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TEMPORAL AND SPATIAL PATTERNS OF BREEDING BROWN-HEADED COWBIRDS IN THE MIDWESTERN UNITED STATES

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ABSTRACT.—Brown-headed Cowbirds (*Molothrus ater*) are an obligate brood parasite and a potential threat to some populations of migratory songbirds. I used radio-telemetry to study temporal patterns in behavior, habitat use, and sociality, as well as spatial patterns and movements among breeding, feeding, and roosting areas. I obtained a mean of 42 locations of 84 radio-tagged female cowbirds on three study sites in Illinois and Missouri. Radio-tagged females usually were located in forest and shrub-sapling habitats with a mean of 1.4 males during the morning breeding period. During midmorning to early afternoon, females commuted to short-grass, cropland, and feedlot habitats; they fed in small flocks. At dusk females roosted singly or in small groups near breeding or feeding areas, or commuted to a large communal roost. Behavior and time of day, behavior and habitat use, and habitat use and time of day were highly associated. For approximately 90% of the radio-tagged cowbirds, breeding, feeding, and roosting locations were distributed nonrandomly within home ranges, and came from distinct utilization distributions. Cowbirds moved an average of 3.6 km between roosting and breeding locations, 1.2 km between breeding and feeding locations, and 2.6 km between feeding and roosting locations. Midwestern cowbirds show the same pattern of commuting between disjunct breeding and feeding areas as elsewhere in their range. *Received 23 June 1993, accepted 24 October 1993.*

THE BROWN-HEADED COWBIRD (*Molothrus ater*) is an obligate brood parasite and a major threat to some populations of Neotropical migratory birds (Mayfield 1977, Brittingham and Temple 1983, Robinson and Wilcove in press). Because cowbirds do not rear their own young, breeding activities (nest searching and laying) and feeding can be separated spatially and temporally. This uncoupling of breeding and feeding allows cowbirds to select separate areas appropriate for each activity (Rothstein et al. 1986). Breeding and feeding areas may be adjacent or disjunct; cowbirds in the Sierra Nevada commuted up to 7 km per day between breeding and feeding areas (Rothstein et al. 1984). Cowbirds usually feed in short-grass habitats or with large grazing mammals (Friedmann 1929, Mayfield 1965, Dufty 1982, Rothstein et al. 1986). They breed in a wide variety of habitats from prairie to forest, but often select habitats with high host densities (Rothstein et al. 1986, S. Robinson unpubl. data).

Numbers of cowbirds and host-parasitism levels are sometimes higher near forest edges (Gates and Gysel 1978, Chasko and Gates 1982, Brittingham and Temple 1983, O'Conner and Faaborg 1992, D. Whitehead pers. comm.). Other studies, however, have found no relationship between parasitism levels and distance to edge (Hoover 1992, Robinson and Wilcove in press). Cowbird numbers and parasitism levels often have been presumed higher near forest edges because of an assumption that movements between nonforested feeding areas and forested breeding areas are restricted. However, cowbirds may also be responding positively to host density, either at edges (Chasko and Gates 1982, Gates and Giffen 1991) or away from edges (S. Robinson unpubl. data).

Although some studies have used color marking to map home ranges of cowbirds (Elliott 1980, Darley 1983, Yokel 1989), radiotelemetry is the most practical method for studying movement and distribution patterns because cowbirds may commute large distances between disjunct areas. Previous studies have used radiotelemetry to map breeding ranges (Dufty 1982), to determine female and male spacing patterns (Teather and Robertson 1985, 1986), and to detect commuting patterns between breeding and feeding areas (Verner and Ritter 1983, Rothstein et al. 1984). These studies used an intensive approach where a modest number of individuals or locations were observed for

up to several hours at a time. None of these studies were undertaken in the highly fragmented forests of the midwestern United States, where the host-rich eastern deciduous forest grades into the Great Plains and where cowbirds reach their greatest abundance (Brittingham and Temple 1983, Robinson 1992, Hoover and Brittingham 1993, Lowther 1993).

I studied spatial and temporal patterns of breeding female Brown-headed Cowbirds on three study sites in Missouri and Illinois. In contrast to previous studies that radio-tracked cowbirds, I used an extensive approach that was based on obtaining numerous independent locations of a large number of individuals. This approach is appropriate for statistical tests of spatial patterns and habitat use (White and Garrot 1990). I report basic patterns in the distribution and movements of cowbirds on these three sites; in a later manuscript I will highlight the differences in these patterns among study sites and relate them to landscape patterns. Relationships between female cowbird behavior, habitat use, and time of day are reported. I examine the spatial distribution of female cowbird locations and determine if female cowbirds use the landscape nonrandomly, and if they use spatially distinct areas for different behaviors. I also report on the distances moved between areas used for morning breeding activities, feeding, and roosting.

STUDY AREA AND METHODS

Study areas.—I selected three study sites in Illinois and Missouri (Fig. 1). All were dominated by oak-hickory (*Quercus* spp. and *Carya* spp.) forest, but the sites varied in the percent of forest cover in the landscape. The predominant nonforest habitat was cool-season pasture (primarily *Festuca* spp.) with varying areas of cropland (corn, soybeans, wheat) and oldfield habitats. The Jonesboro, Illinois site was located in Union County and included private lands, as well as portions of the Jonesboro District of Shawnee National Forest and the Trail of Tears State Forest. The area was approximately 55% forested, with 3% pasture and 32% cropland located along the broader river bottoms and cropland in the Mississippi River floodplain. The Carr Creek, Missouri site was located in Shannon, Reynolds, and Carter counties; it included private lands, Carr Creek State Forest, and Deer Run State Forest. The area was approximately 93% forest and included 4% cool-season pasture located in broad stream valleys. The Ashland, Missouri site was located in southern Boone County and included the Thomas S. Basket Wildlife Education and Research Center, adjacent private lands, and portions of the Cedar Creek District of Mark Twain National Forest. The area is approximately 50% forested, with 32% cool- and warm-season pasture and 13% cropland on level uplands and in broad stream bottoms.

Field methods.—I trapped cowbirds from 10 May to 5 June in both 1991 and 1992 at the Carr Creek and Ashland sites, and in 1992 at the Jonesboro site. I captured cowbirds in walk-in funnel traps (Stoddard 1931) baited with millet in both forested and agricultural habitats near the center of the study sites. Only adult females were radio-tagged. I assumed all radio-tagged females were breeding. This assumption seemed reasonable because host species are parasitized on the study sites throughout May and July (S. Robinson unpubl. data, J. Faaborg unpubl. data), and Payne (1973) reported that all adult females he examined in California from mid-May through June had recently ovulated. Transmitters had a mass of 2 g and a battery life of 30 to 40 days. I attached transmitters to cowbird's backs with a harness made from elastic cord using a technique developed for Mourning Doves (*Zenaida macroura;* Fuemmeller 1992). I tied one elastic loop around the bird's body behind its wings, and around the body in front of the wings; these loops were then tied together on the bird's breast. The transmitter was centered on the birds back between its wings with a 15-cm antenna extending down the bird's back and slightly past the end of its tail.

Cowbirds were radio-tracked by four to six field assistants from 15 May to 30 June each year. We located individual cowbirds one to three times a day and proportionately stratified our searching, so that during each field season we obtained nearly equal numbers of locations for each cowbird in 3-h periods from 0500 to 2000 CST and a nocturnal period from 2000–0500. This sampling was designed to improve the independence of locations and ensure locations were representative of female cowbird activity throughout the day (White and Garrott 1990). Cowbirds were located primarily by homing on a transmitter's signal with a portable receiver and four-element yagi antenna until the bird could be seen, and occasionally by triangulating from two locations within 500 m of the bird. Locations were recorded in the field on aerial photographs (scale 1:12,000) or USGS topographic maps (scale 1:24,000). At each location we recorded the date, time, habitat, bird's behavior, and number of male and female cowbirds in the group.

I classified habitat on the basis of an approximately 0.1-ha patch centered around the bird. Habitats were classified as cropland, short grass, tall grass, feedlot, shrub-sapling, forest, or developed; habitat was listed as unknown if the location was triangulated and it was not clear in which of two adjacent habitats the bird was located. I classified any tilled ground with or without crops present as cropland. Short grass was pasture or native grassland typically mowed or grazed that had a gross height of 10 cm or less. Tall grass

was taller than 10 cm, usually unmowed and ungrazed. Any type of animal pens in which livestock fed were classified as feedlots. Shrub-sapling habitats were oldfields consisting of mixed grasses, forbs, shrubs, and small trees; they also included stands of regenerating seedling and sapling-sized trees (≤10 cm diameter at breast height) that were the result of timber harvest. Mature forest was forest where the overstory trees exceeded 10 cm in diameter. Developed habitats included roads, residences, buildings, and urban areas.

Cowbird behavior was classified as feeding, nonfeeding, roosting, or unknown if the bird was not visually sighted. Birds located after dark on roosts were classified as roosting. During daylight hours birds were observed from as great a distance as possible and only long enough to confirm whether they were feeding or not feeding (typically 1-3 min). Birds observed actively foraging for or gleaning insects or seeds were defined as feeding. All other observed behaviors were classified as nonfeeding. If a radio signal was coming from a large flock of feeding birds, I often did not locate the individual; it was recorded as feeding. If a bird was disturbed by the observer and altered its behavior, I recorded the behavior as unknown.

Analysis.—Cowbird locations were transferred from field maps to a georeferenced raster image in a geographic information system. The raster image was created by scanning aerial photographs of the study areas. Universal transverse mercator coordinators were determined for each cowbird location on the raster image and combined with the date, time, behavior, and habitat of each location for statistical analysis.

For each cowbird, I calculated the percent of the total number of locations for each behavior by time period, in each habitat by time period, and of each behavior in each habitat. I then plotted the means of these values (percents) for all cowbirds. I used log-linear models to test the significance of associations between behavior and time of day, behavior and habitat use, and habitat use and time of day. A full log-linear model containing all main effects and two-way interactions was constructed, then reduced models were constructed with the association (two-way interaction) of interest dropped from the model. The significance of the association is the difference in the maximum-likelihood ratios of the full and reduced models, which follows a chi-square distribution (Freeman 1987). Observations were placed in three time classes for the log-linear analysis. Nocturnal roosting observations were dropped because cowbirds always roosted at night.

I determined the number of males and females in groups that included radio-tagged birds during 3-h blocks beginning at 0500 and ending at 2000. I calculated the median number of females and males in these groups for each 3-h block, as opposed to means, which are more likely to be distorted by occasional observations of large groups during a time period. I calculated the Spearman rank correlation between group size and time period to test the hypothesis that group size increased linearly during the day.

Fig. 1. Location of sites used to study spatial and temporal patterns of Brown-headed Cowbirds in midwestern United States.

I identified locations associated with potential breeding, feeding, and roosting areas to test spatial relationships among them and movements between them. I assumed that morning nonfeeding observations represented females on their breeding areas. This assumption was necessary because we rarely observed birds in activities that could be definitively classified as breeding (i.e. laying, nest searching), and I could not assume a female was on a breeding area based on her location or habitat (this would bias the analysis). Some locations were probably misclassified, but I believe this is a reasonable assumption because female cowbirds usually lay and search for nests in the morning (Friedmann 1929, Hann 1941). Rothstein et al. (1980, 1984) made similar assumptions when studying daily dispersion and commuting patterns of cowbirds in the Sierra Nevada. Observations of birds feeding and roosting (during non-daylight hours) were considered on feeding and roosting areas, respectively.

I calculated the distance moved between consecutive locations of cowbirds on breeding and then feeding areas, feeding and then roosting areas, and roosting and then breeding areas within the same 24-h period. The mean and maximum distance for each type of movement was calculated for individual cowbirds, and the mean and standard error of these for all cowbirds. I also pooled all distance estimates for all cowbirds and report the percent of movements in 1-km distance classes. I also calculated the distance between the geometric center of locations on breeding, feeding, and roosting areas as a measure of the distance between breeding, feeding, and roosting areas.

I used multiple-response permutation procedures (MRPP; Mielke et al. 1981, Biondini et al. 1988, Mielke

1991; Blossom Software, National Ecology Research Center, U.S. Fish and Wildlife Service, Fort Collins, Colorado) to determine spatial patterns of and relationships among breeding, feeding, and roosting locations. MRPP are distribution-free techniques that can be used to identify differences among groups. They can be used to determine spatial relationships among groups or to determine spatial patterns by comparing observed patterns to a reference data set (Reich et al. 1991). MRPP have been used to determine distributional differences of radio-tagged wildlife (Cade and Hoffman 1993). When applied to radio-telemetry locations, MRPP tests if two or more utilization distributions are the same. A utilization distribution is a probabilistic definition of home range; it is the probability of finding an animal at a particular location on a plane (White and Garrot 1990). MRPP are particularly suited to spatial data because they can be based on Euclidean distances, which are commensurate with distances calculated from Cartesian coordinates. The test is based on a comparison of (1) the within-group average of pairwise distance measures between observations with (2) the average pairwise distance measures in groups created by all other possible permutations of the data that create the same number of groups with the observed sample size. A small P-value associated with this test indicates a difference in mean location, dispersion, or both.

I used MRPP to determine if all locations, locations on breeding areas, locations on feeding areas, or evening roosting locations were randomly distributed or aggregated. A reference set was generated for each cowbird by randomly selecting X-Y coordinates from a uniform distribution that fell within a cowbird's home range. I used a convex-polygon estimate of home range because it was a simple and conservative estimate of the area available to each cowbird, and selected a number of random points equal to the number of observed locations for each cowbird. I used MRPP to compare each type of location for each bird to the reference data set; a large P-value suggests the locations do not differ from the randomly generated reference set, while a small P-value suggests a nonrandom pattern.

I also used MRPP to determine if locations on breeding, feeding and roosting areas were from the same utilization distribution. I treated each class of location as a group and included all groups and each possible two-way comparison of groups for each cowbird. A large P-value suggests the locations were not from different areas. All P-values are for individual tests; I did not control for experimentwise error.

RESULTS

Coworkers and I radio-tagged 132 female cowbirds. I analyzed only data from 84 individuals for which I had 15 or more locations. This included 16 cowbirds at the Ashland site and 20 at the Carr Creek site in 1991, and 10, 14, and 27 cowbirds at the Ashland, Carr Creek, and Jonesboro sites, respectively, in 1992. We obtained 15 to 82 locations ($\bar{x}$ = 42 ± SD of 14) of each cowbird in this sample. Individuals that were radio-tagged and not included in the analysis either lost their radio transmitter or died, or we were unable to relocate the birds. In most instances I could not distinguish if a radio was lost or the bird was predated or scavenged. At least two individuals were killed by avian predators. Postmortem exams confirmed two individuals died of salmonella poisoning, which I suspect was contracted from a cattle feeder. I believe as many as six additional individuals also died this way. Two individuals were either killed or scavenged by cats.

Temporal patterns in habitat use, behavior, and group size.—Most cowbirds showed a similar pattern of behavior and habitat use during the day. Females usually were engaged in nonfeeding activities in the forest in the morning (Fig. 2). Cowbird use of forest and shrub-sapling habitats decreased, whereas use of short-grass, cropland, and feedlot habitats increased throughout the day, especially after noon (Fig. 3). While nonfeeding activities and use of forest habitat decreased throughout the day, the greatest decline was during 0800–1400 (Figs. 2 and 3). Occasionally, feeding was observed in the morning in the forest (Fig. 4), usually along trails or abandoned roads. Some early-morning feeding also occurred in short-grass habitats within the forest, such as picnic areas, but these birds still fed in agricultural areas in the afternoon. Cowbirds usually were located in small flocks feeding in agricultural habitats in the afternoon (Figs. 2, 3, and 4). Of 1,351 feeding cowbird observations, 57% were associated with livestock. At night cowbirds roosted singly or in small groups, with the exception of the Jonesboro site where 15 of 28 radio-tagged females were located at a communal roost of at least 200 cowbirds and more than 1,000 Common Grackles (*Quiscalus quiscula*). Results of the log-linear model analysis indicate a high degree of association between: behavior and habitat (G = 1,239.9, df = 6, $P < 0.001$); habitat and time of day (G = 155.5, df = 14, $P < 0.001$); and behavior and time of day (G = 42.5, df = 2, $P < 0.001$).

Cowbirds were more social in the afternoon and evening than early morning. The number of male and female cowbirds observed with ra-

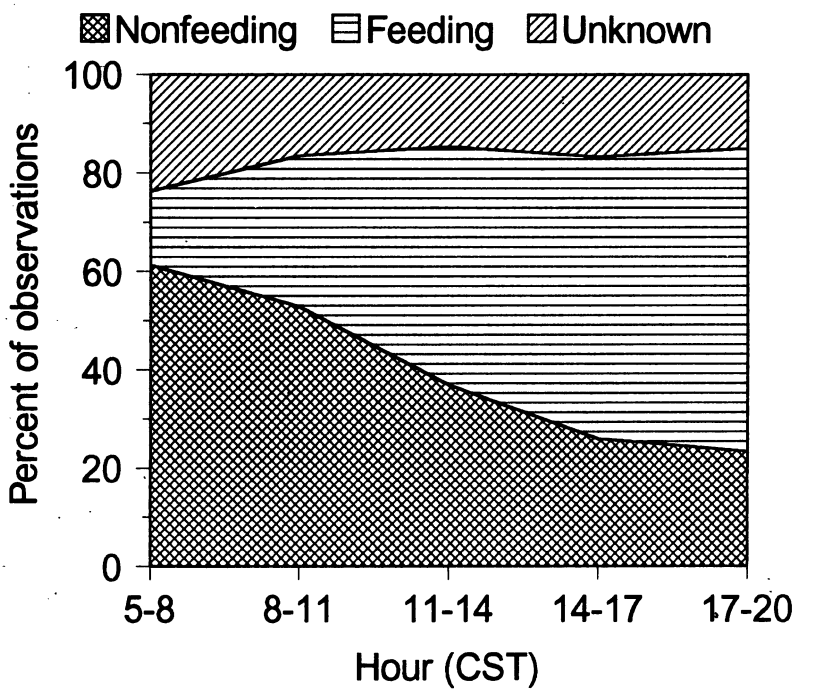

Fig. 2. Diurnal patterns in behavior of breeding female Brown-headed Cowbirds. Hours indicate 3-h blocks beginning with 0500 and ending at 2000.

dio-tagged cowbirds increased from 0500 to 2000 (Spearman $r = 0.4$, $P < 0.001$). On average, radio-tagged females were observed as part of a group of 1.0 females and 1.4 males during 0500–0800, and with 7.0 females and 8.9 males from 1700–2000 when birds were usually feeding (Fig. 5).

Spatial pattern and relationships.—Spatial analysis indicated that locations of most cowbirds were not distributed randomly within their home ranges (Table 1). Distributions of breeding, feeding, and roosting locations of most cowbirds were distinct (Table 2, Fig. 6). Because MRPP is sensitive to differences in dispersion and mean location, differences among breeding, feeding, and roosting distributions could result for different reasons. For cowbirds that had distinct breeding and feeding distributions (78%; Table 2), there was some variation among birds in the pattern of breeding and feeding locations. Breeding and feeding locations of some cowbirds came from clearly defined areas with minimal overlap (Fig. 6A). Most cowbirds,

TABLE 1. Test of nonrandomness of female Brown-headed Cowbird locations from breeding, feeding, and roosting areas in Missouri and Illinois.[a]

Type of location	No. (%) of female cowbirds with Randomly distributed locations	Aggregated locations
All	6 (9)	59 (91)
Breeding	10 (15)	55 (85)
Feeding	5 (8)	60 (92)
Roosting	17 (26)	48 (74)

[a] Determined by MRPP. Null hypothesis is that locations do not differ from locations selected randomly from a uniform distribution ($P < 0.05$).

TABLE 2. Spatial association of locations from breeding, feeding, and roosting areas of female Brown-headed Cowbirds in Missouri and Illinois.[a]

Locations compared	No. (%) female cowbirds with utilization distributions that were Same	Different
All	5 (8)	60 (92)
Breeding and feeding	15 (23)	50 (77)
Breeding and roosting	14 (22)	51 (78)
Feeding and roosting	15 (23)	50 (77)

[a] Determined by MRPP. Null hypothesis is that locations from each area have the same utilization distribution ($P < 0.05$).

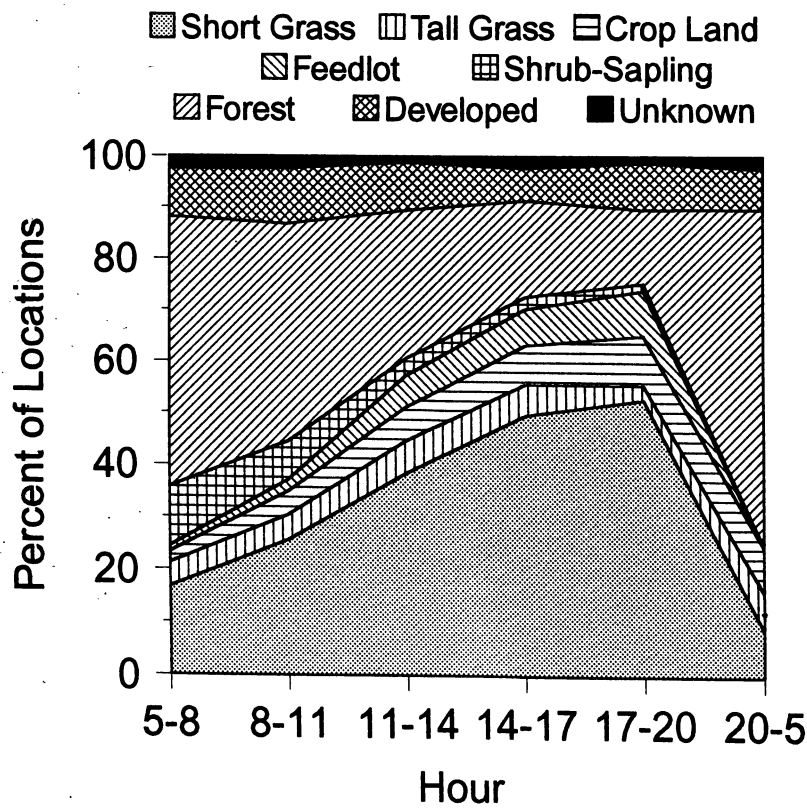

Fig. 3. Diurnal patterns in habitat use by breeding female Brown-headed Cowbirds. Hours indicate time classes covering 24 h beginning at 0500 CST.

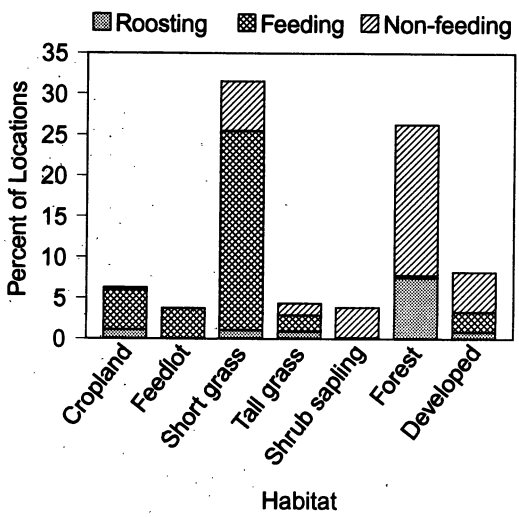

Fig. 4. Behavior of female Brown-headed Cowbirds in different habitats.

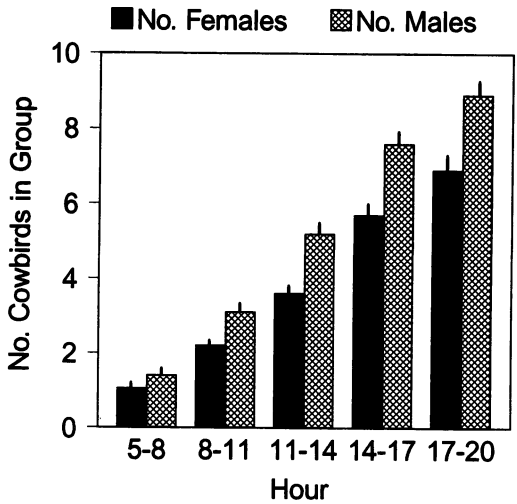

Fig. 5. Diurnal patterns in the mean numbers of female and male Brown-headed Cowbirds in groups. Group size is significantly related to time of day (Spearman $r = 0.4$; $P < 0.001$). Whisker indicates SE.

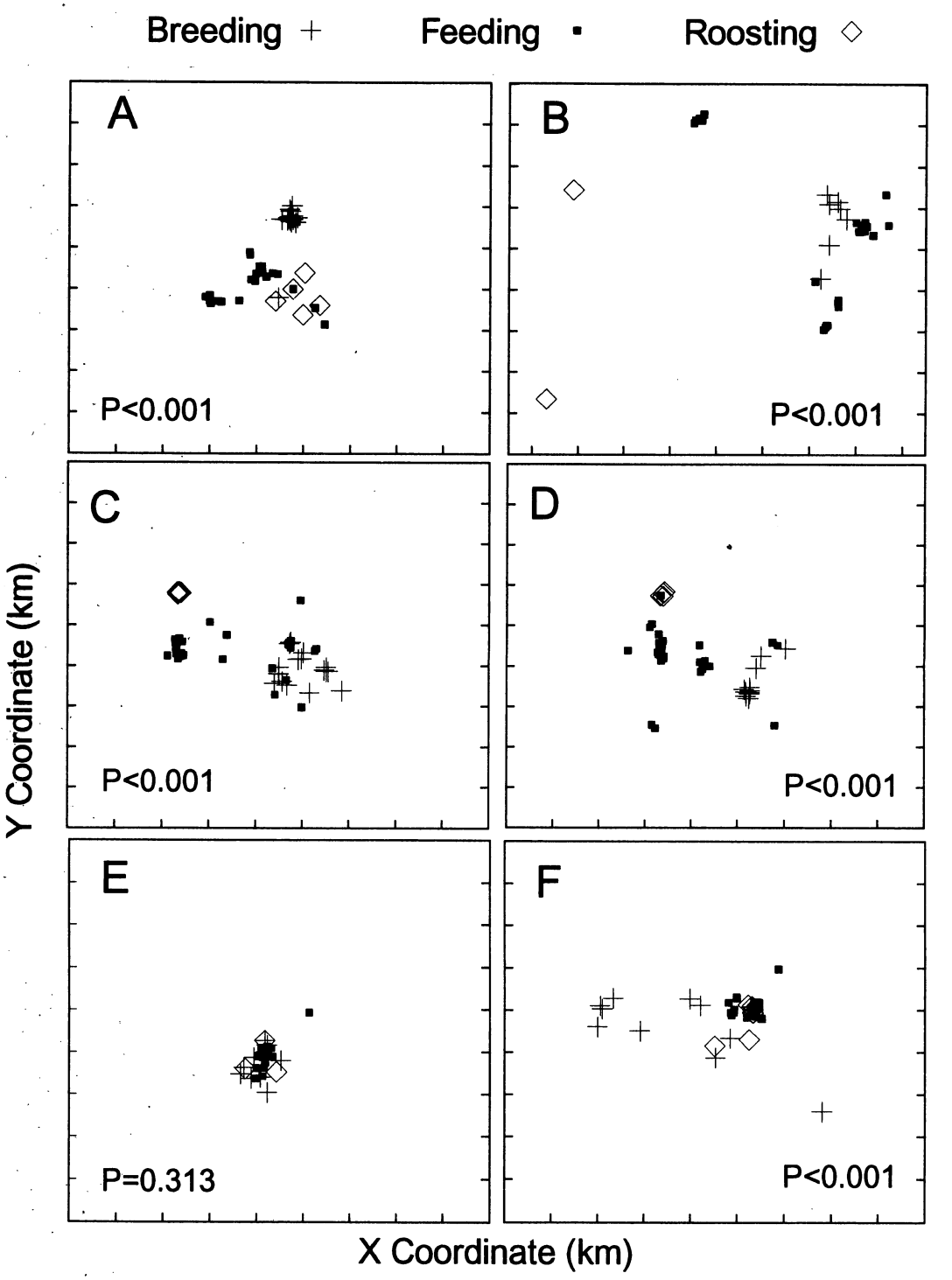

Fig. 6. Locations from breeding, feeding, and roosting areas of six representative female Brown-headed cowbirds. *P*-values are probability that locations from breeding, feeding, and roosting areas are from the same utilization distributions based on MRPP.

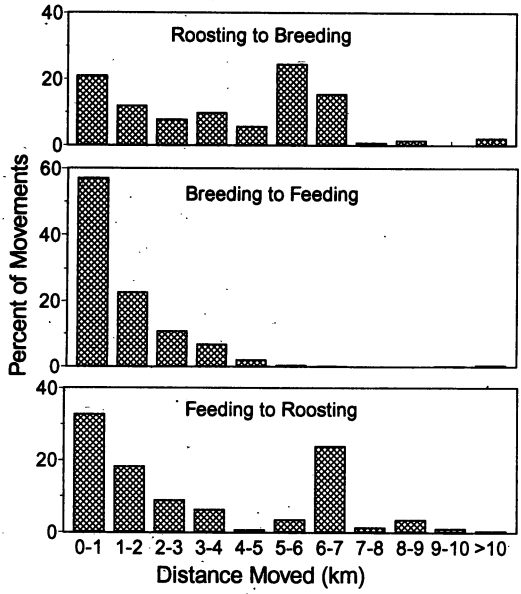

Fig. 7. Movement patterns of breeding female Brown-headed Cowbirds. Movements presented as mean percent of all movements by cowbirds between locations on breeding, feeding, and roosting areas in 1-km distance classes (n = 1,152 movements by 84 radio-tagged cowbirds).

however, had tightly clustered breeding locations, but more widely dispersed feeding locations, with some feeding occurring within breeding areas (Fig. 6B, C, D). A few cowbirds had widely spaced breeding locations that were distinct from feeding locations (Fig. 6F). I found 23% of cowbirds did not have distinct breeding and feeding locations (Table 2, Fig. 6E).

Similarly, the distribution of roosting locations was different than that of breeding and feeding locations for 77% of cowbirds (Table 2). Cowbirds often roosted repeatedly at the same site, so roost locations were often less dispersed than feeding and breeding locations (Fig. 6C, D), or roost sites differed from feeding and breeding locations, and were outside of breeding and feeding areas (Fig. 6B, C). The most extreme example of this was at the Jonesboro, Illinois study site, where cowbirds typically had breeding areas in the forested hills above the Mississippi river floodplain, fed in nearby agricultural habitats, and commuted back and forth from a communal roost site located in a woodlot in the floodplain 6 to 8 km from their breeding and feeding areas. More typically, roosts were located in or near feeding areas, often in single trees or fencerows in agricultural habitats or in developed areas. Occasionally, cowbirds were observed roosting in or near breeding areas.

Movements.—The extent of cowbird movements varied among individuals. For instance, a cowbird moved on average 1.2 km and a maximum of 3.2 km between breeding and feeding locations (Table 3), but some individual movements were greater than 10 km (Fig. 7). Cowbirds generally moved greater distances between roosting and breeding, and feeding and roosting than between breeding and feeding locations (Table 3, Fig. 7). Distances among the geometric centers of breeding, feeding, and roosting locations followed the same patterns as did actual movements (Table 3).

DISCUSSION

Distinct temporal and spatial patterns in behavior and habitat use occurred because cowbirds bred, fed, and roosted during different time periods and in different habitats. Cowbirds can commute among disjunct areas for each of these activities because they do not have to provide parental care to their young. Thus, cowbirds can temporally and spatially segregate activities to time periods and areas that are appropriate for each activity. The ability of cowbirds to uncouple breeding and feeding, and commute between disjunct areas used for each activity has been reported by other investiga-

TABLE 3. Mean distances moved (km) by breeding female Brown-headed Cowbirds from breeding, feeding, and roosting areas in Missouri and Illinois. $\bar{x} \pm$ SE (n).

Distance measure	Roosting to breeding	Breeding to feeding	Feeding to roosting
Mean[a]	3.6 ± 0.39 (56)	1.2 ± 0.08 (86)	2.6 ± 0.28 (70)
Maximum[a]	4.7 ± 0.76 (56)	3.2 ± 0.48 (86)	3.5 ± 0.37 (70)
Between geometric centers[b]	2.9 ± 0.30 (87)	1.1 ± 0.11 (87)	2.4 ± 0.28 (87)

[a] Distance moved between consecutive locations in appropriate areas.
[b] Distance between geometric centers of locations from appropriate areas.

tors studying radio-tagged cowbirds in the east (Dufty 1982) and west (Verner and Ritter 1983, Rothstein et al. 1984, 1986).

Temporal patterns.—Cowbird behavior and habitat use shifted from primarily nonfeeding behavior (and presumably breeding) in forest and shrub-sapling habitats in the morning to feeding in short grass, cropland, and feedlots in the afternoon. Cowbirds generally prefer breeding habitats with high host densities (Verner and Ritter 1983, Rothstein et al. 1986). Forest and shrub-sapling habitats had greater host densities on my study sites than other habitats (S. Robinson unpubl. data, F. Thompson pers. obs.). The high number of cowbird locations in forest and shrub-sapling habitats in the early morning likely reflects cowbird preferences for these habitats for breeding due to their high host density (Rothstein et al. 1980) or more tolerant hosts (Friedmann 1929). From 0600 to 0900, 17% of cowbird observations were in short-grass habitats. Early-morning observations of cowbirds feeding in short-grass habitat were cowbirds that either bred immediately around the edges of these habitats, cowbirds that had already left their breeding areas within the forest to feed, or cowbirds feeding in small patches of short-grass habitat within the forest and their breeding area.

Cowbirds are often associated with large grazing mammals, but it is not clear what benefit they receive from foraging with grazing mammals. Prior to European settlement, cowbirds occurred on the prairies and fed on insects stirred up by grazing bison (*Bison bison;* Friedmann 1929, Mayfield 1965). Cropping and trampling of tall prairie grass by bison may have been an equally or more important reason for the cowbird's association with bison, because cowbirds feed on the ground (Mayfield 1965). In my study, short grass was the most important feeding habitat for cowbirds, and cowbirds usually foraged with livestock.

Cowbirds also fed in cropland, usually immediately following any type of tillage. Tillage probably exposed soil invertebrates and made them available to feeding cowbirds. I also observed females feeding in feedlots, but males appeared much more numerous there (though I did not count them). Females may have been less numerous at feedlots during the breeding season because insects become a more important component of their diet when laying (Ankney and Scott 1980). Males do not have the same nutritional demands and may feed more on waste grain at feedlots than females.

Diurnal patterns in group size are consistent with those reported in other parts of the cowbird's range (Dufty 1982, Darley 1983, Rothstein et al. 1980, 1984, 1986). Observations of single females with one or more males during the early morning are consistent with the hypothesis that females maintain breeding territories. However, females were not directly observed for long enough periods to determine if these areas were defended territories or simple breeding areas. During late morning and afternoon, cowbirds fed in small to large groups (Fig. 5). These flocks may have occurred for a variety of social reasons, such as increased predator detection and escape from predatory attack (Lima 1993). Rothstein et al. (1986) suggested these afternoon aggregations were not important for courtship or breeding, but likely the result of birds concentrating at prime feeding locations and deriving the benefits of increased predator detection.

Cowbirds have previously been reported to roost during their breeding season on their breeding areas (Rothstein et al. 1984), in small groups near feeding areas, or in large flocks in willow thickets (Verner and Ritter 1983). I observed cowbirds exhibiting all these patterns. The large communal roost I watched in Illinois was in a stand of flooded, dense sapling-sized silver maples (*Acer saccharinum*) along a drainage ditch, which may be structurally similar to the willow thickets in which Verner and Ritter (1983) observed large flocks roosting. In general, it is thought that birds roost communally to avoid predation or exchange information regarding resources (Ward and Zahavi 1973, Weatherhead 1983), to reduce thermoregulatory costs (Chaplin 1982), or for a combination of these reasons (Weatherhead and Hoysak 1984). It is unlikely that cowbirds roosted together to share information on resources because they dispersed from the roost to individual breeding ranges, or that reducing thermoregulatory costs was a concern during this season. I believe the likely reason for this roost was to reduce predation. The large number of birds in the roost could be due to a combination of the benefits of large group size in reducing predation, and selection of a unique habitat consisting of flooded dense vegetation. Many nonparasitic blackbirds roost in large flocks when not nesting, and some nest communally

and disperse to feed. This pattern of roosting and feeding in large groups and being solitary on breeding ranges during the same 24-h period may be unique to Brown-headed Cowbirds.

Spatial patterns.—Most cowbirds did not use the area in their home range randomly. Results of MRPP comparing breeding, feeding, and roosting locations to random locations were statistically significant because average pairwise distances between locations in breeding, feeding, and roosting areas were smaller than those between random locations. Thus, for many cowbirds observations in each of these areas tended to be clumped, indicating fidelity to areas for each behavior.

Locations in breeding, feeding, and roosting areas of most cowbirds were from distinct utilization distributions. Feeding locations usually were more dispersed than breeding locations, with little overlap except for some morning feeding locations being on breeding areas. Cowbirds that did not appear to have distinct breeding and feeding areas (Table 2) spent most of their time in agricultural habitats, possibly parasitizing hosts in the grassland, fencerows, and forest edge. It is also possible that these individuals were not breeding. Most females limited their movements to relatively compact breeding areas and were observed without other females during the early morning, suggesting these could be breeding territories. However, I did not radio-tag a sufficient proportion of the total female population to determine if these areas overlapped, and females were not observed for long enough time periods to determine if these areas were defended.

I concur with Rothstein et al. (1986) that spatial segregation is a result of both the cowbird's foraging behavior and parasitic breeding behavior. Forest fragmentation has interspersed potential cowbird feeding areas with host-rich forest habitats, increasing the benefits for cowbirds to commute between breeding and feeding areas in different habitats. Prior to European settlement, cowbirds probably followed bison herds, and fed and bred in the prairies (Friedmann 1929, Mayfield 1965). In present-day grasslands, there does not appear to be any segregation of breeding and feeding activities (Elliott 1980).

Movements.—I found that 80% of movements from breeding to feeding areas were less than 2 km. Distances between breeding and feeding areas, however, ranged from 0.03 to 7.34 km. This variation is likely due in part to differences in landscape pattern, such as the amount of forest and interspersion of feeding areas.

Similar variation in movements and spatial relationships of breeding and feeding areas occur in the Sierra Nevada. In the eastern Sierra Nevada, cowbirds commuted a minimum of 2.1 km and mean of 4.0 km between breeding areas in the forest and the pack stations where they fed (Rothstein et al. 1984). On the western slope, some cowbirds showed similar commuting patterns, whereas others bred and fed around nearby meadows with grazing cattle (Verner and Ritter 1983).

Peaks in the distribution of movements between locations on roosting and breeding areas, and between locations on feeding and roosting areas occurred at 6 to 7 km (Fig. 7). These were largely the result of the use of a single communal roost located away from breeding and feeding areas at the Jonesboro site. However, individuals at all sites occasionally made long flights to roosting areas. The occurrence of these long flights to communal roosts suggests these roosts serve an important function.

Conservation implications for host populations.—My study has implications for the conservation of host species that are heavily parasitized in fragmented midwestern forests. Cowbirds that breed in the forest commute daily to feed in short grass and cropland habitats. I believe the distribution of these feeding habitats can be an important limiting factor for cowbirds. Conservation efforts should provide ample breeding habitat for host populations and minimize the interspersion of cowbird feeding areas (Robinson et al. 1993). Cowbird movements were as great as 10 km, but most movements between breeding and feeding areas were less than 2 km. Providing forest-core areas more than 2 km from potential feeding habitats may reduce levels of brood parasitism in those forests.

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