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COWBIRDS BREEDING IN THE CENTRAL APPALACHIANS: SPATIAL AND TEMPORAL PATTERNS AND HABITAT SELECTION

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Abstract. To help minimize the impact of brood parasitism by female Brown-headed Cowbirds (*Molothrus ater*) on Nearctic-Neotropical migrants, we studied their spatial and temporal patterns and habitat selection throughout the breeding season. The study was conducted on an anthropogenic forest landscape in the central Appalachian Mountains of western Maryland. This landscape was characterized by different forest types and stages of succession resulting from logging, agriculture, and low-density housing development, as well as by natural and human-made corridors. Using radiotelemetry, cowbird movements were monitored in 3-h time periods during the day, beginning at 0500 hours Eastern Standard Time. Females were generally alone or with one or two other individuals from 0500 to 1100 hours. They were located in deciduous forest and brush near edges formed by road, power line, or stream corridors and other clearings, presumably searching for nests to parasitize. Breeding core ranges of individual females tended to be spatially separated from one another. Females would travel, on average, 2.3 km from breeding to feeding areas. From 1100 hours until dusk, feeding aggregations of ≥12 individuals could be found in grazed pasture or other areas of short grass. Feeding core ranges overlapped considerably. At dusk, cowbirds would fly an average of 3.0 km to roosting areas in deciduous forest near ($\bar{X}$ = 1.3 km) where they would be found the next morning, presumably breeding. Cowbirds roosted singly or in small aggregations in trees near forest edges. Although the mean home range was 1592 ha, only 3.5% or 31.6 ha, on average, was actually used for different activities. Most individuals had at least two feeding core ranges ($\bar{X}$ = 16.5 ha total), one breeding core range ($\bar{X}$ = 9.5 ha), and one roosting core range ($\bar{X}$ = 1.8 ha) or combination roost/breed core range ($\bar{X}$ = 9.8 ha). Multiple-use core ranges were generally larger than single-use core ranges. Breeding and roosting core ranges were often elongated, with the long axis paralleling a linear canopy opening, e.g., a road, power line, or stream corridor. Multiple-use core ranges were more circular in shape. Breeding and roosting core-range centroids in the forest were often <50 m from a forest-road, brush, power line, or stream edge. Feeding core ranges were nearly always associated with agricultural land. In selecting home ranges, cowbirds incorporated brush and deciduous forest in greater proportions than those found within the study area. At the next level of habitat selection, agricultural land and deciduous forest were the most important habitat types within core ranges. Breeding core ranges had higher numbers of seedlings and saplings and large (>22.5 cm dbh) snags than were found within forest interior >250 m from an edge. Conservation measures designed to reduce use of large forest tracts by cowbirds in this region would include eliminating feeding areas, minimizing canopy openings or edges, and perhaps managing existing edges in order to disperse nests of potential host species.

Key words: Appalachian Mountains; Brown-headed Cowbird; canopy openings; corridors; edge effects; forest fragmentation; habitat selection; Molothrus ater; spatial patterns; temporal patterns.

Introduction

Forest canopy openings, created naturally and by humans, are major landscape features throughout North America. These openings range from small canopy gaps to larger openings created by logging, wildfires, insect outbreaks, and road and utility corridors. These openings have different impacts upon the surrounding landscape depending upon their form (Gates 1991, Askins 1994, Rich et al. 1994, Forman 1995). Fragmentation of forest land into smaller and smaller patches is considered detrimental to forest-interior breeding birds, especially Nearctic–Neotropical migrants. It has been associated with an increase in competition from edge species, nest predation, and brood parasitism (Gates and Gysel 1978, Whitcomb et al. 1981, Ambuel and Temple 1982, 1983, Brittingham and Temple 1983, Lynch and Whigham 1984, Temple 1984, Wilcove 1985, 1988, Small and Hunter 1988, Robbins et al. 1989, Rothstein and Robinson 1994, Robinson et al. 1995a).

PLATE. 1. A portion of the study area within the Ridge and Valley physiographic province of western Maryland. Grazed pasture (foreground) was used by Brown-headed Cowbirds for feeding. Mixed oak forest near pasture, power line, and brush (cutover areas) edges (background) was an important breeding habitat.

The Brown-headed Cowbird (*Molothrus ater*) is an obligate brood parasite and a factor in the decline of some populations of Nearctic–Neotropical migrants (Mayfield 1977, Brittingham and Temple 1983, Robinson et al. 1995b). If our large forest tracts are to maintain biological diversity and to provide breeding habitat for Nearctic–Neotropical migrants, we must understand the behavior and ecology of this species and the roles that canopy openings, as well as other landscape features, play in their distributional patterns (Robinson et al. 1995b). It was not until the vast expanses of eastern deciduous forests were cleared for farms, pastures, towns, and wood products at the end of the 18th century that the cowbird expanded its range eastward (Mayfield 1965, 1977). Although cowbirds tend to be associated with edges and clearings and are most abundant in fragmented landscapes having a high edge/area ratio, cowbirds have been found deep within the interior of large tracts of forest land near rights-of-way, stream corridors, and other such openings (Chasko and Gates 1982, Verner and Ritter 1983, Rothstein et al. 1984, Gates and Giffen 1991, Hahn and Hatfield 1995). Both host and cowbird densities are often high along forest–field edges and in riparian zones (Gates and Gysel 1978, Rothstein et al. 1984, Gates and Giffen 1991). Additionally, Chasko and Gates (1982) found higher numbers of cowbirds along forest–power line corridor edges and correspondingly higher rates of cowbird parasitism. Nevertheless, such areas rarely provide suitable foraging habitat for cowbirds. Therefore, they must generally seek short-grass feeding areas outside the forest, often traveling several

kilometers (Rothstein et al. 1984, Thompson 1994). It is also thought that livestock are needed to support those cowbird populations inhabiting large tracts of forest land (Rothstein et al. 1980, 1984, Verner and Ritter 1983, Thompson 1994, Coker and Capen 1995).

Many Nearctic–Neotropical migratory bird species nesting in forests in western Maryland have experienced population declines in other parts of the country since the 1950s (Robbins et al. 1989). Information on home ranges and daily movements of cowbirds throughout the breeding season may help us to better design or manage different landscape features to minimize detrimental effects on breeding Nearctic–Neotropical migrants. Furthermore, additional studies are needed to improve our understanding of regional differences in cowbird spatial ecology and habitat selection (Hahn and Hatfield 1995, Thompson et al., *in press*). The specific objectives of our study were to determine the distances traveled (home range), daily spatial use, and habitat affinities of cowbirds in the central Appalachian Mountains of western Maryland.

THE STUDY AREA

The study area (39°36′ N, 78°30′ W) covered 18 038 ha of the Ridge and Valley physiographic province in eastern Allegany County, Maryland, and included a large portion of Green Ridge State Forest (GRSF) as well as agricultural lands along Town Creek to the west (Plate 1). In Allegany County, 78.5% of the land area is forested, totalling ~85 628 ha (Stone and Matthews 1977, Frieswyk and DiGiovanni 1988). The 15 699-ha GRSF makes up 18.2% of this forest land. The study

area itself was 88.9% forested. Habitat types included 30.8% deciduous forest, 56.8% mixed forest, 1.3% evergreen forest, 3.5% brush, 0.3% power line corridor, 7.2% agriculture, and 0.2% developed land. Deciduous forest was typically mixed oaks [chestnut (*Quercus prinus*), red (*Q. rubra*), white (*Q. alba*), black (*Q. velutina*), or scarlet (*Q. coccinea*) oaks]. Mixed forests consisted of hardwood–pine, where the hardwood component was generally an oak species and the pine consisted of Virginia (*Pinus virginiana*), shortleaf (*P. echinata*), pitch (*P. rigida*), table mountain (*P. pungens*), or white (*P. strobus*) pines. Evergreen forests included mixed hard pines, i.e., nearly pure stands of Virginia, pitch, table mountain, or shortleaf pines. Brush included abandoned orchards and regenerating cutover areas. A 46 m wide power line corridor crossed from east to west through the central portion. Other corridors included a telephone line right-of-way; a multilane divided highway, Interstate 68 (I-68); and an undivided highway, Route 40, located in the northern portion. Several light-duty gravel and unimproved dirt roads were located along the ridges and in several stream valleys. Agricultural activities, principally beef cattle farming, occurred largely to the west of GRSF along Town Creek. One farm was located within the central portion of GRSF. Developed land included residential and institutional developments. Elevations ranged from ~165 m along Town Creek to ~620 m on the highest ridge.

MATERIALS AND METHODS

Between 16 and 28 May 1994, we trapped cowbirds in grazed pasture land on Rader's Farm within GRSF. For each captured female cowbird, we estimated age, assessed reproductive condition, and attached a radio transmitter and harness assembly with mass of 1.56 g (Rappole and Tipton 1991). Monitoring began on 19 May and continued through 15 July 1994, well within the cowbird laying season (Rothstein et al. 1986, Fleischer et al. 1987, Holford and Roby 1993). Each of four field assistants tracked 12–13 cowbirds. Individual cowbirds were located 1–3 times per day, and our searching was proportionately stratified to obtain nearly equal number of locations for each cowbird in 3-h time periods from 0500 to 2000 hours and a nocturnal period from 2000 to 0500 hours EST (White and Garrott 1990, Thompson 1994).

We located female cowbirds from vehicles, using a scanning receiver. Each cowbird was then tracked on foot until it could be observed. We then recorded date, time, behavior, numbers of female and male cowbirds associated with the radio-tagged cowbird, habitat type, and distance from an edge. Behavior was classified as feeding (feeding, feeding with livestock); nonfeeding (courting, perching, flying); roosting; and unknown (if the cowbird could not be seen). Nonfeeding that occurred between 0500 and 1100 hours was considered to be breeding behavior (Thompson 1994). Cowbirds located after dark were classified as roosting. Habitat type was classified on the basis of an ~0.1-ha patch centered around the cowbird, with the same general categories used to describe the study area. However, we did subdivide agricultural land into tall-grass (>10 cm) farm fields (e.g., old field, ungrazed pasture, and crop field) and short-grass (≤10 cm) mowed/grazed pasture. A Global Positioning System (GPS) receiver was used to record and store the location of the cowbird within the landscape. We tried to accumulate at least 180 positional fixes (3-min time interval) at each location for a postprocessing accuracy of ±2–5 m using a base station. We used an airplane three times during the field season to locate those cowbirds that we were having difficulty in finding on the ground.

To avoid pseudoreplication, we used median values of each category being examined for differences for each radio-tagged female cowbird, e.g., consecutive movements among activity areas. The reported means (±1 SE) represent those calculated from the median values; therefore, sample sizes (n) are numbers of individual cowbirds. One-way ANOVA and Tukey's studentized range test were used to test for significant differences (SAS Institute 1990). Variables were checked for normality and were then transformed, if needed, using either logarithmic ($\log_{10}$) or square-root transformations. For particular analyses, sample sizes differed due to missing values.

To relate temporal patterns of habitat use and patterns of vegetation strata use within habitats, we plotted the frequency distributions of fixes of all 50 radio-tagged female cowbirds. Because the total number of fixes differed among the 50 radio-tagged individuals, we checked our results against a subsample of 20 individuals having five randomly chosen fixes in each of the six time intervals, i.e., 30 fixes in total. The results were the same as for those using the total sample.

Home ranges were estimated using the minimum convex polygon (MCP) method (Mohr 1947); core ranges were identified using incremental cluster analysis, i.e., multinuclear polygons by clustering (Kenward 1987). We used a subsample of 27 cowbirds that had ≥30 fixes, with ≥1 fix in each time interval. We plotted the utilization distribution for each individual and used the slope discontinuity to determine the percentage of fixes defining a core range (Kenward 1990). The innermost 90% was most often used as the core range. We delineated a minimum-sized study area by determining the outermost boundary of MCP home ranges for these 27 female cowbirds. A vegetative habitat map of the study area was then prepared from available databases, using a geographic information system, or GIS (PC ARC/INFO, ESRI, Redlands, California, USA). Features not present and corrections were added to our coverage by digitizing from aerial photography, current United States Geological Survey 7.5-minute quadrangle maps, or by using the GPS receivers in the field to determine boundary locations. The area of each

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FIG. 1. Mean (+1 SE) of the median number of male and female Brown-headed Cowbirds associated with individual radio-tagged females at different daily time intervals. The number of radio-tagged individuals in the sample is in parentheses.
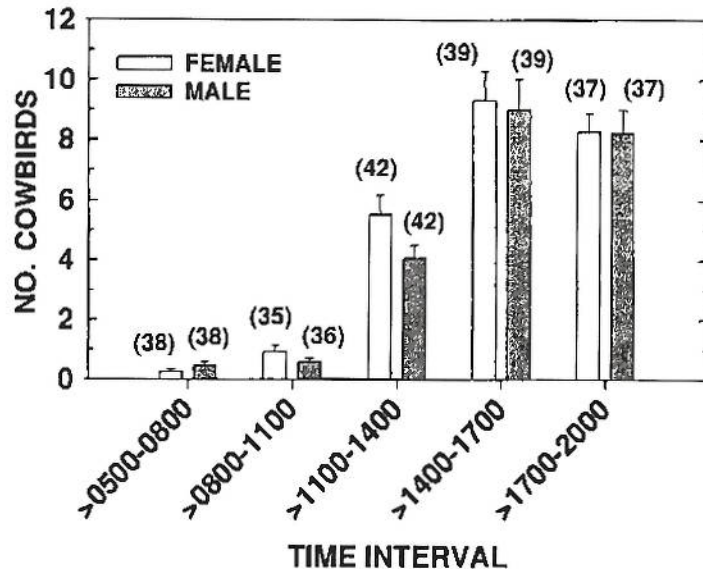
habitat type within each cowbird's MCP home range and core range was determined using PC ARC/INFO.

Habitat selection and use were examined using methods based on the log ratio analysis of compositions or compositional analysis (Aitchison 1986). Habitat use was estimated either by the proportion of home range occupied by each habitat or by the proportion of core range occupied by each habitat. This analysis technique overcomes the problem of lack of independence between proportions that sum to 1 (unit-sum constraint) by converting the n proportions to $n - 1$ log ratios, using one proportion as the denominator (Aebischer et al. 1993). Compositional analysis was done following a two-step approach (Johnson 1980, Aebischer et al. 1993). First, the animal selects its home range from an arbitrarily defined study area. Second, the animal selects core ranges within that home range.

The forest habitat within breeding core ranges was compared with that within forest interior by sampling vegetation composition and structure from 5 to 29 June 1995. Using a GPS receiver, we centered plots at breeding core-range centroids of the 27 cowbirds monitored during the 1994 field season. For comparison, 25 forest interior points, defined here as ≥250 m from an edge, were randomly located and sampled. A 16 m radius circular plot (0.08 ha) was used to sample number and diameter at breast height (dbh, 1.4 m in height) of snag and tree (≥7.5 cm dbh) species. Seedlings and saplings (≥1.4 m in height, <7.5 cm dbh) were sampled in two 16-m, arm's-length transects (0.006 ha) centered on the sample point. Overstory canopy height was measured (in meters) with a range finder or ruler. Percentage of canopy cover was determined with a spherical densiometer.

Canonical discriminant analysis was used to statistically distinguish the two types of habitats, i.e., breeding core range and forest interior (SAS Institute 1990).

Variables measured at each sample point were initially tested for their fit to a normal distribution. Values of variables not meeting the assumption of normality were transformed using either logarithmic ($\log_{10}$) or square-root transformations. Based on the success of normalizing the variables, differences between core ranges and forest interior were compared using either t tests or Wilcoxon-Mann-Whitney tests. Variables that met the assumption of normality and exhibited significant ($P < 0.05$) group differences were used in canonical discriminant analysis.

RESULTS

Of the 51 female cowbirds captured, 78% were taken during the first 3 d of the 13-d capture period, with captures usually reaching a peak near dusk. By palpating the abdomens of captured females, we determined that 86.8% of our sample birds had an oviducal egg, indicating that most would lay an egg the next morning (Fleischer et al. 1987). We accumulated 1467 radio fixes for the 50 radio-tagged female cowbirds during the breeding season. Twenty-five cowbirds had ≥5 locations in the five diurnal time intervals, whereas 20 cowbirds had ≥5 locations in all six. At the end of the field season, 52% of the cowbirds ($n = 50$) had functioning transmitters and were known to be alive. The remaining cowbirds were classified as missing (18%), missing with the transmitter found on the ground (16%), or mortalities resulting from predation (12%) or shooting (2%).

Temporal patterns

Radio-tagged female cowbirds were generally alone in the morning, 0500–1100 hours (Fig. 1). In the afternoon until dusk, groups tended to increase in size and reached an average maximum of 8–9 cowbirds of each sex (16–18 cowbirds total) per radio-tagged fe-
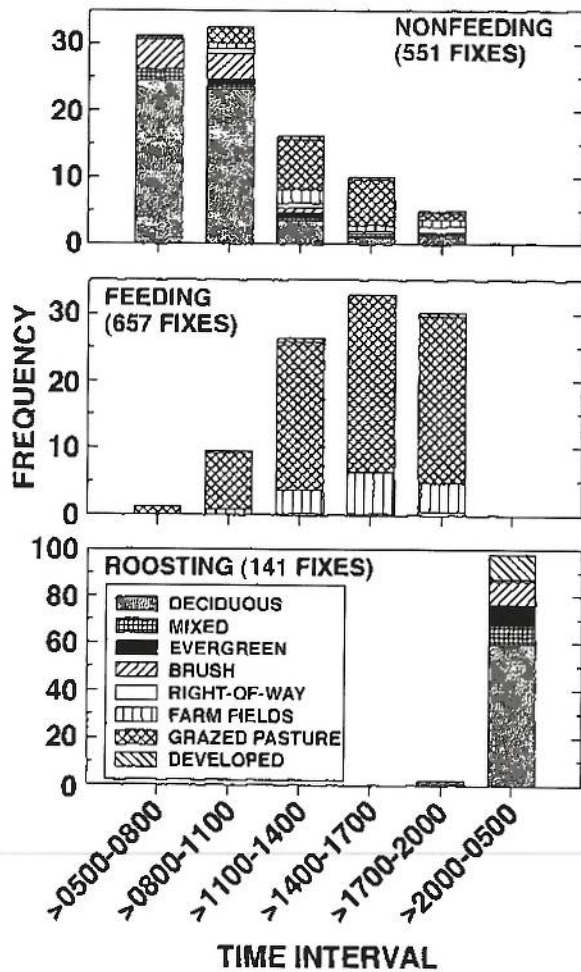
FIG. 2. Daily patterns of habitat use for different activities by 50 radio-tagged female Brown-headed Cowbirds throughout the day. The number of fixes is indicated in parentheses.
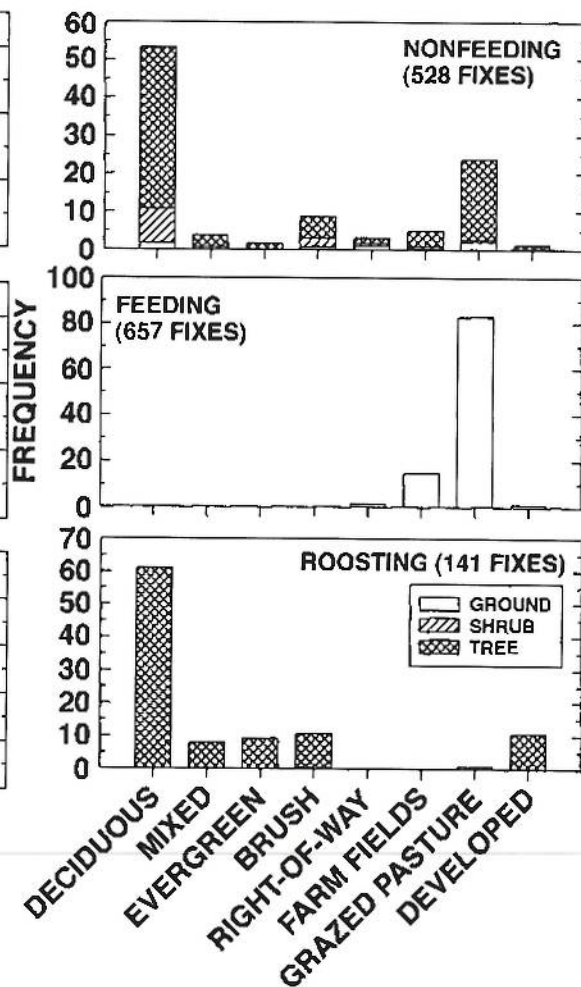
FIG. 3. Use of vegetation strata for different activities by 50 radio-tagged female Brown-headed Cowbirds located in different habitat types. The number of fixes is indicated in parentheses.

male after 1400 hours. In the morning from 0500 to 1100 hours, most fixes were from nonfeeding female cowbirds located in deciduous forest and brush (Fig. 2). Females were assumed to be breeding or searching for host nests at that time. Most fixes of females not feeding occurred in trees, but some were in shrubs and on the ground (Fig. 3). Fixes of female cowbirds identified as feeding tended to increase throughout the day, reaching a peak in the afternoon after 1400 hours (Fig. 2). Agricultural land, primarily grazed pasture (82.8% of fixes), contained 97.5% of fixes at which cowbirds were observed feeding. Some fixes of feeding females did occur in recently mowed road verges along I-68 (1.4%), developed land with mowed lawns (1.1%), and in other types of farm fields (cropland, 2.4%; old field/ ungrazed pasture, 12.3%). Feeding took place on the ground (Fig. 3). Roosting occurred at night after 2000 hours (Fig. 2). Roosts occurred in a wide range of habitat types, but particularly in deciduous forests. Some roosting did occur on developed land near houses (Fig. 2). Nearly all roosting occurred in trees (Fig. 3). Based

on observations made just before dusk, most roosts were composed of a single or only a few individuals.

Spatial ecology

Home and core ranges.—During any 24-h time period, distances representing consecutive movements by individual female cowbirds between breeding, feeding, and roosting sites were often considerable. Several kilometers would separate areas used for different activities (Table 1). Movements from feeding to roosting areas were significantly ($P < 0.05$) greater than those from roosting to breeding areas. Movements from breeding to feeding areas did not differ from those in the other two categories. As a result of these movements, home ranges were large, ranging from 105 to 6958 ha (1592 $\pm$ 287 ha, $\bar{X} \pm 1$ sE, $n = 27$). However, much of the area included within home ranges was little used by female cowbirds. Core ranges were generally much smaller, covering only 3.5 $\pm$ 0.5% ($\bar{X} \pm 1$ sE, $n = 27$, range 0.7–11.2%) of the home range, i.e., 31.6 $\pm$ 2.2

TABLE 1. The median distances between consecutive fixes resulting from movements between activity areas by radio-tagged female Brown-headed Cowbirds within a 24-h time interval, and the median distance between individual core-range centroids.

| | Distance between different activity areas or core-range types (km) | | | | | |
Statistic	Roost/ breed–feed	Breed–feed	Feed–feed	Feed–roost	Roost–breed	Overall
Consecutive movements						
Minimum		0.30		0.29	0.08	
Mean ± 1 SE		2.27[ab] ± 0.25		2.96[a] ± 0.43	1.35[b] ± 0.32	
n†		35		25	20	
Maximum		6.14		9.84	4.91	
Distance between centroids						
Mean ± 1 SE	3.88[ab] ± 0.39	4.15[ab] ± 0.45	3.39[b] ± 0.21	5.89[a] ± 1.10	3.10[b] ± 0.64	3.39 ± 0.29
n†	12	17	17	9	8	27

Note: Tukey's studentized range test was performed on all main effect means. Significant ($P < 0.05$) differences are indicated by dissimilar letters.

† The sample size indicates the number of radio-tagged individuals.

ha ($n = 27$, range 11.8–56.7 ha). These core ranges were also less variable in area (CV = 36.6) than were home ranges (CV = 93.7). Our radio-tagged female cowbirds exhibited little overlap of nonfeeding core ranges in comparison to core ranges used for feeding (Fig. 4).

Core-range types were identified based on the occurrence of a particular activity at at least two locations. Most of the 27 female cowbirds maintained separate breeding and feeding core ranges (Table 2). Roosts were either separate or combined with breeding core ranges. A smaller percentage of cowbirds maintained combined breeding/feeding or feeding/roosting core ranges. Individual core ranges usually numbered four per female cowbird, each averaging 7.3 ha (range 1.1–20.4 ha) in area (Table 2). Cowbirds generally had two feeding, one breeding, and one roosting core range, or some combination thereof. Multiple-use core ranges were often larger than those used for just one activity (Table 2). Breeding/feeding core ranges were significantly larger than breeding, feeding, roosting, or roosting/breeding core ranges. In these multiple-use core ranges, cowbirds feeding on agricultural land would often breed in adjacent forest. Feeding/roosting core ranges were not significantly different among core-range types. Because cowbirds typically had only one core range of a particular type, total area of core-range types was usually similar to that of individual core-range types (Table 2). Because there were normally two feeding core ranges per cowbird, the total area used for feeding was double that of an individual feeding core range (Table 2). Single-use core ranges were often oval or elongated in shape, with a higher edge/area ratio than multiple-use core ranges (Table 2). Hypothetical circular core ranges, which would have the lowest edge/area ratio for the same-sized range, are shown for comparison (Table 2). The long axis of the core range often paralleled a habitat edge formed by a linear opening in the forest canopy. Roosting core ranges had significantly larger edge/area ratios, i.e., were longer and narrower, than any other type of core range. In contrast, core ranges used for more than one activity were more circular in shape.

The nearest edge to a core-range centroid was dependent on the particular activity characterizing that centroid (Fig. 5). Breeding core-range centroids were typically located within forest, but near edges formed by roads, brush areas, or streams. Although there was no feeding within forest (see Fig. 3), centroids of feeding core ranges did occur near a forest edge if within agricultural land, or near an agricultural edge if within forest. A road or stream was also often the closest edge to a feeding core-range centroid when it was found within forest. A majority of cowbirds (92.6%) had road or stream openings within their core ranges; roads averaged 329 ± 69 m ($n = 27$, range 0–1367 m) in total length, and streams 248 ± 46 m ($n = 27$, range 0–862 m). Centroids of core ranges where roosting occurred were found within forest, near road, power line, and other forest-dividing corridors, which probably explains their high edge/area ratio. Core-range centroids were separated by 3.1–5.9 km, with feeding–roosting distances significantly ($P < 0.05$) greater than feeding–feeding or roosting–breeding distances (Table 1). Distances between centroids of the other core-range types were not significantly different. Distances between core-range centroids were somewhat greater than actual distances moved between activity areas over a 24-h period (Table 1).

Distribution of cowbirds and core-range centroids in relation to edge.—Of the 197 total morning breeding fixes of female cowbirds occurring within forest, 94.4% were ≤220 m from a forest edge. This zone included ~73.9% of the total forest area, leaving only 26.1% of the forest as core interior with little cowbird activity. Although sometimes occurring several hundred meters into the interior, female cowbirds often were <50 m from an edge in all major habitat types except grazed pasture (Fig. 6A). In grazed pasture, female cowbirds tended to be located more often 50–100 m from an

Power line
Road
2nd order or higher stream
Agricultural/developed land
Brush land
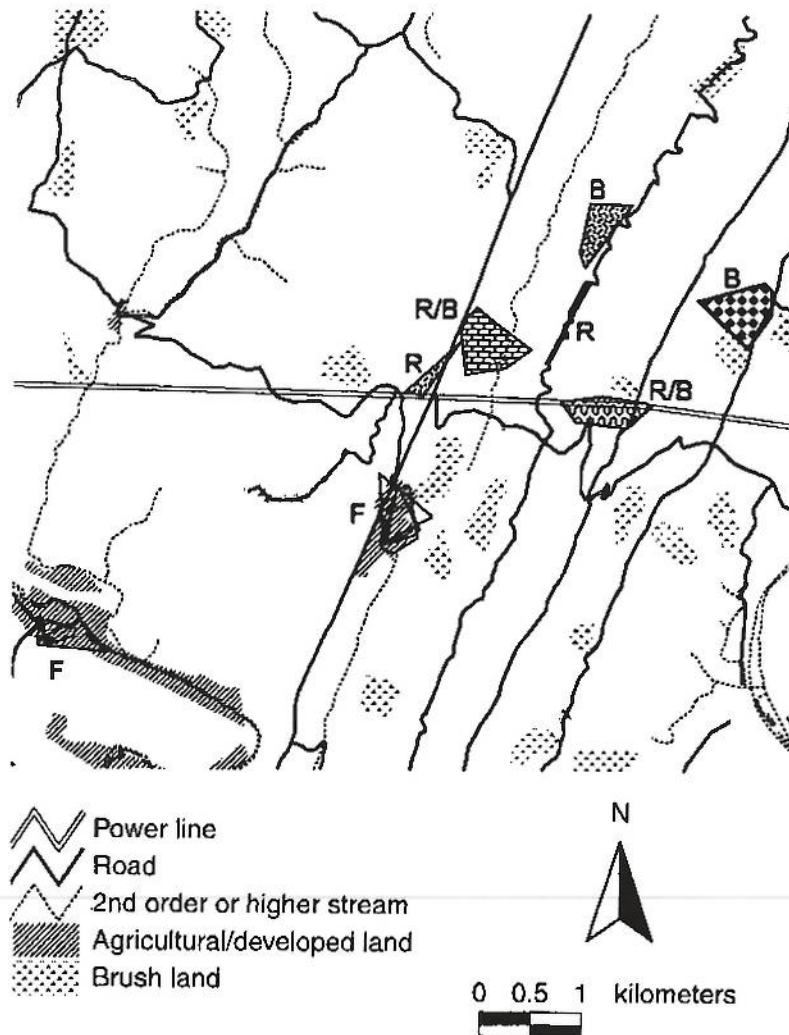
N

0 0.5 1 kilometers

FIG. 4.   Core ranges of four radio-tagged female Brown-headed Cowbirds on the central study area, western Maryland. Several corridor types, agricultural/developed land, and brush land are depicted; the remainder is composed of different forest types. All four cowbirds had two separate, overlapping feeding (F) core ranges. Two individuals had separate roosting (R) and breeding (B) core ranges, and the other two had combination roost/breed (R/B) core ranges. Nonfeeding core ranges of each individual are identified by a different fill pattern. A linear roosting core range is depicted along an unimproved dirt road. The central feeding area coincides with our trapping site on Rader's Farm. Note the association of feeding core ranges with agricultural/developed land. Nonfeeding core ranges were associated with power line, road, and second-order or higher stream corridors and brush (logged) land.

edge. The centroids of core ranges followed a similar pattern (Fig. 6B). Centroids located within forest had the highest occurrence within 0–50 m of an edge, whereas centroids within agricultural land had the highest frequency at least 50–100 m from an edge.

Habitat selection

Study area, home and core ranges.—The overall comparison of habitat use from MCP home ranges in relation to habitat availability within the study area gave $\lambda = 0.1298$ ($P < 0.0001$, by randomization); i.e., cowbirds did not establish home ranges at random. A ranking matrix ordered the habitat types in the sequence brush > deciduous > agriculture > mixed > power line > evergreen > developed (Table 3). There was no detectable difference within home ranges in the proportion of the top two habitats, implying that the order of their assigned ranks meant little. Agricultural land and mixed forest had significantly lower proportions within home ranges than did deciduous forest and brush, but higher proportions than did evergreen forest and developed land (Fig. 7). The proportion of power line corridors within home ranges was significantly greater than that of evergreen forest and developed land (Table 3). The proportional habitat use of evergreen forest was less than all other habitat types except for developed land (Fig. 7).

Habitat use within core ranges in comparison to hab-

TABLE 2. Core-activity-area spatial ecology of female Brown-headed Cowbirds in western Maryland. Significant ($P < 0.05$) differences in means ($\pm$ 1 SE) are indicated by dissimilar letters; the number of radio-tagged individuals in the sample is in parentheses.

Variable	Core-range type						Overall
	Breed	Breed/feed	Feed	Feed/roost	Roost	Roost/breed	
Percentage of birds	70.4 (27)	14.8 (27)	88.9 (27)	16.7 (24)	41.7 (24)	54.2 (24)	
No. core ranges	1.2 ± 0.1 (19)	1.0 ± 0.0 (4)	1.8 ± 0.1 (24)	1.0 ± 0.0 (4)	1.0 ± 0.0 (10)	1.0 ± 0.0 (13)	3.7 ± 0.2 (24)
Individual core-range area (ha)	8.8^b ± 1.9 (19)	21.8^a ± 2.8 (4)	8.2^b ± 1.1 (24)	11.2^{ab} ± 3.6 (4)	1.8^b ± 0.8 (10)	9.8^b ± 2.7 (13)	7.3 ± 0.9 (27)
Total core-range area (ha)	9.5^{ab} ± 1.9 (19)	21.8^a ± 2.8 (4)	16.5^a ± 1.9 (24)	11.2^{ab} ± 3.6 (4)	1.8^b ± 0.8 (10)	9.8^{ab} ± 2.7 (13)	31.6 ± 2.2 (27)
Edge/area ratio							
Actual	0.11^b ± 0.07 (19)	0.01^b ± 0.00 (4)	0.11^b ± 0.05 (24)	0.02^b ± 0.01 (4)	0.84^a ± 0.32 (10)	0.03^b ± 0.01 (13)	0.04 ± 0.01 (27)
Circle†	0.03 ± 0.01 (19)	0.01 ± 0.00 (4)	0.04 ± 0.01 (24)	0.02 ± 0.01 (4)	0.17 ± 0.06 (10)	0.02 ± 0.00 (13)	0.01 ± 0.00 (27)

Note: Tukey's studentized range test was performed on all main-effect means.

† The edge/area ratio of a hypothetical circular core range covering the same area as the actual core range.

itat availability within MCP home ranges also differed significantly from random ($\lambda = 0.0349$, $P < 0.0001$ by randomization; Table 3). The ranking matrix for core ranges indicated agriculture > deciduous > evergreen > mixed > brush > developed > power line. Agricultural land was used significantly more than most other habitat types (Table 3, Fig. 7). Deciduous forest was used significantly more than mixed, evergreen, brush, and power line. Except for significantly higher use of agricultural land than developed land within core ranges, there was no difference in proportional habitat use of developed land within core ranges compared to that within MCP home ranges. Proportional habitat use of power lines was significantly less than that of deciduous forest and agriculture within core ranges, when compared to their availability within MCP home ranges.

Breeding core range vs. forest interior.—Based on point counts, forest interior ≥250 m from an opening was not used by female Brown-headed Cowbirds (Evans and Gates 1997). There were significant ($P < 0.05$) differences in forest habitat characteristics between cowbird breeding core ranges and forest interior sites (Table 4). Breeding core ranges had significantly ($P < 0.005$) higher numbers of seedlings and saplings and large (≥22.5 cm dbh) snags than did forest interior sites. In contrast, forest interior habitats had higher numbers of small trees (≥7.5–30 cm dbh) and small snags (≥7.5–22.5 cm dbh) than did breeding core ranges, whereas there was no difference in the number of large (≥30 cm dbh) trees. Forest interior habitats also had significantly ($P < 0.01$) higher overstory canopy cover, i.e., a more closed canopy, than did breeding core ranges. There was no difference in overstory canopy heights between the two habitat types.

Variables that were significant and normally distributed were used in canonical discriminant analysis (Table 5). A test of homogeneity of within-covariance ma-

trices was not significant ($\chi^2 = 10.907$, df = 15, $P = 0.759$); therefore, a pooled covariance matrix was used in the discriminant analysis. The eigenvalue and associated canonical correlation denote the relative ability to separate the two groups. The canonical correlation indicated that the first canonical variable (CAN-I) was highly correlated with the groups. Wilks' λ, an inverse measure of the discriminating power in the original variables, demonstrated that the variables contained a significant amount of discriminating power ($\lambda = 0.648$, $F = 4.987$, df = 5, 46, $P < 0.001$). One canonical variable (CAN-I) was derived from the analysis. Correlation of each habitat variable with CAN-I represents its relative contribution to that function and identifies those habitat variables that contributed most to differentiation (Table 5).

To evaluate differences in the segregation of breeding core range and forest interior habitats, we looked at the location of the two types along CAN-I. Non-overlap of the 95% CI of the univariate means on CAN-I verified the significant separation of the two habitat types on this axis. CAN-I can be categorized by inspecting the sign and magnitude of the correlation of the associated variables (Table 5). Cowbird breeding core ranges had higher numbers of seedlings and saplings and large snags, and lower numbers of small snags and deciduous trees in the size categories ≥15–22.5 and ≥22.5–30 cm dbh than did forest interior habitats. Using cross validation classification, our statistical model was able to correctly classify 74.1% ($n = 27$) of breeding core range and 72.0% ($n = 25$) of forest interior habitats, indicating that the model had high predictability in classifying habitat types.

DISCUSSION

Spatial and temporal patterns

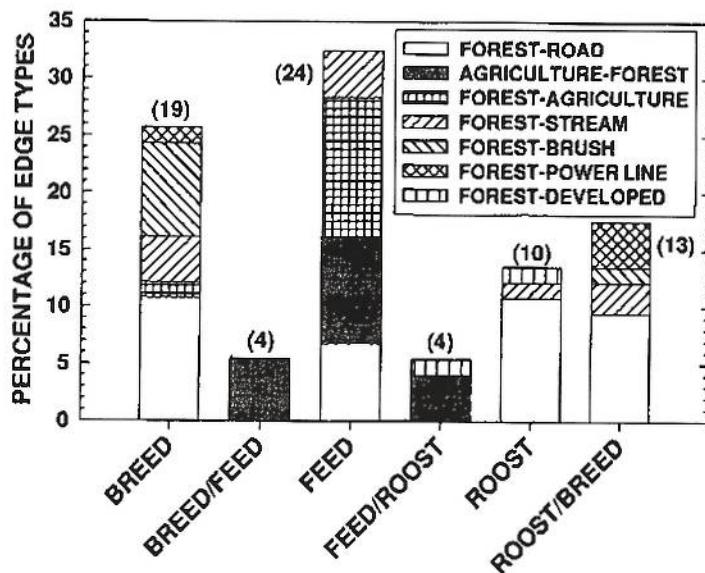The spatial and temporal patterns of habitat use by female cowbirds in western Maryland were similar to

FIG. 5. Percentage of different edges nearest the core-activity-area centroid, where the centroid is located in the first-named habitat type. The number of radio-tagged individuals in the sample is in parentheses.
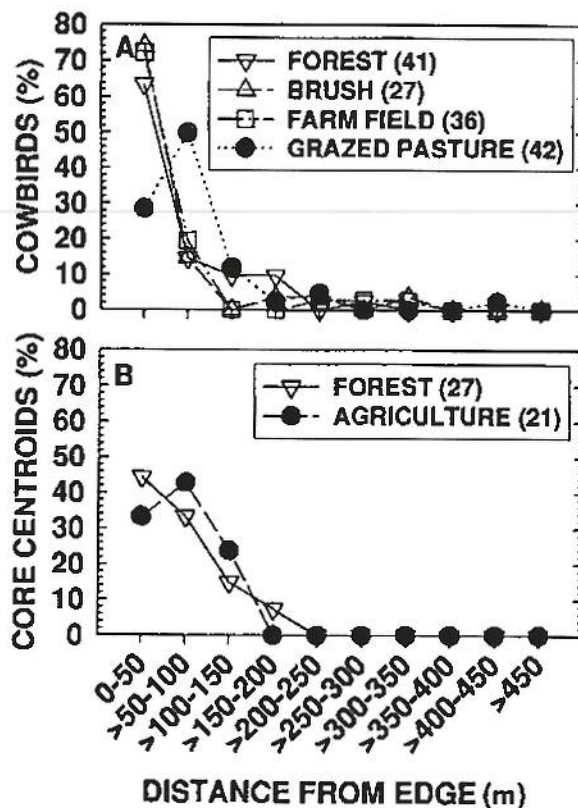

FIG. 6. The frequency distribution of median distances (by 50-m intervals) from an edge of (A) different radio-tagged female Brown-headed Cowbirds and (B) their core-range centroids in different habitat types. The forest habitat type includes deciduous, mixed, and evergreen forests. The agriculture habitat type for cowbirds has been subdivided into farm fields and grazed pasture, where farm fields include old field, ungrazed pasture, and crop field, i.e., areas of taller vegetation where livestock are absent. The number of radio-tagged individuals in the sample is in parentheses.

those reported elsewhere (Rothstein et al. 1980, 1984, 1986, 1987, Dufty 1982, Verner and Ritter 1983, Thompson 1994, Coker and Capen 1995). Home ranges covered hundreds to thousands of hectares ($\bar{X} = 1592$ ha, $n = 27$). Home ranges in western Maryland were much larger than the 405 ha reported for cowbirds in the Sierra Nevada (Rothstein et al. 1984). However, only ~10 ha of the home range in Maryland was actually used by female cowbirds for breeding. This value is much smaller than the 78 ha reported for female morning ranges in the Sierra Nevada, or the 20.4 ha reported for New York (Dufty 1982, Rothstein et al. 1984). If the female cowbirds in New York actually fed on their breeding ranges (Dufty 1982), then this range size would be comparable to our 21.8-ha breeding/feeding core range. Differences could also be related to the density of conspecifics or potential host nests, the landscape mosaic, or even to differences in methodology (Rothstein et al. 1984).

In the central Appalachians, radio-tagged female cowbirds usually maintained breeding and feeding core ranges spatially separated from one another. Most individuals used one core range for breeding; these core ranges tended to overlap minimally, suggesting that there may be some type of spatial segregation among females (Dufty 1982, Rothstein et al. 1984). Females in the Sierra Nevada also had one morning range or breeding site (Rothstein et al. 1984). Commuting distances between breeding and feeding locations averaged 2.3 km in western Maryland, but 1.2–1.5 km in the Midwest (Raim 1978, Thompson 1994) and 4.0 km in the Sierra Nevada (Rothstein et al. 1984). In New York, some females had feeding sites lying entirely within their breeding range (Dufty 1982). We observed that 14.8% ($n = 27$) of radio-tagged individuals in western Maryland showed temporal and spatial overlap of breeding and feeding activities. Females with a com-

TABLE 3. Simplified ranking matrices for 27 cowbirds, based on comparing proportional habitat use within MCP home ranges with proportions of total available habitat types and comparing the proportional habitat use within core ranges with the proportion of each habitat type within the bird's MCP home range. Each element in the matrix was replaced by its sign; a triple sign represents significant deviation from random at $P < 0.05$. A positive value indicates that the row habitat was used more than the column habitat; a negative value indicates the opposite.

	Deciduous	Mixed	Evergreen	Brush	Power line	Agriculture	Developed	Rank
Study area vs. home ranges								
Deciduous								2
Mixed	– – –							4
Evergreen	– – –	– – –						6
Brush	+	+++	+++					1
Power line	–	–	+++	–				5
Agriculture	– – –	+	+++	– – –	+			3
Developed	– – –	– – –	– – –	– – –	– – –	– – –		7
Home range vs. core ranges								
Deciduous								2
Mixed	– – –							4
Evergreen	– – –	+						3
Brush	– – –	–	–					5
Power line	– – –	–	–	–				7
Agriculture	+++	+++	+++	+++	+++			1
Developed	–	–	–	–	+	– – –		6

bination breeding/feeding core range were assumed to parasitize bird nests located in pasture or nearby forest edges.

In western Maryland, most cowbirds had at least two feeding core ranges separated by an average of 3.4 km. Females in the Sierra Nevada also had two ($\bar{X} = 1.6$) feeding sites; however, they were separated by only 1.1 km (Rothstein et al. 1984). Feeding aggregations of ≥12 individuals occurred in late afternoon in western Maryland. They were most often found in grazed pasture on agricultural lands on the periphery of the forest. When feeding in grazed pasture, female cowbirds tended to be located more often 50–100 m from an edge where cattle or other livestock were most often grazing. Cowbirds probably gather in such locations because of

abundant food, presence of livestock, and/or short grass (Rothstein et al. 1986). The sparse occurrence of female cowbirds in more distant categories could reflect limits imposed on distribution by the area and configuration of farm fields or grazed pasture.

Cowbirds in western Maryland would normally fly 3.0 km from feeding to roosting locations in deciduous forest or other habitat types near a linear canopy opening. They roosted closer to their breeding core ranges (1.3 km) than was reported for the Midwest (3.6 km; Thompson 1994). Roosting occurred within a separate core range or, frequently, in conjunction with the breeding core range. Rothstein et al. (1984) also reported that females returned to their morning ranges just before dark, i.e., they roosted near breeding ranges. We
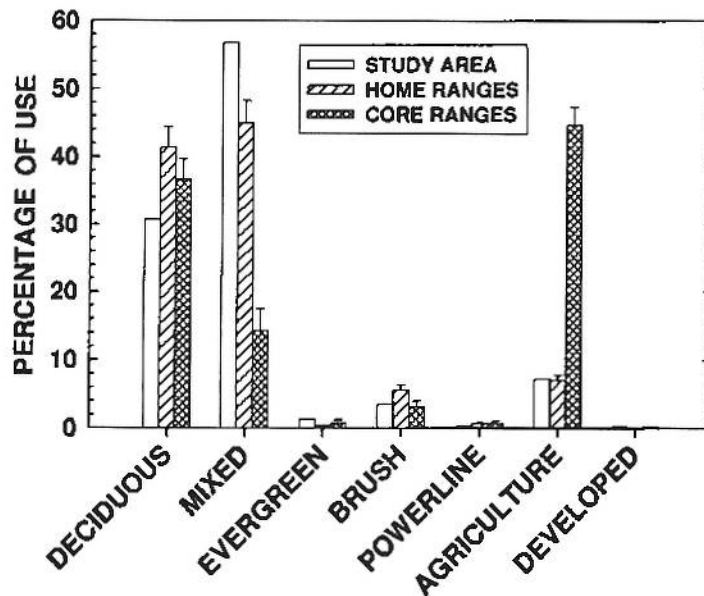
FIG. 7. Habitat use by 27 female Brown-headed Cowbirds in the central Appalachian Mountains of western Maryland (mean + 1 SE). For significance of observed differences, see Table 3.

TABLE 4. Means and 95% CI (in parentheses) of variables sampled in forest at breeding core-range centroids ($n = 27$) of female Brown-headed Cowbirds and at random sites ($n = 25$) within forest interior, i.e., ≥ 250 m from an opening, in western Maryland.

Variable	t test	Wilcoxon (z score)	Breeding core	Forest interior
Seedlings/saplings (no./0.006 ha)				
≥ 1.4 m in height, <7.5 cm dbh†,‡	3.267**	−2.870**	23.0 (17.3–30.3)	12.1 (9.0–16.2)
Deciduous trees (no./0.08 ha)				
$\geq 7.5–15$ cm dbh§	−1.890	1.934	11.4 (8.3–14.9)	16.5 (12.1–21.4)
$\geq 15–22.5$ cm dbh†,‡	−3.830***	3.414***	4.0 (2.7–5.7)	10.0 (7.0–13.9)
$\geq 22.5–30$ cm dbh‡,§	−3.281**	3.039**	5.0 (3.3–7.0)	9.4 (7.5–11.5)
≥ 30 cm dbh	−0.794	0.735	8.1 (6.7–9.5)	9.2 (6.7–11.6)
Evergreen trees (no./0.08 ha)				
≥ 7.5 cm dbh‖		1.296	0.7 (0.1–1.2)	5.4 (1.2–9.5)
Snag trees (no./0.08 ha)				
$\geq 7.5–22.5$ cm dbh‡	−3.184**	2.871**	7.1 (0.1–1.2)	11.8 (9.5–14.2)
≥ 22.5 cm dbh‡,§	2.254*	−2.224	2.9 (2.1–3.8)	1.7 (1.1–2.4)
Overstory canopy				
Height (m)	1.509	−1.365	22.5 (21.2–23.8)	21.2 (20.0–22.4)
Cover (%)‖		2.731**	94.1 (89.6–98.7)	98.8 (97.8–99.8)

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.
† Variable was transformed using $Y = \log_{10}(X + 1)$. Means and 95% CI were derived from the antilogarithms.
‡ Variable was used in canonical discriminant analysis.
§ Variable was transformed using $Y = \sqrt{X + 1}$.
‖ Variable could not be normalized; therefore, the Wilcoxon-Mann-Whitney two-sample test was used to determine significant ($P < 0.05$) differences.

and other investigators have also observed individuals roosting on feeding core ranges (Rothstein et al. 1984, Thompson 1994). Although large communal roosts have been reported for cowbirds elsewhere (Verner and Ritter 1983, Thompson 1994), in the central Appalachians of western Maryland, cowbirds roosted singly or in small aggregations in trees near edges.

Landscape or biogeographic factors may influence the use of forest edges by cowbirds (Thompson 1994, Hahn and Hatfield 1995, Thompson et al., *in press*). In

TABLE 5. Summary of canonical discriminant analysis conducted on female Brown-headed Cowbird breeding core-range and forest-interior habitats in western Maryland. Only one canonical variable, CAN-I, was derived from the analysis.

	CAN-I
Eigenvalue	0.542
Relative percentage of eigenvalue associated with CAN-I	100.0
Canonical correlation	0.593
Total-sample correlations between CAN-I and the original habitat variables	
Seedlings/saplings (no./0.006 ha)	
≥ 1.4 m in height, <7.5 cm dbh†,‡	−0.707***
Deciduous trees (no./0.08 ha)	
$\geq 15–22.5$ cm dbh†,‡	0.803***
$\geq 22.5–30$ cm dbh‡,§	0.710***
Snag trees (no./0.08 ha)	
$\geq 7.5–22.5$ cm dbh‡	0.692***
≥ 22.5 cm dbh‡,§	−0.512***

*** $P < 0.001$.
† Variable was transformed using $Y = \log_{10}(X + 1)$. Means and 95% CI were derived from the antilogarithms.
‡ Variable was used in canonical discriminant analysis.
§ Variable was transformed using $Y = \sqrt{X + 1}$.

our study area, we found cowbirds to be associated with edges when in deciduous forest during the morning breeding period. Use of meadows in forested areas, riparian corridors, or open coniferous forest near patches of shrubs or small aspens, i.e., edges, have also been reported in the Sierra Nevada (Verner and Ritter 1983, Rothstein et al. 1984). This association with edges is perhaps due to the high numbers of nesting birds in such habitats that could serve as hosts (Gates and Gysel 1978, Rothstein et al. 1980, Chasko and Gates 1982, Evans and Gates 1997). Furthermore, significantly greater proportions of species inhabiting forest edges or second growth are reported to be cowbird hosts (Robinson et al. 1995b). Presumably, in moderately fragmented landscapes with scattered feeding areas and no scarcity of hosts, cowbirds would be less numerous and more likely to be associated with forest edges (<250 m from forest edges) (Rothstein and Robinson 1994, Robinson et al. 1995a, b). In highly fragmented landscapes with numerous feeding areas, cowbirds would be quite abundant and, because of the scarcity of hosts, more likely to saturate the available breeding habitat (>600 m from forest edges) (Robinson et al. 1995a, b, Hahn and Hatfield 1995, Thompson et al., in press).

Habitat selection

Habitat selection differed at each level, with female cowbirds initially selecting a home range with higher proportions of brush and deciduous forest than available within the study area (first level), followed by the selection of core ranges with high proportions of agriculture and deciduous forest (second level). The first level of habitat selection appeared to focus primarily on potential breeding habitats (deciduous forest near the edge, e.g., forest–brush edges), whereas the second level included both feeding (agricultural land) and breeding (deciduous forest) habitats. The overall importance of deciduous forest is demonstrated by its prominence at each level of habitat selection, whereas agricultural land did not attain its highest ranking until the second level of habitat selection. Noteworthy was the drop of brush in the ranking from number one for home ranges to number five for core ranges. In the Midwest, cowbirds were frequently located in forest and shrub–sapling, i.e., brush, habitats in the early morning (Thompson 1994). We suggest that the importance of brush may be due to the formation of edge habitats, not that brush is a prerequisite cover type. Breeding core ranges typically did not include a high proportion of brush, but were often located in deciduous forest next to brushy openings.

Breeding core ranges had higher numbers of seedlings and saplings and large snags, and a more open canopy than that found within forest interior >250 m from an opening. Brittingham and Temple (1996) found a more open canopy and a higher density of small shrubs and saplings (0.5–1 m) at nests parasitized by

cowbirds. In addition, cowbirds frequently move about in the lowest vegetation zones (≤1 m) in the forest (Hahn and Hatfield 1995). Although Brittingham and Temple (1996) found no relationship with number of dead trees, snags were not tallied into individual dbh size classes for comparison. Others have reported that parasitism rates can be higher on nests near snags (Anderson and Storer 1976). Cowbirds often use snags as perches from which they may observe nesting activities of potential host species (Norman and Robertson 1975; J. E. Gates and D. R. Evans, personal observation).

Conservation implications

To provide additional forest interior free of cowbirds in western Maryland, it would be necessary to have interior habitat >250 m from openings. Unfortunately, many managed forests have extensive road networks, leaving little interior, closed-canopy forest available. Roads with open canopies (<10% canopy cover) tend to be more attractive to cowbirds than roads with closed canopies (>90% canopy cover) (Evans and Gates 1997). To minimize cowbird use, roads should be kept as narrow as possible to avoid opening the canopy and creating edge habitat. Some roads, especially those forest roads used only for timber extraction, should be evaluated for permanent closure and allowed to revegetate naturally or to be planted with native plants. However, because cowbird numbers may be regulated by large-scale biogeographic and regional landscape patterns, minimizing internal edges within forest landscapes in other biogeographic regions may not produce the expected results (Thompson et al., in press).

The interspersion of cowbird feeding areas should be minimized within forest landscapes, taking into account known commuting distances (Thompson 1994, Thompson et al., in press). The power line corridor has the potential to provide both breeding (forest–power line corridor edge) and feeding habitat (mowed grass). To eliminate any possible use as a feeding area, we suggest that the corridor not be mowed or planted with food plants, and that shrubby vegetation within it be maintained by active management. Mowing of grass within utility corridors and along roadsides within forested areas merely creates feeding areas for cowbirds, particularly during the breeding season. Because of the occurrence of dispersed feeding areas, trapping and removal of cowbirds at any one or two feeding areas are unlikely to be successful in reducing numbers in breeding habitats (Rothstein et al. 1987).

Selective removal of large snags near certain edge types should be evaluated as a management option; however, its impact on cavity-nesting birds and other wildlife should be weighed against the potential benefits to open-nesting passerines. Furthermore, the loss of canopy cover following the mortality of large overstory trees near forest edges, particularly along closed-canopy roads, probably contributes to the increase in numbers of seedlings and saplings. This vegetation lay-

er provides cover for ground- and shrub-nesting birds. Breeding bird density is often positively associated with vegetation volume (Mills et al. 1991, Evans and Gates 1997). Where edges are a permanent landscape feature, managers might explore ways of reducing the density of seedlings and saplings in the edge zone, particularly where it is feasible. Alternatively, one could create a wider zone of seedlings and saplings at the forest edge, particularly in forest tracts where the loss of interior habitat would be negligible. The management goal would be to reduce the number of nests or to disperse the nests of potential host species within the edge zone, making these areas less profitable for cowbirds searching for nests to parasitize.

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