

REGIONAL VARIATION IN COWBIRD PARASITISM OF WOOD THRUSHES

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ABSTRACT.—Population declines of Neotropical migrant songbirds breeding in the eastern deciduous forest have been attributed, in part, to low reproductive success resulting from high rates of brood parasitism by Brown-headed Cowbirds (*Molothrus ater*). Wood Thrush (*Hylocichla mustelina*) nest records from the Cornell Laboratory of Ornithology were used to test whether rates of parasitism and the number of cowbird eggs or young per parasitized nest varied regionally with distance from the historic range of the cowbird. Rates of parasitism differed significantly ($P < 0.001$) among the Midwest (42.1%), Mid-Atlantic (26.5%), and Northeast (14.7%). Mean number of cowbird eggs or young per parasitized nest differed significantly ($P < 0.001$) among regions and displayed similar regional trends with means of 2.09, 1.64, and 1.21, respectively. Rates of parasitism were correlated positively ($r = 0.64$, $P = 0.002$) with relative abundance of cowbirds and negatively correlated ($r = -0.70$, $P = 0.001$) with relative abundance of Wood Thrush. In the Midwest, relative abundance of cowbirds was significantly higher and Wood Thrushes significantly lower than in the other two regions. Because of the high abundance of cowbirds, high percentage of nests parasitized, and high number of cowbird eggs per parasitized nest, the effects of cowbird parasitism are particularly severe in the Midwest. Received 17 April 1992, accepted 22 Oct. 1992.

Neotropical migrant songbirds breeding within the eastern deciduous forest have undergone apparent population declines since the late 1940s (Robbins 1979, Whitcomb et al. 1981, Askins et al. 1990). One suggested cause of the declines has been low reproductive success resulting from high rates of brood parasitism by Brown-headed Cowbirds (*Molothrus ater*) (Gates and Gysel 1978, Brittingham and Temple 1983, Robinson 1988). In addition, the cowbird has been implicated in the near extinction of the Kirtland's Warbler (*Dendroica kirtlandii*) and other rare species (Rothstein 1975, Mayfield 1977).

Although cowbird parasitism appears to have a large effect on reproductive success of forest songbirds in the Midwest (Brittingham and Temple 1983, Robinson 1988), the magnitude of the problem for songbirds nesting throughout the eastern deciduous forest is unknown. Because the historic range of the cowbird was west of the Mississippi River, and because cowbirds are associated ecologically with open habitat (Mayfield 1965, Dufty 1982), their abundance and impact on forest songbirds may be highest close to this historic range and in regions with more open habitat. As a result, rates of cowbird parasitism and the importance of cowbird parasitism as a factor responsible for declines of forest songbirds

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may vary regionally with distance from the historic range of the cowbird. To reverse declining trends in populations of forest songbirds, we need to understand regional differences in the causes of decline.

We analyzed Wood Thrush (*Hylocichla mustelina*) nest records from the Cornell Laboratory of Ornithology Nest Record Program to test whether rates of cowbird parasitism of Wood Thrush varied regionally and to test whether parasitism rates were correlated with differences in abundance of cowbirds or Wood Thrushes. We also tested whether rates of parasitism changed from 1960–1989 within each region. We chose the Wood Thrush because it is a Neotropical migrant that breeds throughout the eastern deciduous forest and has experienced population declines in recent decades (Robbins 1979, Robbins et al. 1989, Askins et al. 1990). It also is a common host of the cowbird (Friedmann 1963), accepts cowbird eggs (Rothstein 1975), and its blue eggs are easily distinguishable from cowbird eggs. In addition, there is a large sample of Wood Thrush nest records.

METHODS

We obtained 896 Wood Thrush nest records from the Cornell Laboratory of Ornithology Nest Record Program. These records dated back to the 1940s, but most (>95%) were from 1960 to the present. Nest records included information on when and where (geographic location) the nest was found, stage of nesting, nest contents (including cowbird eggs or young), and nest outcome. All Wood Thrush nests that contained cowbird eggs or young and all that contained Wood Thrush young or at least two Wood Thrush eggs were included in this study. Forty-one nests for which nest contents were not observed, or that were found empty and not subsequently used, were removed from the initial pool of nests.

Nest records were reported from the entire range of the Wood Thrush, covering southeast Canada and the eastern half of the United States (Fig. 1). This range and the nest records were separated into three longitudinal regions: Northeast (longitudes < 77°), Mid-Atlantic (longitudes 77°–87°), and Midwest (longitudes > 87°) (Fig. 1). We defined regions by longitude rather than ecologically because all of our nests were from deciduous forest habitat. We examined differences in rates of parasitism within one ecological region (deciduous forest) based on location in reference to the historic range of the cowbird. We named the regions according to the location of the majority of nest records. For a regional comparison of brood parasitism, we used all nest records (855) regardless of the year the nest was found. The nests were also separated into three decades, 1960–1989, to determine if there were any temporal differences within regions. For the temporal comparison of parasitism, only nests found from 1960–1989 were used.

We used chi-square tests-of-independence to determine if frequency of brood parasitism varied among regions or among three decades within each region. Over 100 nest records were reported from Pennsylvania (105), New York (136), and Delaware (142). Because a large number of nest records reported from a small area might bias results, we were particularly concerned about the potential influence the large number of records from Delaware might have on our regional analysis. To test for a bias, we omitted Delaware's nest records and re-analyzed the data. Although the χ^2 value changed, the overall trend and significance level did not. We also calculated the mean number of cowbird eggs or young per parasitized Wood Thrush nest and used a two-way analysis of variance to test for regional and temporal

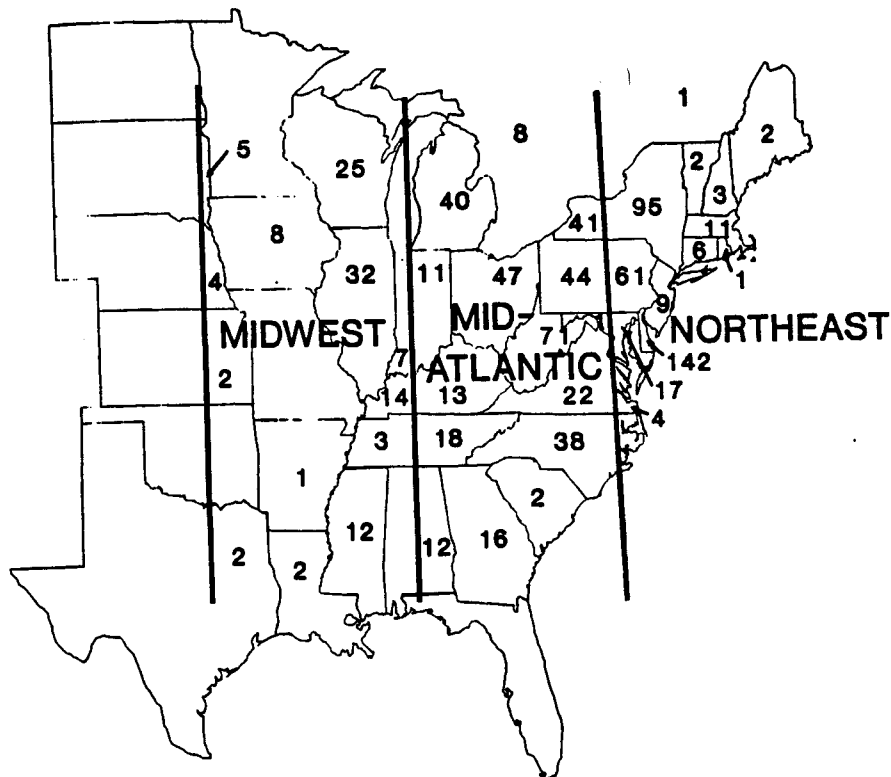


FIG. 1. Number and location (state, region) of Wood Thrush nest records reported to the Cornell Nest Record Program.

differences among means. A Tukey test ($\alpha = 0.05$) was used to determine which means were significantly different.

We obtained Breeding Bird Survey (BBS) data from the Fish and Wildlife Service's Office of Migratory Bird Management and used these data to compare the average relative abundance of Wood Thrush and Brown-headed Cowbirds among the three regions. The comparison was based on average numbers of birds tallied per BBS route per state during 1966–1989. If a state was located in two regions, that state was assigned to the region in which the majority of the state was located. Only states that had at least 10 BBS routes completed within them were used for this comparison. Using the regional description above, there were nine states in the Northeast, 12 in the Mid-Atlantic, and eight in the Midwest that fit the criterion for use. The Office of Migratory Bird Management has calculated average number of birds per BBS route by state from 1966 to 1989 (for methods see Robbins et al. 1980). We then calculated and compared the means of those state averages for states in the different regions. A one-way analysis of variance was used to test for differences among means, and a Tukey test ($\alpha = 0.05$) was used to determine which means were significantly different. We used correlation analysis to test whether the percentage of nests parasitized was correlated with number of Brown-headed Cowbirds or number of Wood Thrushes detected per BBS route by state (1966–1989). For these analyses, we omitted nine states that had fewer than eight nest records (Table 1).

TABLE 1
PERCENTAGE OF WOOD THRUSH NESTS PARASITIZED BY STATE (1960-1989) AND AVERAGE
NUMBER OF BROWN-HEADED COWBIRDS AND WOOD THRUSH REPORTED ON BREEDING BIRD
SURVEY ROUTES (1966-1989)

| State | Percentage of nests parasitized (N) ^a | Average number per route ^b | |
|-------|--|---------------------------------------|-------------|
| | | Cowbirds | Wood Thrush |
| AL | 0.0 (12) | 13.83 | 11.27 |
| DE | 12.7 (142) | 4.52 | 13.59 |
| GA | 56.0 (16) | 5.69 | 8.10 |
| IL | 37.5 (32) | 12.35 | 1.16 |
| IN | 44.4 (18) | 14.05 | 3.95 |
| IA | 62.5 (8) | 25.99 | 0.07 |
| KY | 44.4 (27) | 13.53 | 10.57 |
| MD | 22.2 (18) | 10.22 | 19.35 |
| MA | 18.2 (11) | 6.09 | 16.02 |
| MI | 32.5 (40) | 12.19 | 2.17 |
| MS | 25.0 (12) | 11.52 | 8.79 |
| NJ | 11.1 (9) | 4.46 | 9.46 |
| NY | 22.0 (136) | 10.57 | 14.57 |
| NC | 18.4 (38) | 7.52 | 18.05 |
| OH | 34.0 (47) | 10.18 | 6.16 |
| PA | 20.9 (105) | 9.80 | 16.18 |
| TN | 23.8 (21) | 9.93 | 8.59 |
| VA | 11.5 (26) | 6.58 | 18.24 |
| WI | 72.0 (25) | 20.01 | 1.68 |
| WV | 12.7 (71) | 10.63 | 22.29 |

^a Number of Wood Thrush nest records reported to the Cornell Nest Record Program. States with < eight nest records were not included.

^b Average number per route was calculated by the Fish and Wildlife Service Office of Migratory Bird Management as the average number of birds per BBS route for all routes within each state between the years 1966 and 1989.

TABLE 2
REGIONAL AND TEMPORAL VARIATION IN BROWN-HEADED COWBIRD PARASITISM OF WOOD
THRUSH NESTS

| Region and decade | Percentage of nests parasitized (N) | Number of cowbird eggs or young per parasitized nest ^a (N) |
|--------------------|-------------------------------------|---|
| Northeast | | |
| Total ^b | 14.7 (348) | 1.21 ± 0.08 (52) |
| 1960–1969 | 13.8 (210) | 1.25 ± 0.13 (28) |
| 1970–1979 | 20.4 (54) | 1.18 ± 0.18 (11) |
| 1980–1989 | 16.7 (72) | 1.08 ± 0.07 (13) |
| Mid-Atlantic | | |
| Total ^b | 26.5 (381) | 1.64 ± 0.09 (99) |
| 1960–1969 | 30.5 (141) | 1.53 ± 0.12 (43) |
| 1970–1979 | 29.4 (160) | 1.68 ± 0.13 (47) |
| 1980–1989 | 11.3 (70) | 2.00 ± 0.49 (8) |
| Midwest | | |
| Total ^b | 42.1 (126) | 2.09 ± 0.17 (53) |
| 1960–1969 | 43.6 (39) | 1.59 ± 0.27 (17) |
| 1970–1979 | 45.5 (44) | 2.09 ± 0.29 (21) |
| 1980–1989 | 48.5 (33) | 2.40 ± 0.21 (15) |

^a Mean ± one SE.

^b Total number of nests found in each region prior to 1990.

The Office of Migratory Bird Management calculated the percentage of BBS routes per state where Wood Thrush showed a decline from 1966–1989. We determined the number of decreasing routes and total routes in each region and used a chi-square test-of-independence to determine whether there was a difference in the percentage of BBS routes where Wood Thrush numbers decreased among our three regions.

RESULTS

The percentage of Wood Thrush nests parasitized was significantly different ($\chi^2 = 40.54$, $df = 2$, $P < 0.001$) among regions and was highest in the Midwest and lowest in the Northeast (Table 2). The mean number

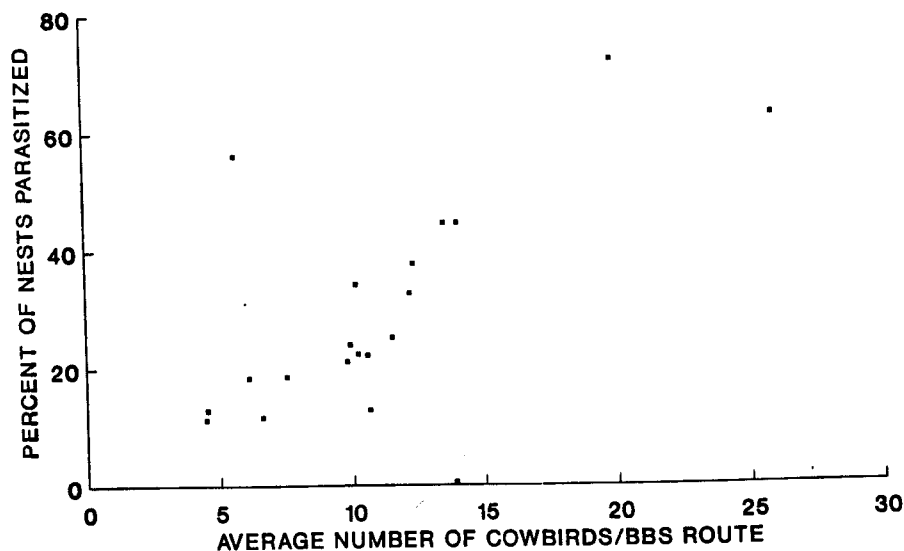


FIG. 2. Average number of Brown-headed Cowbirds per BBS route (1966-1989) reported by state and percentage of Wood Thrush nests parasitized per state.

of cowbird eggs or young per parasitized Wood Thrush nest was also significantly different among regions and followed a similar regional trend ($F = 11.31$, $df = 2, 200$; $P < 0.001$) (Table 2).

Within each region, the percentage of nests parasitized did not differ by decade (1960-1989) in the Northeast ($\chi^2 = 1.51$, $df = 2$, $P > 0.5$) or in the Midwest ($\chi^2 = 0.04$, $df = 2$, $P > 0.5$) but did differ ($\chi^2 = 10.33$, $df = 2$, $P < 0.01$) in the Mid-Atlantic and was lowest during 1980-1989 (Table 2). The mean number of cowbird eggs per parasitized Wood Thrush nest did not differ temporally in any region ($F = 1.63$, $df = 2, 198$; $P = 0.199$).

The average number of Brown-headed Cowbirds detected per BBS route was significantly different ($F = 14.90$, $df = 2, 26$; $P < 0.001$) among regions and was higher in the Midwest region than in the Mid-Atlantic or Northeast regions (Table 3). The average number of Wood Thrushes detected per BBS route was significantly different ($F = 16.73$, $df = 2, 26$; $P < 0.001$) among regions and was lower in the Midwest than in the Mid-Atlantic or Northeast (Table 3). The percentage of Wood Thrush nests parasitized per state was positively correlated ($r = 0.64$, $df = 18$, $P = 0.002$) with the average number of cowbirds detected per BBS route (Fig. 2) and negatively correlated ($r = -0.70$, $df = 18$, $P = 0.001$) with the average number of Wood Thrushes detected per BBS route (Fig. 3).

The proportion of BBS routes where Wood Thrush declined in abun-

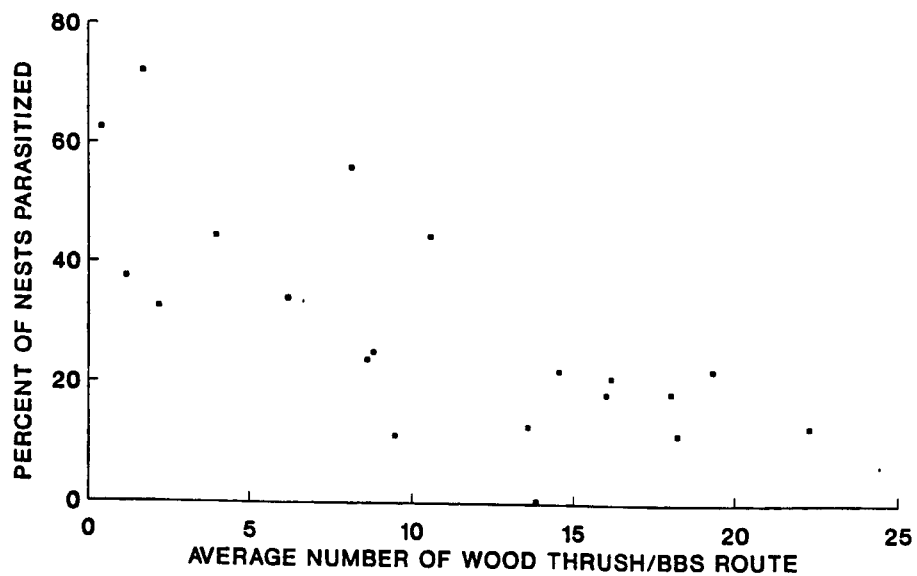


FIG. 3. Average number of Wood Thrushes per BBS route (1966-1989) reported by state and percentage of Wood Thrush nests parasitized per state.

dance from 1966 to 1989 did not differ ($\chi^2 = 0.169$, $df = 2$, $P > 0.5$) among routes in the Midwest (59%), Mid-Atlantic (58%), or Northeast (60%).

DISCUSSION

The Brown-headed Cowbird was originally a nesting species of the grasslands in the Plains region west of the Mississippi River (Friedmann 1929, Mayfield 1965). Regional differences in cowbird numbers are likely a result of regional differences in the landscapes and habitat suitability. The Midwestern landscape is primarily agricultural with scattered patches of forest while the Northeast, conversely, has much more forest habitat and less open habitat. In addition, cowbird abundance appears to decrease with distance from the cowbird's historic range.

Because the rate of cowbird parasitism is a direct function of cowbird density (McGeen 1972, Mayfield 1977), the significant regional differences in rates of parasitism and numbers of cowbird eggs per parasitized nest were probably a direct result of the greater abundance of cowbirds in the Midwest. An alternative explanation is that Wood Thrushes were starting to recognize and eject cowbird eggs in the Northeast. However, we do not consider this to be a plausible explanation. Ejection behavior would likely develop first in areas where parasitism rates are highest and the most

TABLE 3
AVERAGE RELATIVE ABUNDANCE OF WOOD THRUSHES AND BROWN-HEADED COWBIRDS
REPORTED BY REGION, 1966-1989

| Region | Mean \pm SE relative abundance ^a per BBS route by state (1966-1989) | |
|--------------|--|---------------------------------------|
| | Wood Thrush (N) ^b | Brown-headed Cowbird (N) ^b |
| Northeast | 15.77 \pm 1.14 ^c (9) | 6.88 \pm 0.73 ^c (9) |
| Mid-Atlantic | 11.62 \pm 1.79 ^c (12) | 9.84 \pm 0.95 ^c (12) |
| Midwest | 2.72 \pm 1.03 ^d (8) | 16.51 \pm 1.88 ^d (8) |

^a Average relative abundance was calculated by the Fish and Wildlife Service Office of Migratory Bird Management and represents the average number of birds per BBS route for all routes within states between the years 1966 and 1989.

^b Number of states.

^{c,d} Means within a column sharing a letter are not different ($P > 0.05$).

harm is done to the host (Rothstein 1975). Ejection behavior has no adaptive value until a species is parasitized. Because cowbirds were at one time uncommon in the eastern deciduous forest, and the duration of exposure to parasitism is relatively shorter in the Northeast than in the Midwest, we would expect to see ejection behavior occurring first in the Midwest (Rothstein 1975). The strong positive correlation between numbers of cowbirds and rates of parasitism make higher numbers of cowbirds a more logical explanation.

Rates of parasitism were highest in areas where Wood Thrush numbers were lowest. This inverse density dependent relationship is possible because cowbirds are not host specific. As a result, their numbers are not dependent on the density of any one particular host (Mayfield 1965, 1977, Rothstein 1975). The consequences of this inverse density dependent relationship are that the effects of parasitism are most severe in areas where a particular host species is rare. Compared to the Northeast, there are higher numbers of cowbirds in the Midwest and lower numbers of many species of Neotropical migrant forest songbirds (Robbins et al. 1986). The number of cowbird eggs per parasitized nest, an additional indication of cowbird pressure, was also highest in the Midwest. Because nests containing two or more cowbird eggs are often unsuccessful at fledging any host young (Temple and Cary 1988), the effects of cowbird parasitism are particularly severe in the Midwest.

Although cowbirds have increased in abundance from 1900-1980 (Brittingham and Temple 1983), we did not find a significant increase in rates of parasitism between 1960-1989, and in the Mid-Atlantic states, rates of parasitism were lower 1980-1989 than during the previous two decades.

The increase in cowbird numbers and the expansion of the cowbird's range into the East occurred when eastern forests were cleared prior to 1960 (Brittingham and Temple 1983). Currently, numbers of cowbirds in the Mid-Atlantic and Northeast states appear to be leveling off or actually declining (Robbins et al. 1989). However, fragmentation of the remaining forest continues to be a concern (Brooks and Birch 1988). Although rates of parasitism in the Midwest did not increase between 1960–1989, they remained high as did the number of cowbird eggs per parasitized nest. In addition, many ongoing studies in the Midwest are reporting extremely high rates of parasitism (Robinson 1992).

Because rates of brood parasitism were highest in the Midwest, we predicted that the Wood Thrush would show greater rates of decline in the Midwest than in the other two regions. The BBS data did not support our prediction. Instead, proportions of BBS routes reporting declining numbers of Wood Thrush were similar among regions.

The Wood Thrush may be less adversely affected by cowbird parasitism than other host species. The Wood Thrush is one of the larger host species and can often raise its own young along with cowbird young (Friedmann 1963, Rothstein 1975). The Wood Thrush incubation period is similar to the cowbirds so the cowbird young will normally not gain an advantage over the Wood Thrush young by hatching first (Rothstein 1975). Also, the Wood Thrush can re-nest in the same season and increase its chances of fledging young. Brood parasitism may have much more of a negative influence on the warblers (Parulidae), flycatchers (Tyrannidae), and vireos (Vireonidae) that are smaller host species, have longer incubation periods, and have inadequate defenses against brood parasitism (Rothstein 1975, Robbins 1979, Ambuel and Temple 1982). On the other hand, the Wood Thrushes may actually be declining more rapidly in the Midwest, but the BBS method may not be sensitive enough to detect differences in rates of decline among regions.

The large number of nest records, extensive geographic coverage, and long-term nature make the Cornell nest record data base an extremely valuable data set that may eventually be used to monitor trends in reproductive success and to test hypotheses concerning factors that influence reproductive success. The nest record program provided us with information regarding the condition of the nest and its contents upon discovery, but nest outcome information was included for only 18% of the Wood Thrush nests. Data on nest outcomes are needed to understand fully the factors affecting breeding success. To increase the usefulness of the Cornell nest records, we recommend that nest finders monitor nests to a final outcome, include this information when filling out nest record cards, and report these nest records as often as possible. Also, it would be beneficial

for local or state organizations that maintain separate nest record programs to submit their records to Cornell, making the Cornell program a centralized source of nest record data. In addition, we encourage all researchers who are conducting nesting studies to send nest records to the Cornell Nest Record Program.

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