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# Movement behavior of radio-tagged European starlings in urban, rural, and exurban landscapes

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**Abstract:** Since their intentional introduction into the United States in the 1800s, European starlings (*Sturnus vulgaris*) have become the fourth most common bird species and a nuisance bird pest in both urban and rural areas. Managers require better information about starling movement and habit-use patterns to effectively manage starling populations and the damage they cause. Thus, we revisited 6 radio-telemetry studies conducted during fall or winter between 2005 and 2010 to compare starling movements ( $n = 63$  birds) and habitat use in 3 landscapes. Switching of roosting and foraging sites in habitat-sparse rural landscapes caused daytime (0900–1500 hours) radio fixes to be on average 2.6 to 6.3 times further from capture sites than either urban or exurban landscapes ( $P < 0.001$ ). Roosts in urban city centers were smaller (<30,000 birds, minor roosts) than major roosts (>100,000 birds) 6–13 km away in industrial zones. Radio-tagged birds from city-center roosts occasionally switched to the outlying major roosts. A multitrack railroad overpass and a treed buffer zone were used as major roosts in urban landscapes. Birds traveling to roosts from primary foraging sites in exurban and rural landscapes would often pass over closer-lying minor roosts to reach major roosts in stands of emergent vegetation in large wetlands. Daytime minimum convex polygons ranged from 101–229 km<sup>2</sup> ( $\bar{x} = 154$  km<sup>2</sup>). Anthropogenic food resources (e.g., concentrated animal feeding operations, shipping yards, landfills, and abattoirs) were primary foraging sites. Wildlife resource managers can use this information to predict potential roosting and foraging sites and average areas to monitor when implementing programs in different landscapes. In addition to tracking roosting flights, we recommend viewing high-resolution aerial images to identify potential roosting and foraging habitats before implementing lethal culls (e.g., toxicant baiting).

**Key words:** agriculture, concentrated animal feeding operations (CAFO), European starling, invasive species, radio-tracking, spatial ecology, *Sturnus vulgaris*, urban ecology, wildlife damage, winter roost

**EUROPEAN STARLINGS** (*Sturnus vulgaris*; starlings; Figure 1) are a medium-sized, Old World passerine species introduced in the United States in the late 1800s. The North American starling population was recently estimated at 140 million (Jernelöv 2017) and ranked fourth in the United States in total numbers tallied during the 2018 North American Breeding Bird Survey (Pardieck et al. 2019). Starlings are abundant and have exhibited a swift expansion throughout North America (Kessel 1953, Bodt et al. 2020), but they along with many other avian species are exhibiting population declines in both their introduced and native ranges (Chamberlain et al. 2000, Rosenberg et al. 2019). Still, large congregations of starlings at fall and winter roosts result in flocks being drawn to foraging sites in human-modified environments, where they

cause inordinate economic damage (Linz et al. 2018; Figure 2). Starling damage reported to the U.S. Department of Agriculture, Animal and Plant Health Inspection Service, Wildlife Services (USDA APHIS WS) averages <\$2 million USD per year, but this is a fraction of total damage (Homan et al. 2017). Agricultural damage alone was estimated at nearly \$1 billion per year in the United States (Pimentel et al. 2005). Other damage costs are unknown, including costs of cleaning and maintaining city centers, loss of production and increased veterinary care at concentrated animal feeding operations (CAFO), and public health care (Shwiff et al. 2012). Starlings, rather than rock doves (*Columba livia*), may be the most economically harmful bird species in the United States (Lowe et al. 2004).



**Figure 1.** European starling (*Sturnus vulgaris*; photo courtesy of U.S. Department of Agriculture, Animal and Plant Health Inspection Service, Wildlife Services).



**Figure 2.** Flock of European starlings (*Sturnus vulgaris*) at a dairy (photo courtesy of N. Dunlop, U.S. Department of Agriculture, Animal and Plant Health Inspection Service, Wildlife Services).

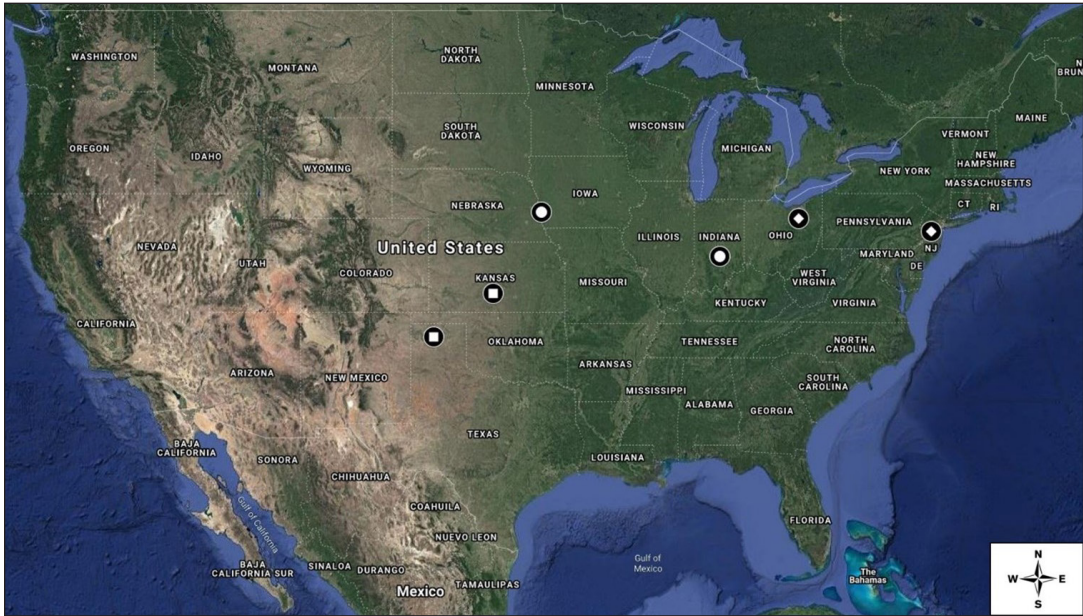
Starlings are attracted to urban environments because of anthropogenic foods and sheltered roosting sites (Peach and Fowler 1989, Clergeau and Quenot 2007). A city-center roost will number about 30,000 starlings spread out over several buildings (Potts 1967). Urban roosts draw the most complaints because the roosts' metabolic wastes despoil buildings, city infrastructures, and public amenities that affect the ambience and attractiveness of commercially active areas (Bernardi et al. 2009). Starling roosts also cause public health issues including the increased risk of histoplasmosis, a respiratory fungal infection (Clark and McLean 2003). In rural areas, complaints about starlings arise because massive flocks, some in the hundreds of thousands, forage on livestock feed at CAFO, particularly those with open feeder troughs (Glahn et al. 1983, Homan et al. 2010, Gaukler et al. 2012). A flock of

1,000 starlings using a CAFO for 60 days will eat about 1.5 tons of cattle feed, representing a loss of \$200 to \$400 (Homan et al. 2017); perhaps more importantly, starlings contaminate feed and nutritionally deplete mixed-rations, effectively reducing dairy cow (*Bos taurus*) performance and weight gains in beef livestock (Deppenbusch et al. 2011, Medhanie et al. 2014, Carlson et al. 2017). Large flocks of starlings are correlated with poorer herd health (Carlson et al. 2011a, b, c; Carlson et al. 2015, 2020) and probably amplify and transmit pathogens within and among CAFO (Gaukler et al. 2012, Chandler et al. 2020). Night roosts are likely point sources for pathogenic dissemination among CAFO (Swirski et al. 2014). Lastly, starlings cause damage to fruit crops (Conover and Dolbeer 2007, Anderson et al. 2013, Campbell et al. 2016) and are found in mixed flocks of blackbirds (Icteridae) damaging mature and sprouting grains (Stickley et al. 1976, Dolbeer et al. 1986).

Understanding the movement behavior and habitat use of starlings associated with large fall and winter aggregations among different regions in the United States will inform the implementation of management strategies at landscape scales. We describe the distances traveled by starlings to forage and roost and the habitats used to fulfill these behaviors in 3 landscapes. Better information regarding differences in starling behavior among urban, exurban, and rural landscapes may help wildlife managers adopt effective plans for managing pest birds and address various human-wildlife conflicts ranging from nuisance complaints and agricultural damage to public health threats.

## Study area

We conducted 5 radio-telemetry studies at the request of USDA APHIS WS state directors after receiving nuisance complaints from the private sector. We completed a sixth study in conjunction with an epidemiological study done through the Ohio Agricultural Research and Development Center, Food Animal Research Program (The Ohio State University, Wooster Campus). We conducted 2 studies on night roosts in urban centers (Indianapolis, Indiana and Omaha, Nebraska, USA) and 4 studies at CAFO, including dairies (Ohio, USA), beef feedlots (Texas and Kansas, USA), and a gamebird farm (New Jersey, USA; Homan et al. 2006, 2010; Gaukler et



**Figure 3.** A map of the 6 study sites across the United States used to evaluate the habitat use and movement behavior of European starlings (*Sturnus vulgaris*) during fall or winter between 2005 and 2010. The sites incorporated 2 studies at night roosts in urban centers (circles; Indianapolis, Indiana and Omaha, Nebraska) and 4 studies at concentrated animal feeding operations, including dairies (Ohio) and a gamebird farm (New Jersey) in exurban landscapes (diamonds) and beef feedlots (Texas and Kansas) in rural landscapes (squares).

al. 2012; Homan et al. 2012, 2013; Figure 3). From the total 17 capture sites used for radio tagging, we selected 2 roosting sites and 6 foraging sites for evaluation. We pooled locations ( $n = 7$ ) from 5 birds at the Indianapolis roost with 6 birds ( $n = 12$  locations) captured at a foraging site used by most of the roost's radio-tagged birds. We pooled 2 foraging sites that were 1 km apart in the Ohio CAFO study because of high rates of exchange between radio-tagged cohorts. We selected the foraging site where the most birds were radio-tagged at the remaining 3 CAFO studies.

We assigned each of the 6 studies to the predominant landscape of the study area (i.e., urban, rural, and exurban). We defined an exurban landscape as an amorphous boundary lying between suburban and rural landscapes. The exurban landscapes were characterized by large single-residence tracts surrounded by farms, fields, and recreational parks. We divided the 4 CAFO studies into rural (beef feedlots in Texas and Kansas) and exurban (dairy in Ohio and gamebird farm in New Jersey) landscapes.

## Methods

Our target sample size was 50 radio-tagged birds for each study, allocated proportionately,

based on the population size at multiple capture sites (2–5) per study area. We aged and sexed the birds according to external characteristics (Kessel 1951, Schwab and Marsh 1967, Smith et al. 2005), and the sex ratio of radio-tagged birds matched that of captured birds. We used spring-loaded box traps and hoop nets to capture starlings at urban roosts and drop-in traps and mist nets at CAFO. We also used drop-in traps to capture urban starlings at foraging sites with trappable populations, which were found through monitoring of radio-tagged birds.

We used very-high frequency radio transmitters (mass with harness = 2.2 g; frequency range = 164.000–167.999 MHz; radio pulses = 40 min<sup>-1</sup>; warranted battery life = 50 days). The transmitter was mounted on the anterior dorsal surface of the bird's fused pelvic region using a leg harness made of 0.8-mm elastic beading cord (Rappole and Tipton 1991; Figure 4). We followed the U.S. Geological Survey (USGS) Bird Banding Laboratory guidelines indicating the radio and harness pack must be  $\leq 3\%$  of body mass (i.e., starling mass >73 g). We released the radio-tagged birds at the capture site immediately after banding them on the left leg with a No. 2 USGS aluminum band. We collected radio



**Figure 4.** European starling (*Sturnus vulgaris*) being fitted with a radio-telemetry harness (photo courtesy of U.S. Department of Agriculture, Animal and Plant Health Inspection Service, Wildlife Services).

frequency, capture date and site, mass, sex, leg-band number, and date and time of locations for each bird. Birds not radio tagged were banded with a USGS leg band and released. We provided a minimum 2-day acclimation period prior to collecting movement data.

We used 2 mobile receiving units consisting of a rotatable set of dual 6-element Yagi antennas attached to an aircraft aluminum pole mounted through the roof of a pickup truck and cabled to a null-peak box, a data recorder, and global positioning system. We attached a compass rose to the pole aligned to the North Magnetic Pole and used the antenna null to acquire bearings. The optimum line-of-sight transmission range was 2–3 km, but field testing showed ranges were generally  $\leq 1$  km (Homan et al. 2006). The mobile units were operated 5–7 days per week from 6–10 hours per day. Search routes included all drivable roads and trails in the study area. An onboard PC-laptop with a Geographical Information System was used to store the mobile unit's unique route, directional track, and geographical coordinates of prior detections. Search radii from capture sites were 50 km in urban and exurban and 100 km in rural landscapes.

We defined a valid radio-frequency signal (fix) as the logging of  $\geq 3$  signals per minute averaging  $\geq 100$  dBm in strength (maximum signal strength: 155 dBm). If signal strength was  $< 130$  dBm, we attempted to move closer to get a sighting on the bird or its flock. When multiple signals from the same frequency were received within 60 minutes, we used the strongest signal to determine the radio fix. The data recorder stored the radio frequency, time, date, signal

strength, radio pulse, and decimal degree coordinates of the mobile unit. We self-entered a description of the location (e.g., residence, park, airport). If multiple fixes per bird were made on the same day, we required them to be separated by  $> 1$  hour for spatially independent fixes (White and Garrott 2012). Nighttime fixes on roosting birds consisted of a single fix  $> 1$  hour past local sunset.

We cleaned the raw data generated from the data recorder by culling false positives using Visual Basic® for Applications. We only used fixes obtained between 0900 and 1500 hours and  $\geq 1$  km from the capture site because we wanted to focus on offsite daytime activities. We considered hours outside the 6-hour time frame as periods for transiting to and from roosts (Homan et al. 2013). We measured the distances of mobile locations from the capture sites using the haversine-distance formula or the great-circle distance between 2 points on a sphere given longitudes and latitudes (Sinnott 1984). We discarded bearings emanating from the direction of a capture site if  $< 1$  km. We imported the fixes into Google Earth® for identification of habitat, distances to roosts and foraging sites, and minimum convex polygons (MCP) of cohorts. The base map was a mosaic of high-resolution (1 m), digital orthoimage quadrangles, with roadways.

We used geographical coordinates of the urban roosts and CAFO capture sites as center points for measuring offsite distances to the respective foraging and roosting sites. We used means ( $\pm$ SE) to describe average distances traveled, whereas means ( $\pm$ SD) were used for MCP and distances from major (primary) and minor (secondary) roosts to the most-used (primary) foraging sites in the urban studies and vice versa in the CAFO studies. By the nature of our study designs, the CAFO capture sites were primary foraging sites (PFS), so we designated the next-most used foraging site as the PFS to those capture sites. We used a 1-way analysis of variance (ANOVA) on ranked-transformed data to test differences ( $P \leq 0.05$ ) among landscapes in offsite average distance measurements between fixes and capture sites. We used Tukey-Kramer multiple comparisons to compare differences among landscape means with distance (single fix) or average distance (multiple fixes) of each bird from its capture site.

**Table 1.** Movements and habitats used by 63 radio-tagged European starlings (*Sturnus vulgaris*) in 6 behavioral studies done between 2005 and 2010 in the United States. Movements included (1) average linear distance (km) between capture sites and geographic points where birds were detected between 0900 and 1500 hours, (2) linear distances (km) from primary (1<sup>0</sup>) and secondary (2<sup>0</sup>) roosts to primary foraging sites (PFS), (3) minimum convex polygons (km<sup>2</sup>) with (MCP+) and without (MCP) roosts, and (4) dominant habitat of the PFS.

State	Date	Landscape	Birds	Radio fixes	Avg. dist. (SE)	1 <sup>0</sup> Roost <sup>a</sup> ↔ 1 <sup>0</sup> PFS	2 <sup>0</sup> Roost ↔ 1 <sup>0</sup> PFS	MCP+	MCP	PFS habitat <sup>b</sup>
IN	Dec–Jan	Urban	11	19	7 (3.2)	7	8 <sup>c</sup>	131	116	LF
NE	Dec–Jan	Urban	18	33	6 (3.6)	1	6 <sup>c</sup>	229	229	AB
NJ	Dec–Jan	Exurban	10	21	5 (3.7)	34	6	485	172	RT
OH	Sep–Oct	Exurban	11	34	3 (3.3)	23	7	282	101	DA
KS	Dec–Feb	Rural	11	61	19 (9.2)	13	6	273	146	GR
TS	Dec–Jan	Rural	2	54	18 (1.4)	39	7	461	157	DA
			63	222	10 (7.0)	20	7	310	154	

<sup>a</sup>Primary and secondary roosts were those attended by the largest and next largest populations, respectively.

<sup>b</sup>Primary foraging sites were those attracting the largest populations. In exurban and rural concentrated animal feeding operations (CAFO) studies, where the CAFO themselves were PFS, PFS represent those sites second in intensity of use. Abbreviations are as follows: LF = landfill, AB = abattoir, RT = residential tracts, DA = dairy, GR = granary.

<sup>c</sup>Secondary roost was the capture site

## Results

### Movements

Of 176 radio-tagged birds, 63 individuals (male = 31, female = 30, and unknown = 2) provided data after passing our entry criteria. Linear distances traveled from capture sites during daytime activities in rural landscapes ( $\bar{x}$  = 19 km, SE = 8.4,  $n$  = 2) were 2.6–6.3 times further than urban and exurban landscapes ( $F_{2,60}$  = 40.27,  $P$  < 0.001; Table 1). We did not detect differences in distances traveled in urban and exurban landscapes ( $\bar{x}$  = 5 km, SE = 2.0,  $n$  = 4;  $P$  > 0.05). The greater distances traveled in rural landscapes were primarily from birds using or switching to other feedlots 15–20 km from capture sites; 19% and 10% of radio-tagged birds in the Kansas and Texas studies, respectively, temporarily used or switched CAFO.

Both capture sites in urban landscapes were secondary roosts ( $\leq$ 30,000 birds). These urban-centered roosts averaged 9 km (SD = 4.9) from primary roosts ( $\geq$ 100,000 birds) in outlying industrial zones with less public access. Radio-tagged birds from urban-center roosts would intermittently use the primary roosts. The primary roost in Omaha was only 1 km from the PFS; otherwise, distances between PFS and both roost classes in urban landscapes were similar ( $\bar{x}$  = 7 km, SD = 1.0). In exurban and rural land-

scapes, primary roosts were >10 km ( $\bar{x}$  = 27 km, SD = 11.6) from PFS with sizable variation in distances (Table 1). In contrast, secondary roosts in all landscapes were <10 km ( $\bar{x}$  = 6 km, SD = 0.6) from PFS with little variation. The average MCP size was 154 km<sup>2</sup> (SD = 45.3). The Ohio study, conducted in early fall, had the smallest daytime MCP (Table 1). The area of the daytime MCP doubled when we included locations of primary roosts (MCP+; Table 1).

### Habitat use and food sources

In urban landscapes, primary roosts were under a multitrack railroad overpass and in a treed buffer zone surrounding an airport. In exurban and rural landscapes, all primary roosts were in large wetlands ( $\bar{x}$  = 196 ha, SD = 89.7) with dense stands of emergent vegetation, including cattail (*Typha* spp.) and phragmites (*Phragmites australis*). Secondary roosts in urban centers extended throughout downtown areas on building ledges and facades, fire escapes, monuments, decorative conifer plantings, signage, and central air units atop multistoried buildings. Expansive industrial structures (e.g., power plants, refineries, and shipping-yard granaries) were also used as secondary roosts in urban and rural landscapes. In exurban land-

scapes, we located starlings in numerous small roosts (100–5,000 birds) scattered among barns, outbuildings, CAFO, and tree stands in parks, residences, university grounds, and along roadways.

Sources of directly or indirectly supplied anthropogenic foods were foci of PFS across all landscapes. The PFS in urban landscapes were landfills and abattoirs (Table 1). Other lesser-used sites were zoos, water treatment plants, grassy tracts of industrial and business parks, and shipping-yard granaries. All of these sites were <15 km from urban roosts. In exurban landscapes, CAFO were often PFS; lesser-used sites included groomed lawns of residential tracts and business parks, fields, roadsides, and grassy extents of airports, fairgrounds, and recreational parks. In rural landscapes, most PFS were large, open-troughed CAFO ( $\geq 5,000$  head); lesser-used sites in rural areas were small towns and cities, small CAFO ( $\leq 500$  head), and granaries.

## Discussion

We demonstrated that the distribution of food and roosting resources across landscapes affected starling movements between foraging and roosting sites. The feedlot studies in Kansas and Texas were conducted in the Interior Plains physiographic region, known for its large swaths of scrublands, grasslands, and grainfields. These are not ideal habitats for wintering starlings, which have few foraging options but to use cities, towns, CAFO, and the industries serving CAFO (e.g., granaries). In the vastness of the Interior Plains, CAFO used by starlings lie far apart in comparison to the availability of anthropogenic food resources in urban and exurban landscapes.

Although strong fidelity was shown for major roosts as indicated by consecutive days of use per individual and overall use by cohorts, roost site choice was not rigid. Similarities in distances from primary roosts to PFS in exurban and rural landscapes indicated starlings spent more time and energy to join primary roosts, usually passing over smaller secondary roosts. For example, in the Ohio study the distance between the primary roosting site and the PFS was 23 km, whereas the secondary roost was only 7 km away. The primary roost was a phragmites-dominated, 100-ha wetland in a wooded complex of industrial sites and suburban develop-

ments on the outskirts of Akron, Ohio. The unique characteristics of the roost were likely the sole cause for it being preferred; the roost was large and had stable water depths and expansive emergent cover, making it more attractive than woodlot habitats, which were available and used but at magnitudes far less than the primary roost. The birds may have preferred the wetland's seclusion or perhaps derived some thermal benefits from the aquatic roost. The secondary roost was also a secluded, emergent-dominated wetland but was only 40 ha. This secondary roost held  $\leq 30,000$  birds and thus its smaller area likely explained its status as a secondary roost.

Our observations of strong site fidelity for specific CAFO indicates that morning departure lines taken by roosting flocks to foraging sites from primary and secondary roosts are not random. However, we found birds did switch CAFO foraging sites, which indicates some mixing of flocks at roosting sites, either prior to roosting (e.g., staging) or upon departure the next morning. In the Texas study, we followed the flightline emanating from the primary roost and never witnessed diverging flightlines for the entire 40-km flight to the CAFO. However, a secondary roost (an abandoned refinery) 7 km away from the CAFO capture site supported several thousand birds and was used sporadically by 11 of our 20 radio-tagged birds. Thus, birds from our cohort probably followed birds from this roost that were using another CAFO. In the Kansas study, radio-tagged birds that we captured at another CAFO used the same primary roost as members of our radio-tagged cohort. As in Texas, a few members of our cohort joined the flock that was using the unselected CAFO about 20 km away and the nearby town of Great Bend, Kansas, USA. The switching of CAFO has implications for distribution of bacterial and viral pathogens that impact herd health. Of the total 51 birds radio tagged at the 2 CAFO in Kansas and Texas, 8 (16 %) established temporary or permanent residence at a feedlot different than the capture-site feedlot. With an average MCP+ of 367 km<sup>2</sup> in rural landscapes, disease transmission among neighboring CAFO is likely.

Basically, no adventurism was displayed other than movement within the confines of daytime MCP, which were small for birds capable of flying 60–80 km/hour (Feare 1984).

For example in New Jersey, starlings continued to use the same foraging area, despite a switch to a less preferred food at the gamebird CAFO. Although starlings curtailed their use of the CAFO after a switch from high-protein meal to whole kernel corn (*Zea mays*), they continued foraging on nearby residential lawns, a habitat capable of providing abundant prey resources, especially during a mild and open winter (Morrison and Caccamise 1985, Olsson et al. 2002). This type of starling behavior, wherein a small-sized activity area is maintained and used consistently over time, has been observed previously in several different studies (Morrison and Caccamise 1985, 1990; Caccamise 1991, 1993; Homan et al. 2013). Long-term use of small-sized areas may confer a survival advantage through increased foraging efficiency and reduced predation (Tinbergen 1981, Caccamise and Morrison 1986). In some instances, it may have roots in a desire to remain near reproductive territories (Morrison and Caccamise 1985, Caccamise 1993). In our study, the presence of reliable anthropogenic food resources may have also contributed to small activity areas.

We do believe that the small-sized MCPs were not an artifact of inefficient sampling but indeed a result of strong site fidelity (Caccamise 1991). In the Ohio study, we traversed over 8,500 km of roads, illustrating the intensive nature of our searches for radio-tagged birds. The extent of our searches in Ohio far exceeded starling movements and MCPs as evidenced by minimal mixing of the cohorts from 5 capture sites. We only found the daytime mixing of cohorts at a maximum distance of 6 km. Birds seldom visited dairies >5 km away from the capture sites unless transiting to roosts, and these visits were usually of short duration compared to the time spent at the capture sites. In the New Jersey study where the average distance of all capture sites from the average of their geographical coordinates was 20 km, we did not observe interactions among cohorts at any of the capture sites ( $n = 3$ ), alternate foraging sites, or secondary roosts. Thus, our study areas were effectively sampled by our mobile receiving units as evidenced by the lack of finding intermingled cohorts during the daytime (i.e., mingling of cohorts occurred at roosts and not foraging sites).

Previous studies have shown how landscape

composition (e.g., pasture) influences population density, nest box occupancy, reproductive success, foraging distances, and winter roost distribution of starlings (Smith and Bruun 2002, Bruun and Smith 2003, Clergeau and Fourcy 2005, Heldbjerg et al. 2016, Pfeiffer et al. 2019). Seasonal variation in temperatures may also influence movement and habitat-use behaviors of starlings. We observed instances of starlings foraging in lawns, parks, fields, and roadsides during all studies, but mostly in the New Jersey and Ohio studies. Given we started the Ohio study in late September and experienced a mild winter in New Jersey, starlings were able to exploit foraging habitats that would have otherwise been unavailable during colder periods. Starlings are omnivorous, with a natural diet of invertebrates and wild fruits (Feare 1984). A major portion of their invertebrate diet consists of coleopteran (beetle) and lepidopteron (butterfly and moth) larvae foraged from soils (Fischl and Caccamise 1987). Starlings encountering harsher fall or winter conditions would have quickly lost access to soil invertebrates and wild fruits found in pastures, fields, and lawns, likely forcing them to expand their MCP to acquire reliable sources of anthropogenic foods. Starlings are attracted to sites where human-produced foods are processed (e.g., distiller's grain, suet, pet food, and livestock feed). During colder periods, starlings develop a preference for high-energy fatty foods, which are available at landfills and food processing plants (Homan et al. 2011).

Caccamise and Morrison (1988) hypothesized that large communal roosts develop over time by passive convergence of individual flocks staging and foraging at sites adjacent to the roost ("patch-sitting"). The birds gather at these sites because they are forced to forage outside the usual confines of their breeding home ranges because of seasonal changes in food preference from invertebrates to plant materials, the latter being unavailable in the diurnal home ranges. However, the communal roost in Ohio did not apparently develop by "patch-sitting," potentially due to various seasonal, agricultural, and landscape differences between the Ohio study area and the New Jersey study area used by Caccamise and Morrison (1988). Those differences included an Ohio landscape with (1) high-energy foods or supplemental feedings areas provided at the dairies; (2) abundant invertebrates on a heterogeneous landscape containing

numerous dairy farms juxtaposed among large pastures, extensive lawns of rural homes, housing developments, and towns; (3) availability of maturing cultured and wild fruits in orchards and roadsides; and (4) availability of corn, small grains, and weed seeds in pastures and fields surrounding the dairy operations. Indeed, the roosting behavior we observed was inverse of that observed by Morrison and Caccamise (1985), where birds used a roost in rural habitat and left to forage in suburban habitats. Ultimately, the availability, distribution, and environmental and physical quality of roosting sites combined with consistency in availabilities of anthropogenic food resources are important factors in explaining fall and winter movements and habitat use of starlings across all landscapes, urban, exurban, and rural.

### Management implications

Starling roosts in urban centers remain a chronic problem in the United States because of the lack of management options. Even if the use of physical frightening agents (e.g., alarm calls, pyrotechnics, and lasers) is feasible, their efficacy is generally short-lived. Roosts that develop on multistoried buildings in commercial districts are generally inaccessible, and removal of starlings is complicated by proximity to heavily used public areas. In the Omaha, Nebraska study, we used radio telemetry to find secluded areas where birds concentrated after departing the roost that could be used for lethal control (i.e., Judas technique; Woolnough et al. 2006). We avoided additional public encounters with sick or dead birds by collecting carcasses early in the morning at the urban roosts. Daily movement radii of birds in rural and exurban landscapes can be so large that they include small towns, suburbs, and urban areas. Resource managers should be aware of this when conducting toxicant baiting (e.g., DRC-1339) on starlings in these landscapes for effective public notification of lethal management activities (Homan et al. 2017). Small activity areas also suggest that localized control of starlings may be achievable if immigration is limited (Rollins et al. 2009, Campbell et al. 2016), but well-established populations can act as sources of individuals that disperse short distances into nearby favorable landscapes (e.g., proliferation of human development in

exurban areas) if starling populations are not controlled (Zufiaurre et al. 2016).

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