

EUROPEAN STARLING FIDELITY TO DIURNAL ACTIVITY CENTERS: ROLE OF FORAGING SUBSTRATE QUALITY

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ABSTRACT.—The information center hypothesis, the most commonly cited explanation for communal roosting behavior, assumes a roost-centered foraging distribution. Nonetheless, European Starlings (*Sturnus vulgaris*), as well as several other communally roosting species, have a foraging distribution centered on a single diurnal activity center (DAC) which is central to the distribution of roosts they use. The “patch-sitting hypothesis” integrates DAC-based foraging behavior into an alternate explanation for communal roosting behavior. One prediction of this hypothesis is that foraging substrate quality should decline on DAC’s as increasing proportions of the local roosting population become associated with large roosting congregations, i.e., when more individuals leave their DAC’s to forage elsewhere. I examined this prediction by assessing foraging substrate quality on DAC’s through measures of feeding success on the most commonly used DAC-based foraging substrate—lawns. My goals were to determine the importance of foraging substrate quality in DAC fidelity and to identify the factors contributing to the decline in use of lawns during late summer. I found a substantial seasonal decline in foraging success, suggesting lower foraging substrate quality on DAC’s when (1) use of lawn habitats normally declines, and (2) starlings leave their DAC’s to forage and roost at distant sites. These results agree with the prediction that foraging substrate quality declines when starlings leave their DAC’s to forage elsewhere, and thereby provide new support for the patch-sitting hypothesis. Received 19 Sept. 1989, accepted 27 Aug. 1990.

During the post-breeding roosting season (June–November) European Starlings (*Sturnus vulgaris*) show ardent fidelity to the same small (2–4 km²) diurnal activity center (DAC) over many weeks, while at night they use a variety of different communal roosts (Caccamise et al. 1983, Morrison and Caccamise 1985). Such DAC-based roosting behavior has been directly observed in Common Grackles (*Quiscalus quiscula*, Morrison and Caccamise 1990), American Robins (*Turdus migratorius*, Bovitz 1991), American Crows (*Corvus brachyrynchos*, Stouffer and Caccamise, unpubl. data), and may be indirectly inferred in Red-winged Blackbirds (*Agelaius phoeniceus*, Johnson 1979), wing-tagged starlings in Great Britain (Feare 1984), Cattle Egrets (*Bubulcus ibis*, Siegfried 1971), and Great Blue Herons (*Ardea herodias*, Krebs 1974).

The information center hypothesis (Ward and Zahavi 1973) is the most commonly cited explanation for communal roosting behavior (Mock et al. 1988). It carries the implicit assumption of a roost-centered foraging distribution. If roosts are the location where individuals “learn” the lo-

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cation of new feeding sites, then the roost should lie at the center of the group of feeding sites used by individual birds. DAC-based species have a foraging distribution that is DAC-centered, with foraging concentrated on a single small area which itself is central to the distribution of the roosts that are used (e.g., Morrison and Caccamise 1985). This is clearly contrary to the roost-centered assumption of the information exchange hypothesis. Violation of the roost-centered assumption casts serious doubt on the importance of information transfer (*sensu strictu*, Ward and Zahavi 1973) as the primary cause for the formation of roosting assemblages in any DAC-based roosting species.

Based primarily on observations of communally roosting European Starlings, the "patch-sitting hypothesis" integrates DAC-based foraging behavior into an alternate explanation for communal roosting behavior (Caccamise and Morrison 1986). Early in the roosting season DAC-based starlings forage almost entirely on their DAC's where they prefer substrates providing soil invertebrates (e.g., managed lawns, pastures; Fischl and Caccamise 1986). Night-time roosts are usually near the DAC and are small (25–500 birds). As the season progresses towards the seasonal peak in numbers of roosting birds (mid to late August, Caccamise et al. 1983), starlings increasingly frequent larger, more distant roosts. The diversity of foraging habitats also increases, and the diet changes with the inclusion of far greater proportions of plant materials (fruits, seeds, Fischl and Caccamise 1985, 1986). The commute between DAC and roost plays a key role in the change in diet. This is because DAC's always contain foraging substrates suitable for collecting invertebrates (e.g., lawns), but they often hold no apparent alternate foraging substrates. For example, suburban neighborhoods and pastures are habitats where starling DAC's are common, yet they clearly offer little by way of sources for the plant foods that become important later in the season. When starlings commute between DAC's and distant roosts, they often make foraging stops at sites with particularly abundant food sources where they supplement their diet (e.g., fruiting trees, feed lots, grain fields). These supplemental feeding areas (SFA's) provide the bulk of the plant foods important late in the season (Caccamise and Morrison 1988). Despite dramatic changes in foraging substrates and the often long commuting distances (e.g., to 38 km, Wynne-Edwards 1929; 50 km, Hamilton and Gilbert 1969) common later in the season, starlings remain faithful to the same DAC where they return each day to spend most of the daylight hours.

The patch-sitting hypothesis is based on three assumptions: First, DAC fidelity provides benefits in addition to those associated with foraging there. Otherwise, there would be no reason to return to the DAC at times when birds travel to SFA's to supplement their diets. Though benefits of

DAC fidelity remain unclear, DAC-based roosting behavior appears widespread among communally roosting species (Morrison and Caccamise 1990). The second assumption requires that birds move to distant roosts in order to utilize high quality foraging sites (SFA's) located nearby. The third assumption is that birds use foraging areas (including SFA's) in ways that tend to minimize commuting distance. One expected outcome of the patch-sitting hypothesis is that a DAC-based bird would be expected to forage on its DAC so long as it is able to satisfy dietary requirements there. This leads to the prediction that foraging substrate quality should decline on DAC's as increasing proportions of the local roosting population become associated with large roosting congregations, i.e., when more individuals are leaving their DAC's to forage elsewhere.

In this study I tested this prediction by examining changes in foraging substrate quality on DAC's through the post-breeding roosting season of European Starlings. I evaluated changes in substrate quality by measuring feeding success on the most commonly used DAC-based foraging substrate. In my central New Jersey study area, managed lawns are the preferred foraging substrate on DAC's and are used throughout the post-breeding season (Fischl and Caccamise 1985). My goals were to: (1) identify factors contributing to the decline in use of lawns during late summer, and (2) determine the seasonal relationships between foraging success in lawn habitats and the formation of large roosting associations. I found a substantial seasonal decline in foraging success occurring at the same time that: (1) use of lawn habitats normally declines, and (2) starlings begin leaving their DAC's to forage and roost at distant sites. This outcome agrees with the prediction that foraging substrate quality declines when starlings leave their DAC's to forage elsewhere. These results, like some earlier tests (Caccamise and Morrison 1988), provide support for the patch-sitting hypothesis.

STUDY SITE AND METHODS

My study took place during the post-breeding roosting seasons (June–September) of 1984–1986 on and near the Rutgers Univ. campus in central New Jersey. I worked in the north-central quarter of same larger study area that has been used for several other recent studies of starling roosting and foraging (e.g., Caccamise and Morrison 1988). The area is a typical mixture of urban and suburban habitats (shrubbery, lawns, gardens) interspersed with small (mainly <2 ha) woodlots and agricultural fields. I sampled birds feeding only in managed lawn habitats, the most important habitat during the post-breeding season (Fischl and Caccamise 1985).

I recorded foraging behavior between 06:30 and 10:30 h by watching starlings through a car window with binoculars or a 20× spotting scope. Individual foraging bouts began when a bird attempted to feed (probed soil with bill) and continued until I recorded approximately 100 feeding attempts (probes), or until the bird flew away. Feeding bouts of <10 sec were

later removed from the data set. At the end of each observation, flock size, species composition and meteorological information were recorded.

I used a hand-held computer (Radio Shack TRS-80, Model PC-2) programmed to store time of day (± 0.5 sec) and the keyboard character for each key depression. By coding individual keys for particular foraging activities, I was able to directly produce a computer-compatible data file from field observations. At the end of the day, I transferred the field data to a personal computer (IBM-AT) where a data base management program (dBASE III) performed initial calculations. Each activity was summarized (tally, mean duration and rate) over individual foraging bouts; these then became my sample units for statistical purposes.

I recognized five activities associated with foraging. (1) A *probe* consisted of a downward thrust of the bill into the substrate, presumably in an attempt to locate a food item. (2) A *successful feeding* followed a probe and was generally recognized by a very deliberate raising of the bill followed by a bobbing of the head, and generally a visible swallow. Or, when birds loaded several food items for nestlings, the items were manipulated in the bill, usually quite visibly, before foraging recommenced. *Feeding success* within each bout was represented by number of food items gathered per number of probes with the bill $\times 100$. (3) *Handling time* was elapsed time from when a food item was first sought (probe) until it was swallowed. When birds loaded several items handling time ended when the bird resumed foraging. (4) *Vigilant scanning* occurred when a bird temporarily stopped foraging activities and raised its head in an apparent effort to search for potential danger. (5) I recorded all *aggressive acts* directed at nearby birds.

I used one-way ANOVA's to make comparisons among flock size classes and among 10-day sample intervals. For the latter, I used covariance analyses to evaluate main effects (10-day sample intervals) while holding constant the effect of a secondary variable (flock size). In both cases tests were preformed on untransformed data using the GLM procedure of SAS for personal computers. Mean comparison tests were performed using the Duncan's multiple range test ($\alpha = 0.05$).

RESULTS

I evaluated a total of 553 foraging bouts of adult European Starlings feeding in lawn habitats. Bouts lasted an average of 3.5 ± 0.15 min and included a mean of 59 ± 2.9 probes each. The average probe rate was $16.9 \pm 0.28/\text{min}$ and ranged from 0.5–40.0/min. Bouts often ended before 100 probes were recorded. Usually birds were frightened, but sometimes they left of their own accord. By including these shorter observations (>10 sec) in the analysis, I reduced the possibility of bias from over-representing birds foraging in the best sites, i.e., where they remained for the longest intervals.

Foraging behavior.—Seasonal changes in size of foraging flocks were indicated by significant differences among 10-day sample intervals ($F = 5.56$, $P = 0.0001$). Mean comparison tests revealed that size of foraging flocks generally increased through 29 August, and thereafter declined (Table 1, Fig. 1A). I was not able to detect seasonal patterns in either amount of total foraging time devoted to scanning (scan rate; $F = 1.29$, $P = 0.2212$) or aggression (aggression rate; $F = 0.71$, $P = 0.7414$). How-

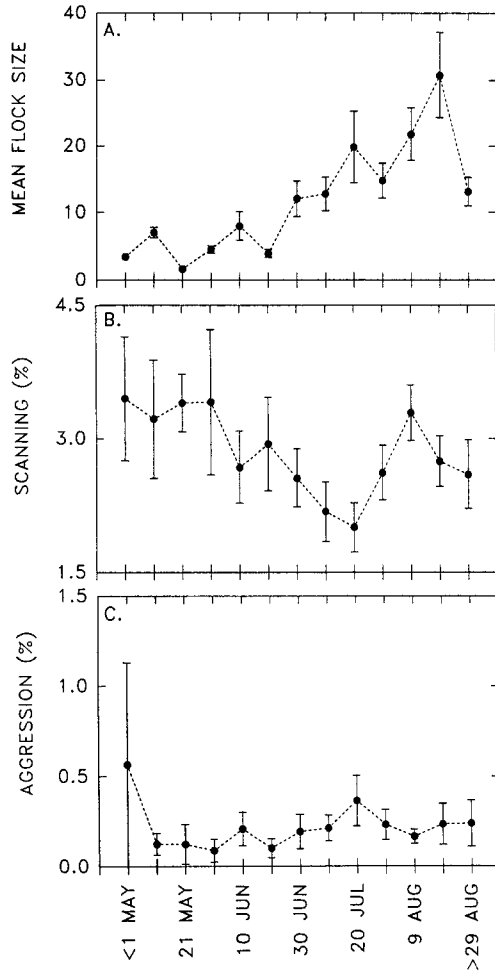


FIG. 1. Seasonal patterns in mean flock size (A), scan rate (B), and aggression rate (C) for European Starlings foraging on lawns. Dotted lines connect means, and vertical lines represent standard errors.

ever, during the earliest interval aggression rates were highly variable, and this may have masked actual elevated rates of aggression early in the season.

Flock size was related to other aspects of foraging behavior. A relationship was apparent between flock size and scan rate, however the response was not uniform over the full range of flock sizes (Fig. 1B, Fig. 2). Rather, highest scan rates occurred for solitary birds, while in larger

TABLE 1
COMPARISONS OF 10-DAY INTERVAL MEANS FOR GROUP SIZE AND HANDLING TIME
(DUNCAN'S MULTIPLE RANGE TEST)

Flock size			Handling time		
Date	Mean	Duncan*	Date	Mean	Duncan
19 Aug.	30.7	A	10 May	4.7	A
9 Aug.	21.8	AB	19 June	4.0	AB
20 July	19.8	AB	20 May	3.5	ABC
30 July	14.7	B	30 May	3.4	ABC
29 Aug.	13.1	BC	20 July	2.7	BC
10 July	12.7	BC	9 June	2.6	BC
29 June	12.0	BC	30 July	2.6	BC
9 June	8.0	BC	30 April	2.5	BC
10 May	7.0	BC	9 Aug.	2.3	BC
30 May	4.5	BC	10 July	2.1	BC
19 June	3.9	C	29 Aug.	2.1	BC
30 April	3.4	C	19 Aug.	1.8	C
20 May	1.6	C	29 June	1.7	C

* Means for dates with the same letter are not significantly different at the 0.05 level of probability.

flocks scan rates seemed much lower. To examine this relationship I divided foraging flocks into size classes, and performed analysis of variance. I found significant differences in scan rates among flock size classes ($F = 4.43$, $P = 0.0001$). Mean comparison tests indicated that scan rates for solitary birds were significantly higher than for all other flock sizes. Despite the suggestion of a declining scan rate for flock sizes above one,

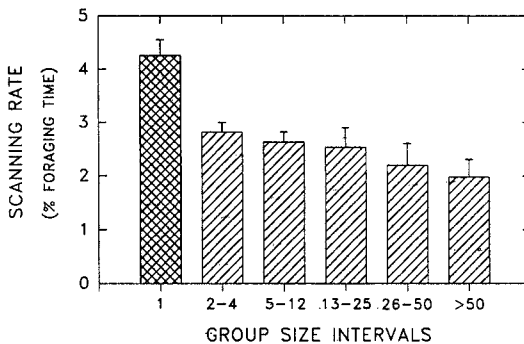


FIG. 2. Mean percent of total foraging time spent in vigilant scanning for each flock size category. Vertical lines on bars represent standard error, differing hatch patterns represent significant differences between means at 0.05% level.

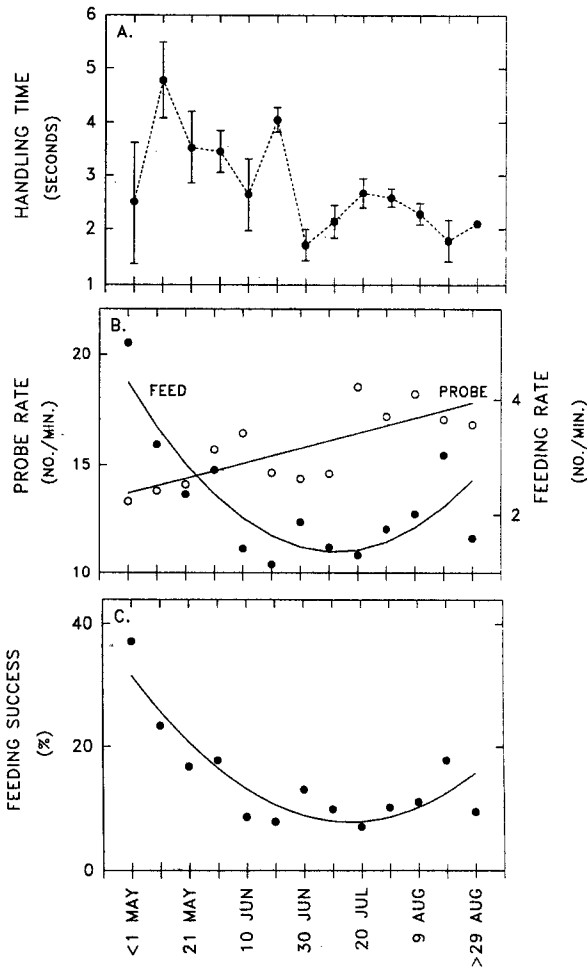


FIG. 3. Seasonal patterns in mean handling time (A), probe and feeding rate (B), and feeding success (C) for European Starlings feeding on lawns. Solid lines represent significant regressions (see text for equations).

mean comparison tests failed to detect any differences among the larger flock size categories (Fig. 2).

Rates of aggression were very low for the foraging starlings I observed, accounting for <0.3% of their total foraging time (Fig. 1C). I failed to detect significant differences in aggression rates among flock size classes ($F = 2.22$, $P = 0.0509$).

Foraging success.—Handling time varied significantly over the season

($F = 2.94$, $P = 0.0006$) with longer values occurring earlier in the season (Table 1). The short handling time of the earliest period was an exception, as such brevity was more typical later in the season (Fig. 3A).

I found significant differences among 10-day intervals for probe rate ($F = 3.35$, $P = 0.0001$), feeding rate ($F = 3.44$, $P = 0.0001$), and feeding success ($F = 3.12$, $P = 0.0001$). Probe rates increased significantly with seasonal advance ($Y = 12.98 + 0.35X$, $R^2 = 0.59$, $t = 4.01$, $P < 0.01$; Fig. 3B). However, feeding rates showed an overall decline with seasonal advance, although the response was not linear. Because feeding rates were lowest in middle to late July and higher towards both the beginning and end of the season, a second degree polynomial provided the best fit ($Y = 4.2920 - 0.0810X_1 + 0.0006X_2^2$; $R^2 = 0.73$; $t_{a1} = 4.8$, $P = 0.01$; $t_{a2} = 4.1$, $P = 0.01$; Fig. 3B). I combined responses of probe rate and feeding rate to arrive at an overall measure of feeding success. Feeding success was greatest early in the season, falling to its lowest levels in mid-summer, before rising again late in the season. Therefore, a second degree polynomial again best represented the data ($Y = 38.3 - 7.1X_1 + 0.4X_2^2$; $R^2 = 0.79$; $t_{a1} = -5.3$, $P < 0.01$, $t_{a2} = 4.4$, $P < 0.01$; Fig. 3C).

DISCUSSION

Foraging pattern.—Size of foraging flocks increased markedly through the season (Table 1, Fig. 1A). Others have reported similar seasonal changes for starlings (Williamson and Gray 1975, Fischl and Caccamise 1985). Enhanced predator protection through increased vigilance is a common explanation, although recent evidence suggests that individual risk may not always decline in larger flocks (Lindström 1989). Jennings and Evans (1980) found that time spent in vigilant behavior by foraging starlings decreased both as flock size increased, and as the location of individuals was nearer the center of the flock. I did not measure vigilance as defined by Jennings and Evans. In their study it represented intervals between my foraging bouts. They found that vigilance accounted for up to 50% of total foraging time. My measures of scan rate were much lower (3–6%), appearing more similar to their “head-up” display (4–5%). However, for this behavior they were not able to detect any relationships to flock size or position.

I found significantly higher scan rates for individual birds, although I did not detect differences among larger group size classes. The uniformly declining mean scan rates over the larger group size classes makes it tempting to speculate on a legitimate relationship. Nonetheless, variability inherent in visually measured behaviors of such short duration is difficult to manage, even with very large sample sizes. If such a relationship exists,

its detection will be easier with recorded media (e.g., film, video tape) where precision can be increased.

I found no effects for either group size or season on rates of aggression. Nonetheless, it is clear from Fig. 1C that variance in the earliest sample was much larger than the others. It is quite possible that this represents a real difference in behavior since starlings in the study area were still in relatively early stages of breeding during the first interval (Stouffer 1989). Failure to detect changes in rates of aggression would seem to preclude "despotic" (Fretwell 1972) monopolization of foraging resources on DAC's. This was the case even in late July and early August when group sizes were largest and foraging success on lawns was far below earlier levels.

Handling time tended to decline later in the season. The low values during the first 10-day interval may reflect the relatively high proportion of birds loading items for transport back to the nest. The nature of the data collection precluded separating these birds from individuals feeding for themselves; however the data were confounded in this way only during the earliest intervals. Nonetheless, beyond the first interval handling time declined significantly, indicating a change in the characteristics of food items being gathered. A decrease in average size of invertebrates taken would yield such a pattern.

The decline in feeding rate in late July and August represented an increase in search time between successful feeding encounters, likely resulting from a lower density of available invertebrates. Several studies have documented the transition in starling diets from mainly invertebrates in summer to largely plant foods in late summer and fall (e.g., Kalmbach and Gabrielson 1921, Dunnet 1955, Fischl and Caccamise 1986). Working in my study area, Maccarone (1985) attempted to relate changes in food abundance to this dietary transition. He worked in several foraging substrates, including lawns, but his results on invertebrate abundance in lawns were inconclusive. He did find lower soil moisture in late summer which may result in lower availabilities for certain moisture sensitive organisms (e.g., earthworms).

The higher probe rates in late July in combination with lower feeding rates resulted in a significant decline in feeding success (Fig. 3B, C). At its lowest levels in mid-summer, feeding success was three times lower than at the beginning of the season. Taken together with the shorter handling time (e.g., smaller items), this represents strong evidence that quality of lawn as a foraging substrate declines during the mid-summer interval when starlings are most actively engaged in roosting and foraging away from the DAC.

Foraging success and use of distant roosts. — Though DAC-based roosting behavior appears widespread among communally roosting species,

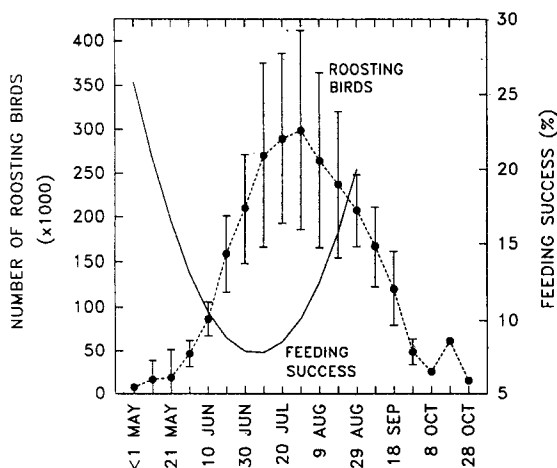


FIG. 4. Mean size (taken over four years) of total roosting population within 1000 km² study area in relation to a regression of feeding success over the roosting season. Size of roosting populations adapted from Caccamise et al. (1983); vertical lines through means present standard error.

benefits of DAC fidelity remain unclear. DAC-based birds can save up to 50% of the costs of travel to distant feeding sites by roosting near these sites and feeding during the morning and evening commute (Caccamise and Morrison 1986). While this provides an explanation for how DAC-based birds use distant feeding sites efficiently, it provides no insight into why they return each day to their DAC. Benefits of DAC fidelity likely exceed those simply associated with foraging because starlings maintain ardent fidelity to their DAC even when foraging success diminishes and they travel long distances to forage at alternate sites. Nonetheless, each day they return to their DAC where they spend most of the daylight hours.

The seasonal change in size of roosting populations in my census area has been shown to approximate a bell-shaped curve, with small populations early and late in the season, and large populations during a mid-summer peak (Caccamise et al. 1983). Although it is assumed that the size of the local population of starlings is approximately constant through this period (June–October) the change in size of the roosting population is believed to result from birds moving between small, scattered roosts (early and late in the season) and large associations (mid-season). Because the small roosts (25–1000 birds) are difficult to detect and monitor on a large regional basis these roosts remain uncensused. Thus, as birds move between the small undetected roosts associated with DAC's to the large censused roosts associated with SFA's, measures of the roosting population change accordingly.

I calculated mean size of the roosting population in my study area over the four years for which data were available (Caccamise et al. 1983) and plotted these results in Fig. 4 along with the regression describing seasonal changes in feeding success (Fig. 3). The results show that feeding success reaches its lowest levels at just about the same time that number of birds using large roosting associations reaches its maximum. Furthermore, as feeding success begins to increase again near the end of July, size of the roosting population again decreases as birds leave the large associations to return again to the small roosts associated with DAC's. It is possible that the concurrence of these events is entirely coincidental. Yet, other changes in foraging-related behavior occur at the same time and are likely related to the processes; size of foraging flocks increase (Fig. 1A; Williamson and Gray 1975), foraging substrate preference changes (Fischl and Caccamise 1985), and diet progresses from mainly insectivorous to frugivorous and granivorous (Kalmbach and Gabrielson 1921, Fischl and Caccamise 1986).

My results are consistent with the predictions that declining foraging substrate quality on DAC's occurs when roosting populations are largest, and that starlings leave their DAC's in order to improve their foraging opportunities. The patch-sitting hypothesis holds that formation of large communal roosts is a secondary effect resulting from passive convergence of many individuals near high quality food patches (SFA's) at times when DAC's do not provide adequate foraging opportunities. By roosting near distant foraging sites and feeding during morning and evening commutes, DAC-based starlings are able to minimize commuting costs (Caccamise and Morrison 1986) at times when foraging substrate quality in preferred habitats on DAC's is relatively low.

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