

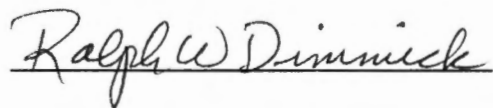
To the Graduate Council:

I am submitting herewith a thesis written by Richard Kirk Miles entitled "Modeling the Effects of Landscape Structure on the Spatial Distribution of Brown-headed Cowbirds and Nest Parasitism in Forest Openings." I have examined the final copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Wildlife and Fisheries Science.



David A. Buehler, Major Professor

We have read this thesis and
recommend its acceptance:





Accepted for the Council:



Associate Vice Chancellor and
Dean of The Graduate School

**Modeling the Effects of Landscape Structure on the Spatial Distribution
of Brown-headed Cowbirds and Nest Parasitism in Forest Openings**

A Thesis

Presented for the

Master of Science

Degree

The University of Tennessee, Knoxville

Richard K. Miles

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ABSTRACT

Apparent declines of breeding neotropical migrant land bird populations in the United States over the last 25 years have been associated with increases in populations of brown-headed cowbirds (*Molothrus ater*). Because cowbirds parasitize nests of many of these species, such parasitism may be a major contributing factor to these declines. I used avian-census data and landscape-level habitat variables to develop models predicting the presence/absence of cowbirds and nest parasitism in forest openings in a predominately forested (89%) landscape at Land Between the Lakes in Kentucky and western Tennessee.

Cowbird populations were surveyed in forest-opening and interior-forest settings between 15 May and 1 July 1993 and 1994, using 10-minute, 50-m fixed-radius point counts. Cowbirds were present within 50 m in 62 (27%) of 227 forest-opening and interior forest points. Cowbirds were present at forest-opening edges more often than at interior forest points ($P \leq 0.05$). Cowbird presence did not differ by distance from edge for interior-forest points (200, 300, 400, and 500-m points) ($P > 0.05$). Overall cowbird abundance per point (forest-opening and interior-forest points) was 0.53 cowbirds/point. Cowbirds were more abundant at forest-opening edges than at interior forest points ($P \leq 0.05$). Cowbird abundance did not differ by distance from edge for interior-forest points ($P > 0.05$).

Potential cowbird host nests were located and monitored between 15 May and 1 July 1994. A total of 195 active nests of 20 species known to be parasitized by brown-

headed cowbirds were located and monitored. Of these nests, 23.6% (46 nests) were parasitized by cowbirds. The percentage of nests parasitized did not differ across distance from nest to nearest edge categories ($P > 0.05$). Forest species were more heavily parasitized (30.5% of 82 nests) than were edge species (18.6% of 113 nests parasitized) ($P = 0.03$).

A logistic regression model was developed to predict cowbird presence/absence in forest openings based on 17 landscape and avian census variables associated with each opening. Forest opening size (ha), average height of vegetation in the opening (m), and the number of potential cowbird foraging locations within a 2-km radius of the opening were the best predictors of cowbird presence/absence in forest openings. Larger forest openings, with lower average vegetation heights that were near a high concentration of foraging locations were the most likely to have cowbirds present. Using these model variables, predicted and observed responses were concordant 90.0% of the time, and forest openings were correctly classified for cowbird presence/absence 82.9% of the time.

A logistic regression model was developed to predict the presence/absence of nest parasitism in forest openings based on 20 landscape and avian census variables associated with each opening. Forest opening size (ha), average height of vegetation in the opening, and the number of potential cowbird foraging locations within 2 km of the opening were the best predictors of the presence of nest parasitism presence/absence in forest openings. Smaller forest openings, with higher average vegetation heights that were near a high concentration of foraging locations were most likely to have nest parasitism present.

Using these model variables, predicted and observed responses were concordant 85.2% of the time and forest openings were correctly classified for nest parasitism presence/absence 81.8% of the time.

A total of 148 point counts and recorded playback sessions of cowbird vocalizations were conducted in forest-opening and interior-forest settings between 15 May and 1 July 1993. I assessed the effects of point-count duration cowbird detection and estimates of cowbird abundance. I also compared the efficiency of point-count versus recorded-playback techniques for detecting cowbirds and estimating cowbird abundance. Ten-minute point counts were suggested to be the best option for managers initiating efforts to monitor cowbird populations. Point count and playback techniques yielded similar results ($P > 0.05$) for detecting cowbird presence and estimating cowbird abundance.

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CHAPTER 1

I. GENERAL INTRODUCTION

The brown-headed cowbird (Molothrus ater) is the only obligate brood parasite in North America whose range extends into Tennessee and Kentucky. Prior to European settlement, the brown-headed cowbird was confined primarily to the plains and prairies west of the Mississippi River (Brittingham and Temple 1983). In this setting, cowbirds were closely associated with herds of nomadic bison (Bison bison), and were dependent on the grazing activity of these large ungulates to create suitable feeding conditions (Robinson et al. 1993).

The clearing of eastern forests for farming and the widespread introduction of livestock allowed brown-headed cowbirds to gradually expand their range eastward (Mayfield 1965). By the late 1800's, cowbirds were widely distributed but uncommon in the eastern United States. The impact of cowbird parasitism on forest songbirds was probably minimal (Brittingham and Temple 1983).

Although the range expansion of cowbirds in eastern North America has apparently stabilized, in recent decades cowbird abundance has generally increased (Brittingham and Temple 1983, Mayfield 1965). Brittingham and Temple (1983) examined regional Audubon Christmas bird count records from 1900 to 1980 for 11 southern states (below 37° latitude from Texas to the Atlantic Ocean) where most cowbirds in the eastern United States migrate to spend the winter. The number of counts on which cowbirds were recorded ranged from 1 in 1900 to 205 in 1980. Cowbirds were

reported with increasing frequency throughout the time period, indicating that cowbird numbers were steadily increasing. Peterjohn and Sauer (in press) analyzed 27 years (1966-1992) of North American Breeding Bird Survey Data and reported that cowbird populations nationwide actually declined during this period at an average rate of 0.9% per year. Cowbird populations were generally increasing during 1966-1976, but populations began to decline during 1977-1984, with the most extensive declines occurring after 1985. These declines were most evident from the Maritime Provinces south along the Appalachian Mountains, around the upper Great Lakes, and in the southern Great Plains.

In the past 20 years, there has been a marked increase in concern over population declines of many avian species that breed in temperate North America and winter in the tropics (neotropical migrants) (e.g., Askins et. al 1987, Robbins et. al 1989, Terborgh 1989, Finch 1991). Forest fragmentation on the breeding grounds and deforestation in the tropics have frequently been mentioned as likely causes of these population declines (Askins et al. 1990, Terborgh 1992). Numerous studies have shown that local avian populations in the eastern United States are clearly reduced by forest fragmentation (Robbins 1979, Whitcomb et al. 1981, Ambuel and Temple 1982, Wilcove 1988, Terborgh 1989, Askins et al. 1990 Wilcove and Robinson 1990).

Habitat fragmentation occurs when a large, fairly continuous tract of vegetation is converted to different vegetation types such that only scattered fragments of the original type remain (Faaborg et al. 1993). In general, habitat fragmentation results in both a quantitative and qualitative loss of habitat (Temple and Wilcox 1986). The most obvious

effect of fragmentation is an outright loss of a particular habitat that a species or groups of species may depend on. Fragmentation can also lead to a decrease in habitat quality for many songbirds. Habitat quality decreases for some species when there is an increase in the amount of edge relative to interior area (Faaborg et al. 1993). Negative edge effects may include: (1) high rates of nest predation near edge habitat (Gates and Geysel 1978, Wilcove 1985, Small and Hunter 1988, Yahner and Scott 1988); (2) high rates of interspecific competition in edge habitat (Ambuel and Temple 1983); and (3) high rates of brown-headed cowbird parasitism near edge habitat (Brittingham and Temple 1983, Gates and Geysel 1978, Robinson et al. 1993).

Cowbirds pose a potential threat to many hosts because of the extraordinary fecundity of the female cowbird and the extent to which cowbird parasitism reduces reproductive success of host species (Robinson et al. 1993). Female cowbirds lay, on average, 30-40 eggs per season (Payne 1965, Payne 1976, Scott and Ankey 1980, Scott and Ankey 1983, Rothstein et. al 1986). Thus, relatively small numbers of female cowbirds can parasitize many nests. Robinson et al. (1993) listed the following reasons for the negative impact of nest parasitism on host productivity: (1) female cowbirds usually remove one host egg from 33% to 90% of all parasitized nests (Friedmann 1963, Weatherhead 1989, Sealy 1992); (2) cowbird eggs are unusually thick and when laid often break host eggs (Spaw and Rowher 1987, Roskaft et al. 1990); (3) cowbird eggs have a short incubation period of 11 days when compared with 12-14 days for most hosts (Nice

1953, Friedmann 1963); and (4) cowbird nestlings grow faster, beg more loudly, and have larger gapes than host nestlings (Friedmann 1929, Ortega and Cruz 1991).

Because cowbirds do not raise their own young, their two major activities during the breeding season, foraging and nest searching, can be carried out in different locations. Rothstein et al. (1984) found that cowbirds in the Sierra Nevada Mountains regularly commuted up to 7 km between feeding and nest searching areas. Similarly, Smith (1981) noted that cowbirds breeding on small islets off Vancouver Island regularly commuted up to 7 km to feed on larger islands. Cowbirds typically forage in areas such as pastures, livestock feedlots, mowed lawns and roadsides, recently plowed and planted row crop fields, campgrounds, bird feeders, gravel roadsides, and logging roads (Robinson et al. 1993). Breeding areas are typically host-rich zones such as open or partially harvested forest (Rothstein et al. 1984), riparian zones (Airola 1986), clear cuts (Verner and Ritter 1983), and edges between forests and forest openings (Gates and Geysel 1978). The ability of cowbirds to commute between preferred feeding and breeding areas suggests that the dispersion small feeding areas may allow access to large expanses of breeding habitat (Rothstein et al. 1984).

The relationship between cowbirds, nest parasitism, and landscape patterns in highly fragmented settings has been well documented (Robinson 1988, Wilcove and Robinson 1990, Robinson 1992, Bollinger and Linder 1994). However, relatively little research has focused on these relationships in predominately forested matrices with limited fragmentation which typifies large expanses of forested land in eastern North America. In

addition, most attempts to characterize cowbird-habitat relationships have been descriptive in nature. I found only 2 studies (Coker and Capen in review, and Gustafson and Crow 1994) that attempted to build predictive models of cowbird landscape-level habitat relationships.

Baseline data on local cowbird distribution and abundance are essential for managers to determine the potential threat of cowbird parasitism to songbird populations across a given landscape. Most avian censusing techniques (i.e., point-counts) are primarily designed to detect singing males on relatively small breeding territories (Ralph and Scott 1981). However, during the breeding season, cowbirds are highly mobile (Rothstein et al. 1984, Robinson et al. 1993), less territorial and have larger home ranges (Scott and Ramsey 1981). No one has evaluated techniques specifically designed for censusing brown-headed cowbirds.

This study represents the first step in identifying potential problem areas and developing management strategies associated with nest parasitism by the brown-headed cowbird in a primarily forested (89%) landscape in Tennessee and Kentucky. I used point-count surveys, landscape-level habitat variables, and habitat modeling with multivariate statistical techniques to identify the landscape-habitat variables that most accurately predicted the presence of cowbirds and nest parasitism in forest openings. I also evaluated two avian censusing techniques (point-counts and recorded playbacks) specifically for monitoring brown-headed cowbird populations.

Results from this research can assist land managers by predicting the possible impacts of land management activities on the distribution of cowbirds and nest parasitism across the landscape. Accordingly, management alternatives can be weighed based on their relative impacts.

CHAPTER 2

II. LANDSCAPE LEVEL MODELS

INTRODUCTION

Brown-headed cowbird abundance, spatial distribution, and nest parasitism frequencies are often strongly related to levels of habitat fragmentation and the interspersions of cowbird foraging habitats across a given landscape (Airola 1986, Robinson et al. 1993, Donovan et al. in press, Thompson et al. in press). In highly fragmented settings, cowbirds may be abundant and saturate the available habitat. Conversely, in predominately forested settings cowbirds may be less abundant and limit their breeding activity in and around existing edge habitat.

Traditionally, "edge effect" has been defined as an increase in abundance and diversity of wildlife found along the boundary between two habitat types (Leopold 1933). In many cases, wildlife management has been considered synonymous with creating edge habitat (Harris 1988). The creation of forest openings (i.e., wildlife food plots) is a common tool used by land managers, usually in an effort to increase habitat quality for game species such as white-tailed deer (Odocoileus virginianus) and eastern wild turkey (Meleagris gallopavo). There is little information on how the creation of edge habitat in

extensively forested areas may affect cowbird abundance and parasitism frequencies where cowbirds may not have had previous access.

The application of mathematical models predicting cowbird distribution and nest parasitism across landscapes managed under different strategies could help land managers decide where the creation of edge-habitat would produce the least negative impact from cowbird parasitism on songbirds. A thorough literature review revealed only 2 studies that attempted to build predictive models of cowbird landscape-habitat relationships.

Coker and Capen (in review) developed an empirical landscape-level habitat model predicting cowbird presence in disturbance patches in a primarily forested (94%) portion of the Green Mountain National Forest in central Vermont. Disturbance patch size, distance to closest chronic (permanently maintained) disturbance patch, and the number of livestock areas within 7 km of disturbance patches were the best predictors of cowbird presence/absence in disturbance patches (80.3% of patches correctly classified for cowbird presence/absence). Larger disturbance patches, that were either chronic or close to a chronic disturbance patch and near a high concentration of livestock areas were most likely to contain cowbirds. However, they had no data on nest parasitism in disturbance patches or cowbird penetration from patches into surrounding forest habitat.

Gustafson and Crow (1994) developed a theoretical landscape model using model relationships that were developed based on recent studies of cowbird nest parasitism. The relative vulnerability of forest birds to cowbird parasitism at a given location was produced by applying a theoretical function relating cowbird parasitism rates to the values

in 2 input variables. These variables were a weighted total of cowbird feeding habitat within a 2.5-km radius of the location, and the distance from the location to the nearest habitat edge. The model was applied in a geographic information system (GIS) to assess the impacts of simulated forest management strategies on the vulnerability of a generalized forest bird to nest parasitism by cowbirds.

The purpose of this research was to help fill in existing gaps in the knowledge of landscape-level cowbird and nest parasitism habitat relationships. The study objectives were to: (1) determine if forest openings serve as focal points for cowbird penetration into surrounding forest lands; (2) develop models predicting the probability of cowbird presence in forest openings and the presence of nest parasitism associated with forest openings as a function of measurable landscape and avian parameters associated with the openings; and (3) make management recommendations based on observed results.

The following research hypotheses were tested as part of this study: (1) cowbird presence, cowbird abundance, and the presence of nest parasitism would be highest in forest opening edge habitat and would decrease with increasing distance from edge habitat; and (2) variation in measurable landscape and/or avian parameters could explain the observed variation in the presence of cowbirds and nest parasitism associated with forest openings.

STUDY AREA

This study was conducted on Land Between the Lakes (LBL) in western Kentucky and Tennessee. LBL occupies a 70,000 ha strip of land approximately 13 km wide and 61 km long, which separates Kentucky Lake from Lake Barkley. A canal linking the two reservoirs serves as the northernmost boundary of the area, in effect making it an inland peninsula (Figure 1). LBL was established in 1963 and has been developed and maintained by the Tennessee Valley Authority (TVA) as a national outdoor recreation and environmental education area.

About 89% of LBL's landbase is forested (Tennessee Valley Authority 1994). Currently, the tree species composition is roughly 80% oak (Quercus spp.) - hickory (Carya spp.), 5% maple (Acer spp.) - beech (Fagus grandifolia), 4% pine (Pinus spp.), and 11% other tree species. These forest resources are managed by LBL to create a diversity of successional growth stages across the area. The primary goal of this management is to provide habitat for a variety of wildlife species for recreational and educational purposes and to generate timber resource revenue. This management has generally resulted in a mid-successional, even-aged, oak-hickory forest, except where recent disturbance (e.g., wildfire, timber harvest) has occurred. Stand age classes are distributed as follows: hardwood old growth 10%; hardwood sawtimber 66.4%; hardwood poletimber 10.1%; hardwood young growth 10.1%; pine (all ages) 3.4%.

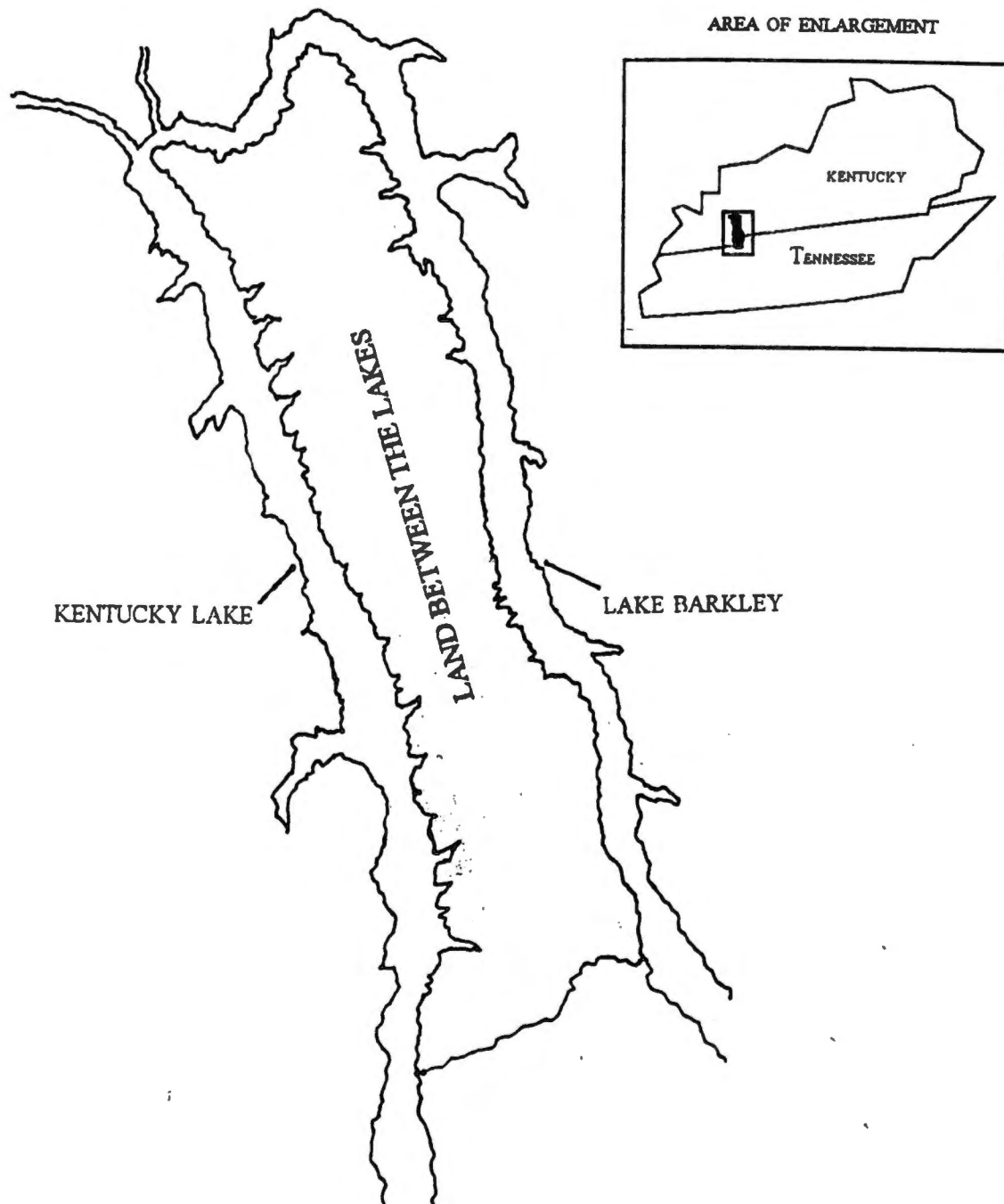


Figure 1. Land Between the Lakes study area in Tennessee and Kentucky.

LBL conducts an active open land management program on approximately 5,079 ha (7.4% of LBL lands). These open lands are relatively evenly distributed across the landscape (Figure 2). Open land habitat plans are developed and implemented to: (1) provide food and habitat for wildlife; (2) to prevent loss of landscape-level biological diversity as a result of reversion of open lands to forest; and (3) to provide vistas and wildlife viewing opportunities (Tennessee Valley Authority 1994). There are five categories of open lands currently managed: cooperative farmlands, woods openings, wildlife plantings, maintained open lands, and miscellaneous open lands.

Approximately 1,625 ha (32%) of open lands are maintained in row crops or hay as part of the cooperative farming program. These openings are often integrated into large, complex field systems located in narrow valleys draining to Kentucky and Barkley lakes. Fields maintained annually through the cooperative farming program contain corn (*Zea mays*), soybeans (*Glycine max*), wheat (*Triticum aestivum*), millet (*Setaria italica*), clover (*Trifolium* spp.), and cool season grasses. Fallow fields contain annual plants such as ragweed (*Ambrosia artemisiifolia*), Johnson grass (*Sorghum halepense*), foxtail (*Alopecurus* spp.), and morning glory (*Ipomoea purpurea*).

Woods openings, wildlife plantings, and other maintained open lands account for 47% (2,387 ha) of LBL's open land management program. During the initial years of developing LBL, 245 forest openings were created to enhance wildlife habitat, distributed

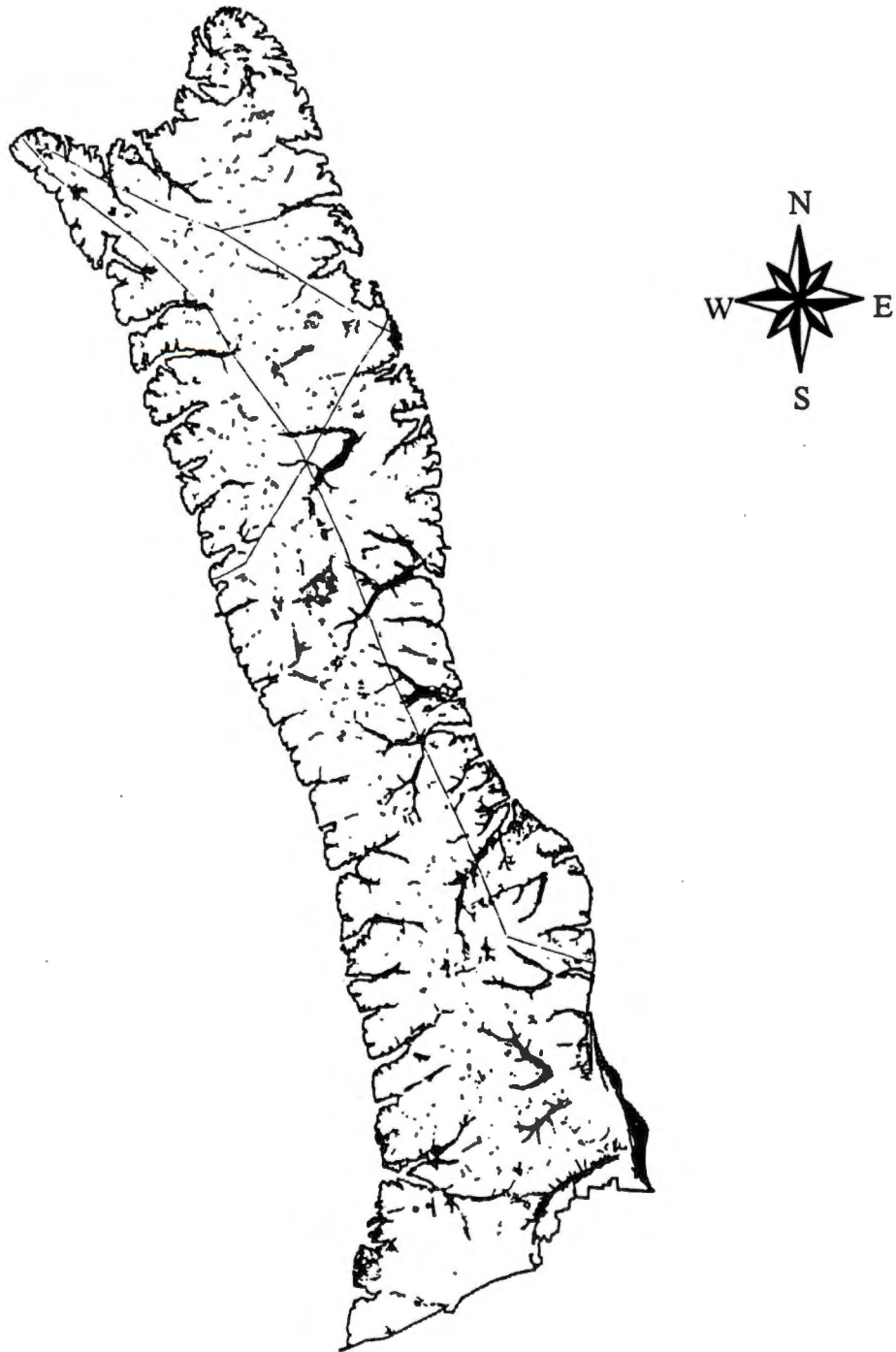


Figure 2. Distribution of open-lands at Land Between the Lakes, Kentucky-Tennessee 1994.

evenly throughout the forest. Some of the original openings reverted to forest because of poor access for maintenance equipment. Existing forest openings average 2 ha in size with irregular borders that follow the topography of the land. These openings and other maintained open lands are maintained primarily by mowing on 2- to 4-year rotations resulting in a great diversity of plant species. Early successional stages are typically represented by annual and perennial grasses, legumes, and broadleaf weeds. Later successional stages (old field) often contain sumac (Rhus spp.), persimmon (Diospyros virginiana), black cherry (Prunus serotina), black locust (Robinia pseudoacacia), eastern redcedar (Juniperus virginiana), goldenrod (Solidago spp.), and native warm season grasses. Wildlife openings (food plots) are planted annually with crops such as corn, milo, or millet, specifically for wildlife.

The remaining 21% (1,067 ha) of LBL's open lands contain a variety of maintained recreational areas. This includes campgrounds, lake access areas, visitor centers, and other recreational areas. Many of these open areas are regularly maintained (mowed) in short-grass cover. Also included in this category are the Wrangler's Campground, an area providing trails and barns for housing horses, and the Buffalo Range, an area consisting of two adjacent 40-ha pastures used by a herd of 70 - 80 bison.

Unlike LBL, surrounding counties in Kentucky and Tennessee are only 50% forested. The non-forested land use is dominated by agriculture, with primary crops being corn, wheat, and soybeans. Private tourism development in the surrounding counties occurs primarily in areas close to the lakes. Resorts, recreation facilities, private homes,

and residential subdivisions are scattered along the shoreline. Kentucky and Tennessee also manage several state resort parks along the lakes.

METHODS

Selection of Avian Census Points

Forest-opening and interior-forest avian-census points were randomly selected from an existing GIS coverage of LBL lands using PC Arc/Info computer software (Environmental Systems Research Institute, Redlands, Calif.).

Forest Opening Points

Forest openings were defined as areas in which vegetative succession was permanently suppressed, such as maintained wildlife openings, campgrounds, and agricultural fields in row crops, pasture, or hay. Selection of forest openings across the study area was stratified based on the size of each opening and the relative isolation of each opening (number of forest openings within a 2-km radius of a selected forest opening). The maximum size of selected forest openings was limited to 12 ha, as larger forest openings were generally integrated into complex field systems which were difficult to census accurately. Management in these large field systems was extremely varied and individual fields were often indistinguishable from the larger field system.

I selected a random sample of 80 forest openings, balanced across the size and isolation strata. Ultimately, only 76 forest openings were surveyed because 4 of the selected openings had reverted to forest cover. This sampling strategy resulted in an even distribution of studied forest openings across the area (Figure 3) and generally maintained the balanced sample design across the two stratification variables (Table 1).

Forest-opening census points were established on a random compass bearing from the center of selected forest openings, at the opening/forest edge. One census point was located in each forest opening regardless of the size of the opening.

Interior Forest Points

Interior-forest census points were defined as forested points at least 200 m away from any surrounding edge (i.e., forest openings, primary roads). For each selected forest opening point an associated interior forest point was selected by the following method. Selected forest openings, and landscapes surrounding the openings, were individually displayed on a computer monitor using the LBL land cover database in Arc/Info. A randomly-selected compass bearing (N, S, E, W, NE, NW, SE, SW) was identified that would place interior-forest census points 200 m from each opening and at least 200 m from other habitat edges. These compass bearings were adjusted, as needed, by researchers in the field to ensure that interior-forest points were ≥ 200 m from all surrounding habitat edges.

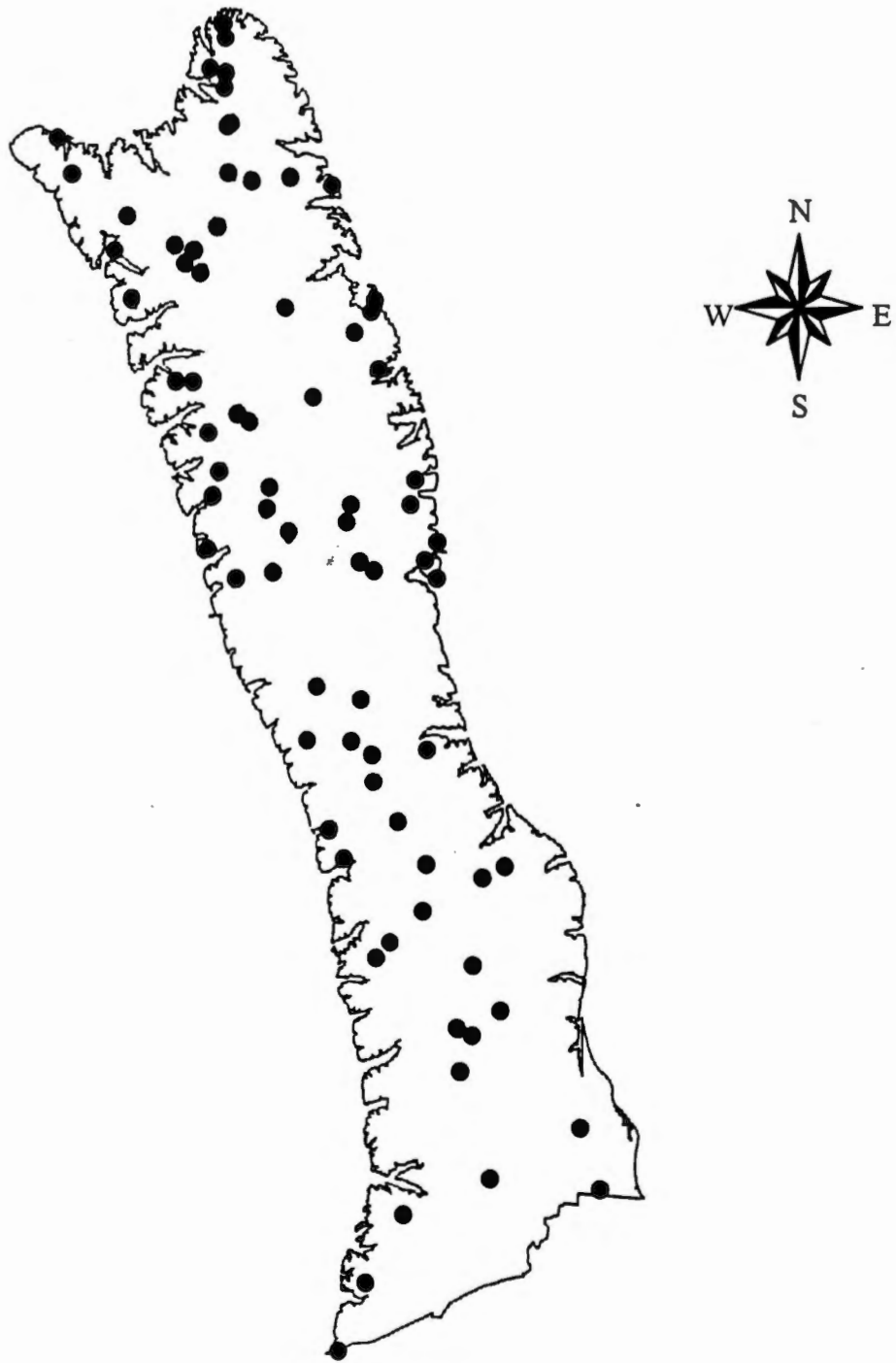


Figure 3. Distribution of surveyed forest openings on Land Between the Lakes, 1993-1994.

Table 1. Distribution of points censused for cowbirds on Land Between the Lakes (1993-1994) by forest opening size, relative isolation of forest openings, and distance from point to nearest edge.

Forest Opening Size (ha)	Number of Openings Within 2 km				TOTAL
	0 - 3	4 - 7	8 - 11	> 12	
Distance from Point to Nearest Edge = 0 m					
0 - 1.9	3	5	5	5	18
2 - 3.9	4	5	5	5	19
4 - 5.9	4	5	6	5	20
> 6	3	6	5	5	19
TOTAL	14	21	21	20	76
Distance from Point to Nearest Edge = 200 m					
0 - 1.9	3	5	5	5	18
2 - 3.9	4	5	5	5	19
4 - 5.9	4	5	6	5	20
> 6	3	6	5	5	19
TOTAL	14	21	21	20	76
Distance from Point to Nearest Edge = 300 m*					
0 - 1.9	2	2	1	2	7
2 - 3.9	2	1	0	0	3
4 - 5.9	2	2	3	2	9
> 6	1	2	2	1	6
TOTAL	7	7	6	5	25

Table 1 (continued)

Forest Opening Size Class (ha)	Number of Opening Within 2 km				TOTAL
	0 - 3	4 - 7	8 - 11	> 12	
Distance from Point to Nearest Edge = 400 m*					
0 - 1.9	1	2	2	2	7
2 - 3.9	1	2	3	2	8
4 - 5.9	1	1	1	1	4
> 6	1	2	1	2	6
TOTAL	4	7	7	7	25
Distance from Point to Nearest Edge = 500 m*					
0 - 1.9	0	1	2	1	4
2 - 3.9	1	2	2	3	8
4 - 5.9	1	2	2	2	7
> 6	0	2	2	2	6
TOTAL	2	7	8	8	25
				GRAND TOTAL	227

* Note: Points located at 300, 400, and 500 m from the nearest edge were only censused during the 1994 field season.

* Note: Points located at 300, 400, and 500 m from the nearest edge were only censused during the 1994 field season.

In 1994, in addition to the paired forest-opening and original interior-forest census points, an additional interior-forest census point was located at either 300, 400, or 500 m from the edge of the opening and all other surrounding habitat edges (Table 1). At one forest opening it was impossible to locate an interior-forest census point at least 300 m from surrounding edge, thus only 75 additional interior-forest census points were established. In most cases these additional census points were located on the same compass bearing as were the 200-m census points. Again, researchers in the field made adjustments to ensure that census points were the correct distance from the surrounding habitat edge.

Avian Censusing

1993 Field Season

A total of 152 50-m fixed-radius point-counts were conducted at 76 paired forest-opening and interior forest (200 m) census points during the 1993 field season (15 May-1 July 1993). Point-counts were conducted between sunrise and 10:30 a.m. EST. Counts were broken into 0-3, 3-5, 5-10, and 10-20 minute intervals. All avian species seen or heard were recorded as being within 50 m of point center, outside the 50-m radius, or as "flyovers". Special attention was given to cowbirds seen or heard, specifically noting the sex of the individual, song heard, and activity (i.e., perched, flying, foraging). Census protocols were identical for forest-opening and interior-forest point-counts.

1994 Field Season

Based on analysis of 1993 data for point-count efficiency (Chapter 2), point-count duration was shortened from 20-min point-counts in 1993 to 10-min point counts in 1994. These 10-min counts were broken into 0-3, 3-5, and 5-10 min intervals, allowing for comparison between 1993 and 1994 point-count results. Seventy-five additional interior-forest point counts were conducted at either 300, 400, or 500 m from habitat edge, resulting in a total of 227 point-counts conducted during the 1994 field season. Point-count protocols were identical in every other respect for both field seasons.

Nest Searching and Monitoring

Bird nests were located and monitored only during the 1994 field season. Nest searching efforts focused on the same 76 forest openings selected for avian census point locations. Forest openings were searched for nests in random order on days that the openings were not being censused to avoid disrupting counts. Nest searching was conducted in the morning (6:00 a.m. - 1200 p.m. EST) and nest monitoring was conducted in the afternoon (1:00 p.m. - 6:00 p.m. EST). Technicians spent approximately equal amounts of time searching the forest opening/edge and surrounding forest at each forest opening site. In general, the guidelines outlined by Martin and Geupel (1993) for locating and monitoring nests were followed.

Nest searching and monitoring was accomplished by 2 teams made up of 2-3 technicians each. Technician experience ranged from individuals experienced at both bird identification and nest searching, to individuals experienced only with bird identification,

to individuals without experience at either. Technicians were trained to distinguish cowbird eggs from eggs of avian hosts. Team were assigned to either the northern or southern half of LBL, consequently teams were responsible for roughly the same number of forest openings.

Although data were collected on all nests found, nest searching efforts were concentrated on 4 species: acadian flycatcher (Empidonax virescens), wood thrush (Hylocichla mustelina), indigo bunting (Passerina amoena), and northern cardinal (Cardinalis cardinalis). This limited the required training for technicians, as they were only required to be thoroughly familiar with locating nests for 4 species. It also helped ensure that adequate data would be collected on forest-interior species (acadian flycatcher and wood thrush) and opening/edge species (indigo bunting and northern cardinal).

When a nest was found the following information was recorded: avian species, nest location (description), date located, height from nest to ground, distance from nest to nearest edge, tree or other plant species in which the nest was located, number of host eggs or chicks present, number of cowbird eggs or chicks present, and detailed notes on nest status (i.e., nest being built, female incubating, etc.).

Nests were revisited every 3–4 days until the nest either failed or chicks successfully fledged. On each visit, the number of host eggs or chicks present and the number of cowbird eggs or chicks present was recorded. Detailed notes were recorded on failed nests (i.e., nest abandoned, evidence of predation, etc.) and on nests that successfully fledged (i.e., fledglings heard or seen, parents seen carrying food, etc.)

Model Building

General

Descriptive statistics, model building, and model assessment functions were run with SAS (SAS Institute, Inc., Cary, N.C.) and BMDP (BMDP Statistical Software, Inc., Los Angeles, Calif.) statistical software packages. Variables describing each sampled forest opening were derived using PC Arc/.Info computer software.

Model Variables

Dependent Variables. Cowbirds were considered “present” at a forest opening if a cowbird was ever observed within 50 m of point center during a forest-opening point count (1993 or 1994 or both years). Cowbird presence/absence formed one response variable used in the logistic regression modeling. Forest openings were considered to be parasitized by cowbirds if any nest found in the opening, opening/forest edge, or in the surrounding forest (for which the selected forest-opening was the nearest edge) was parasitized. Thus, the presence/absence of nest parasitism formed the second response variable used in the logistic regression modeling.

Independent Variables. The area and perimeter of each forest opening was calculated as a standard data field in Arc/Info polygon attribute tables (PAT's). These measurements were used to derive the variables OPENSIZE and SHAPINDEX (Table 2). The height of vegetation (VEGHEIGHT) in forest openings was visually estimated when each opening was censused. These estimates were averaged over 1993 and 1994 field

Table 2. Variables describing forest openings surveyed for cowbirds and nest parasitism on Land Between the Lakes, 1993-1994.

Abbreviation	Variable Name	Variable Description
Forest Opening Intrinsic Variables		
OPENSIZ	Forest Opening Size	Size of forest opening (ha) measured from GIS
VEGHEIGH	Vegetation Height	Average height of vegetation in forest opening (m) measured when censused (ocular estimate)
SHAPINDX ¹	Shape Index	Shape of forest opening: $D_i = P/2(A\pi)^{1/2}$ where D_i = shape index P = forest opening perimeter (from GIS) A = forest opening area (from GIS)
Landscape Variables		
ISOLINDX ²	Isolation Index	Isolation of forest opening: $r_i = (1/n)\sum_{j=1}^n d_{ij}$ where r_i = isolation index n = number of neighboring forest openings within a 2-km radius d_{ij} = distance between forest opening i and neighboring forest opening j
DISTLGOP	Distance to Large Openings	Distance from forest opening to nearest large (>12 ha) opening (km)
DISTFORG	Distance to Foraging Areas	Distance from forest opening to nearest potential cowbird foraging location (km)
DISTNRRD	Distance to Nearest Road	Distance from forest opening to nearest primary (asphalt) or secondary (gravel) road (km)
#FORGE2K	Number of Foraging Areas (2 km)	Number of potential cowbird foraging locations within a 2-km radius of forest opening
#OPEN2K	Number of Openings (2 km)	Number of neighboring forest openings within a 2-km radius of forest opening
#COVER2K	Number of Covertypes (2 km)	Number of different covertypes within a 2-km radius of forest opening
EDGE2K	Edge habitat (2 km)	Total edge (neighboring forest opening perimeters (km) plus primary and secondary road lengths (km) within a 2-km radius of forest opening

Table 2 (continued)

Abbreviation	Variable Name	Variable Description
OPENAREA	Area of openlands (2 km)	Total area (m ²) of openland within a 2-km radius of forest opening
HDYGAREA	Area of hardwood young growth (2 km)	Total area of hardwood young growth within a 2-km radius of forest opening (m ²)
HDPLAREA	Area of hardwood pole-timber (2 km)	Total area of hardwood pole-timber within a 2-km radius of forest opening (m ²)
HDSTAREA	Area of hardwood saw-timber (2 km)	Total area of hardwood saw-timber within a 2-km radius of forest opening (m ²)
PIYGAREA	Area of pine young growth (2 km)	Total area of pine young growth within a 2-km radius of forest opening (m ²)
PIPLAREA	Area of pine pole-timber (2 km)	Total area of pine pole-timber within a 2-km radius of forest opening (m ²)
PISTAREA	Area of pine saw-timber (2 km)	Total area of pine saw-timber within a 2-km radius of forest opening (m ²)
Avian Census Variables		
HOSTABUN	Host species abundance (1993 & 1994)	Number of potential cowbird hosts within 50-m (average for 1993 and 1994 forest-opening points)
HOSTAB94	Host species abundance (1994)	Number of potential cowbird hosts within 50-m (1994 forest-opening points only)
FCWBRD94	Female cowbird abundance (1994)	Number of female cowbirds within 50-m (1994 forest-opening points only)
MFCWBD94	Male & female cowbird abundance (1994)	Number of male and female cowbirds within 50-m (1994 forest-opening points only)
FCW/HOST	Female cowbird to host species ratio (1994)	Female cowbird to host ratio: FCWBRD94/HOSTAB94

¹ Sources: Patton, D.R. 1975. A diversity index for quantifying habitat edge. *Wildl. Soc. Bull.* 395:171-173.
 Game, M. 1980. Best shape for nature reserves. *Nature* 287:630-632.

² Source: King, L.J. 1969. *Statistical analysis in geography*. Englewood Cliffs, New Jersey: Prentice Hall.

seasons. All measured distances used to calculate the variables ISOLINDX, DISTLGOP, DISTFORG, and DISTNRRD were measured from the geometric center (centroid) of selected forest polygons to the centroid of surrounding polygons. A 2-km radius buffer was generated around each selected forest opening in Arc/Info. Within this buffered area, variable measurements were either tallied (#FORGE2K, #OPEN2K, #COVER2K, EDGE2K) or area measurements from Arc/Info PAT's were summed (OPENAREA, HDYGAREA, HDPLAREA, HDSTAREA, PIYGAREA, PIPLAREA, PISTAREA). For the variables DISTFORG and #FORGE2K, potential cowbird foraging areas were identified as areas maintained in short-grass conditions, areas with livestock present, maintained (mowed) roadsides, agricultural areas, and areas where cowbird were observed foraging.

Avian census datasets for 1993 and 1994 were combined (HOSTABUN) and only birds recorded within 50 m during 10-min forest-opening point counts were entered into model building (Table 2). Because data on nest parasitism were only collected during the 1994 field season, only 1994 avian census data were entered into the model building process for nest parasitism models. Cowbird host species for the variables HOSTAB94 and FCW/HOST were identified as all birds which build open cup nests and were known to be parasitized by cowbirds.

Multicollinearity Analysis

A Pearson correlation coefficient analysis (SAS 1990) was performed on all of the independent variables measured and derived for forest openings. Variable pairs with correlation coefficients ≥ 0.70 were considered redundant (explaining the same variance) and one variable in the pair was excluded from subsequent analyses. Two variables were excluded from all analyses based on results from this procedure. The variable HDPLAREA was excluded because of a positive correlation ($r = 0.88$, $P = 0.0001$) with the variable HDYGAREA. The variable HDSTAREA was excluded because of a negative correlation ($r = -0.96$, $P = 0.0001$) with the variable OPENAREA.

Model Development

Model development strategy was the same for both the cowbird and nest parasitism models. First, a full model was fit using all landscape and avian census variables derived for forest openings. Second, a stepwise-selection method was used in which all landscape and avian census variables were selected either for inclusion or exclusion from the final model in a sequential fashion (SAS 1990). A significance level of $P = 0.10$ was required for variable entry into the selection process and a significance level of $P = 0.05$ was required for variables to remain in the final model.

As a comparative technique, I also used a best subset selection method based on the minimum of Akaike's Information Criteria (AIC) (Akaike 1973, Bozdogan 1987). AIC is an information-based or entropic measure used for identifying an "optimal

statistical model”. In the best subset selection method, an AIC score is calculated for all possible independent variable combinations and the combination of variables that results in the minimum AIC score represents the optimal model (Akaike 1973). Because final AIC-selected model variables were identical to final stepwise-selected model variables, I reported only the stepwise model results.

Logistic Regression Equations. The probability of the presence of cowbirds and nest parasitism in forest openings was quantified by creation of a linear regression line for each final model (cowbird and nest parasitism models). The slope and origin of this line for a particular model is determined by the function $g(x)$, defined as the estimated logit of the probability of an event occurring (i.e., cowbird presence in a forest opening) (SAS 1990). The straight line equation has the form:

$$g(x) = \beta_0 + \beta_1 x_1 + \dots + \beta_p x_p$$

where: $g(x) = \text{logit}(p) =$ the estimated logit of the probability of an event

$\beta_0 =$ y-intercept (value of y when $x = 0$)

$\beta_1 =$ slope of the straight line (change in y for a unit change in x)

The value for $g(x)$ was calculated for each forest opening. Finally, the predicted probability of either cowbird presence in a forest opening or the presence of nest parasitism associated with a forest opening was calculated using the following equation:

$$p = e^{g(x)} / (1 + e^{g(x)})$$

where: p = the predicted probability of an event

Tests of Model Predictive Power. The predictive power of resulting models was tested using two separate statistical procedures available in the SAS LOGISTIC procedure (SAS 1990). The first procedure (concordance) compared model-predicted probabilities for positive (i.e., cowbirds present) and negative (i.e., cowbirds absent) observed responses. A pair of different observed responses was said to be concordant if the positive observed response had a higher model-predicted probability than the negative observed response. The concordance test criteria (model-predicted probabilities) were developed including the observed responses being tested, therefore, this test is considered biased.

The second procedure (classification table) utilized a fixed probability (0.5) to predict positive and negative observed responses. A predicted response was said to be positive if the predicted probability was greater than 0.5. Model-predicted responses were compared with observed responses in a classification table and the percent of observed responses correctly predicted was calculated. This test utilized a “jack-knife” (SAS 1990) procedure in which observed responses were individually removed and evaluated against test criteria (model-predicted responses) that were developed without the tested observed response, therefore, this test is considered unbiased.

Goodness of Fit Test. To determine the adequacy of fitted logistic models in describing the relationship between the independent and dependent variables (goodness of fit), the Hosmer-Lemeshow statistic (Hosmer and Lemeshow 1989) was calculated with BMDP statistical software. The Hosmer-Lemeshow test uses 'deciles of risk' grouping to categorize points into 10 groups - ranked and separated according to their estimated probabilities. Models that fit the data well show small differences between observed and expected frequencies in each group, and generally have large P-values (> 0.05). Small P-values (< 0.05) indicate large differences between within-group observed and expected frequencies and indicate a poor fit of the model to the data (Hosmer and Lemeshow 1989).

The significance of independent model variables in predicting dependent variable responses was tested using the Wald chi-squared statistic, computed as the square of the dependent variable's parameter estimate divided by its standard error estimate (SAS 1990). Independent variables with Wald chi-squared P-values ≤ 0.05 were considered significant predictors of dependent variable responses.

RESULTS

Cowbird Presence and Abundance

Cowbirds were present within 50 m in 62 (27 %) of 227 forest-opening and interior-forest points. Cowbirds were observed at forest-opening edges more often than at interior-forest points ($P \leq 0.05$) (Figure 4). No differences in cowbird presence were detected among interior forest-points with varying distances from edge ($P > 0.05$).

Cowbird abundance per point (within 50 m in forest-opening and interior-forest points) averaged 0.53 cowbirds/point. Mean cowbird abundance per point was higher at forest-opening edges than at interior-forest points ($P \leq 0.05$) (Figure 4). No differences in cowbird abundance were detected among interior forest points with varying distances from edge ($P > 0.05$). The sex ratio was strongly male biased at 1.5 male cowbirds to 1 female cowbird. The overall female cowbird to male host ratio was 0.04.

Nest Parasitism

One hundred ninety five active nests of 20 species known to be parasitized by brown-headed cowbirds were located and monitored. Of these nests, 23.6% (46 nests) were parasitized by cowbirds (Table 3). Multiple parasitism was common, with an overall average of 1.3 cowbird eggs per parasitized nest. The number of cowbird eggs per parasitized nest ranged from 1-6 eggs/nest, with 2 eggs/nest occurring most frequently (Figure 5).

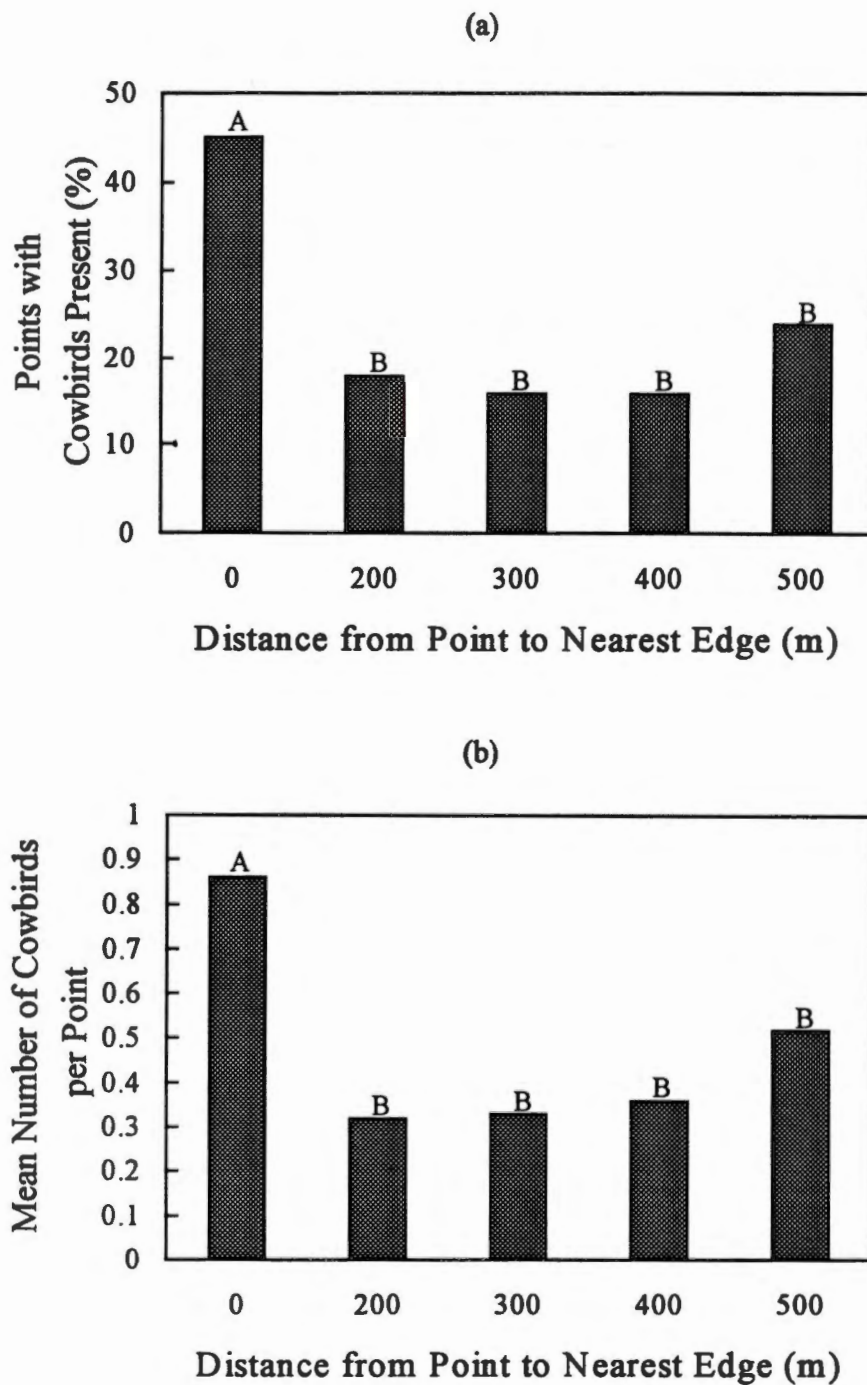


Figure 4. Percentage of points with cowbirds present (a) and mean number of cowbirds per point (b) by distance from point to nearest edge. Columns with different letters differed significantly ($P \leq 0.05$), based on pairwise tests.

Table 3. Cowbird nest parasitism frequencies for all host species nests found on Land Between the Lakes, 1994.

Species	Active Nests ¹	Average Distance from Nest to Nearest Edge (m)	Average Height of Nest (m)	Percent of Active Nests Parasitized (n) ²	Average Number Host Eggs/Chicks per Active Nest	Average Number Cowbird Eggs/Chicks per Active Nest	Average Number Cowbird Eggs/Chicks per Parasitized Nest
Acadian Flycatcher (<i>Empidonax virescens</i>)	47	168.0	5.1	19.2 (9)	3.1	0.26	1.4
Blue-gray Gnatcatcher (<i>Polioptila caerulea</i>)	1	20.0	9.0	0	5.0	0	0
Brown Thrasher (<i>Toxostoma rufum</i>)	17	4.4	2.0	11.8 (2)	3.1	0.12	1.0
Blue-winged Warbler (<i>Vermivora pinus</i>)	2	0	0	0	4.0	0	0
Common Yellowthroat (<i>Geothlypis trichas</i>)	2	0	0.18	0	3.5	0	0
Field Sparrow (<i>Spizella pusilla</i>)	4	0.40	0.65	25.0 (1)	3.0	0.25	1.0
Indigo Bunting (<i>Passerina cyanea</i>)	41	0.98	0.84	7.3 (3)	2.9	0.10	1.3

Table 3. (continued)

Species	Active Nests ¹	Average Distance from Nest to Nearest Edge (m)	Average Height of Nest (m)	Percent of Active Nests Parasitized (n) ²	Average Number Host Eggs/Chicks per Active Nest	Average Number Cowbird Eggs/Chicks per Active Nest	Average Number Cowbird Eggs/Chicks per Parasitized Nest
Louisiana Waterthrush (<i>Seiurus motacilla</i>)	2	241.0	0	0	4.0	0	0
Northern Cardinal (<i>Cardinalis cardinalis</i>)	19	15.3	2.1	36.8 (7)	2.5	0.63	1.7
Orchard Oriole (<i>Icterus spurius</i>)	2	10.0	4.5	100 (2)	2.5	1.0	1.0
Pine Warbler (<i>Dendroica pinus</i>)	1	0	9.0	0	3.0	0	0
Prairie Warbler (<i>Dendroica discolor</i>)	6	0.83	1.4	33.0 (2)	3.3	0.33	1.0
Rufous-sided Towhee (<i>Pipilo erythrophthalmus</i>)	2	94.0	2.2	0	3.5	0	0
Red-winged Blackbird (<i>Agelaius phoeniceus</i>)	4	1.3	1.5	0	3.25	0	0

Table 3. (continued)

Species	Active Nests ¹	Average Distance from Nest to Nearest Edge (m)	Average Height of Nest (m)	Percent of Active Nests Parasitized (n) ²	Average Number Host Eggs/Chicks per Active Nest	Average Number Cowbird Eggs/Chicks per Active Nest	Average Number Cowbird Eggs/Chicks per Parasitized Nest
Summer Tanager (<u>Piranga rubra</u>)	4	108.0	5.1	100 (4)	1.8	1.0	1.0
White-eyed Vireo (<u>Vireo griseus</u>)	9	11.0	0.74	33.0 (3)	1.8	0.33	1.0
Worm-eating Warbler (<u>Helmitheros vermivorus</u>)	1	300.0	0	0	3.0	0	0
Wood Thrush (<u>Hylocichla mustelina</u>)	25	130.1	4.1	48.0 (12)	2.85	0.92	1.9
Yellow-breasted Chat (<u>Icteria virens</u>)	3	0	0.83	33.0 (1)	3.0	0.67	2.0
TOTALS	195			23.6 (46)			1.3

¹ Nests found with eggs or chicks present that were monitored to termination or fledging.

² Number of nests parasitized.

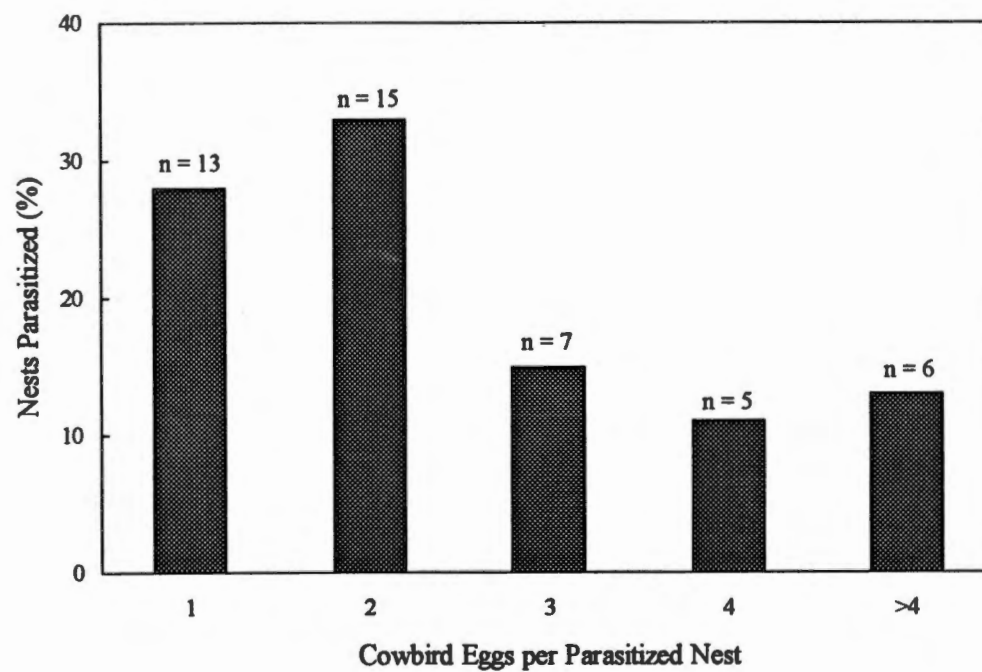


Figure 5. Percentage of active nests parasitized and number of cowbird eggs per parasitized nest. Numbers above columns are the number of nests per column.

Wood thrushes were the most heavily parasitized (48% of 25 nests) of the 4 species on which nest searching efforts were focused. Northern cardinals were second (36.8% of 19 nests), followed by acadian flycatchers (19.2% of 47 nests), and finally indigo buntings with 7.3% of 41 nests parasitized. (Table 3). Although sample size was limited, host species productivity appeared to be markedly reduced by cowbird parasitism ($P \leq 0.05$) (Table 4).

The percentage of nests parasitized was not significantly different across distance from nest to nearest edge categories ($\chi^2 = 3.63$, $P > 0.05$) (Figure 6). The percentage of nests parasitized averaged 26.2% for nests within 200 m of the nearest edge; beyond 200 m average parasitism frequency dropped to 12.7%. Forest species (average distance from nest to nearest edge ≥ 100 m) were more heavily parasitized, 30.5% of 82 nests, than were edge species (average distance from nest to nearest edge < 100 m), 18.6% of 113 nests ($P = 0.02$) (Table 3). It appeared that ground and shrub nesting species (average height of nest ≤ 2 m) suffered less parasitism, 29% of 95 nests, than sapling and canopy nesting species (average height of nest > 2 m), 34% of 100 nests parasitized, although these differences were not significant ($P = 0.07$) (Table 3).

Active nests were located in 66 of the 76 forest openings that were searched for nests. Overall parasitism frequency on a per-opening basis was 45% (33 of 66 forest openings) (Table 5). Forest openings with 5-6 and >6 active nests were parasitized more frequently (80%; 12 of 15 openings) than forest openings with 1-2 or 3-4 active nests (35%; 18 of 51 openings) ($P \leq 0.05$).

Table 4. Host species productivity in non-parasitized and parasitized nests monitored to successful fledging on Land Between the Lakes, 1994.

Species	Average Number of Host Eggs/Chicks per Non-parasitized Nests (n) ¹	Average Number of Host Eggs/Chicks per Parasitized Nest (n) ²	T-test P-Value ³	Average Number of Host Chicks Fledged from Non-parasitized Nests (n) ¹	Average Number of Host Chicks Fledged from Parasitized Nests (n) ²	T-test P-Value ³
Wood Thrush	3.5 (4)	1.6 (7)	0.05	3.5 (4)	1.0 (7)	0.03
Northern Cardinal	2.5 (6)	1.0 (5)	0.06	2.5 (6)	0.6 (5)	0.04
Acadian Flycatcher	2.6 (25)	1.7 (3)	0.17	2.5 (25)	0.7 (3)	0.01
Indigo Bunting	3.1 (14)	0 (1)	0.07	2.8 (14)	0 (1)	0.11

¹ Nests found with host eggs or chicks present that were monitored to successful fledging.

² Nests found with host and/or cowbird eggs or chicks present that were monitored to successful fledging.

³ Based on Wilcoxon Rank Sum Test.

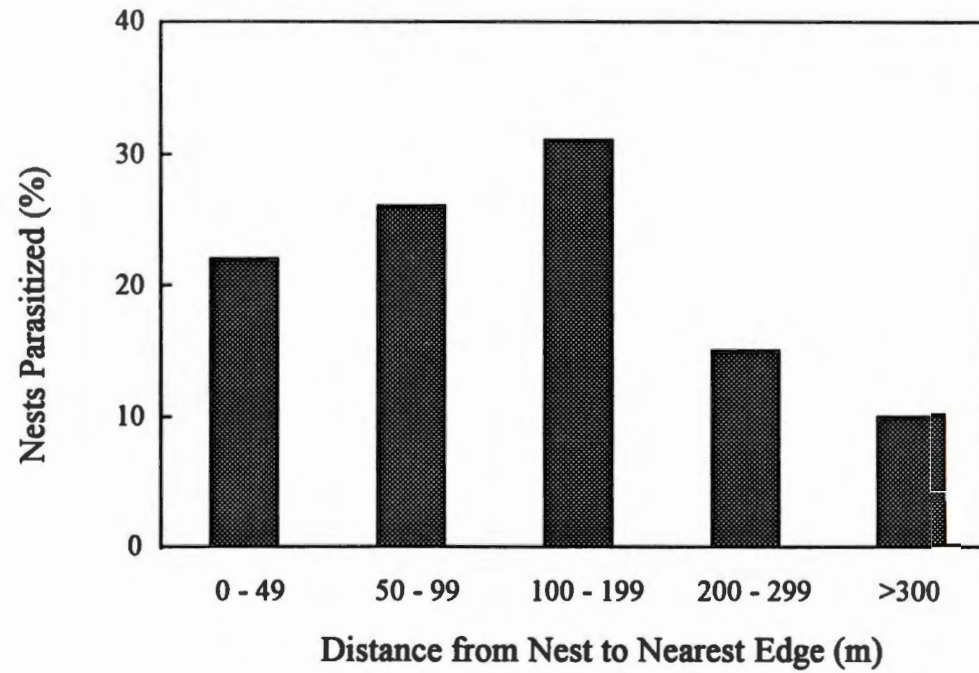


Figure 6. Percentage of nests parasitized and distance from nests to nearest edge (no significant differences were found across distance categories).

Table 5. Percentage of forest openings with active host nests parasitized by cowbirds on Land Between the Lakes, 1994.

Active Nests per Opening	Number of Openings	Percent of Openings Parasitized (n) ¹	Percent of Openings with Cowbirds (n) ¹	Host Abundance per Point-Count ¹
0	10	**	20 (2) _A	2.45 _A
1-2	22	32 (7) _A	36 (8) _A	3.95 _A
3-4	29	38 (11) _A	45 (13) _A	2.96 _A
5-6	12	83 (10) _B	75 (9) _A	3.58 _A
≥ 6	3	67 (2) _B	67 (2) _A	5.83 _A

¹ Different letters indicate significant differences ($P \leq 0.05$), based on pairwise tests.

Cowbird Models

Full Model

A total of 17 variables were used to build a full model predicting cowbird presence in forest openings (Table 6). Predicted and observed responses were concordant 93.6% of the time and classification table results indicated that forest openings were correctly classified for cowbird presence/absence 86.8% of the time. The Hosmer-Lemeshow goodness of fit test indicated that the model fit the data well ($P = 0.406$). Wald chi-square scores indicated that 4 variables (OPENSIZE, #FORGE2K, VEGHEIGHT, and DISTLGOP) were significantly related to cowbird presence ($P \leq 0.05$).

Stepwise Selected Model

Three variables (OPENSIZE, #FORGE2K, and VEGHEIGHT) were selected by the stepwise selection procedure for inclusion in a final model predicting cowbird presence in forest openings (Table 6). Wald chi-square scores indicated that all 3 variables were significantly related to cowbird presence in forest openings ($P \leq 0.05$). The variables OPENSIZE and #FORGE2K were positively related to cowbird presence and the variable VEGHEIGHT was negatively related to cowbird presence (Figure 7).

The resulting logistic regression equation was:

$$g(x) = 4.0808 + 1.2863(\text{\#FORGE2K}) + 0.5279(\text{OPENSIZE}) - 0.9668(\text{VEGHEIGHT}).$$

Predicted and observed responses were concordant 90.0% of the time, and forest openings were correctly classified for cowbird presence/absence 82.9% of the time, based on

Table 6. Results of full model and stepwise selection procedures for predicting cowbird presence in forest openings at Land Between the Lakes.

Variable	Parameter Estimate	Wald chi-square Pr > χ^2	Tests of Model Predictive Power		Goodness of Fit Indicator
			Concordance of Predicted and Observed Responses (% Concordant)	Classification Table (% Correctly Classified)	Hosmer Lemeshow Statistic
FULL MODEL RESULTS					
OPENSIZE	1.0695	0.0016	93.6	86.8	df = 8 $\chi^2 = 8.283$ P = 0.406
#FORGE2K	1.4493	0.0041			
VEGHEIGH	- 2.1690	0.0179			
DISTLGOP	- 0.0021	0.0342			
PIPLAREA	162.40	0.1572			
OPENAREA	- 6.8795	0.1713			
DISTNRRD	0.0021	0.1762			
#OPEN2K	- 0.1859	0.1969			
PISTAREA	- 932.60	0.2973			
PIYGAREA	- 825.60	0.3036			
HDYGAREA	- 61.258	0.3421			
DISTFORG	- 0.0006	0.4045			
HOSTABUN	0.1361	0.5384			
SHAPINDX	0.9130	0.5244			
ISOLINDX	- 0.0012	0.6584			
#COVER2K	- 0.2816	0.6832			
EDGE2K	0.0001	0.7380			
STEPWISE SELECTION RESULTS					
#FORGE2K	1.2863	0.0001	90.0	82.9	df = 8
OPENSIZE	0.5279	0.0001			$\chi^2 = 10.05$
VEGHEIGH	- 0.9668	0.0502			P = 0.261

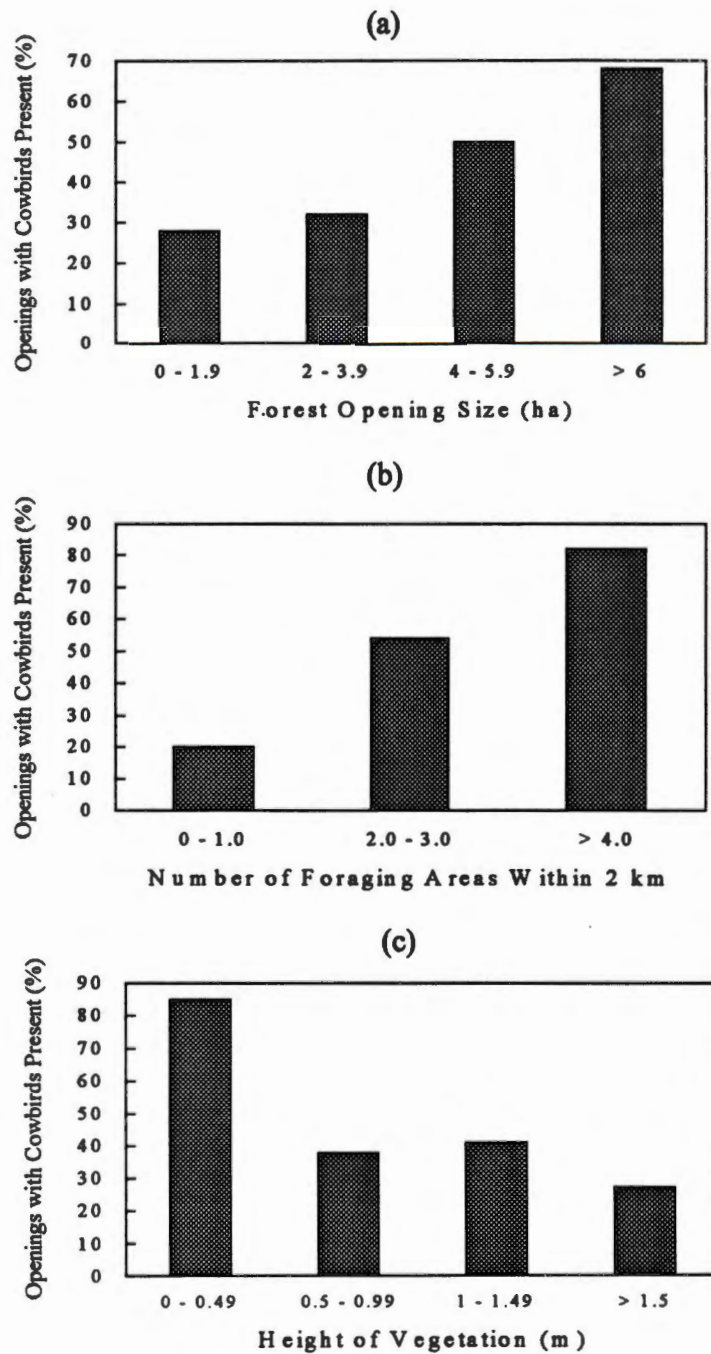


Figure 7. Percentage of forest openings with cowbirds present by forest-opening size (a), number of optimal foraging areas within 2 km (b), and vegetation height in forest openings (c).

classification table results (Table 6). The Hosmer-Lemeshow goodness-of-fit test indicated that the model fit the data well ($P = 0.26$).

Nest Parasitism Models

Full Model

A total of 20 variables were used to build a full model predicting the presence of nest parasitism associated with forest openings (Table 7). Predicted and observed responses were concordant 94.4% of the time and classification table results indicated that forest openings were correctly classified for the presence/absence of nest parasitism 86.4% of the time. The Hosmer-Lemeshow goodness of fit test indicated that the model fit the data well ($P = 0.266$). Wald chi-square scores indicated that 5 variables (OPENSIZE, VEGHEIGHT, #FORGE2K, SHAPINDEX, and HDYGAREA) were significantly related to the presence of nest parasitism associated with forest openings.

Stepwise Selected Model

Three variables (OPENSIZE, #FORGE2K, and VEGHEIGHT) were selected by the stepwise selection procedure for inclusion in a final model predicting the presence of nest parasitism associated with forest openings (Table 7). Wald chi-square scores indicated that all 3 variables were significantly related to the presence of nest parasitism in forest openings ($P \leq 0.05$). The variables #FORGE2K and VEGHEIGHT were positively related to the presence of nest parasitism and the variable OPENSIZE was negatively related to the presence of nest parasitism (Figure 8).

Table 7. Results of full model and stepwise selection procedures for predicting the presence of nest parasitism in forest openings at Land Between the Lakes.

Variable	Parameter Estimate	Wald chi-square Pr > χ^2	Tests of Model Predictive Power		Goodness of Fit Indicator
			Concordance of Predicted and Observed Responses (% Concordant)	Classification Table (% Correctly Classified)	Hoemer Lemeshow Statistic
FULL MODEL RESULTS					
#FORGE2K	1.5509	0.0040	94.40	86.36	df = 8 $\chi^2 = 3.441$ P = 0.2660
OPENSIZ	- 1.4100	0.0065			
VEGHEIGH	0.7966	0.0134			
HDYGAREA	111.50	0.0309			
SHAPINDX	6.7280	0.0454			
ISOLINDX	0.0057	0.0682			
EDGE2K	0.0001	0.4724			
HOSTAB94	0.2219	0.4780			
MFCWBD94	0.7428	0.5251			
FCWBRD94	1.4651	0.5439			
PTYGAREA	560.20	0.5952			
DISTNRRD	0.0007	0.6096			
#COVER2K	0.3984	0.6206			
DISTFORG	0.0004	0.6497			
FCW/HOST	- 3.3271	0.6820			
DISTLGOP	- 0.0005	0.7054			
PISTAREA	397.00	0.7319			
#OPEN2K	0.0493	0.7627			
PIPLAREA	- 15.017	0.8465			
OPENAREA	0.6172	0.9110			
STEPWISE SELECTION RESULTS					
#FORGE2K	1.0095	0.0055	86.10	84.20	df = 8
OPENSIZ	- 0.3328	0.0002			$\chi^2 = 6.256$
VEGHEGH	0.0836	0.0102			P = 0.6190

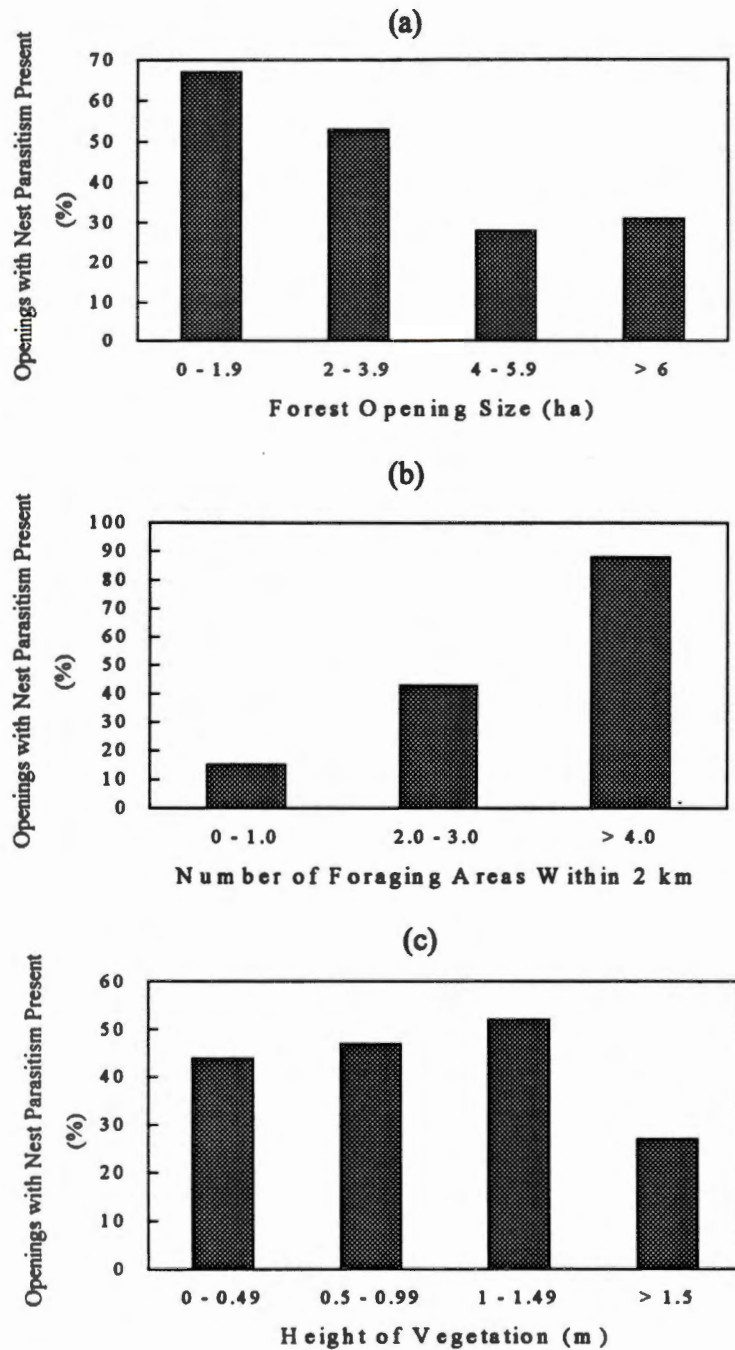


Figure 8. Percentage of forest openings with nest parasitism present by forest opening size (a), number of potential foraging areas within 2 km (b), and vegetation height in forest openings (c).

The resulting logistic regression equation was:

$$g(x) = 1.1221 + 1.0095(\text{\#FORGE2K}) - 0.3328(\text{OPENSIZE}) + 0.0836(\text{VEGHEIGHT}).$$

Predicted and observed responses were concordant 85.2% of the time and forest openings were correctly classified for the presence/absence of nest parasitism 81.8% of the time based on classification table results (Table 7). The Hosmer-Lemeshow goodness-of-fit-test indicated that the model fit the data well ($P = 0.619$).

Host Species Abundance

Host-species abundance per point count (forest-opening and interior-forest points) averaged 3.3 host-species/point. Host species abundance per point was higher at forest-opening edges than at interior forest points ($P \leq 0.05$) (Figure 9). Host species abundance did not differ across interior-forest points ($P \geq 0.05$). The variables $\text{\#FORGE2K}$ and VEGHEIGHT were positively correlated with host species abundance ($r = 0.21$, $P = 0.01$) (Figure 10). The variables VEGHEIGHT and OPENSIZE were not correlated with host species abundance ($P > 0.05$).

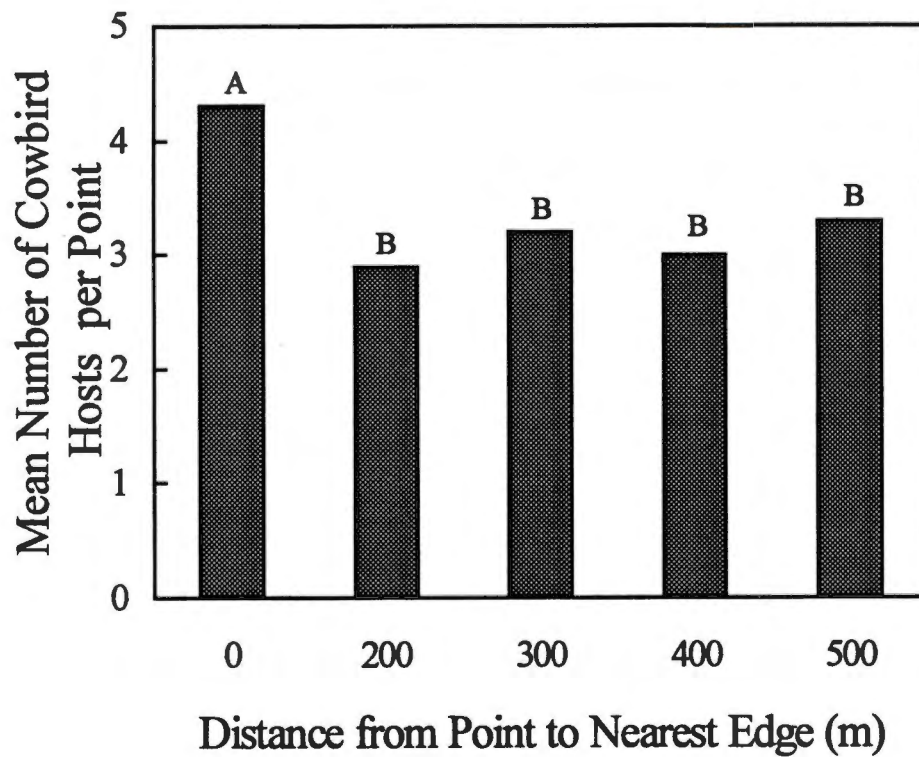


Figure 9. Mean number of cowbird hosts per point by distance from point to nearest edge. Columns with different letters differed significantly ($P \leq 0.05$), based on pairwise tests.

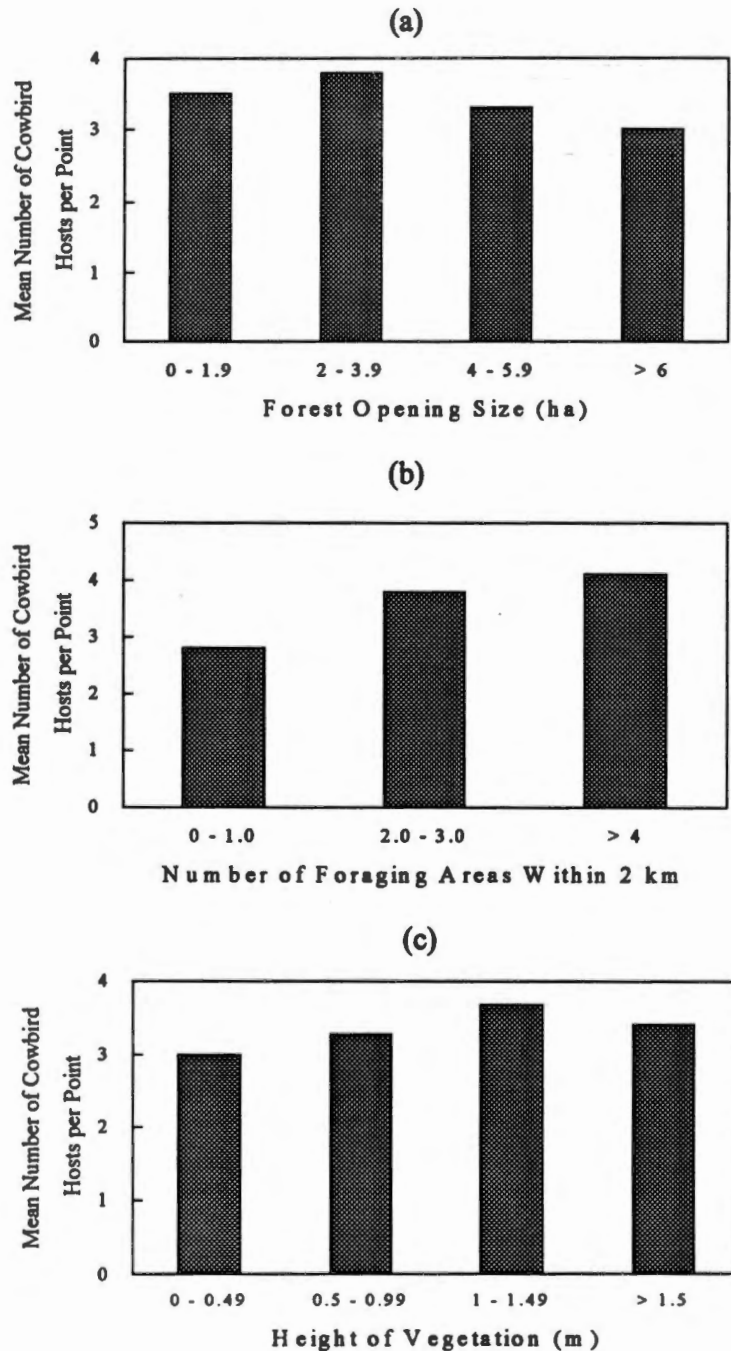


Figure 10. Mean number of cowbird hosts per point by forest-opening size (a), number of potential foraging areas within 2 km (b), and vegetation height in forest openings (c).

DISCUSSION

Forest Openings and Cowbirds

The Cowbird Edge Effect

In this study, both cowbird presence and cowbird abundance were higher at forest-opening edges than at interior-forest points (Figure 4). The presence of nest parasitism was also highest within 200 m of forest openings (Figure 5). Thus, forest openings appeared to serve as focal points for cowbird penetration into surrounding forest, supporting my first research hypothesis.

This “cowbird edge-effect” has been demonstrated in some landscapes, but not in others. Overcash and Roseberry (1987) found cowbird abundance to be 4-5 times higher around small (<4 ha) wildlife openings than in interior forest settings in the Shawnee National Forest of southern Illinois, but lack data on nest parasitism. Brittingham and Temple (1983) reported an inverse relationship between cowbird density and distance to open habitat in an extensively forested area of Wisconsin. They also found that nest parasitism frequencies declined from 65% within 99 m of an edge to less than 18% at >300 m from an edge. In contrast, Robinson (1992) found no appreciable decreases in nest parasitism rates even 800 m from the nearest edge in a moderately (50%) forested area of the Shawnee National Forest in southern Illinois, probably due to the saturation of available forest habitat by an extremely high cowbird population.

The Importance of Scale

Thompson et al. (in press) suggested that on a local scale, edges may only affect cowbird distribution and not abundance, and that cowbird abundance may actually be regulated at larger spatial scales. On a biogeographic scale, cowbird abundance was closely related to their historic distribution in the Great Plains. Abundance of cowbirds in states east of the Great Plains is negatively correlated to the distance of the state from the Great Plains (Thompson et al., in press). For example, based on Breeding Bird Survey data (1966-1971), the average number of cowbirds per route in midwestern states (North Dakota, South Dakota, Nebraska, Kansas, and Oklahoma) was 35 (124 total routes), whereas in Kentucky and Tennessee it was only 12 (72 total routes) (Van Velzen 1972). Similarly, Hoover and Brittingham (1993) found that the percentage of wood thrush nests parasitized was significantly higher in the midwest (45%) than in mid-Atlantic (24%) and northeast (16%) regions, based on three decades of wood thrush nest records from the Cornell Laboratory of Ornithology Nest Record Program. Kentucky and Tennessee were included in the mid-Atlantic region.

On a landscape scale, cowbird distribution and abundance and levels of nest parasitism are often strongly related to the amount of forest habitat and interspersions of cowbird foraging habitats. In this study, the number of potential cowbird foraging locations within 2 km of a forest opening was positively related to cowbird presence in the opening and the presence of nest parasitism associated with the opening. Similarly, Coker and Capen (in review) reported a positive relationship between cowbird presence in a

disturbance patch and the number of livestock areas (cowbird foraging locations) within 7 km of the patch. Donovan et al. (in press) compared nest parasitism rates in a heavily forested environment (81% forest cover) with limited cowbird foraging areas versus a highly fragmented landscape (25% forest cover) with many foraging areas in Missouri. Nest parasitism was significantly higher in the fragmented landscape (50% of nests parasitized) than in the heavily forested landscape (3% of nests parasitized).

Thus, on a local, or opening-intrinsic scale, the cowbird-edge effect at forest openings observed in this study may be a reflection of local cowbird abundance that is regulated at a larger scale. Where abundant, (i.e., highly fragmented landscapes) cowbirds may saturate the available forest habitat, but where less abundant (i.e., heavily forested areas) they may limit breeding activity near edge habitat (Thompson et al., in press).

Finally, host abundance may be an ultimate factor determining local cowbird distribution and abundance. In this study, host abundance was highest at forest-opening edges (Figure 9), corresponding with higher cowbird presence and abundance at forest-opening edges. Similarly, Gates and Geysel (1978) found 51% of 194 nests within 15 m of edge habitat in contiguous field and forest habitats in Michigan. Parasitism rates were as high as 15-25% near the edge to as low as 0-5% farther from it, and they noted that cowbirds were observed more often in edge habitat than in interior forest habitat.

Vulnerability of Forest Birds

Results from this study indicate that canopy-nesting forest birds may be especially vulnerable to nest parasitism (Table 3). Nests in the forest canopy are generally more conspicuous than well concealed nests near or on the ground, and thus may be easier for cowbirds to find and parasitize. Consistent with this observation, Robinson et al. (in press) found species nesting in early successional and grassland habitats were less heavily parasitized than forest species in a fragmented Illinois landscape. Robinson (1992) reported that, within forests, ground nesters suffered less parasitism (41% of 17 nests) than shrub, sapling, and canopy nesters (75% of 56 nests). Hahn (in press) reported a significantly higher percentage of parasitized nests in a 1300-ha forest (22% of nests parasitized) than in adjacent open habitat (5% of nests parasitized). However, in contrast to what I observed, Hahn reported higher parasitism of shrub and ground-nesting species (36% of nests parasitized) than sapling and canopy nesting species (23% of nests parasitized) within forest habitat. Some species with apparently well concealed nests were parasitized significantly more often (e.g., ovenbird 50%, hermit thrush 46%, veery 23%) than species with more conspicuous nests (e.g., wood thrush 8%).

Landscape-Habitat Models

The size of forest openings (OPENSIZE), average height of vegetation in openings (VEGHEIGHT), and number of foraging areas within 2 km of openings (#FORGE2K) were the best predictors of both cowbird presence in forest openings and the presence of nest

parasitism associated with forest openings. Larger forest openings, with lower average vegetation heights, that were near a high concentration of suitable cowbird foraging locations were most likely to contain cowbirds (Figure 7). Smaller forest openings, with higher average vegetation heights, that were near a high concentration of foraging locations were most likely to contain nest parasitism (Figure 8). Using these variables, openings were correctly classified for cowbird presence/absence 82.9% of the time (Table 6), and for the presence/absence of nest parasitism 81.8% (Table 7). Thus, the strong performance of both models supports my second research hypothesis.

Landscape Scale

On a landscape scale, cowbirds in this study appeared to select areas with higher concentrations of suitable foraging areas (#FORGE2K). Within these broad landscape-level areas, both cowbird presence and the presence of nest parasitism were highest. This relationship was not surprising as, throughout North America, cowbird distribution seems to be limited primarily by the availability of suitable foraging habitat, with the birds feeding mostly on the ground in areas of short grass (Friedmann 1929; Hamilton and Orians 1965; Mayfield 1965; Robinson et al. 1993; Rothstein et al. 1987). Coker and Capen (in review) also reported a positive relationship between the number of livestock areas (cowbird foraging areas) within 7 km of openings and the presence of cowbirds in the openings. Gustafson and Crow (1994) suggested that the relative position of openings in a landscape (i.e., proximity of openings to foraging areas) was more

important than the size of openings in assessing areas for nest parasitism. Finally, Airola (1986) demonstrated that the distance from a cowbird feeding area was a significant indicator of cowbird parasitism rates as areas that were closer to feeding areas had higher parasitism rates.

Local Scale

On a local, or forest-opening intrinsic scale, cowbirds in this study appeared to spatially separate individual forest openings as either breeding or feeding locations. Cowbird presence was highest in larger forest openings (OPENSIZE) with lower average vegetation heights (VEGHEIGHT), probably corresponding to use of these openings as foraging habitat. Large openings at LBL were usually more intensively managed than smaller openings, thus creating more suitable foraging habitat in larger openings. Management regimes in these large openings included row crops, campgrounds, pasture (livestock grazing), and recreational (short-grass) areas.

The presence of nest parasitism was highest in association with smaller forest openings with higher average vegetation heights, probably in response to higher host densities in and around these small openings (Figure 10). Small openings at LBL were usually maintained by periodic mowing (2-4 yr rotations), and many of the openings existed in later (old field) successional stages. The presence of isolated trees and scattered areas of stout, shrubby vegetation in these small openings often provided suitable nesting cover for many mixed-habitat species (e.g., indigo bunting, northern cardinal, field

sparrow), not only at the opening/forest edge, but throughout the opening. Thus, these small openings were comparatively host-rich areas for cowbird parasitism.

The spatial separation of breeding and feeding areas observed in this study is one of the few aspects of cowbird ecology that shows little geographic variation. Coker and Capen (in review) also reported higher cowbird presence in larger disturbance patches than in smaller patches, and noted that many of these large patches were maintained as short-grass lawns. Using radio-telemetry, Rothstein et al. (1984) demonstrated that cowbirds in California commuted up to 7 km between prime feeding and breeding habitats. Cowbirds seem to maintain this separation of breeding and feeding habitat even in areas where the two habitats are not significantly spatially separated. Workers in the East and Midwest (Payne 1965, Kennard 1978, Dufty 1982) have noted that daily breeding and feeding activities were separated spatially, but the pattern is not as well defined as in California (e.g., Rothstein et al. 1984) as prime breeding and feeding areas generally occurred closer together on their study areas. Thompson (in press) reported that cowbirds in a radio-telemetry study moved an average of only 1.2 km between breeding and feeding locations, and stated that cowbirds did not seem to separate breeding and feeding areas based solely on their proximity to one another.

Cowbird-Nest Parasitism Link

Results from this study suggest that there was at best a weak relationship between the observed presence of cowbirds at a specific forest opening and observed presence of nest parasitism associated with the opening. There are several possible explanations for this. First, cowbirds may have been feeding and nest searching in spatially separate forest openings. Thus, some of the cowbirds recorded during point-counts may not have been involved in activities directly related to nest parasitism of an opening. Cowbirds, especially females, are secretive when searching for nests and might be missed during point-counts (see Chapter 2). In contrast, cowbirds often gather in large social flocks when foraging (Rothstein et al. 1984, Rothstein et al. 1987) and consequently may be more conspicuous during point-counts.

Alternatively, the relationship might have been obscured by the limited ability in this study to accurately detect nest parasitism in forest openings where very few active nests were found. In 13% of the openings (10 of 76 forest openings), no nests were found, despite relatively intense nest searching efforts (Table 5). In 29% of the openings (22 of 76 forest openings), only 1-2 nests were found. Given the small sample of nests in these openings, the likelihood of detecting nest parasitism, if it existed, was limited. However, cowbird presence and host species abundance were lowest in fields where we found few or no host nests (Table 5), suggesting that these particular fields had less suitable nesting habitat and consequently were poor areas for cowbirds to search for nests to parasitize.

Model Interpretation and Application

Example Calculation

Using the logistic regression equations and the parameter estimates for variables selected in final models (Tables 6 and 7), I calculated the predicted probability of cowbird presence and nest parasitism presence associated with a given forest opening. For example, the presence of cowbirds in a forest opening “A” that has no suitable foraging locations within 2 km, and is 0.5 ha in size, with an average vegetation height of 2.5 m, would have an estimated logit probability equal to:

$$g(x) = [4.081 + (1.286 \times 0) + (0.528 \times 0.5) - (0.967 \times 2.5)] = 3.214.$$

Opening “A” would therefore have a probability of cowbird presence equal to:

$$p = e^{3.214} / (1 + e^{3.214}) = 0.873 \text{ (87\% probability of cowbird presence).}$$

The presence of nest parasitism associated with the same opening “A” would have an estimated logit probability equal to:

$$g(x) = [1.122 + (1.010 \times 0) - (0.333 \times 0.5) + (0.084 \times 2.5)] = 1.165.$$

Opening “A” would therefore have a probability of nest parasitism presence equal to:

$$p = e^{1.165} / (1 + e^{1.165}) = 0.762 \text{ (76\% probability of nest parasitism).}$$

In contrast, a forest opening “B” that has 1 suitable foraging area within 2 km, is 9.0 ha in size, with an average vegetation height of 0.05 m would yield a $g(x) = 10.07$, $p = 0.999$ (100% probability of cowbird presence); and $g(x) = -0.861$, $p = 0.297$ (30% probability of nest parasitism presence). Thus, the likelihood of cowbirds occurring in forest opening “B” (100%) is slightly higher than in forest opening “A” (87%). However,

the likelihood of nest parasitism occurring in forest opening “A” (76%) is substantially higher than in forest opening “B” (30%). Similarly, probabilities can be generated and compared for any forest opening using the cowbird and nest parasitism models.

GIS Application

Model-predicted probabilities of cowbird and nest parasitism presence were calculated for each forest opening. These probabilities were entered into the existing land-use GIS coverage for LBL and maps were developed illustrating the spatial distribution of model-predicted cowbird presence (Figure 11) and nest parasitism presence (Figure 12) in forest openings.

Mathematical models that produce visual outputs such as the maps in Figures 11 and 12 provide a valuable tool for evaluating alternative management strategies on a given landscape. For example, the relative impacts of large forest openings clustered in management blocks versus smaller openings scattered across the landscape can be evaluated using this spatial model. Similarly, the importance of landscape-level variables (i.e., potential cowbird foraging locations) when evaluating cowbird edge-effects can easily be visualized under a range of conditions (e.g., different relative amounts or spatial distributions of forest openings) using this model.

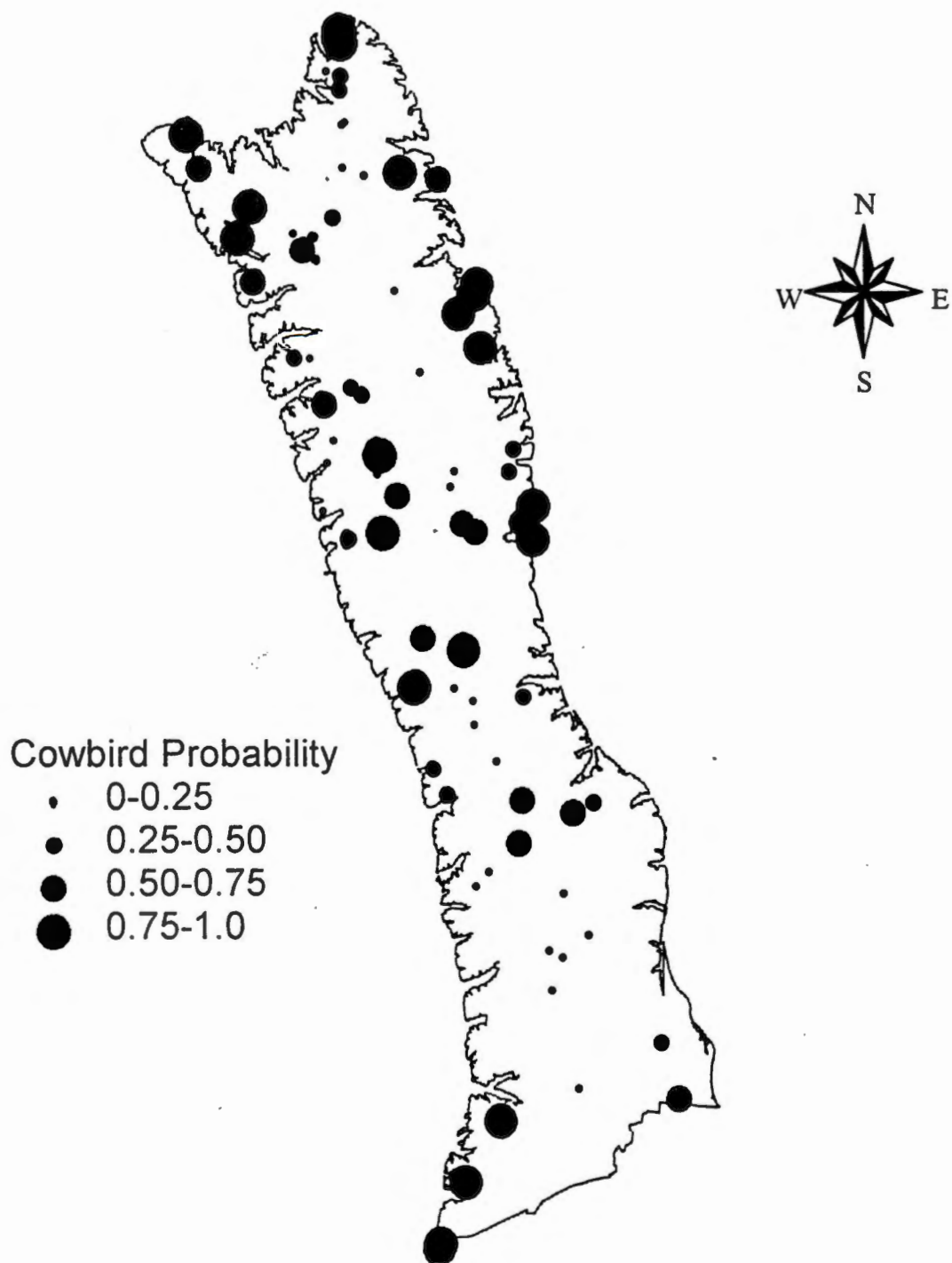


Figure 11. Model-predicted probabilities of brown-headed cowbird presence in surveyed forest openings on Land Between the Lakes, 1993-1994.

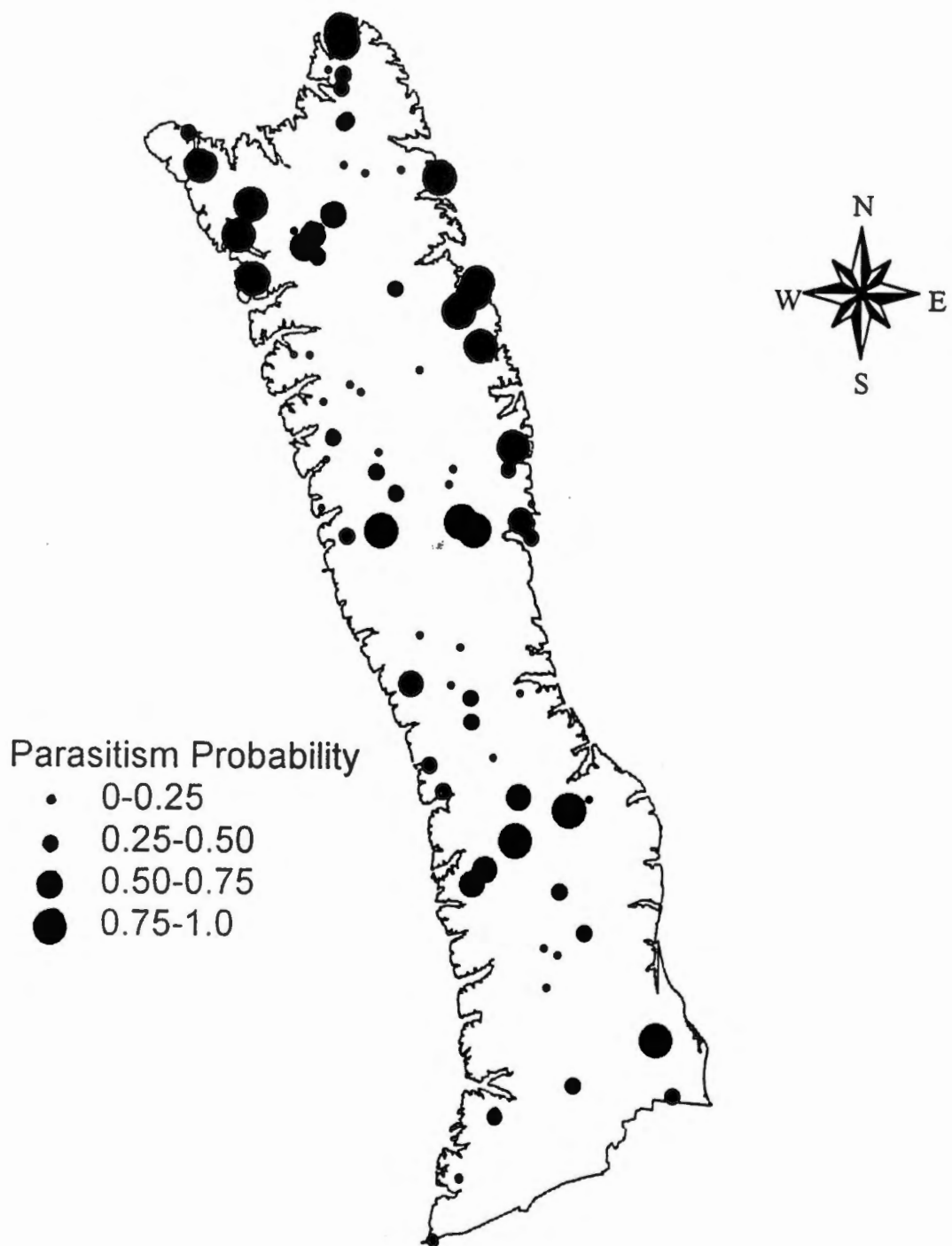


Figure 12. Model-predicted probabilities of the presence of nest parasitism by brown-headed cowbirds associated with forest openings nest-searched on Land Between the Lakes, 1994.

MANAGEMENT IMPLICATIONS

Because of the high degree of geographic variation in most cowbird-habitat relationships, it is inadvisable to make broad application of the predictive models in this study without testing the model relationships on a local level. For instance, in highly fragmented landscapes with extremely high cowbird populations, cowbirds may saturate the available forest habitat in which case the usefulness of predictive models is limited. Conversely, in areas with very low cowbird populations these relationships may exist but be hard to detect. The models in this study should be most applicable in forested landscapes characterized by low to moderate fragmentation and moderate cowbird populations. These conditions are currently found in many deciduous forest settings in the eastern United States.

From a management perspective, the positive relationship between the concentration of foraging areas around a forest opening and cowbird presence and/or parasitism at the opening may be particularly important for 3 reasons: (1) it seems to apply throughout the geographic range of the cowbird (Friedmann 1929; Hamilton and Orians 1965; Mayfield 1965; Robinson et al. 1993; Rothstein et al. 1987); (2) it was the strongest predictor of both cowbird presence and the presence of nest parasitism associated with forest openings; and (3) because it is a landscape-scale relationship, landscape-scale management actions may benefit broad areas.

Results from this study suggest that nest parasitism by cowbirds has a negative impact on host species productivity (Table 4). Several studies have reported a similar negative impact of cowbird parasitism on host productivity (Gates and Geysel 1978, Weatherhead 1989, Robinson 1992). High nest predation and increased interspecific competition associated with edge habitat may also negatively impact songbird productivity. However, from a management perspective, controlling nest parasitism in a given landscape may be the most attainable goal for land managers.

If minimization of nest parasitism is a management goal, landscape-level management is perhaps the best and most permanent way to reduce the negative impacts of cowbird parasitism on host species (Robinson 1993). Managers should be aware of surrounding land-use patterns and incorporate the possible effects of surrounding land-use patterns into management strategies. Within large forest tracts, any practice that creates cowbird feeding opportunities (i.e., mowing roadsides and campgrounds, allowing cattle grazing) will increase the likelihood of nest parasitism in these areas. Therefore, elimination of these foraging habitats on a management area may reduce the potential for high parasitism frequencies on the area. If this is not possible or feasible, potential cowbird feeding sites should be concentrated as much as possible. Cowbird trapping programs might be established in these areas during the breeding season to locally control cowbird populations (Robinson et al. 1993).

Large areas of contiguous forest habitat, in general, may be relatively immune to the effects of cowbird parasitism. In forested areas managed for timber, the establishment

many potential cowbird foraging sites. Robinson et al. (1993) suggested that making one large cut rather than many small ones, clustering cuts near existing edge, and avoiding irregularly shaped cuts may reduce parasitism.

It is theoretically possible to maintain specific levels of timber volume production and maintain certain amounts of undisturbed forest interior habitat simply by harvesting large blocks, and clustering these blocks (Gustafson and Crow 1994). Results from this study support a strategy of designing landscapes to provide a mix of resource outputs by clustering or zoning management activities (Probst and Crow 1991, Thompson et al. 1993, Gustafson and Crow 1994).

CHAPTER 3

III. COWBIRD CENSUSING TECHNIQUES

INTRODUCTION

The spatial distribution and abundance of brown-headed cowbirds must be known to determine the potential threat of cowbird parasitism to songbird populations across a given landscape. Parasitism levels vary geographically for most host species (Robinson et al. 1993). Therefore, it is important that land managers collect local data on cowbird presence and abundance to assess a potential cowbird problem. To make this assessment, researchers and managers require techniques that monitor cowbird populations efficiently and accurately

Point-counts of various types are widely used for censusing avian populations (Ralph and Scott 1981). These counts are primarily designed to detect singing males on relatively small breeding territories. Although general avian censusing techniques have been reviewed (Ralph and Scott 1981), no one has evaluated techniques specifically designed for censusing brown-headed cowbirds.

Cowbirds maintain relatively large home ranges (Dufty 1981; Darley 1982, Darley 1983; Teather and Robertson 1985) and are highly mobile during the breeding season (Rothstein et al. 1984, Robinson et al. 1993). Counts of longer duration (e.g., 20-min) may overestimate densities of birds like the cowbird that are highly mobile, less territorial

and have larger home ranges (Scott and Ramsey 1981). Thus, the duration of point-counts may be particularly important when censusing cowbirds.

Response of both sexes of brown-headed cowbirds to playbacks of the recorded female "chatter" call is well documented (Dufty 1981, Yokel 1989). However, little information is available on the potential use of playbacks for censusing cowbirds. Playbacks may be especially effective for enhancing detection of female cowbirds because they are secretive while searching for nests. Information on female cowbirds is especially important because females are directly responsible for nest parasitism. Playbacks also allow positive identification of male and female cowbirds as both sexes will approach playback equipment closely (Dufty 1981, Yokel 1989).

I assessed the effects of point-count duration for detecting cowbirds and estimating their abundance. I also compared the efficiency of point count versus recorded playback techniques for detecting cowbirds and estimating their abundance.

STUDY AREAS

I conducted point-counts and playbacks on two study areas, Land Between the Lakes (LBL) and Natchez Trace Wildlife Management Area, in Kentucky and western Tennessee (Figure 13). LBL is a 70,000-ha inland peninsula separating Kentucky and Barkley lakes, developed and managed by the Tennessee Valley Authority (TVA) as a national outdoor recreation and environmental education area. TVA maintains 7.4% of

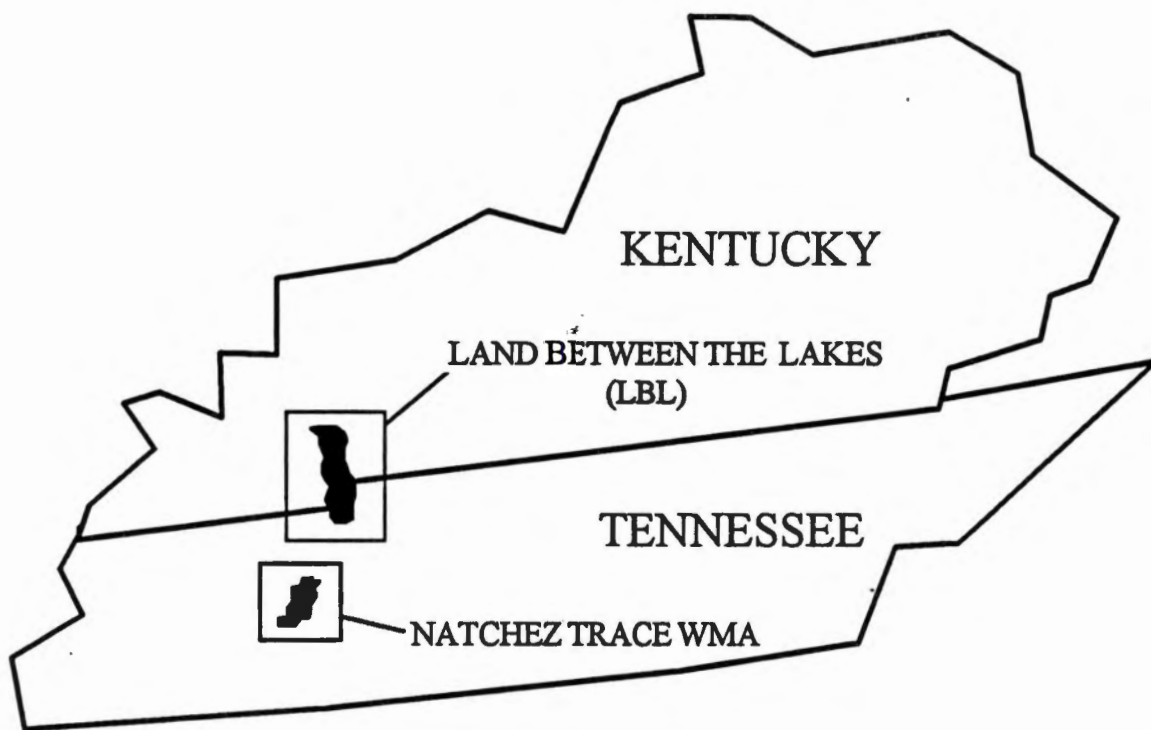


Figure 13. Location of Land Between the Lakes and Natchez Trace WMA study areas in Kentucky and Tennessee, 1994.

the total LBL area in forest openings. LBL is surrounded on three sides by water.

Predominant land-use patterns beyond the reservoirs are agricultural.

Natchez Trace is a 16,000-ha wildlife management area, state forest, and state park with 2% of the area maintained as forest openings. Tennessee Wildlife Resources Agency (TWRA) maintains both linear forest openings and smaller (>1 ha) polygonal forest openings on Natchez Trace. Surrounding land-use is primarily agricultural.

Most forest openings on both areas were managed as wildlife openings; however, some campgrounds and recreational areas were censused on LBL. All forest openings were permanently maintained, usually by mowing. Forest types on both areas included oak (Quercus spp.) - hickory (Carya spp.), pine (Pinus spp.), or mixed.

METHODS

Avian Censusing

Fifty-meter, fixed-radius point-counts were conducted at 296 paired, randomly selected forest-opening and interior-forest points from 17 May-15 July 1993. Counts were conducted between sunrise and 10:30 EST. Forest-opening counts were conducted at the opening/forest edge. Interior-forest points were located on a randomly selected compass bearing 200 m from the nearest forest opening.

Counts were broken into 0-3, 3-5, 5-10, and 10-20 min intervals. All birds seen or heard were recorded as being within 50-m of point center, outside the 50-m radius, or as "flyovers". Special attention was given to cowbirds seen or heard, specifically noting the sex of the individual, song heard and activity. Census protocols were the same for forest-opening and interior-forest points, although birds were easier to see and hear at forest opening points.

Recorded Playbacks

Recordings of the female "chatter" call were used to detect both male and female cowbirds. Free-ranging female cowbirds were recorded in Boise, Idaho in 1991 with a Marantz PMD 221 cassette recorder and a Sennheiser K3-U power unit and condenser microphone (A. Dufty, Jr., pers. comm.). Playbacks were broadcast with a Sony CFS-208 radio cassette-recorder. The playback emitted two chatters every 10 sec. Playbacks were played at a volume clearly audible up to 100 m by humans.

Playback sessions were conducted immediately after standard point-counts. We conducted playbacks at either the forest-opening or the paired interior-forest point to avoid the possibility that tapes were audible to cowbirds from both points. Thus, there were 148 points in which both techniques were applied. Tapes were played for five minutes, followed by a 5-min observation period. All cowbirds observed during the 10-min period were recorded, including sex of the bird and its activity, e.g., flying or perched.

Statistical Analyses

Point-count Duration

Power Function Equations. To predict results for point-counts longer than 20 minutes, a power function regression curve (Smith et al. 1993) was fitted to cowbird presence (cumulative number of points with cowbirds) and mean cowbird abundance (cumulative individual cowbirds per count), as a function of point-count duration for both forest-opening and interior-forest points. Power function regression equations had the form: $y = \beta_0(x)^{\beta_1}$. This approach allowed us to compare cowbird presence, mean abundance and habitat effects across a wide range of point-count durations.

Habitat Effects. Twenty-minute point-count data were used to determine if point-counts of different durations led to differences in cowbird detection frequency between forest-opening and interior-forest points. A logistic regression was performed, modeling cowbird presence as a function of point-count duration (3-, 5-, 10-, and 20-min counts) and habitat type (forest-opening or interior-forest). Finally, a two-way ANOVA was performed, modeling mean cowbird abundance as a function of point-count duration and habitat type.

Comparison of Point-count and Playback Techniques

The first 10-min interval of point-counts was compared with the 10-min playback period. A χ^2 -test for independence was performed to determine if detection patterns differed between the two techniques. Estimated mean cowbird abundance per point was

also compared for each technique, and a three-way analysis of variance (ANOVA) was performed modeling estimated mean abundance per point as a function of technique (point-count or playback), sex (male or female cowbird), and habitat type (forest-opening or interior-forest points) and their interactions.

RESULTS

Point-count Duration

Cowbird Presence

Male and female cowbird presence, predicted by the power-function regression equations, continued to increase throughout the 60-min count interval (Figure 14). However, cumulative female presence was consistently lower than cumulative male presence.. In both cases, cumulative presence began to decrease after 10 minutes.

Cowbird Abundance

A sharp increase in cumulative abundance was evident in male and female cowbird curves between 5- and 10-min intervals (Figure 15). After 10 minutes, cumulative abundance continued to increase throughout 60-min counts, although at a decreasing rate. Cumulative female cowbird abundance was consistently lower than cumulative male cowbird abundance.

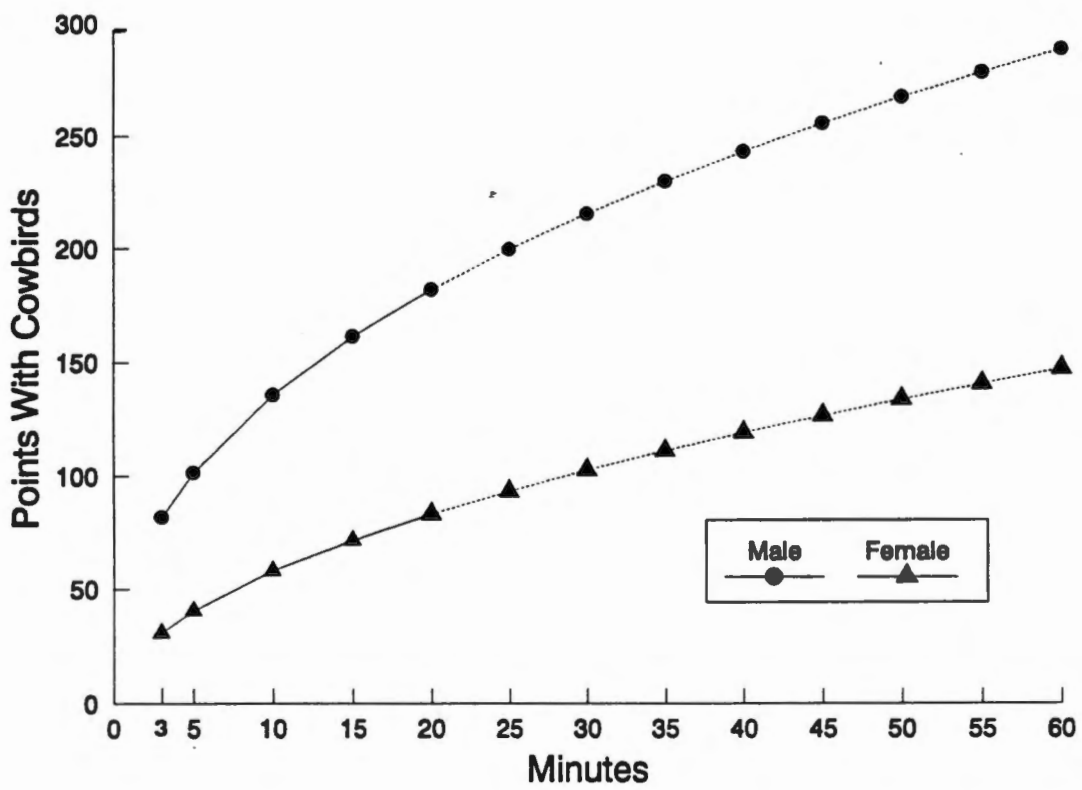


Figure 14. Cumulative number of points with male and female cowbirds present over time (dotted line represents extrapolation from power function regression equations).

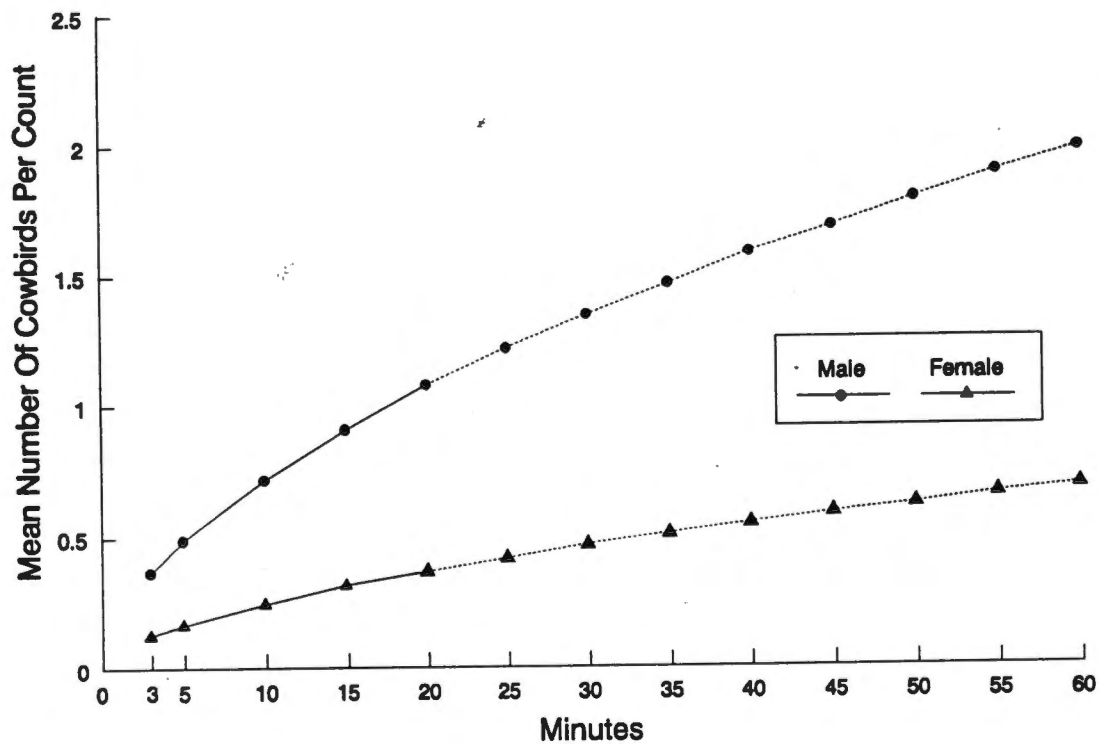


Figure 15. Cumulative mean number of individual male and female cowbirds per point count over time (dotted line represents extrapolation from power function regression equations).

Habitat Effects

Cowbird Presence. Female cowbird presence appeared to be greater in forest-opening than interior-forest points (Figure 16). However, there was little difference in male cowbird presence between the two habitat types. A logistic regression analysis using 20-min point-count data detected no significant interaction between point-count duration and habitat type for both curves ($P > 0.05$). Habitat type explained no significant variation for male cowbird presence ($P > 0.05$), whereas it was significant in explaining female cowbird presence ($P = 0.005$). Point-count duration was significant for both male and female cowbird presence ($P \leq 0.05$).

Cowbird Abundance. Female and male cowbird mean abundance appeared to be greater in forest-opening than interior-forest points (Figure 17). A 2-way ANOVA using 20-min point-count data detected no significant interaction between point-count duration and habitat type for both curves ($P > 0.05$). Main effects of point-count duration and habitat type were significant ($P \leq 0.05$) for both curves.

Comparison of Point-count and Playback Techniques

Cowbird Presence

Both methods detected cowbirds at similar frequencies, but not at the same points ($P < 0.05$) (Table 8). Point-counts and playbacks detected male cowbirds at 62 and 56 points, respectively. Point-counts detected female cowbirds at 27 points, whereas playbacks detected females at 33 points.

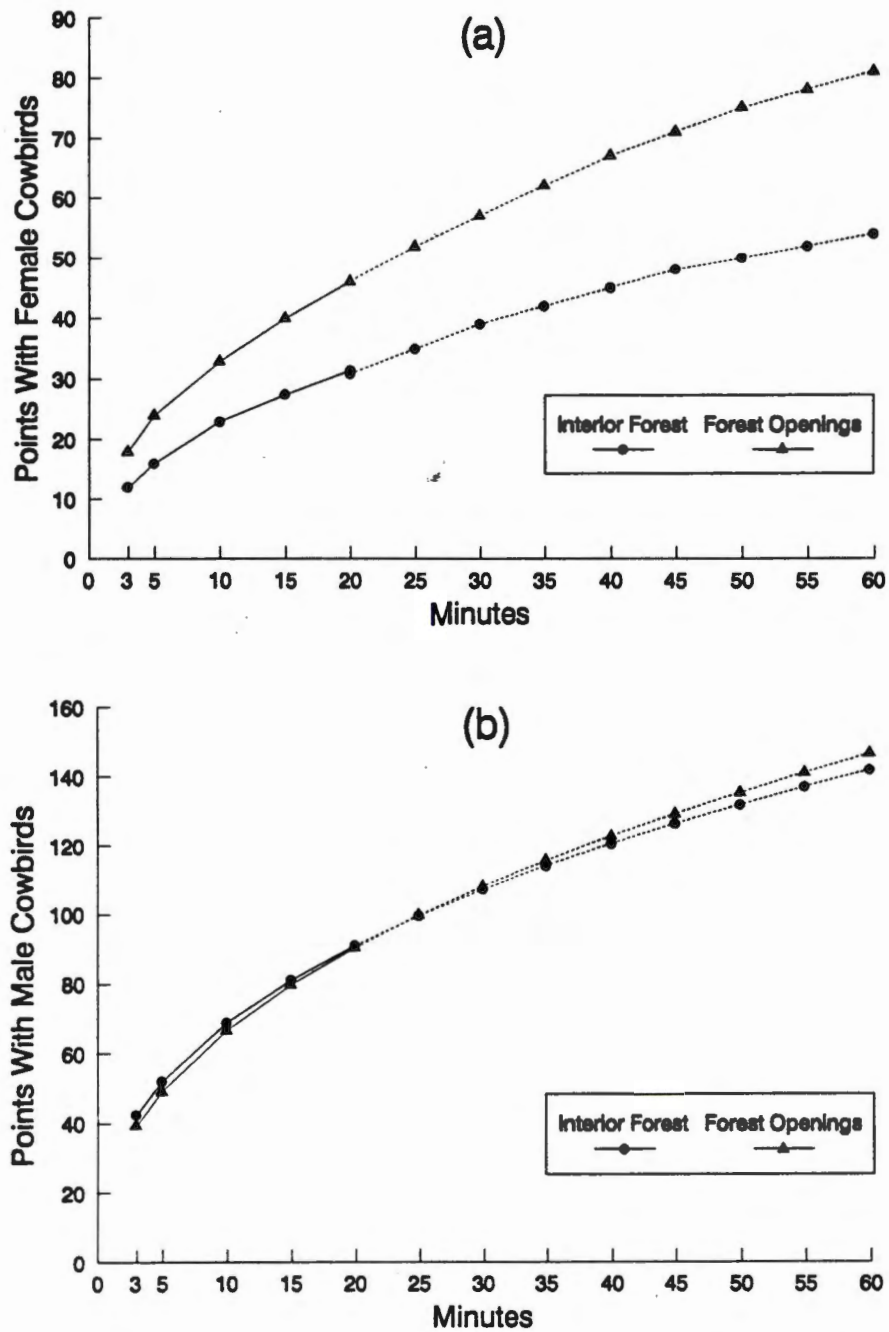


Figure 16. Cumulative number of interior-forest and forest-opening points with female (a) and male cowbirds (b) present over time (dotted line represents extrapolation from power function regression equations).

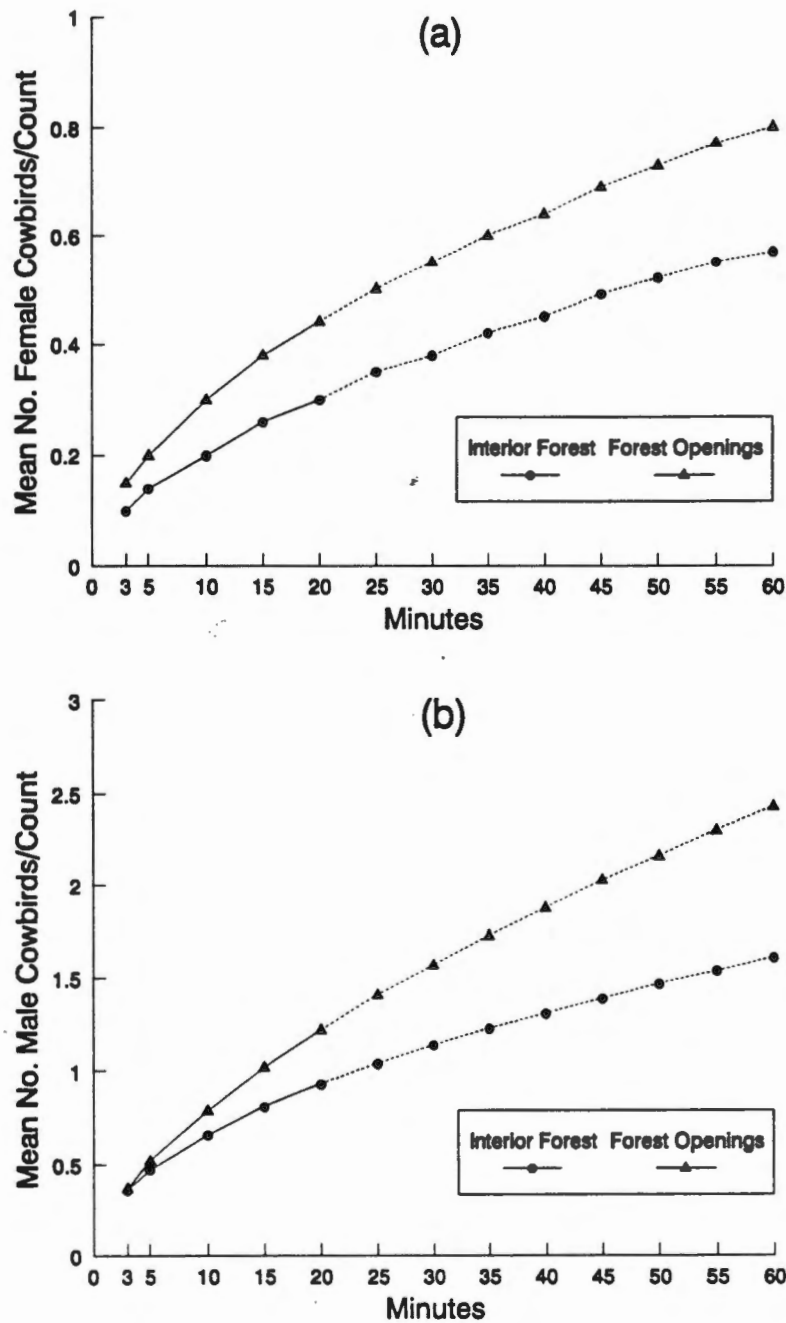


Figure 17. Cumulative mean number of female (a) and male cowbirds (b) per point count in interior-forest and forest-opening points over time (dotted line represents extrapolation from power function regression equations).

Table 8. Number of point counts and playbacks in which male and female cowbirds were present or absent.

		MALES		
		Playback		Total
		Absent	Present	
Point-Count	Absent	63	23	86
	Present	29	33	62
	Total	92	56	148
$\chi^2 = 10.74, df = 1, P = 0.001$				
		FEMALES		
		Playback		Total
		Absent	Present	
Point-Count	Absent	98	23	121
	Present	17	10	27
	Total	115	33	148
$\chi^2 = 4.14, df = 1, P = 0.042$				

Cowbird Abundance

Point-counts estimated slightly greater abundances for males (0.65 vs. 0.54 males per count) and playbacks estimated slightly greater abundances for females (0.28 vs. 0.24 females per count) (Table 9). However, abundance did not differ significantly between the two methods ($P > 0.05$).

Based on a 3-way ANOVA I detected no significant interactions between techniques, sex or habitat variables ($P > 0.05$) (Table 9). Sex and habitat type were the only variables that explained any significant variation in mean abundance ($P < 0.05$). Estimated male abundance was consistently greater than estimated female abundance ($P = 0.0001$).

DISCUSSION

Point-count Duration

Presence and abundance estimates for both male and female cowbirds continued to increase throughout 60-min point counts (Figures 14 and 15). This suggests that increasing point-count duration does not lead to a fixed estimate of the total number of points with cowbirds or the number of cowbirds per point. In addition, prolonged censuses are not viable alternatives for managers facing constraints of personnel, time and other responsibilities (Smith et al. 1993). Prolonged censuses also greatly increase the

Table 9. Mean cowbird abundance per point count ($n = 148$) and playback ($n = 148$) for male and female cowbirds in interior-forest, forest opening, and all points combined.

Technique	Sex	Interior Forest		Forest Opening		All Points	
		Mean	S.E.	Mean	S.E.	Mean	S.E.
Playback	Male	0.40	0.08	0.68	0.12	0.54	0.07
Point Count	Male	0.54	0.09	0.76	0.14	0.65	0.08
Playback	Female	0.23	0.06	0.32	0.08	0.28	0.05
Point Count	Female	0.19	0.06	0.28	0.07	0.24	0.05

Three-way Analysis of Variance			
Source	DF	F-Value	Pr > F
Technique	1	0.27	0.6037
Sex	1	26.02	0.0001
Habitat Type	1	6.89	0.0089
Technique*Sex	1	1.29	0.2565
Technique*Habitat Type	1	0.05	0.8264
Sex*Habitat Type	1	1.43	0.2318
Technique*Sex*Habitat Type	1	0.06	0.8135

likelihood of multiple counts of the same birds (Scott and Ramsey 1981). Thus, census methods must be based on measures of relative cowbird abundance. The ultimate question, then, is what count duration provides the best estimates for these relative measures?

Cowbird Presence

The optimal count duration must be a compromise between two competing objectives. The first objective is to ensure that any cowbirds present during the count are detected. The second objective is to ensure that additional time spent after the first detection is minimized. Ten-min point-counts appear to provide a reasonable balance between these competing needs. For example, 10-min counts accounted for 70% and 40% of the total female presence for 20- and 60-min counts, respectively. In contrast, 5-min counts accounted for only 49% and 28% of the total female presence for 20- and 60-min counts, respectively. Thus, a substantial increase in female cowbird presence was recorded from 5 to 10 minutes. After the 10-min period, however, the relative gain in female detections decreased.

Cowbird Abundance

Ten-min point-counts also appear to be suitable for estimating mean cowbird abundance. For example, 10-min counts accounted for 68% and 36% of the estimated female mean abundance for 20- and 60-min counts, respectively. Five-min counts

accounted for 46% and 25% of the estimated female mean abundance for 20- and 60-min counts, respectively. Thus, a substantial increase in estimated female abundance was recorded between 5- and 10-min intervals.

Habitat Effects

Because of obvious differences in vegetative cover between forest-opening and interior-forest settings, cowbirds are likely to be more detectable during point-counts in forest-opening than in interior-forest settings. This difference in detectability could obscure real differences in cowbird presence or abundance as point-count duration increased. However, there was no significant interaction between point-count duration and habitat type when they were used to estimate cowbird presence or mean abundance for counts up to 20 minutes.

Comparison of Point-count and Playback Techniques

Cowbird mobility probably accounted for the differences in where cowbirds were detected by the two techniques. Because we used only the first 10 minutes of point-counts to compare with the 10-min playback period, a 10-min window existed in which cowbirds could move in or out of a point. This time interval appeared to be sufficient to allow birds detected by the point-counts to move out of the area by the time playbacks began. Similarly, cowbirds detected by the playbacks were not necessarily present during the earlier point-count. Perhaps as important as where birds were detected, however, was

the frequency of detection. Both male and female presence and abundance estimates were similar for both techniques.

Differences in Male and Female Detections

Male cowbird abundance in this study was consistently greater than female cowbird abundance, regardless of detection technique. This is consistent with other studies reporting a strongly male-biased sex ratio (Rothstein et al. 1986, Yokel 1989).

Of the 198 points at which males were observed on our study areas, females were absent 65% of the time (128/198). Conversely, of the 85 points at which females were observed, males were absent only 21% of the time (15/85). Robinson et al. (1993) suggested that many males in nest-searching areas may be unmated and searching for mates rather than nests, whereas females are more likely to be searching for nests. Unmated males provide little insight into the actual breeding population of cowbirds, and consequently may be of little value for predicting parasitism frequencies.

MANAGEMENT IMPLICATIONS

We suggest that 10-min counts, broken into 0-3, 3-5 and 5-10 min intervals, would be best for managers initiating efforts to monitor cowbird populations. After reviewing first-year results, managers can decide which count duration works best for their particular situation. For high-density cowbird populations, shorter counts may be more efficient.

Point-count and playback techniques yielded similar results in our study.

Playbacks may be useful to managers as a training tool for cowbird identification (including distinguishing cowbird sex) or as a check to ensure that cowbirds are not being overlooked during point-counts. Playbacks may also be useful on areas where cowbird densities are low

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