

# EPHEMERAL ROOSTS AND STABLE PATCHES? A RADIOTELEMETRY STUDY OF COMMUNALLY ROOSTING STARLINGS

DOUGLAS W. MORRISON<sup>1</sup> AND DONALD F. CACCAMISE<sup>2</sup>

<sup>1</sup>Department of Zoology, Rutgers University, Newark, New Jersey 07102 USA, and

<sup>2</sup>Department of Entomology and Economic Zoology, Cook College, New Jersey Agricultural  
Experiment Station, Rutgers University, New Brunswick, New Jersey 08903 USA

**ABSTRACT.**—Radiotelemetry observations on 15 adult European Starlings (*Sturnus vulgaris*) during two roosting seasons (June–November) in central New Jersey indicate that individuals are more faithful to their “diurnal activity centers” (DACs) than to their communal roosting sites. Our findings contrast sharply with the model of stable roosts and ephemeral patches central to many current explanations of communal roosting. For the 3–4-month life of their transmitters, 13 of 15 starlings commuted to their individual DACs from 1–5 different communal roosts. Some evidence suggests that nonmigratory, adult starlings use DACs as year-round bases of operation for both feeding and nesting and that they join major roosts (>2,000 birds) on a temporary basis to exploit rich sources of supplemental food near those roosts. Received 11 January 1985, accepted 2 May 1985.

NUMEROUS selective factors have been implicated in the evolution of avian coloniality (Wittenberger 1981). These include predation pressure, clumping of preferred nesting or roosting habitat, and various energetic considerations involving foraging or microclimatic conditions. The relative importance of these factors varies among species.

European Starlings (*Sturnus vulgaris*) are notorious for forming large, nocturnal roosting flocks, often containing tens of thousands of adults and juveniles in the nonbreeding season (Marples 1934). Several factors can be discounted as relatively unimportant in the evolution of communal roosting by starlings: (1) Starlings sharing a sheltered site do not benefit thermally from the presence of conspecifics (Kelty and Lustick 1977). (2) Starlings in our study area do not aggregate because of a shortage of suitable roosting sites (Lyon and Caccamise 1981). (3) Large roosts are not simply premigratory aggregations. In New Jersey there is a mid-August peak in the number of starlings found using major (>2,000 birds) roosts that is clearly separate from a smaller, October peak associated with premigratory aggregation (Caccamise et al. 1983). (4) Predation pressure is likely to be less important in roosts than in nesting colonies because highly vulnerable eggs and nestlings are absent. Weatherhead (1983) hypothesizes that larger roosts are possible if some members (the dominants) derive anti-predator benefits while others (the subordi-

nates) derive foraging benefits. Unfortunately, no good data on predation rates at avian roosts have been published. However, Pulliam (1973) argues on mathematical grounds that groups as large as those at starling roosts probably could not have evolved due to predation pressure alone.

Previous studies of starlings in New Jersey suggest that communal roosting by this species is integrally related to foraging. The relationship is evident in the seasonal changes that occur in (1) the size, number, and location of major roosting groups (2,000–100,000+ birds) in a 1,000-km<sup>2</sup> area (Caccamise et al. 1983) and (2) the availability and utilization of foraging habitats in this area (Fischl and Caccamise 1985). In 3 of 4 years the peak in the number of starlings using major roosts occurred in mid-August. The peaks were produced by an influx of starlings that previously, and subsequently, used smaller, more dispersed roosts. Censuses of foraging starlings indicate that August is a month of transition. Lawns, favored for their insects early in the year (April–July), became hard and dry, and postharvest corn fields, strongly preferred later in the year (October–November), were not yet available. During August and September, starlings foraged over a greater diversity of habitats. Whether this diversity reflects “hard times” for foraging remains to be determined.

Here we report results of an intensive, radiotelemetry study that indicate starlings are more

faithful to their feeding sites than to their roosting sites. Most individuals commuted for months to a single "diurnal activity center" (DAC) from a variety of communal roosts. Adult foraging activity clearly is centered around a DAC, not a roost. We also have evidence that suggests that the fidelity of nonmigratory adults to DACs is a year-round phenomenon that includes both overwintering and nesting sites.

The DAC-centered pattern we observed contrasts sharply with the "roost-centered" model (i.e. ephemeral food patches and relatively stable roosts) central to several, frequently cited explanations of communal roosting (e.g. Horn 1968, Ward and Zahavi 1973). Our observations suggest that nonmigratory starlings fly to more distant, major roosts (>2,000 birds) in late summer and fall as food available on the DAC declines. Major roosts form near locally superabundant food patches available at that time of year ("patch sitting"). DAC-based starlings appear to select roost sites that enable the birds to use supplemental food patches efficiently while maintaining a daily presence on their DACs.

#### STUDY AREA AND METHODS

*Study area.*—We studied the same 1,000 km<sup>2</sup> of the piedmont and inner coastal plain provinces of central New Jersey censused for starling roosts by Caccamise et al. (1983). The types of habitat found in this area are described in Fischl and Caccamise (1985).

In 1982 we focused our radio-tracking efforts on adult starlings from two major roosts. North roost (40°29'N, 74°31'W; Roost No. 4 in Caccamise et al. 1983) is on the piedmont and is largely surrounded by suburban development. South roost (Roost No. 23) is 36 km to the southeast on the inner coastal plain and is surrounded by agriculture and forest. We calculated habitat availability around North roost using the 290 sample points listed by the U.S. Soil Conservation Service (USDA 1979, 1982) for the northern third of our study area. For South roost we used the 869 points in the southern third. Habitats subsequently were lumped into four broad categories: residential (including urban, suburban, and rural), agricultural (soybeans, corn, vegetables, hay, pasture, barnyard, and orchard), forested (woodlot >0.5 ha), and other (open water, marsh, etc.).

*Roost census.*—In 1982 we continued the census of major roosts (>2,000 starlings and Common Grackles, *Quiscalus quiscula*) conducted by Caccamise et al. (1983) in 1977–1981. The size and composition of the flocks at all active roost sites were estimated every 6–8 days by counting the birds by species as they arrived in the evening. Minor roosts (<2,000 birds) were

included in the census only after radio-tagged birds led us to them.

*Radiotelemetry.*—During the local roosting seasons (June–November) of 1981 and 1982, we radio-tagged 18 adult starlings. Sixteen were captured at major roosts in the early evening using a mist net (3 × 12 m) suspended from pulleys atop a pair of telescoping, 15-m antenna masts set near the center of the roosting area. Two birds were captured on feeding grounds with decoy or baited walk-in traps. The transmitter package consisted of a 1-g transmitter (Model SM-1, AVM Instrument Co., Dublin, California 94566), 2.4-g mercury battery, 30-cm whip antenna, and protective coatings (wax and dental acrylic). The 5-g package was attached to the starling (80–85 g) with a "vest" of cotton lacing (AVM Instrument Co.). The vest and most of the "back pack" settled in and became covered with feathers after 1–2 days in the field. Newly radio-tagged birds were released inside their roosts after dark.

The expected life of each transmitter was calculated by dividing battery capacity (8.0 milliamp-days) by the transmitter's current drain (0.076–0.097 milliamps). Actual transmitter life, excluding Male 350 found eaten 5 days after release, was usually longer, averaging 104 days (SD = 21, *n* = 17). A radio was assumed to have ceased transmitting if the expected life of the battery had been exceeded and no signal was present at any of the known roosts in the area. In only one case did we lose a signal before the expected life of the transmitter had been reached. In this case and two others we were able to confirm visually that the radio was still on the bird but had ceased transmitting.

Because the starlings usually flew directly from the roost to their feeding areas, we searched initially for diurnal activity sites by driving along the vanishing bearings recorded as the birds left the roost at dawn. Diurnal activity sites were first located using a car-top, omnidirectional antenna (range approximately 1 km) and then pinpointed using a hand-held, directional antenna. Sunlight reflecting off the whip antenna often helped us recognize the radio-tagged individual in a group of conspecifics. We were able to pinpoint the roosts and diurnal activity sites used by all 18 radio-tagged starlings.

*Characterization of habitat, substrate, and activity.*—Our analysis of habitat and substrate utilization is based on intensive radio-tracking observations made in August 1982. August marked the beginning of the transition from minor to major roosts in 3 of the 4 previous years. Five adult starlings were radio-tagged at North roost on 27 July and 5 at South roost on 3 August. On each of 10 days between 12 and 24 August, a team of five observers attempted to locate and observe each bird for 30 min in the morning (0600–1100, EDT) and 30 min in the afternoon (1400–1900). At this time of year, starlings leave the roost shortly after 0600 and return shortly after 1900. Midday ob-

servations (1100-1400) were omitted for logistical reasons and because starlings spend most of this time in trees preening or resting. One of the 5 birds tagged at North roost was found dead 5 days after release, between the first and second day of observation (13-14 August). We substituted a sixth starling that used North roost but that had been captured and radio-tagged on 14 June while feeding. Unfortunately, this individual's transmitter battery expired after only 5 days of observation.

The sequence of observations was determined randomly within a framework that scheduled 2, 30-min observations on each of the 10 birds during each of the 10 study days, for a total of 100 observations on the birds from each roost. We successfully located the birds for the scheduled observation 93% of the time in the north and 79% of the time in the south. Twelve of the 21 missed observations in the south involved a single bird whose feeding area (near the periphery of the study area, 12 km south of the roost) was not located until the second week. These 12 and 9 other missed observations subsequently were filled by scheduling "make-up" observations at the appropriate time of day on 1 of 6 days (27 August to 2 September) selected at random. The 7 missed observations in the north could not be made up because they involved the substitute bird whose radio had ceased transmitting.

During a 30-min observation most birds used more than one location, habitat, or substrate. Habitat changes, substrate changes, and movements of >100 m were recorded as "subobservations." Our analysis of habitat and substrate utilization is based on a total of 439 such subobservations made during 193 observation periods. The observation periods totaled 94.2 h: 2,514 min in the north and 3,137 min in the south.

Habitats used by the radio-tagged birds initially were assigned to 1 of 15 categories that were somewhat different from the 15 USDA categories, having been modified to more accurately differentiate feeding habitats used by starlings. For analysis, these were lumped into the same four categories used for habitat availability: residential (including urban, suburban, rural, cemetery, and managed park), forested (oak/maple and other), agricultural (tilled, immature, mature, harvested, pasture, barnyard, and orchard), and other. Preferences for broad habitat categories were detected by comparing the frequency of use (minutes used/total minutes of observation) with occurrence.

Fifteen categories used to record substrate also were later reduced to 8: lawn, fruiting and nonfruiting trees, fruiting and nonfruiting shrubs, agricultural, commensal (e.g. garbage, handouts, roadside), and unidentified. Determinations of substrate and activity (feeding, perching, flying) usually required seeing the bird. However, the categories "tree" and "tree in fruit" sometimes were assigned in cases where the radio signal was clearly coming from a tree, but the bird could not be seen through the foliage. "Uniden-

tified" was used most frequently when a signal came from behind a house whose backyard was inaccessible to us.

*Longer-term observations.*—Our description of long-term roosting and foraging patterns is based on the behaviors of 15 adult starlings for whom we have 3 or more months of tracking data. These include 5 adults (4 male, 1 female) tracked in 1981 and the 10 adults (6 male, 4 female) whose movements in August 1982 were used in our analysis of habitat utilization. We excluded the radio-tagged starling found dead 5 days after release and 2 birds tagged very early (28 May) and very late (10 September) in the season.

We were almost always able to locate the roosts and feeding sites used by the 15 starlings tracked for the life of their transmitters. In 1981, we successfully located the 5 radio-tagged starlings during the day in all but 4 of 191 attempts. In 1982, we were able to locate the diurnal activity sites of the 5 northern birds in all but 7 (3%) of 227 attempts. We failed to locate the diurnal activity sites of the 5 southern birds in 39 (16%) of 251 attempts, but 12 of these failures involved the starling whose DAC was 12 km from its roost.

During the period of intensive observation in August 1982, more than one subobservation usually was recorded during each observation. However, in the rest of 1982, as in 1981, the birds were located but not followed to other sites that day. To reduce sample bias, we excluded all but the first site used during an observation from our analysis of the spatial distribution of diurnal sites.

## RESULTS

*The roosting population.*—During the 1982 roosting season (June–November), 17 major roosts were located and counted in the 1,000-km<sup>2</sup> study area. These mixed-species roosting flocks contained roughly equal numbers of starlings and Common Grackles, and the total population using major roosts peaked at about 350,000 in late September (Fig. 1A).

The buildup and decline of the flock at South roost, peaking at 100,000 in mid-September (Fig. 1C), closely paralleled the seasonal pattern for the study area as a whole. In contrast, the roosting flock at North (Fig. 1B) remained relatively stable at 15,000 before declining abruptly in late August. The North roost decline was accompanied by an even sharper buildup at Park roost (No. 42 in Caccamise et al. 1983), 6.5 km to the southwest. Park roost peaked at 130,000 birds in late October. The pattern of roosting in the northern area is complicated by the presence of several minor roosts.

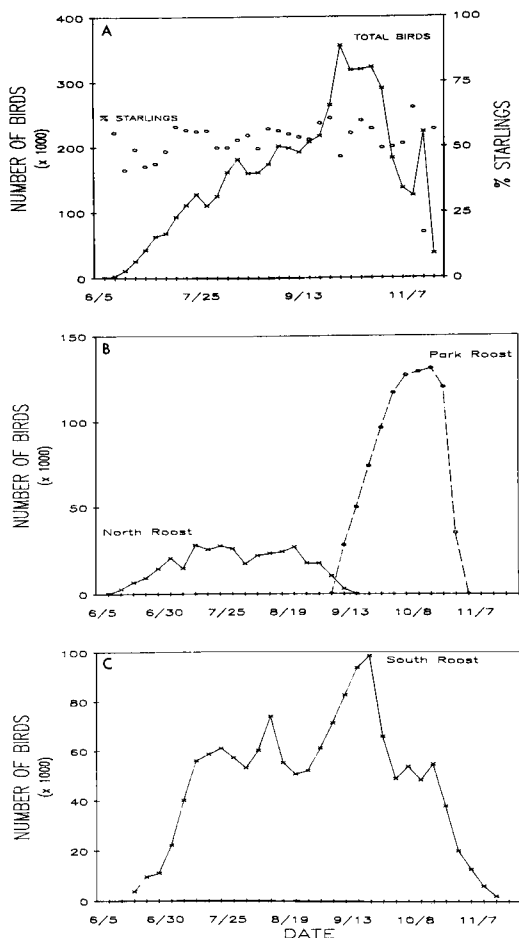


Fig. 1. Total number of birds and percent starlings in all major roosting flocks within the study area (A) and starlings and grackles present at major roosts used by radio-tagged starlings in 1982 (B, C).

None of the starlings radio-tagged at South roost in 1982 used minor roosts. With the exception of 2 birds that stayed away for 3 nights immediately following their capture and tagging, all 5 were present during all 23 nocturnal checks of South roost made between 4 August and mid-October, when their transmitters expired. In contrast, each of the North birds used 1-3 minor roosts and 1-3 major ones. Since we usually were led to minor roosts only after they were well established, we are able to show their decline phase only (Fig. 2). The one exception is minor roost 48, which had been used by a starling radio-tagged during a pilot study in 1980. Four of the 5 minor roosts declined just

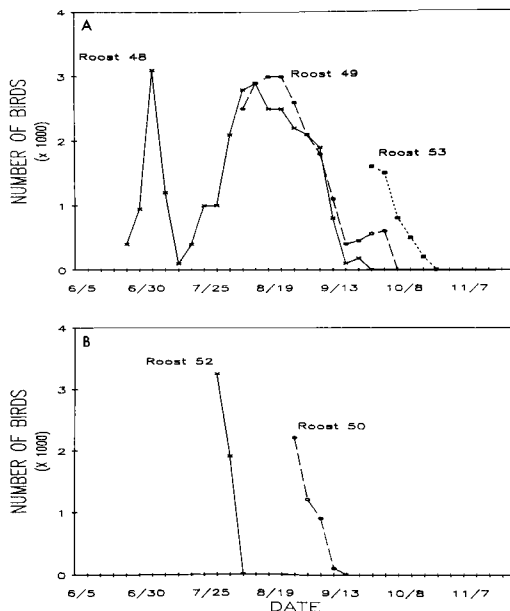


Fig. 2. Size of roosting flocks at five minor roosts in 1982.

prior to the buildup at Park roost. The exception (52) was abandoned one month earlier. A temporary decline at roost 48 in early July was caused by the release of firecrackers in the roost on 4 July.

*Diurnal home ranges.*—During the period of intensive observation in August 1982, we recorded 227 diurnal sites used by the northern birds and 251 used by the southern birds. At that time there were approximately 30,000 starlings and Common Grackles at North and 60,000 at South roost (Fig. 1). The starlings from North used feeding sites closer to the roost; their mean commuting distance to feeding sites was 4 km, compared with 8 km for South birds. The diurnal home ranges of individual birds were somewhat smaller in the North: 95% confidence ellipses (Koepl et al. 1975) around each individual's feeding sites averaged 33 km<sup>2</sup> for North and 49 km<sup>2</sup> for South birds. The diurnal home ranges of the North birds overlapped broadly, and their foci were much closer together: 95% confidence ellipses around all the diurnal sites used by North birds averaged 30 km<sup>2</sup>, compared with 525 km<sup>2</sup> for South birds.

*Habitat, substrate, and activity.*—Habitat preferences can be inferred by comparing habitat availability with habitat use. Potential feeding habitats differed in their availability in the

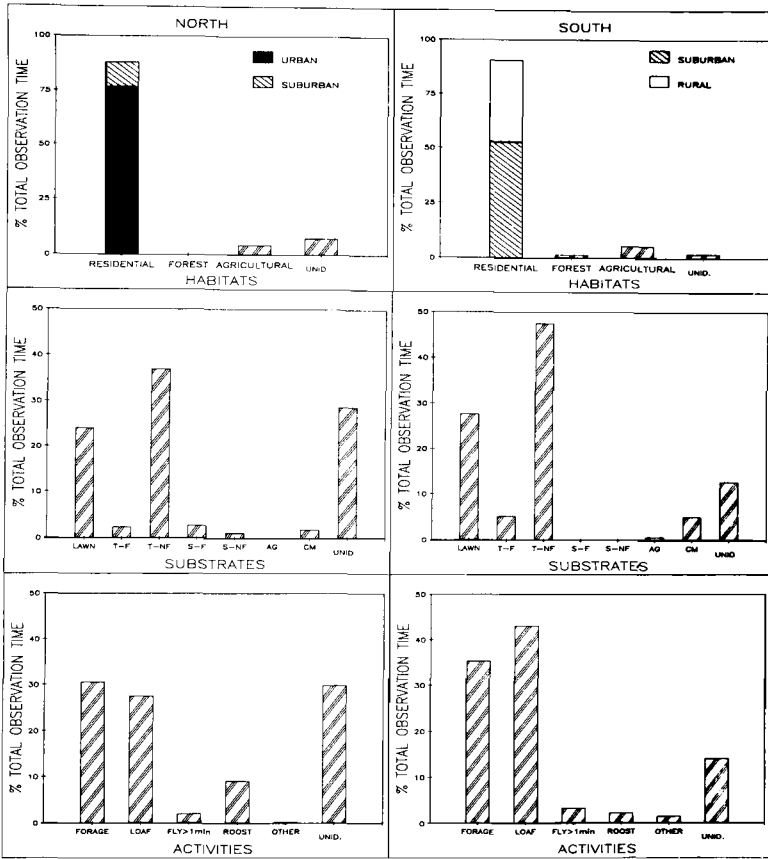


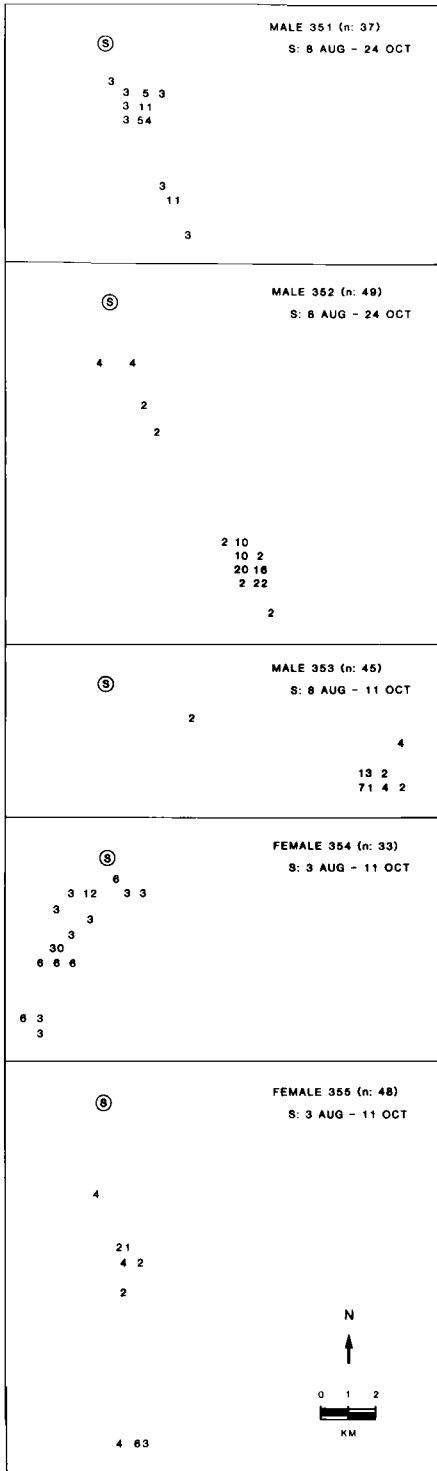
Fig. 3. Percentage of total observation time spent by starlings from North (left column) and South roosts (right) in habitats (top), substrates (middle), and activities (bottom). Substrate categories are lawn, fruiting tree (T-F), nonfruiting tree (T-NF), fruiting shrub (S-F), nonfruiting shrub (S-NF), agricultural (AG), commensal (CM), and unidentified (UNID).

north and south: residential (81% and 29%, respectively), forested (2% and 27%), and agricultural (4% and 18%). Yet the percentage of total observation time spent by the birds in each of the habitats was very similar (Fig. 3, top). The starlings from North and South roosts showed equally heavy use of residential areas (88% and 91%, respectively), even though these habitats were only one-third as common in the south.

Northern and southern birds were also very similar in the way they apportioned their time among substrates (Fig. 3, middle) and activities (Fig. 3, bottom). Both spent about 25% of the time on lawns, where they actively foraged. Over half the time was spent in trees, where they usually engaged in a nonforaging activity like preening or resting. For both substrate and

activity, the "unidentified" category was more common in the north because inaccessible areas (backyards) are more common in residential areas.

*Fidelity to diurnal activity centers.*—Over the 3–4-month life of the transmitters, the diurnal activities of starlings from both roosts tended to cluster in one or two relatively small areas. Figures 4–6 plot the percentage of an individual's diurnal sightings that fell into each 0.25-km<sup>2</sup> square of a grid centered at the first roost used by that bird. All 5 birds from South roost commuted daily to DACs south of the roost (Fig. 4). The few sightings outside these centers fell within 5–10° of the line connecting the roost to the DAC. In other words, the birds sometimes stopped at sites en route, but they were never seen to "wander."



Long-term fidelity to a DAC is even more apparent in the 5 starlings tagged at North roost (Fig. 5). All 5 showed tightly clustered diurnal activity sites, even though they used 3 or 4 different roost sites. This fidelity is also evident in the behaviors of the 5 starlings tracked in 1981 (Fig. 6).

*Mortality.*—Of 18 adults radio-tagged in 1981 and 1982, 2 died. Male 350 (replaced by female 316 in this study) was an apparent victim of predation. He was found eaten on his DAC, a cemetery 4 km from North roost. Female 350 was killed accidentally by a snap trap set at a private bird feeder.

Of 10 juvenile starlings radio-tagged in a concurrent study in 1982, 3 died. Two were apparently victims of predation. Juvenile 315 was found eaten on a tree limb 200 m from its nest box, and juvenile 345 was eaten in a corn field 2 km from its minor roost. Juvenile 302 died after feeding from a dumpster filled with insecticide bags. No adult or juvenile deaths occurred at a roost.

DISCUSSION

Our 1,000-km<sup>2</sup> census of communal roosts supports the conclusion that roosting groups are dynamically interrelated over broad areas (Caccamise et al. 1983). The sharp rise in the number of starlings using the major roost at Park (P) clearly coincided with declines in the major roost at North and in several minor roosts nearby (Figs. 1, 2). The movement of birds between roosts, suggested by the changes in roost size, is confirmed by the case histories of numerous radio-tagged individuals. For example, starlings 346, 347, and 349 all abandoned North, used minor roosts for 2 weeks, and then joined Park at about the same time (see Fig. 5).

The 10 starlings tracked intensively in August 1982 showed a marked preference for lawns in residential areas. Frequent rains during the summer of 1982 kept the lawns from drying, so the birds were able to continue feed-

Fig. 4. Spatial distribution of diurnal sightings of starlings radio-tagged at South roost (S) in 1982. Each number represents the percentage of the total (n) observations that fell within a 0.25-km<sup>2</sup> square. Dates shown are the periods the birds used South roost.

ing on lawn insects into September. Rainfall in August 1982 was 168 mm, 46% greater than normal for this area. This may partly explain why in 1982 the number of starlings using major roosts did not peak until late September. The peak had been in August in 3 of the 4 previous years (Caccamise et al. 1983). The one exception (1979) also had a comparatively wet August (140 mm) and a roosting peak in late September. August rainfall in 1978, 1980, and 1981 was less than half the normal (50, 37, and 53 mm, respectively).

Seasonal patterns in the utilization of feeding habitats (Fischl and Caccamise 1985) and the availability of food in these habitats (Maccarone unpubl. data) suggest that August peaks in major roosts occur in dry years and coincide with the drying of lawns, the major source of insect food in the DACs. In wet years the peak is delayed, probably because the productivity of lawns is prolonged by the summer rains. The September peak in wet years immediately precedes a change to feeding in postharvest corn fields, where energy-rich food items are more readily available.

Despite differences in the size and surroundings of their roosts, the northern and southern birds showed remarkably similar habitat, substrate, and activity profiles (Fig. 3). In the south, where the availability of the preferred foraging habitat was lower, the birds simply flew farther to get to it. Residential areas (lawns) were one-third as common around South roost (81% vs. 29%), and the southern birds commuted twice as far to forage (8 km vs. 4 km).

The additional cost of commuting to a more distant site could be well worth the investment if the bird can forage more efficiently at a more distant site (Hamilton et al. 1967). If an 84-g starling flies the extra 8 km (4 km each way) at 10.38 m/s (37.4 km/h), the "velocity of maximum range" for a bird this size (Pennycuick

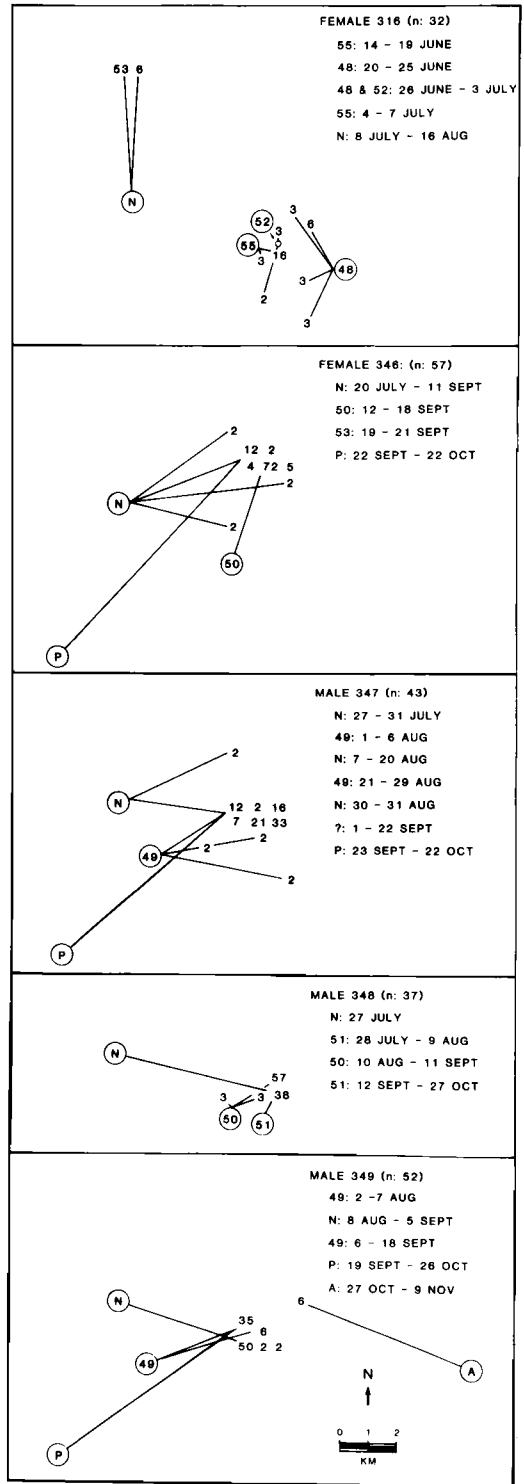


Fig. 5. Spatial distribution of diurnal observations of starlings associated with North roost in 1982. Each number represents the percentage of the total (n) observations that fell within a 0.25-km<sup>2</sup> square. Dates that birds used specific major roosts (letters) and minor roosts (circled numbers) are listed in the upper right corners. Lines connect roosts with diurnal sites each bird used while at those roosts.

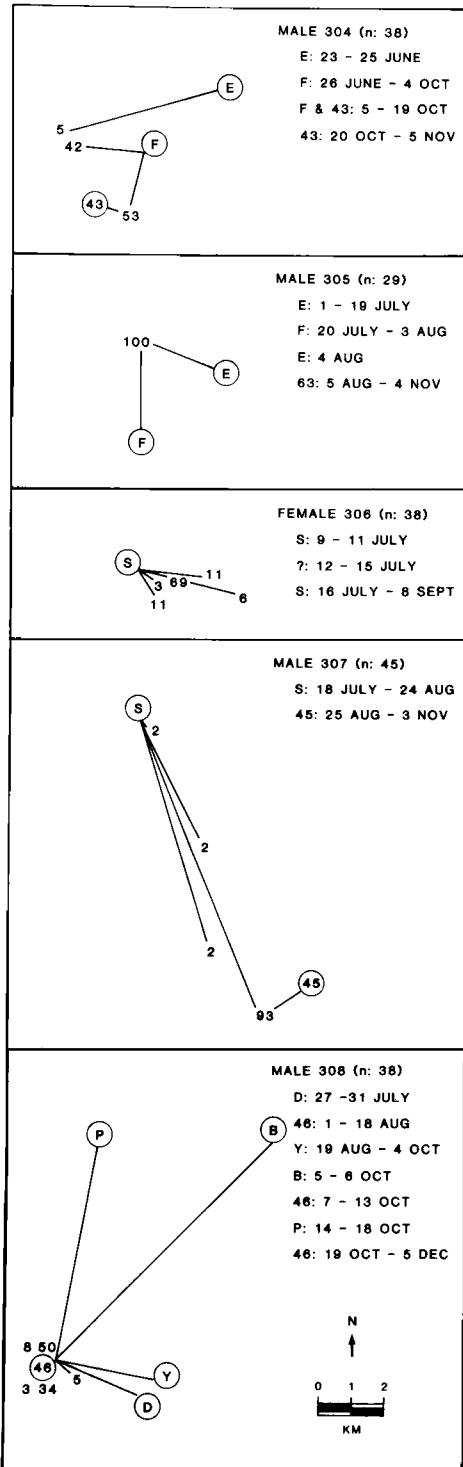


Fig. 6. Spatial distribution of diurnal observations on starlings radio-tagged in 1981. See Fig. 5 for explanation of symbols.

1969), it would require a power input of 7.6 W (or J/s; Cacçamise and Hedin 1985) for 12.8 min, or an extra daily expenditure of 5.8 kJ. Assuming 40% digestive efficiency, a starling can obtain this much energy from less than 0.5 g of corn (dry weight), or three average-size kernels.

The dispersal distances of the birds in this study were very similar to those reported for wing-tagged starlings (Feare 1984) and are consistent with the radii of "radar ring angels" produced when dispersing starlings are detected on radar screens (Eastwood et al. 1962). Starlings have been observed dispersing 50 km and more from a huge, winter roost in the Central Valley of California (Hamilton and Gilbert 1969), but this may reflect a lower density of suitable foraging sites in this arid area in winter.

*Fidelity to DACs.*—Our most significant finding was that many starlings showed longer-term fidelity to their DACs than to their communal roosts. This was true of the birds that roosted in the more urban, northern portion of the study area. Two of the 3 northern starlings tracked in 1981 and 3 of the 5 radio-tagged at North roost in 1982 used a complex of major and minor roosts while continuing to commute to a single DAC. The 3 exceptions were female 316, male 304, and male 347. Female 316 changed her roost and DAC at the same time, male 304 changed his roost but did not begin using his second DAC until 1 month later, and male 347 was absent from his DAC and two previously used roosts for 3 weeks.

In contrast, most of the starlings that roosted in the less-developed south used a single, major roost (South) for the life of their transmitters. This was true of the 5 southern birds tracked in 1982 and southern female 306, tracked in 1981. However, the other 2 southern birds from 1981 used more than 1 roost: male 307 used South roost for 1 month before changing in early September to a minor roost 10 times closer to his DAC, and male 308 used a complex of 1 minor and 4 major roosts. However, each of the 7 southern birds used a single DAC, although each occasionally visited sites along the flight line between the roost and the DAC.

Other studies also suggest little roost-site fidelity for starlings. Feare (1984: 249) showed that wing-tagged starlings fed daily at a farm and roosted 6.5 km to the south. These birds continued to feed at the farm even after the



roost split into two, with some going consistently to a site 3 km to the northwest and others 6 km to the southeast. In winter roosts studied by Heisterberg et al. (1984), the population turnover for starlings averaged 30% per night.

*Possible functions of communal roosts.*—Why fly to a major roost when there are sites physiologically suitable for roosting closer to the DAC? Considering four of the most frequently cited explanations for communal roosting, elements of two (1 and 4 below) are probably involved in the starlings' use of major roosts.

(1) Starling roosts could reduce nocturnal predation (Lack 1968). Suitable nocturnal roosting sites within the DAC may be sufficiently limited that an individual runs an increased risk of predation if he uses one or a few roosts year-round. Leaving the DAC in the evening to join a minor roost nearby makes adaptive sense. Of 3 cases of apparent predation on radio-tagged starlings (1 adult and 2 juveniles), none occurred at a roost. These data are consistent with the prediction that predation at even minor roosts (100–2,000 birds) should be low (Pulliam 1973). The lower the rate of predation at minor roosts, the less likely it is that predation alone can explain the formation of much larger roosts.

(2) Starling roosts do not appear to be "central places" (*sensu* Horn 1968). A roost may be quite acentric before the energetic advantage of shorter mean commuting distance is lost for average individuals (Wittenberger and Dollinger 1984). Nevertheless, the roost locations we observed appear to exceed this threshold, since most individuals commuted to a single DAC rather than to several patches in various directions from the roost.

(3) Another frequently cited explanation for avian communal roosting is the "information center" hypothesis (Ward and Zahavi 1973). One problem with this hypothesis has been explaining why successful foragers return to roost with unsuccessful foragers. Weatherhead (1983) suggested that successful foragers may use unsuccessful foragers as buffers against predation. Starling roosts, however, do not appear to be information centers, at least as envisioned by Ward and Zahavi. Their model, like Horn's above, depicts a stable roost surrounded by ephemeral patches of superabundant food. Of 3 starlings that changed their DACs, 2 (316 and 347) changed roosts at the same time. We do not know, however, whether the roost

change preceded the change in DAC, as required by this hypothesis. Since 12 of 15 starlings did not change their DACs, communal roosts do not appear to be used to locate new DACs.

The occasional use of supplemental feeding sites outside the DAC leaves open the possibility that major roosts may be centers of information about such sites. However, since these sites tend to fall along a line between the roost and the DAC, a simpler explanation is that these sites are located by some form of local enhancement (see below).

(4) Starling roosts may facilitate the use of "local enhancement" (Hinde *in* Marshall 1961) for finding supplemental feeding areas. Krebs (1974) found that the number and behavior of Great Blue Herons (*Ardea herodias*) on the ground was a reliable indicator of patch quality. He hypothesized that individuals may make more efficient use of such local enhancement opportunities by dispersing each day from a communal roost. Starlings differ from herons in that they already know that a certain (usually sufficient?) amount of food is available at their DAC. However, an important supplement to this food may be obtained by feeding opportunistically at richer, more ephemeral patches outside the DAC.

Most supplemental feeding areas seem to be encountered during flights to and from the roost. The occasional use of sites along the commuting route was evident in 9 of the 15 starlings, especially the 5 that roosted at South in 1982 (Fig. 4). However, local enhancement cues could be used any time a bird flew over areas outside its DAC. For starling roosts to have evolved to facilitate the use of local enhancement, there must be a reason that it is better to search while commuting. Otherwise, the use of local enhancement to locate supplemental feeding areas along the commuting route must be considered a secondary benefit gained by birds that have joined a communal roost for some other reason.

*A DAC-centered view.*—Our observations clearly indicate that the activities of adult starlings are centered at the DAC rather than at the roost. The 3–4-month fidelity to DACs documented by this study may well extend year-round for nonmigratory adults. Unlike their Common Grackle roostmates, which migrate south, more than half the starlings overwinter in the study area (Caccamise et al. 1983).

Limited observations suggest that the DACs of overwintering starlings include small but stable sources of food in winter (e.g. bird feeders, weed seeds, fruits). For example, male 308 was still on his DAC in early December, long after all large premigratory roosts had dispersed, and may have stayed there all winter. In addition, the DAC may include a preferred nesting site, such as a tree hollow. The only starling radio-tagged while still nesting was male 313, captured at his nest hole on 25 May 1982. He returned to a DAC near his nest hole every day (except one day of heavy rain) until his transmitter ceased operation on 2 September. He used a minor roost near his nest hole for 1 month. On 22 June he began flying 10.2 km to South roost, where he roosted each evening until 3 August. He then used a second minor roost until 2 September. This male was excluded from our summary of diurnal movements only because he had been radio-tagged too long before the mid-June start of the roosting season. More nesting starlings will need to be radio-tagged before the influence of nesting sites on DAC fidelity can be evaluated.

Fidelity to a DAC may bestow a number of selective advantages. Foraging in familiar surroundings probably increases foraging efficiency and decreases the risk of diurnal predation (Tinbergen 1981). Residency also may improve the chances of getting a nest hole in the spring, as competition for nest holes can begin as early as February (Kessel 1957).

Leaving the DAC to join a roosting group probably reduces the risk of nocturnal predation (see hypothesis 1 above), and starlings regularly join small, nocturnal roosting groups near their DACs. But why join any but the nearest roosting group? The use of more distant, major roosts is limited to late summer and fall, when the quality of food outside the DAC appears to be significantly greater than that inside. Although major roosts begin to form near the end of the breeding season (mid-June), the population using major roosts does not peak until the availability of food (lawn insects) in the DACs declines: mid-August in dry years and late September in wet ones.

Secondary feeding sites consistently fell along the lines between roosts and DACs. This pattern differs from the potentially omnidirectional pattern predicted by information-center explanations of communal roosts. The ob-

served distribution suggests that information about supplemental sites may be gained by local enhancement while commuting between a roost and a DAC. Individuals in a flight line may assess the quality of food patches from the air (using the number and behavior of conspecifics on the ground), or subgroups of the flight line may land to assess firsthand the quality of food at points along the route. Although individuals could search on their own for supplemental patches, we suggest that it is safer and more efficient to join an evening flight line of conspecifics headed for a major roost. Whether in flight or on the ground, the antipredation benefits of being in a group would apply (Hamilton 1971, Powell 1974). Birds with DACs too distant from a major roost for such flight lines to pass nearby may assemble at "staging areas" (Feare 1984), a well-known and as yet unexplained phenomenon. However, the observed linear distribution also may reflect an individual's decision to use only a subset of the information available to him at the roost. Nevertheless, the selection of supplemental feeding areas clearly is influenced by the location of the DAC and cannot be understood simply on the basis of roost-centered mechanisms.

Finally, starlings at major roosts may be "patch sitting," i.e. using the roost site closest to an especially rich food source. Patch sitting enables an individual to visit the supplemental feeding area twice a day, when leaving the DAC in the evening and when returning to the DAC the next day. Limited observations suggest that major roosts are more likely to form near large grain fields. For example, major roost B formed across the road from a large corn field every September for 4 years (1977-1980). Starlings regularly stopped in this field on their way out in the morning and on their way back to the roost in the evening. Roost size peaked at 24,000-64,000 birds at the time the field was harvested, when grain that was inaccessible while the corn was standing became available. In 1981 the field was not planted, and a much smaller roost (8,500 birds) formed at the site. That year a new major roost (P) formed 5 km to the west at a site surrounded by corn and soybean fields. In 1982 the field was again fallow, and only the P roost formed. The association of major roosts with rich food sources may be missed by investigators if, as in one case,

the corn field was 3 km away, but such distances are short for a starling (5 min of flying at 35 km/h).

Further support for the patch-sitting hypothesis comes from the observation that all 7 radio-tagged starlings using South roost commuted from DACs south of the roost. This directionality is not a sampling artifact. Counts of the population roosting at South have been made on a regular basis since 1976. Typically, 3 major flight lines converge on this roost in the evening, with 65-85% of the birds arriving from the south and east. Very few approach from the north. This directionality correlates with differences in the availability of nonresidential habitats. The areas to the north and west are on the inner coastal plain, where nonresidential habitats are primarily forested. Birds from the south, whose DACs are surrounded by forested habitats, may fly to South roost simply because South roost is adjacent to the closest source of rich supplemental food (grain fields). In contrast, birds to the north, whose DACs are surrounded by agricultural fields, may have more supplemental feeding areas and roosts from which to choose.

In a frequently cited study (Hamilton and Gilbert 1969), spotters observed starlings dispersing 50 km and more from a huge winter roost. Hamilton et al. (1967) theorized that communally roosting starlings dispersed widely from the roost to reduce competition for food. Our patch-sitting hypothesis suggests a different explanation. The starlings may have been flying this far from their DACs because there was a feedlot less than 5 km from this roost. Starlings are notorious feedlot pests.

Hypotheses suggesting an information exchange function for communal roosting have had to explain why successful foragers return to a roost where their information on the location of food can be parasitized, rather than roosting at the feeding site until it is depleted. Our observations suggest that starlings roost as close to patches as possible, within the constraints imposed by the availability of suitable roosting habitat.

Communal roosts undoubtedly serve many functions, with differences both between and within species. Juvenile and migratory adult starlings may have different reasons for joining major roosts. For nonmigratory adult starlings, however, it is clearly the DAC and not the com-

munal roost that is the base of operation. Maintaining a daily presence on the DAC places significant constraints on the selection and use of feeding areas. These constraints, and the availability of food both in DACs and in supplemental feeding areas, are essential for understanding not only why starlings disperse from a roost, but why they converge there in the first place.

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