue Herons *Ardea herodias* (Krebs 1974). DACs will probably be found in other species as more studies are done using marked individuals.

Recognition that DACs are widespread in communally roosting birds is an important milestone. Traditionally, models of communal roosting have been simple extensions of central place models intended to describe colonial nesters. These models assumed that the nocturnal roosting site was stable and that food patches surrounding the roost were short-lived. The assumption that roosts are more stable than feeding areas is reasonable for nesting birds tending immobile eggs and nestlings. However, this assumption is violated by many species that roost communally in the nonbreeding season.

COMMUNAL ROOSTS

By roosting communally, individuals probably gain both foraging and antipredator benefits. The evidence for antipredator benefits is indirect. For example, communal roosts typically form in substrates that are relatively inaccessible to predators (Lack 1968). In theory an individual's predation risk should be lower in larger groups (Hamilton 1971, Pulliam 1973). This hypothesis holds for some foraging groups (e.g., Powell 1974, but see Lindström 1989). The hypothesis has never been tested for roosting groups.

The roost-use patterns that we observed cannot be explained by predation alone. If antipredator benefits are greater at larger roosts, then birds should converge to form larger and larger roosts (Sibly 1983), or roost size should stabilize at a point where antipredator benefits and foraging costs balance (Giraldeau and Gillis 1985). The differences assumed to exist in predation rates at large and small roosts must be extremely small, because actual predation rates at our roosts were very low. None of our recorded predations on starlings occurred at a roost. In addition, major and minor roosts were active concurrently, and individuals switched back and forth between them. Roost switching has also been observed in starlings on their overwintering grounds, but no explanation for the switching was given (Heisterberg et al. 1984).

As DAC-based foragers, starlings, grackles, and robins do not routinely use communal roosts as information centers (*sensu* Ward and Zahavi 1973). Nevertheless, foraging considerations remain essential for understanding how these species select communal roosts. On most nights, all three species joined roosts in protected sites close to their DACs, probably to reduce the risk of nocturnal predation while minimizing commuting costs back to the DAC.

Distant roosts were used only by starlings and grackles, probably to reduce commuting costs to distant food patches being used as supplemental feeding areas. We did not follow grackles en route to distant roosts, but starlings using distant roosts usually stop at orchards, grain fields, or other supplemental food sources near those roosts (Caccamise and Morrison 1988). Roosting overnight near food patches far from the DAC reduces commuting costs to these supplemental feeding areas by up to 50% (Caccamise and Morrison 1986, 1988).

Actual differences in predation rates at large and small roosts are extremely small and do not explain the roost-use patterns documented in this study. Instead, roosts appear to be selected primarily for their proximity to good sources of food.

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