Studies in Avian Biology No. 18:204–217, 1999.

A SPATIAL AND GENETIC ANALYSIS OF COWBIRD HOST SELECTION

D. CALDWELL HAHN, JAMES A. SEDGWICK, IAN S. PAINTER, AND NANCY J. CASNA

Abstract. Molecular genetics makes it possible to measure basic but long elusive parameters of the breeding biology of the Brown-headed Cowbird (*Molothrus ater*). We examined cowbird fecundity and host selection behavior using a combination of molecular genetic techniques to link female cowbirds to the eggs they lay, radio-telemetry techniques to track female cowbirds' daily movements, and geographic information systems (GIS) to integrate these genetic and spatial data. Our study site lay within a forested 1300-ha landscape in New York composed primarily of mature forest with adjacent old fields. We found that female cowbirds used their home ranges as principal egg-laying areas. Individual females used characteristic individual home ranges throughout the breeding season, and they returned to the same home range every breeding season. Over one-half (54%) of females laid all their eggs in host nests inside or close to their home range. Proximity to a female's home range was the only significant ecological or biological feature affecting a cowbird's host selection. Neither host species identity, nest height, adult mass, egg size, incubation period, nor host taxonomic classification predicted which nests would be parasitized. Eggs laid outside the home range were frequently found in multiply-parasitized nests located along common flyways or in conspicuous sites that a cowbird could discover opportunistically. We also found that female cowbirds avoided laying more than one egg in a particular host nest, even though multiple parasitism characterized over one-third of parasitized nests in the study. Finally, we estimated that effective cowbird fecundity lies between a minimum of 1.72 eggs per female and an upper bound of 8.16 eggs per female. Effective cowbird fecundity is defined as the actual number of cowbird eggs laid in appropriate host nests and not ejected; it is lower than raw fecundity or the physiological egg production capacity of cowbirds. We suggest that the female cowbird's use of home range is a critical element in its breeding behavior, enabling cowbirds to use a known-host selection strategy. Experienced female cowbirds selectively parasitize the host pairs that nested in their home ranges in previous breeding seasons and were most successful. The three elements of cowbird breeding behavior reported here challenge the stereotype of the Brown-headed Cowbird as an *r*-selected species that produces a large number of young and invests no parental care. Instead, these results suggest that cowbirds lay fewer eggs in host nests than has been speculated and that they do invest parental care. Two examples of parental care we discuss are observing a host's parental behavior and nest success before parasitizing it, and laying each egg in a different host nest, even though that requires females to search longer and to find a larger number of host nests. Current cowbird trapping programs should be evaluated for their effect on age structure of cowbird populations and resulting parasitism patterns. Yearling females may be associated with higher rates of multiple parasitism and higher rates of parasitism on more conspicuous hosts. Conspicuous hosts such as the Black-capped (*Vireo atricapillus*) and Least Bell's (*Vireo bellii pusillus*) vireos are probably most at risk from cowbird populations with disproportionately high numbers of immigrant yearling female cowbirds such as those created by trapping programs.

Key Words: Brown-headed Cowbird, DNA fingerprinting, fecundity, GIS, home range, management, *Molothrus ater*, telemetry.

To evaluate whether Brown-headed Cowbirds (*Molothrus ater*) pose a threat to particular species or communities, conservation biologists need to measure basic parameters that have long been invisible. Fundamental reproductive traits such as the average laying rate per female, percentage of breeding females in a population, use of a breeding territory, and the number of eggs laid per nest are readily determined in non-parasitic birds, but are still not well established for the Brown-headed Cowbird. These reproductive traits require measurement at the individual level, and in brood parasites this is a feat that was not possible until the recent advent of molecular genetic techniques.

Without genetic information, previous investigators have been limited to analyzing parasitism patterns at the population level rather than at the individual level, focusing on features that generally make host nests more conspicuous to cowbirds, such as proximity to forest edge (e.g., Brittingham and Temple 1983); nest height above the ground, with low nests being more exposed in some sites (Hahn and Hatfield in press) and more camouflaged in other sites (Martin 1993); differences in host density (e.g., Clark and Robertson 1979); and breeding behavior that makes a host's nest more susceptible to parasitism, such as the nest singing of the endangered Least Bell's Vireo (*Vireo bellii pusillus*; Kus *this volume*) and Black-capped Vireo (*Vireo atricapillus*; e.g. Graber 1961).

Examining habitat features or host behavior has been of limited value in deciphering cowbirds' host selection patterns. Determining cowbird fecundity has become increasingly urgent to conservation biologists, since physiological and laboratory data suggested that cowbirds were unusually fecund, potentially laying 20–40 eggs per female each season (Payne 1976, Scott and Ankney 1980, Holford and Roby 1993). However, fecundity under field conditions, the critical parameter, required genetic techniques to be measured.

Our goal in this study was to obtain accurate estimates of cowbird reproductive rate and host selection patterns that could be used to speed recognition of host populations in trouble. We designed this study to estimate the proportion of female cowbirds actively breeding in a local population, the fecundity of individual cowbirds, and the biological or ecological features that guide an individual female's host selection. Previous studies had established that cowbirds use territories or home ranges (Dufty 1982a, Darley 1983, Rothstein et al. 1984, Teather and Robertson, 1985, Smith and Arcese 1994), but no one had looked quantitatively at the relationship between female home range and the locations of parasite eggs throughout an entire host community. This approach required documentation both of the individual female cowbird's movements and of the specific nests where she laid her eggs. We designed a study to locate as many parasitized nests as possible in the study area, then to use molecular genetic techniques to match the cowbird eggs to the individual cowbird females that had laid them. Our strategy was to combine parentage information from cowbird young with radiotelemetry data from females' movements in order to explain their breeding behavior.

METHODS

STUDY AREA

We conducted a study of cowbird parasitism during 1991–1993 near Millbrook, Dutchess County, NY (51° 50 N, 73° 45 W), in a 1300-ha oak-maple-hemlock forest and in old fields adjacent to the forest and within cowbird commuting distance (Fig. 1; Hahn and Hatfield 1995). The study occurred on lands belonging to Rockefeller University and for the portion of the study reported here, we searched for nests within a 226-ha block. The study area is located within the township of Washington, a 38,000-ha area of which 55% is forested and the remaining area is a mosaic of equal parts pasture, livestock, and suburban development (Glitzenstein et al. 1990). The forest contains stands ranging in age from 70–150 years, experiences little disturbance, and is bisected by a seldom-used one-lane dirt road.

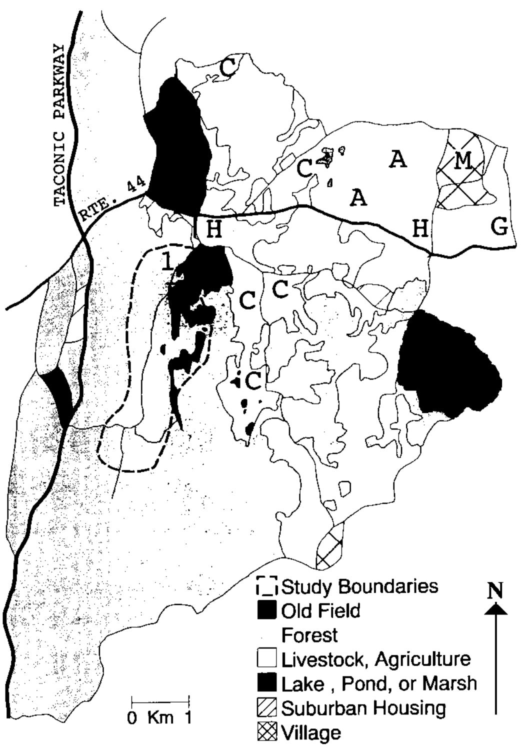

FIGURE 1. The study area in Millbrook, NY, 1991–1993, and surrounding landscape. The study area is numbered "1" and enclosed in dashed lines. A = agricultural fields; C = cattle and dairy farms; G = golf course; H = horse farms; M = village of Millbrook; R = Rockefeller University Field Research Center.

The stands are dominated by chestnut oak (*Quercus prinus*) and northern red oak (*Q. rubra*) on rocky slopes, and by white oak (*Q. alba*), black oak (*Q. velutina*), and pignut hickory (*Carya glabra*) on valley bottoms and mesic uplands. Hemlock (*Tsuga canadensis*), beech (*Fagus grandifolia*), and sugar maple (*Acer saccharum*) are confined to moist habitats such as ravines and streamsides. Understory tree species are flowering dogwood (*Cornus florida*), ironwood (*Ostrya virginiana*), shadbush (*Amelanchier* spp.), and striped maple (*Acer pensylvanicum*). Maple-leaved viburnum (*Viburnum acerifolium*) and blackberry (*Rubus* spp.) are the dominant shrubs. The swamps are vegetated with cinnamon fern (*Osmunda cinnamomea*), skunk cabbage (*Symplocarpus foetidus*), spicebush (*Lindera bezoin*), and tussock sedge (*Carex stricta*).

The old fields are dominated by blackberry (*Rubus* spp.), rose (*Rosa* spp.), alder (*Alnus* spp.), and haw (*Viburnum* spp.). The old field study areas include a 1-ha lawn with ornamental trees and shrubs on the north side of Tyrrell Lake.

TRAPPING ADULT COWBIRDS

Brown-headed Cowbirds were caught at the Rockefeller University Field Research Center (RUFRC) in Millbrook, Dutchess County, New York. A local population of cowbirds has been observed and studied there intermittently during two decades (Dufty 1983; P. Marler, pers. comm., J. Wingfield, pers. comm). There is a large local cowbird population, readily seen at the dairy, beef, and horse farms in the local countryside, as well as at numerous residential bird feeders. Cowbirds are attracted in feeding flocks to the field station lawns and to the nearby trash disposal area, where discarded seed associated with maintenance of captive canaries and finches is available year round.

We trapped cowbirds in funnel (or confusion) traps, which were constructed of 14-gauge wire (2.54 × 5.1 cm mesh) and measured 76.2 × 50.8 × 25.4 cm. Cowbirds walk into the traps through one of two openings in the trap wall and are led via wire tunnels (10.2 cm in length) into the center of the trap. Birds are reluctant to exit because the tunnel (funnel) narrows at the exit end. We set eight traps daily on a 0.25 ha lawn at RUFRC; the field station and trapping area were adjacent to the study site where we searched for parasitized nests and followed radiotagged females. We ran a trapping and banding program here throughout the field season (15 May–25 July) on weekdays from 1600 to 1900 hours, checking traps every 30 minutes. Cowbirds were banded with USFWS aluminum bands and individually unique color bands. Animals were handled and treated in accord with the guidelines and principles of the American Ornithologists' Union animal use practices guidelines (Oring et al. 1988).

NEST SEARCHING FOR COWBIRD YOUNG

A team of six searched for nests over approximately 1500 hours between 15 May–15 July. In the forest, the principal cowbird host species ($N \geq 20$ nests) were Wood Thrush, American Redstart, Veery, and Ovenbird (scientific names in Table 3). Eastern Phoebes were a frequent species in the forest, on the ubiquitous rock faces, and also on sheds in old fields. In the old field community, Song Sparrow and Chipping Sparrow were common species.

POINT-COUNT SURVEY

To obtain an estimate of host density independent of the estimate obtained from nest searching, we conducted six point-count surveys across the breeding season, three in the forest and three in the old fields. Two observers conducted early morning surveys in late May and early June at points spaced 100 m apart on two different transects. We used the program DISTANCE (Burnham et al. 1980, Laake et al. 1993, Buckland et al. 1996) to analyze the survey data.

RADIOTELEMETRY, HOME RANGE MAPPING, AND TERRITORIAL BEHAVIOR

Each year we attached radio transmitters to female cowbirds that we trapped that weighed over 35 g (1991: N = 7; 1992: N = 26; 1993: N = 22). Transmitters, manufactured by Holohil, Inc., Ontario, Canada, weighed 1 g and were equipped with 30-day batteries. We attached the transmitters to the birds' backs between the scapulae using Superglue™. We prepared the transmitters by gluing silk or cotton fabric to one side of the transmitter and allowing it to dry at least one day before putting them on the birds. We selected birds > 35g and prepared the bird for the transmitter by pushing aside feather coverts, then clipping underfeathers to a stubble on the back. We applied glue to the fabric side of the transmitter, then pressed the radio against the feather stubble. We held each bird quietly in our hands for 5 min after affixing the transmitter, gently pressing the radio against the bird's back and allowing the bond to set. We next placed the birds in a large 4 m × 4 m holding cage to let the bond cure for an additional 30 min before releasing them.

We tracked all radiotagged birds daily 0500 to 1200 Monday through Saturday throughout the breeding season. One full-time biologist, assisted by two others part-time, searched for each female daily, tracking both on foot with a hand-held antenna and also with a vehicle carrying a mounted antenna. Our objective was to obtain a daily morning location for each female while she was engaged in non-feeding activities, for the life of the battery.

In addition to mapping daily points on individual topographic maps for each female, we entered the daily telemetry points for all females on an enlarged (2.25 m × 1 m) master map where we also noted all nest locations, so that the study team had an integrated picture of the data being collected and an overview of parasitism on the study site. Subsequently all radiotelemetry points were translated into UTM locations and entered into home range coverages in ARC/INFO.

We designated as the principal group those females that we had followed 10 days and for which we had collected at least 10 location points, although we also analyzed the home range size and location of other radio tagged females for which we had fewer points. We gathered limited baseline data on cowbird territorial behavior during Year 1 of the study to use in the design of the larger radio tracking program in Year 2. We counted boundary disputes between females with adjacent home ranges while following radio tagged individuals. We also studied the responsiveness of female cowbird home range holders to intruder female cowbirds by audiotape playback experiments, using the calls of cowbird females. To conduct the playback experiment, we first established by radiotelemetry that a radiotagged female was in the vicinity of her home range, although not in sight. Along what we identified as the home range boundary, we placed two portable speakers in a canvas field case under shielding shrubs. We then stood nearby, also shielded by shrubs, holding a small portable tape recorder. We played the audiotaped female cowbird vocalizations for 10 s, then waited 30 s, then played another 10 s of tape; 30 s later, we played another 10 s. We then waited 3 min and noted if a marked home range holder female appeared during that period, either checking visually and/or calling. We conducted 6 separate tests with 6 different female cowbirds on their home ranges.

GIS: Integrating Spatial and Genetic Information

To obtain an overview of cowbird parasitism on the study area, we integrated the three datasets using ARC/INFO, namely: (1) spatial information (nest locations and daily location points of radio tagged females); (2) ecological and biological information (for all nests: nest height, host species, parasitized or not, number of cowbird eggs or nestlings); and (3) genetic data (band sharing coefficients showing genetic relationships between pairs of individual cowbirds). To provide accurate land cover information, we scanned aerial photographs of the study area into ARC/INFO; to provide information on elevation and slope, we imported the appropriate U.S. Geological Survey topographic maps.

Individual home ranges were depicted and calculated using the minimum convex polygon function of ARC/INFO, joining the outermost points of each individual's cluster. Maps displayed each female's home range and the location of parasitized nests of cowbird young with known degrees of genetic relatedness. We used three classifications for the spatial relationship between a female's home range boundary and her parasitized nests: "inside," "close to" (within a 50-m buffer zone of the boundary), and "distant from" (beyond a 50-m boundary).

Genetic Analyses

We conducted genetic analyses using multilocus DNA probes on 104 cowbirds trapped or collected from the study site in Year 2 of the study (43 females and 61 eggs or nestlings). The 43 adult females were selected on the basis of weight (> 35 g), the best indicator available to distinguish older, reproductive females; the 61 young cowbirds or eggs represented those we found that yielded viable genetic material.

We collected 10–40 microliters of blood by venipuncture of the brachial vein, added lysis buffer, and stored it in a freezer until analysis. DNA profiles were performed at Therion Corporation, Troy, NY. DNA was isolated, digested with restriction endonuclease *Hae*III, electrophoresed, and transferred to a nylon membrane following standard methods (Haig et al. 1994, 1995). Molecular weight sizing standards (MWSS) were loaded in up to three lanes so that they bracketed samples and facilitated objective identification of bands. Ten samples were run on each gel. The set of standard DNA fragments of known molecular size was composed of 48 bands ranging from 0.504 to 34.679 kilobase pairs. The transferred DNA was probed sequentially with two ^{32}P-labeled proprietary probes, Opt-03 ™ and Opt-05™, washed, and exposed to x-ray film following the protocols of Haig et al. (1994, 1995). The two probes had been selected on the basis of a pilot study that showed that they gave highly variable DNA profile patterns among unrelated cowbirds collected from widely separated sites. To estimate relatedness we calculated band sharing coefficients (BSCs) for all pairs of individuals in the study. Similarity (S) was calculated as the ratio of number of bands shared divided by the total number of bands scored for a pair of individuals (Lynch 1988), and it yielded just over N = 5,000 pairwise comparisons. Because we consider that each probe detected a different set of minisatellites (Georges et al. 1988), we treated these BSC data as independent assessments of relatedness.

DNA fragment scoring and data analyses

We scored fragments within and among gels as described in Haig et al. (1994, 1995). Each DNA fragment (band) was independently scored by two investigators. We eliminated any band that was lighter than the lightest bands in the molecular weight sizing standards. To calculate band-sharing among individuals on all gels, band sizes were hand-digitized and resulting data entered into computer programs designed by Therion Corporation. Prior to making comparisons among cowbirds, MWSS lanes were compared within gels and then among gels to determine the accuracy and precision of our band matching methodology. The program matched identical MWSS bands within and among gels.

Band sizes for each individual were then determined by comparison to the MWSS within the range of 13.823–2.532 kb. Using this method the sizing error within and between gels was estimated to be ± 0.6% of band size (i.e., the total range was equal to 2 SD or 1.2% of band size; Balazs et al. 1989, 1990; Risch and Devlin 1992). Therefore, when determining band-sharing between individuals, bands were considered to be a match when their respective sizes overlapped within a range of ± 0.9% of each band size (i.e., the total range is equal to 3 SD or 1.8% of band size). These values were consistent with those reported by Galbraith et al. (1991) who suggested that the distance between bands be at least 2.8 SD before they are declared different at the 0.05 level.

DATA ANALYSES: INVESTIGATING HOST SELECTION PATTERNS USING GENETIC DATA

Comparing band-sharing coefficients among groups

We examined several factors that might influence cowbird laying behavior: (1) location of female's home range; (2) host nest height (low, medium, high); (3) host adult mass; (4) host egg volume; (5) host body length; (6) host clutch size; and (7) host taxonomic identity (by subfamily). We tested the influence of each factor by comparing average relatedness (BSCs) between groups of cowbirds. Comparison of groups of BSCs maximizes the information that can be gleaned from a large sample of BSCs without assigning maternity. Each factor was tested by comparing the average relatedness of pairs of individuals with a similar value (for that factor) with the average relatedness of individuals with dissimilar values. Standard errors were calculated separately for each group following Lynch (1988, 1990) by taking a random sample of pairs, where no pair shared an individual with any other pair, and treating each pair as uncorrelated. Standard errors for the mean pairwise bandsharing coefficients were then calculated using a conservative estimate of the correlation between pairs with one individual in common. A correlation of 0.5 was used, which was approximately the upper 95% point of a bootstrap distribution of the correlation calculated from uncorrelated pairs of pairs with one individual in common (Lynch 1988). The standard error calculated for the difference was used in the power calculations.

Estimating most likely mother-offspring pairs

We assigned probable maternity of cowbird young on the basis of BSCs using as a cut-off value the upper 95% confidence interval. BSCs have been repeatedly shown to be a robust estimate of relatedness (Lynch 1988, 1990; Webster and Westneat 1998). For most typical outbred avian taxa using the Jeffreys' probe, the band-sharing or similarity index (*S* of Lynch 1988, 1990) varies between about 0.1 and 0.4 among unrelated individuals and between 0.5 and 0.8 for first-order relatives (Burke et al. 1989, Meng et al. 1989, Morton et al. 1990, Westneat 1990, Oring et al. 1992, Stutchbury et al. 1994). Thus, pairs of individuals in populations with *S*-values greater than 0.5 are very likely to be siblings or parents and offspring (Lynch 1988). We confirmed this finding in Year 1 of the study when we did multilocus analyses of cowbird DNA using Jeffreys' probe (Hahn and Fleischer 1995); we found a significant difference between the mean BSCs for unrelated individuals (mean = 0.31 ± 0.08) vs. mothers and offspring (mean = 0.45 ± 0.13). We had confirmed this finding by also calculating a cutoff value to define first-order relatives using the upper 95% confidence limit.

For Year 2, we generated cut-off values to define first-order relatives using the upper 95% confidence limit (probe Opt-03: 0.30 ± 2(0.10) = 0.50; Opt-05: 0.24 ± 2(0.12) = 0.48) as in Haig et al. (1994, 1995) and Hahn and Fleischer (1995). We assigned putative mothers to young when a mother-young pair had a BSC ≥ cut-off value on at least one probe.

RESULTS

CHARACTERISTICS OF FEMALE COWBIRD HOME RANGES

Cowbird females followed at least 10 days and which had at least 10 point locations (N = 12), consistently used an identifiable home range throughout the breeding season. Their point locations created a characteristic cluster of points within a defined spatial area (Fig. 2). The average home range size for these principal females was 9.38 ha ± 7.9 SD, range = 2.6–32.2 ha, median = 7.6 ha.

Cowbirds were commonly seen in feeding flocks in the afternoon and early evening. Flocks congregated at a variety of sites in the Millbrook township including the lawn of the field station at RUFRC as well as at barns and fields associated with local dairies, horse, and cattle farms, and at residential bird feeders (Fig. 1). We did not find a communal evening roost of the cowbirds in this study area. We conducted several searches for individual radio tagged females at

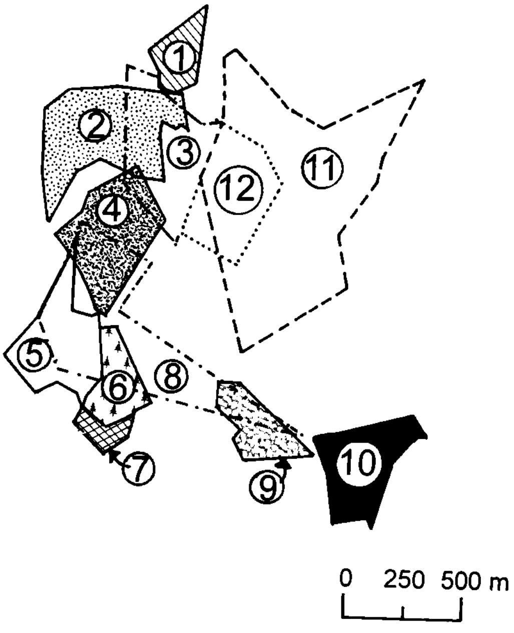

FIGURE 2. The home ranges, showing zones of overlap, of the 12 principal female cowbirds followed by radiotelemetry in Millbrook, NY, 1992.

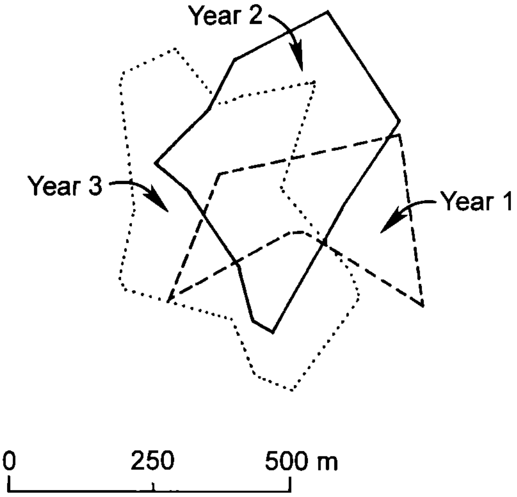

FIGURE 3. The home range fidelity of a female cowbird (F91337) followed by radiotelemetry over three successive breeding seasons in Millbrook, NY, 1991–1993.

dusk and after nightfall, but on each occasion located only a single female on her home range.

HOME RANGE FIDELITY ACROSS SUCCESSIVE BREEDING SEASONS

The characteristic home ranges of females within the host community were re-established from one breeding season to the next. For example, one female (F91337) used a Year 2 home range that overlapped with 53% of her Year 1 home range; in Year 3, she used a home range that consisted of 89% of the area she used as home ranges in Years 1 and 2 (Fig. 3).

We have multi-year data on six females radioed in Year 2 of the study, and each returned to nearly the same spatial area as its previous home range. The mean size of the 13 home ranges established over three years by the six females was 8.0 ha ± 5.3. The mean home range size in Year 2 was 9.38 ± 7.9 when looking at the 12 principal females, and it was 7.0 ha ± 3.2 (Year 2) when looking only at the subset of six females with multi-year data. Home range size did not differ among years (one-way ANOVA: $F_{2,10} = 2.31$, $P > 0.14$).

A multi-year map of home ranges of six of the seven females for which we have telemetry data in more than one year displays how consistently each individual returned to the same distinct home range (Fig. 4). While there was some

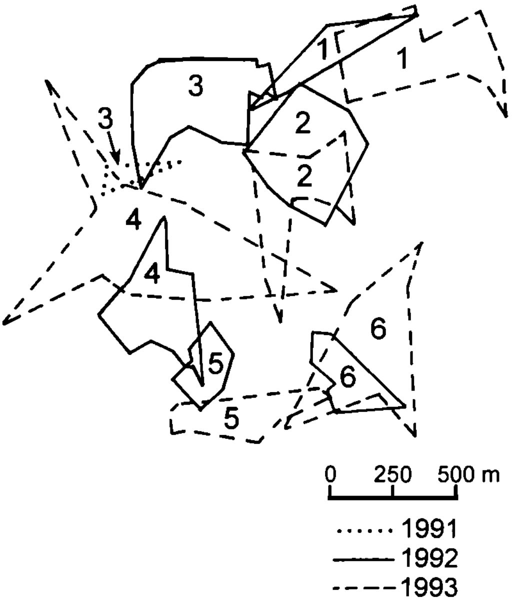

FIGURE 4. The home range fidelity of six female cowbirds that were followed for more than one year via radiotelemetry at Millbrook, NY, 1991–1993. The home range outlined in a dotted line was observed in 1991. Six home ranges outlined in black solid lines were observed in 1992. The five home ranges outlined in dashed lines were observed in 1993.

TABLE 1. SIZE OF THE STUDY POPULATION OF COWBIRDS AT MILLBROOK, NY, 1991–1993, BASED ON INDIVIDUALS TRAPPED ON THE FEEDING GROUND, 15 MAY–25 JULY

	Females		Males		Hatch Year Birds (HY)			
					Eggs and nestlings[a]	Fledglings	Total	HY/
	N	%	N	%	N	N	N	females
1991	53		92		16	109	125	2.36
1992	111		127		72	36	108	0.97
1991 adult returns	23	21%	20	15.7%				
1991 HY returns	7		11					
1993	43		64		61	90	151	3.5

[a] Found in host nests on the study site.

year to year variability, each female returned to a characteristic area within the landscape. Trapping records showed that 21% of the females were returnees and thus were familiar with the study area and the avian host community (Table 1).

Home range overlap zone between neighbors

Neighboring home ranges overlapped in their use of space (Fig. 2). Because it was extremely rare to actually sight the female being radiotracked, disputes between neighbors were observed infrequently. We noted only eight boundary disputes in the form of physical chases or aggressive calling during 3 weeks (approximately 120 hours) of following six radio tagged females during Year 1. However, resident females were highly responsive to unknown "intruders," as indicated by our playback experiments; during Year 1, resident females responded every time to experimental playbacks of cowbird audiotapes, approaching, and making visual or auditory contact in the vicinity of the playback speaker (binomial exact interval 0.607, 1.000; $N = 6$, $P < 0.05$). This suggested that female cowbirds responded to intruders and defended a home range.

We explored the possibility that overlapping home ranges were characteristic of neighboring females that were close relatives; however, we found that the average BSCs of female cowbirds who shared overlapping home ranges was not different from the average BSCs of female cowbirds who did not share overlapping home ranges (Table 2, last hypothesis; $P > 0.1$).

HOME RANGE-BASED HOST SELECTION

Female cowbirds laid their eggs within their home range (Table 2, first hypothesis; $P < 0.001$). We found that female cowbirds were more closely related to the young cowbirds in nests inside their home ranges than to young in nests outside their home ranges, based on the difference between average bandsharing coefficients of the two groups. No other relationship was found between groups of young cowbirds based on other ecological and biological parameters that could have affected females' host selection patterns (e.g., nest height or host species; Table 2). The same pairwise comparisons of the average bandsharing coefficients between two groups were conducted for each hypothesis, but no significant differences were found between any groups.

ESTIMATING MOST LIKELY MOTHER-OFFSPRING PAIRS

Effective cowbird fecundity

We found 298 nests in the study area, belonging to 26 species that are known cowbird hosts, and 31% were parasitized (Table 3). We collected samples from 72 cowbird eggs and nestlings, and 61 yielded successful genetic analyses. Over three-quarters of these 61 young cowbirds ($N = 50$, including one egg laid in the lab by a female held overnight) were assigned to probable mothers ($N = 29$) on the basis that all pairs had BSCs on one or both probes that fell outside the 95% confidence interval. Eleven young cowbirds ($11 / 61 = 18\%$) could not be assigned to a probable mother, because they did not share a high enough BSC with any adult female in our sample. We estimated cowbird fecundity by calculating the ratio of cowbird eggs detected to the number of females to which they were assigned, and at this study site we found it to be 1.7 ± 1.2 eggs per female (i.e., 50 eggs/29 assigned females). The 14 females to whom no young were assigned may have been inactive breeders, or they may have laid eggs that did not yield genetic material ($N = 11$) or that we did not find. Seventeen of the 29 actively breeding females (58.6%) were assigned one egg, and over three-quarters of the known breeding cowbird females ($23/29 = 79.3\%$) were assigned only one or two eggs (Fig. 5). Only one female in our sample ($1/29 = 3.4\%$) was assigned more than three eggs.

This estimate of fecundity (1.7 eggs per fe-

TABLE 2. COMPARISONS OF AVERAGE BAND SHARING COEFFICIENTS BETWEEN GROUPS OF INDIVIDUALS[a]

Hypothesis tested	Groups compared	Observed difference: d	se_d	95% confidence interval	P-value	$q_{.95}$	$q_{.50}$
Young within the range of an adult female are more closely related to that female than are young outside the range of the female	Female–young relatedness: (1) young inside or close to HR vs (2) young outside HR	0.1	0.032	0.036 to 0.165	<0.001	0.110	0.050
Young found in nests at one height range are more closely related than young found in nests at different heights	Host nest height: (1) <1 m vs (2) 1–3 m vs (3) >3 m	0.006	0.028	−0.049 to 0.061	>0.1	0.093	0.046
Young found in nests of hosts with similar mean body mass are more closely related than young in nests of hosts having dissimilar mean body mass	Host mass (adult): (1) <27 gm vs (2) >27 gm	0.002	0.018	−0.033 to 0.038	>0.1	0.059	0.030
Young in nests of host species with similar mean egg volume are more closely related than young in nests of host species having dissimilar mean egg volume	Host egg volume: (1) <175 cm^3 vs (2) >1+75 cm^3	0.002	0.015	−0.028 to 0.032	>0.1	0.051	0.025
Young in nests of host species with similar mean body length are more closely related than young in nests of host species with dissimilar mean body length	Host body length (adult): (1) <6.4 cm vs (2) >6.4 cm	−0.006	0.019	−0.042 to 0.030	>0.1	0.061	0.030
Young in nests of host species with similar mean clutch size are more closely related than young in nests of host species having dissimilar mean clutch size	Host clutch size: (1) <4.25 eggs vs (2) >4.25 eggs	0.002	0.017	−0.031 to 0.035	>0.1	0.056	0.028
Young in nests of hosts within the same taxonomic family are more closely related than young in nests of hosts from different taxonomic families	Host taxonomic relationship: (1) same family vs (2) different family	−0.002	0.016	−0.034 to 0.029	>0.1	0.053	0.027
Females with overlapping home ranges are more closely related than females without overlapping home ranges	Female neighbors: (1) overlapping home ranges vs (2) non-overlapping ranges	0.025	0.271	−0.519 to 0.570	>0.1	0.909	0.454

[a] d is the estimated mean difference in relatedness, se_d is the estimated standard error of this difference, $q_{.95}$ and $q_{.50}$ are estimates of the actual mean difference in the population that would be required to observe a statistically significant difference (at the 0.05 level) with a probability of 95% and 50%, respectively.

TABLE 3. THE COWBIRD HOST COMMUNITY AT MILLBROOK, NY, 1992

	Nests		
Host species	Total N	Parasitized N	%
Eastern Wood-Pewee (*Contopus virens*)	4	0	0
Eastern Phoebe (*Sayornis phoebe*)	21	6	28.6
Least Flycatcher (*Empidonax minimus*)	4	1	25.0
Blue-headed Vireo (*Vireo solitarius*)	2	0	0
Red-eyed Vireo (*Vireo olivaceus*)	11	6	54.5
Carolina Wren (*Thryothorus ludovicianus*)	3	1	33.3
Blue-gray Gnatcatcher (*Poliptila caerulea*)	2	0	0
Wood Thrush (*Hylocichla mustelina*)	60	5	8.3
Veery (*Catharus fuscescens*)	31	7	22.6
Hermit Thrush (*Catharus guttatus*)	13	7	53.8
Blue-winged Warbler (*Vermivora pinus*)	5	1	20.0
Black-and-white Warbler (*Mniotilta varia*)	2	1	50.0
Yellow-rumped Warbler (*Dendroica coronata*)	1	0	0
Worm-eating Warbler (*Helmitheros vermivorus*)	5	0	0
Ovenbird (*Seiurus aurocapillus*)	20	10	50.0
Louisiana Waterthrush (*Seiurus motacilla*)	8	2	25.0
Common Yellowthroat (*Geothlypis trichas*)	4	1	25.0
American Redstart (*Setophaga ruticilla*)	37	13	35.1
Northern Cardinal (*Cardinalis cardinalis*)	6	1	16.5
Eastern Towhee (*Pipilo erythrophthalmus*)	6	2	33.3
Song Sparrow (*Melospiza melodia*)	14	1	7.1
Field Sparrow (*Spizella pusilla*)	4	0	0
Chipping Sparrow (*Spizella passerina*)	18	0	0
Rose-breasted Grosbeak (*Pheucticus ludovicianus*)	10	1	10.0
Scarlet Tanager (*Piranga olivacea*)	4	2	50.0
Red-winged Blackbird (*Agelaius phoeniceus*)	3	0	0
Total	298	68	30.56

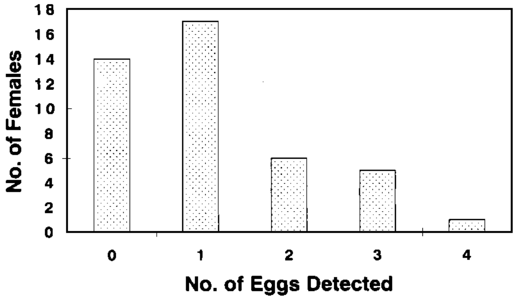

FIGURE 5. Estimate of effective cowbird fecundity at Millbrook, NY, 1992, based on the number of eggs detected in the study area and assigned to probable mothers on the basis of DNA analyses.

male) constitutes a minimum estimate of cowbird fecundity that reflects only the parasitized nests that we found. In effect, the number of nests found gives us an estimate of host density, which in conjunction with genetic analyses defines cowbird fecundity. However, we also calculated an upper estimate of cowbird fecundity to take into account any parasitized nests in the study area that we did not find. We calculated this upper estimate of host fecundity using data on host density from point-count surveys (Table 4). Point-count survey data suggested an upward correction of host density estimates for 10 of 13 parasitized species with correction factors ranging from 1.13 (Wood Thrush) to 13.33 (Red-eyed Vireo). The resulting estimate of effective cowbird fecundity was 8.16 eggs per female.

Home range-based host selection

We used ARC/INFO to display each female's home range and the parasitized nest(s) holding her assigned young. An overview of the study area (Fig. 6) shows the home ranges of nine of the females for which we had radiotelemetry data, genetic data, and assigned young. Seven of the 13 (54%) females in our sample laid their assigned eggs either inside or close (< 50 m) to their home range boundary (Table 5); six laid eggs in nests more distant than 50 m beyond their home range boundaries (mean = 401 ± 331, range = 105–1070 m). Three females had assigned young only in distant nests, but eggs that did not yield genetic material were also found in nests inside their home ranges (Table 5). All but one of the parasitized nests > 50 m from the home range boundary were multiply parasitized and were typically found in conspicuous locations.

MULTIPLY PARASITIZED NESTS

Female cowbirds avoided laying more than one of their own eggs in a single host nest.

TABLE 4. ESTIMATES OF EFFECTIVE COWBIRD FECUNDITY AT MILLBROOK, NY, 1992, BASED ON TWO DIFFERENT MEASURES OF HOST DENSITY

	Fecundity estimates						
	Nest density—based			Point-count density—based			
Species	Host[a] density per 100 ha	No. cowbird eggs found	Female[b] laying rate	Host[c] density per 100 ha	Point[d] count correction factor	Point[e] count adjusted number of eggs	Point[f] count adjusted laying rate
Wood Thrush	27	2	0.07	30.6	1.13	2.3	0.08
Eastern Phoebe	10.2	8	0.28	5.8	1	8	0.28
Ovenbird	8.8	7	0.24	38.7	4.4	30.8	1.06
American Redstart	16.4	8	0.28	147.2	8.98	71.8	2.48
Veery	13.7	5	0.17	96.7	7.06	35.3	1.22
Red-eyed Vireo	4.9	4	0.14	65.3	13.33	53.3	1.84
Blue-winged Warbler	3.1	1	0.03	15.7	5.06	5.1	0.18
Hermit Thrush	5.8	6	0.21	4.5	1	6	0.21
Song Sparrow	10.2	2	0.07	4.8	1	2	0.07
Scarlet Tanager	1.8	1	0.03	12.1	6.72	6.7	0.23
Eastern Towhee	2.7	4	0.14	4.2	1.56	6.2	0.22
Louisiana Waterthrush	3.5	1	0.03	22.7	6.48	6.5	0.22
Rose-breasted Grosbeak	4.9	1	0.03	10.1	2.06	2.1	0.07
Total eggs		50				236.1	
Fecundity estimates			1.72[g]				8.16

[a] Host density based on actual number of nests found.
[b] Laying rate per 29 females with assigned young.
[c] Host density based on point count surveys.
[d] Ratio of point count to nest density.
[e] Number of eggs found × correction factor.
[f] Nest density laying rate × correction factor.
[g] Based on actual number of nests found and cowbird eggs assigned using genetic analyses.

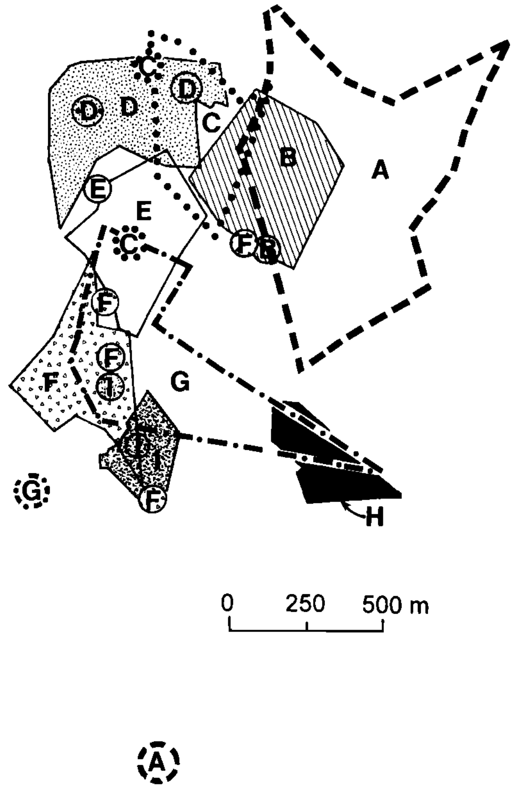

FIGURE 6. Results of integrated radiotelemetry and genetics studies of cowbirds in Millbrook, NY, 1992. The map depicts the spatial relationship between nine female's home ranges and the 16 parasitized nests containing eggs assigned to these females. Nests (small circles) are lettered to match the letter of the home range of the female that parasitized them.

TABLE 5. SUMMARY OF THE LAYING PATTERNS OF COWBIRDS IN RELATION TO THEIR HOME RANGES

Location of parasitized nests	No. females
At least one egg laid inside mother's home range	6
1. All eggs inside	3
2. Some eggs inside and some close	2
3. Some eggs inside, some close, and some distant	1
All eggs laid close[a] to mother's home range	1
All eggs laid distant[b] from mother's home range	3
Some eggs laid distant from mother's home range and some laid inside but with no genetic results	3
Total	13

[a] Close eggs were laid outside of the home range but within a 50-m buffer zone of the boundary.

[b] Eggs laid > 50 m from the home range boundary.

While multiple parasitism characterized nearly one-third of the nests in the study area, we noted multiple parasitism of one nest by the same female in only one case. Nearly three-quarters of the multiply parasitized nests for which we had genetic results (11/15 = 73%) lay in locations within overlap zones covered by more than one known home range.

DISCUSSION

The results presented here, combining genetic and telemetry data, suggest the importance of the home range in cowbird breeding behavior. The three principal results we report are female cowbirds' use of a characteristic home range year after year, lower cowbird fecundity than expected, and avoidance of multiple laying in a single nest by female cowbirds. These three elements of cowbird breeding behavior challenge the stereotype of cowbirds as a species that produces a large number of young and invests no parental care. They substitute the picture of a brood parasite that produces limited numbers of young and does invest parental care, both by selection of known-host parents and by placing each parasitic egg in a separate host nest without a competitive cowbird sibling. The home range is the foundation of the known-host selection strategy, making it possible for female cowbirds to preferentially parasitize successful host pairs observed in previous breeding seasons.

The first result, home range fidelity of female cowbirds, enables breeding cowbirds to learn the physical territory and thus detect more nests as well as observe the relative success of resident songbirds. This information can be used in host selection. The well known site fidelity of songbirds (e.g., Brown 1975, Krebs and Davies 1993) makes it likely that experienced cowbird females return to their previous home range and encounter many of the same host pairs that nested there during the preceding breeding season. Long-term studies of parasitism are rare, but two notable studies of host species reported seemingly strategic parasitism patterns that are explained by home range-based host selection and preferential selection of known hosts by cowbirds. In Song Sparrows, cowbirds preferentially parasitized older females (Smith 1981, Smith and Arcese 1994), and in Willow Flycatchers (*Empidonax traillii*) cowbirds appeared to parasitize superior host parents (Sedgwick and Iko *this volume*). Fidelity to home range has further benefit for cowbirds, allowing females to monitor the progress of their young in host nests. Such monitoring has already been reported for the parasitic Great Spotted Cuckoo (*Clamator glandarius*; Soler et al. 1995), and it would explain how female cowbirds were found associating with their own offspring after fledging (Hahn and Fleischer 1995).

Several previous investigators have shown that cowbirds use a home range (Dufty 1982a, Darley 1983, Teather and Robertson 1985, Yokel 1989, Smith and Arcese 1994, Raim in press), but this is the first report of genetic evidence linking a female cowbird's use of a home range to her egg-laying pattern. In this diverse avian community spanning forest, edge, and old field habitats, female home range was the only predictor of which nests would be parasitized. No other biological or ecological factor predicted where an individual cowbird would lay an egg, including host species identity, body size, clutch size, egg size, incubation period, or nest height. Rather than targeting a particular host species, as some investigators have suggested (e.g., Walkinshaw 1983), each individual female cowbird used a mixture of host species. Such lack of host specialization is, of course, the expected pattern if female cowbirds use their home range as an egg-laying range. Host territorial behavior creates species-specific spacing patterns that effectively limit the number of nests of any one host that occur within a single cowbird's home range.

We observed few instances of aggressive behavior at territorial boundaries, which is consistent with other observations that female cowbirds have non-exclusive home ranges (e.g. Payne 1977, Fleischer 1985). Krebs and Davies (1993) review the concept of territories with renewing resources, using those with flowers for nectar-feeding birds as the classic example of a system in which the owner's knowledge of the pattern of resource renewal and location of recently depleted patches may be so superior to an intruder's that the need for defensive behavior is reduced. Brood parasites similarly depend on renewing resources, a series of host nests that are available for receiving a parasitic egg only at brief, precise time intervals. Since it was not our objective in this study to obtain a thorough description of home range acquisition and maintenance, we did not follow individuals for long periods each day and thus we cannot evaluate how territorial defense may be used. However, future studies of cowbirds may examine whether female cowbirds display more aggressive behavior early in the breeding season when home ranges are being established, as is characteristic in many species (Stamps 1994).

The second principal result of this study is that effective cowbird fecundity is lower than previous studies of fecundity have suggested. We use the term "effective cowbird fecundity" (S.I. Rothstein, pers. comm.) to describe only those eggs that cowbirds succeed in laying in appropriate host nests and that are not subsequently ejected by hosts. Based on ovarian dissections of wild breeding birds, several investigators have independently estimated a high cowbird laying rate of 0.7–0.8 eggs per day with an extrapolation to 20–40 eggs per season (Payne 1976, Scott and Ankney 1983, Rothstein et al. 1986b). However, the physiological egg-laying capacity, or raw fecundity, of cowbirds is likely to be higher than their effective fecundity, because when a cowbird does not find a host nest in which to lay, she may dump the egg in an inappropriate nest (e.g., Mourning Dove, *Zenaida macroura*; D.C. Hahn, pers. obs.) or other site, she may reabsorb the egg in the oviduct (Payne 1998), or she may eat it after laying to regain nutrients (R.C. Fleischer, pers. comm.; D.C. Hahn, pers. obs.). In addition, a number of cowbird eggs are successfully ejected by some hosts (Rothstein 1975a). Effective fecundity is the measurement of interest to conservation biologists and resource managers, since it reflects the true impact cowbirds potentially have on host species' reproductive success.

The average number of eggs that we detected and assigned to individual cowbird females using genetics techniques was 1.7 ± 1.2 eggs per female (range = 1–4). This estimate is a lower bound on effective fecundity, because it does not include cowbird eggs in nests we did not find or eggs that did not yield genetic results. We calculated 8.16 eggs per female as the upper bound of effective cowbird fecundity using host density estimates from point count surveys in the study area (Table 4). Our subjective assessment of the study area based on field experience did not suggest that there were nearly five times more nests present than we found, but many factors hamper a field study in locating all parasitized nests and cowbird eggs in a large study area. Nests located in the forest canopy are particularly difficult to locate, and predation of parasitized nests or removal of a cowbird egg by rival cowbirds can occur before an observer finds the nest. Once a host abandons a parasitized nest, observers are less likely to find it without the cues associated with active nests.

Trapping data offer a third perspective on effective cowbird fecundity. We ran traps until late in the breeding season on lawns adjacent to the study area, and we captured a number of recently fledged cowbirds (with short tails) that appeared to have emerged from nests that we had not found (Hahn and Fleischer 1995). We calculated the ratio of total cowbird young found (including eggs and nestlings found in host nests plus cowbird fledglings trapped) to total adult females trapped during the breeding season (Table 1). For 1992 this yielded a fecundity estimate of 0.97 young per female, a lower estimate than the one we first calculated using only the young found in host nests that could be assigned to adult females using genetic analyses (Table 4). We used our radiotelemetry data to evaluate this ratio of 0.97 and to determine whether it was skewed by females that came to the feeding site but were not breeding in the local area. Specifically, since we had attached radio transmitters to 26 females and subsequently located only 19 (73%) of these females within the study area, we reduced the estimate of trapped females by 27%. This increased the ratio of effective fecundity from 0.97 to 1.33 young per female, still lower than the 1.72 eggs per female estimated from nest searching data alone. It is important to note that this estimate of cowbird fecundity using fledglings and trapping data is both more robust and more limited than the estimate using only nest data, since the number of fledgling cowbirds trapped reflects the number of cowbird eggs laid minus any egg and nestling mortality; at the same time it may include additional cowbird eggs that hatched and fledged from nests that were not detected.

The range of estimates of cowbird fecundity considered here and the proposed difference between effective fecundity and raw fecundity emphasize the difficulty of measuring accurately the pressure of parasitism on a host community. Given this difficulty, the most reliable approach of measuring cowbird impact on host species appears to be the long-term studies that track the cost that parasitism imposes on lifetime reproductive success of individual birds. Such studies have shown that parasitism exerts severe pressure in some communities (e.g., Wood Thrush in southern Illinois; Robinson 1992, Trine in press) and limited pressure in others (Song Sparrow in British Columbia, Smith and Arcese 1994; Indigo Bunting in Michigan, Payne 1998; Willow Flycatcher in eastern Oregon, Sedgwick and Iko *this volume*).

We suggest that the third finding of this study, that individual female cowbirds avoided laying more than one of their own eggs in a host nest, is an indicator of cowbird parental investment. Laying more than one egg in a nest makes breeding easier for the cowbird female because it reduces the number of nests she must find. However, multiple parasitism of single nests probably reduces her reproductive success because it puts her aggressive offspring in competition with one another (Nice 1937, Klaas 1975, Nolan 1978, Walkinshaw 1983). Trine (in press) found that each additional cowbird egg in a Wood Thrush nest reduced cowbird hatching success by 8–10%. Home range-based breeding behavior increases the home range holder's chances of being the first to parasitize a given host nest and to parasitize it at the optimum time because the owner knows her territory and its resources better than any intruder female.

The explanation for the multiply-parasitized nests in our study area may be other pressures that conflict with the strategy of single parasitism to optimize an individual cowbird chick's survival. For example, a cowbird might lay her second egg in a previously parasitized nest if the host nest that she had targeted were unexpectedly lost to predation, weather damage, or other accidents (e.g., Morse 1988, Wiens 1992). As the breeding season progresses, the costs of laying twice in a host nest decline relative to the risk of not finding a better, future laying opportunity.

Finally, multiple parasitism is probably often the result of opportunistic laying by a yearling female cowbird. While experienced female cowbirds may lay most eggs inside their home range, younger females probably lay more eggs outside a home range. Our data do not permit testing this hypothesis, because we lack information on cowbird females' ages. However, two of Darley's (1983) findings suggest that yearling cowbird females may not be mature enough to hold a home range. Darley observed that younger cowbirds were less consistent in their use of home range and that for both male and female cowbirds dominance hierarchies dictate behavior among birds of the same gender. Unable to hold a home range, yearling cowbird females may employ a callow host selection strategy, searching widely throughout the host community and parasitizing any conspicuous nest. The challenges of the brood parasitic breeding strategy probably force yearling females to lay many eggs that have a low probability of success, either in previously parasitized nests or in nests that are not at the optimal stage in the host's breeding cycle. As a female cowbird acquires experience over successive seasons, we suggest that she would master the known host selection strategy: establish a home range, study the host birds within the range, and synchronize her parasitic laying schedule with that of the best pairs.

The frequency of multiple parasitism among communities varies widely according to published reports (e.g., Wiens 1963, Brittingham and Temple 1983, Collins et al. 1988, Robinson 1992, Hahn and Hatfield 1995, Payne 1998, Trine in press). Cowbird density or host density are the factors typically assumed to determine frequency of multiple parasitism. However, our conclusions support Holford and Roby's (1993) suggestion that age structure of the cowbird population may also be a factor, with higher rates of multiple parasitism occurring in cowbird populations that have a larger proportion of yearling and young females. If experienced cowbird females rely on home range-based breeding behavior and on a known-host selection strategy, then a host community parasitized by a stable cowbird population with a diverse age mix would experience lower levels of multiple parasitism and less negative impact from brood parasitism. In contrast, a host community parasitized by a disproportionately high number of yearling cowbirds or new immigrants would experience more multiple parasitism and more negative impact.

MANAGEMENT IMPLICATIONS

The patterns reported here characterize the cowbirds we studied in the northeastern U.S. where cowbird populations are not expanding (Robbins et al. 1989, Peterjohn et al. in press). Comparative studies are required in the West and Southwest to see if the home range-based breeding behavior that we observed also characterizes cowbirds in regions where parasitism exerts severe pressure on host communities and cowbird management programs are underway.

The known-host selection strategy proposed here suggests that knowledge of cowbird population demographics can assist wildlife managers in managing cowbird parasitism and determining whether to initiate cowbird trapping programs. For example, in a stable cowbird population composed of mixed-age birds, a large proportion of females would be experienced breeders that will primarily parasitize a mix of host species within their individual home ranges. However, in communities where cowbird trapping programs are in place, a high proportion of the cowbird population each year will be immigrant, yearling females, which may disproportionately parasitize conspicuous hosts. Endangered species such as the Least Bell's and Black-capped vireos that advertise the nest site by song would be more at risk from a population of younger cowbirds that lay a large proportion of their eggs opportunistically in the nests of conspicuous hosts. Continuous trapping probably prevents the cowbird population from stabilizing and developing a predominance of older, experienced females that would exert a lower parasitism rate on vireos. Managers of endangered species populations should beware of intermittent or inconsistent trapping programs. These may expose conspicuous host species to unexpectedly high parasitism rates by the high numbers of yearling females that characterize a local cowbird population in off years when trapping is not underway.

Host-parasite population dynamics also suggest that host communities that experience steady levels of cowbird parasitism across long time periods may evolve better defenses against parasitism than host communities that experience intermittent parasitism. For example, secretive behavior and camouflaged nest building may be effective against younger, inexperienced cowbirds that search opportunistically, but not against the majority of experienced females that maintain a home range and search it thoroughly for all nests. More aggressive host defense, such as physically preventing a cowbird's access to lay her egg or physically ejecting the parasite egg, may evolve sooner in host communities where cowbird populations are stable and where experienced home range-based females exert steady selection pressure on all hosts. This suggests that resource managers be alert to the negative effect of cowbirds on host communities that are experiencing intermittent parasitism, whether due to natural population cycles or to trapping programs that are inconsistent or short term. In these communities, population stability should be monitored most carefully in species that lack secretive behavior and camouflaged nest building and thus may serve as indicator species.

ACKNOWLEDGMENTS

We thank Rockefeller University Field Research Center, the Institute of Ecosystem Studies, and Mr. Bruce Kovner for permission to use their land. DCH appreciates long term support from R. Jachowski (USGS) and helpful discussion and maps provided by F. Nottebohm (RUFRC) and R. Winchcombe (IES). We are grateful to our skilled and dedicated team of nest searchers, including J. Boone, K. Corey, S. Plentovich, G. Oines, and J. Cherry, and to D. Clugston, J. Koloszar, J. Wisniewski, K. Corey, and G. Oines, who very ably collected home range information on radio tagged cowbirds in difficult terrain. We thank L. Williams for managing the incubator; I. Thomas and H. Bourne for skillful GIS work; L. Loges and P. Osenton for assistance with database management; and K. Boone and D. Crawford for preparing figures. W. Gergits provided invaluable help in presentation of genetic data; J. S. Hatfield provided helpful advice on statistical analysis of genetic data and, with G. A. Gough, carried out preliminary DISTANCE analyses. We appreciate helpful reviews by M. Morrison, J. Rotenberry, M. P. Scott, J. Longmire, J. Rhymer, J. S. Hatfield, and an anonymous reviewer that greatly improved the manuscript. We thank S. I. Rothstein for proposing the term "effective fecundity" to distinguish cowbird eggs that are actually laid in appropriate host nests and not ejected from the total number of cowbird eggs produced by in a population.