Studies in Avian Biology No. 18:200–203, 1999.

# INFLUENCE OF LANDSCAPE AND COWBIRD PARASITISM ON THE REPRODUCTIVE SUCCESS OF PLUMBEOUS VIREOS BREEDING IN COLORADO

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*Abstract.* We studied the impact of Brown-headed Cowbird (*Molothrus ater*) parasitism on the reproductive success of Plumbeous Vireos (*Vireo plumbeus*) nesting in the foothills of the Rocky Mountains west of Boulder, Colorado, between 1984 and 1997. Cowbirds parasitized 51.9% of 185 vireo nests monitored, with a range of 37.5% in 1992 (N = 8) to 65.7% in 1994 (N = 35). Parasitized nests had significantly smaller clutch sizes (3.3 ± 0.10 vs. 3.8 ± 0.06), lower hatching success (43.9% vs. 73.5%), and lower fledging success (14.6% vs. 54.4%) than unparasitized nests. Significantly fewer vireos fledged from parasitized nests (mean 0.5 young/nest) than unparasitized nests (mean 2.1 young/nest). Of eleven variables measured around 81 vireo nests, parasitized nests were significantly closer to openings in the canopy (> 400 sq. m) and had significantly less canopy cover than unparasitized nests. A stepwise logistic regression correctly classified 61.9% of 68 nests based on canopy cover, which was the best predictor of whether a vireo nest was parasitized in 1993–1994. Cowbirds are probably better able to observe host nest building activity from open canopies. Nests found in sites with lower tree density and canopy cover tended to have a higher likelihood of being parasitized, although the differences were not significant. While the ponderosa pine (*Pinus ponderosa*) forest has many natural canopy openings, openings created by roads also tended to increase the local frequency of parasitism. Managers concerned about the reproductive success of birds nesting in ponderosa pine forests should seek to reduce anthropogenic sources of canopy openings, which may not only increase the likelihood of parasitism, but nest predation as well.

*Key Words:* Brown-headed Cowbird, canopy openings, landscape ecology, *Molothrus ater,* Plumbeous Vireo, reproductive success, *Vireo plumbeus.*

Local features of the landscape can influence the distribution and abundance of Brown-headed Cowbirds (*Molothrus ater*) and the frequency of parasitism on host populations. Higher levels of cowbird parasitism have been reported along forest-field edges than in forest interiors (Gates and Gysel 1978, Brittingham and Temple 1983, Johnson and Temple 1990, but see Hahn and Hatfield 1995). Likewise, the frequency of cowbird parasitism has been reported as high on host nests along powerline corridors (Chasko and Gates 1982), in small forest tracts (Robinson et al. *in press*), and near livestock (Verner and Ritter 1983). Cowbirds tend to travel along streams (Gates and Giffen 1991) and are more abundant near clearcuts (Thompson et al. 1992). Frequency of parasitism is high across fragmented Midwestern landscapes where cowbird densities are high (Robinson and Wilcove 1994, Thompson 1994).

Most landscape level studies of cowbird distribution and frequency of parasitism have been conducted in eastern and midwestern deciduous forests where forest-field edges are sharp, and usually caused by anthropogenic disturbance (Gates and Gysel 1978, Johnson and Temple 1990, Gates and Giffen 1991, Robinson et al. 1995a). Coniferous forests of the West are often naturally fragmented, with open meadows and canopy openings occurring because of the patchiness of mature forests, especially of ponderosa pine (*Pinus ponderosa*).

Along the Front Range of the Rocky Mountains in Colorado, lower elevation ponderosa pine forests have been under increasing pressure of urban development. Furthermore, in Boulder County, a large portion of ponderosa pine forest has been set aside as Open Space, which has been an exceedingly popular program and receives over 3 million visitors annually (City of Boulder Open Space statistics, 1997). Thus, the canopy of the ponderosa pine forest is disrupted both naturally, with mature low density forest stands, successional stands, open meadows, and riparian vegetation, and anthropogenically, with trails, roads, homes, and at the edge of the city of Boulder, Colorado. In this study we examined the influence of both natural and anthropogenic sources of canopy disruption on cowbird parasitism of the Plumbeous Vireo (*Vireo plumbeus*). We hypothesize that openings, both natural and anthropogenic, facilitate cowbird observations of vireo nests, and that parasitism should be higher on nests closer to openings in the canopy.

## METHODS

Plumbeous Vireo nest data were collected during the summers of 1984–1986, 1992–1994, and 1997 in the foothills of the Rocky Mountain Front Range west of the city of Boulder, Colorado (40° 00'N, 105° 20'W). Study sites range from 1,800 m to 2,400 m in elevation and had a park-like appearance of open canopy ponderosa pine. Sites contained scattered Douglas fir (*Psuedotsuga menziesii*) and an understory dominated by chokecherry (*Prunus virginiana*), wax currant (*Ribes cereum*), skunkbrush (*Rhus aromatica*), small ninebark (*Physocarpus monogynus*), Oregon grape (*Mahonia repens*), kinnikinnick (*Arctostaphylos uva-ursi*), and various grasses (*Bromus, Achillia,* and *Stipa*).

Plumbeous Vireos were chosen for this study because their low nests were relatively easy to locate and monitor. Additionally, Plumbeous Vireos are relatively abundant on the study sites, and in various parts of their range are known acceptors of cowbird eggs (Friedmann et al. 1977, Curson 1996, this study)

Vireo nests were found during all stages of the nesting cycle and subsequently visited once every 2–4 days. Care was taken to minimize disturbance and attraction of nest predators to the nest site (Major 1990, Ralph et al. 1993). Outcome of each clutch (i.e., parasitism, predation, abandonment, or fledging) was determined. Nest appearance and mode of disturbance were used to determine whether nests were disturbed by predators. Nests that were found empty before young could potentially fledge, i.e., oldest vireo nestling was < 12 days or cowbird < 9 days old, were determined to have been preyed upon. Nests found empty on or after that point were determined to have been preyed upon if adults gave no alarm calls and no juveniles could be found in the nest area after a careful search. Only nests in which the final outcomes were known were used in the analysis. Nesting success was calculated using the Mayfield (1975) method to reduce the error introduced when nests observed for different lengths of time are treated equally.

Following the termination of nest site activity in 1993–1994, eleven landscape measurements were taken around each nest site. Distances to the nearest road (ROAD), trail (TRAIL), natural forest canopy opening (OPEN: an opening was > 400 $m^2$, with at least 10 m on one side and had < 15% canopy cover from the points of measurement), riparian vegetation (RIPAR), town (TOWN: Boulder or Lyons, Colorado), and year-round occupied residence (RESID) were measured from each nest. Using a 5-m and 50-m measuring tape, we measured these distances to the nearest 0.1 m within 50 m, 1 m between 51 m and 200 m, and to the nearest 50 m when distances were > 200 m. Canopy cover (CANOPY) of the site was estimated from 20 forest densiometer (concave) readings taken at uniform points within a 11.3 m radius circular plot centered on the nest. Ground cover (GROUND) was estimated from 20 ocular tube readings taken within the circular plot from the same points as canopy cover (James and Shugart 1970, Noon 1981). The number of trees (woody plants with a dbh ≥ 8 cm) were counted per 11.3 m radius circle around the nest and extrapolated to density per ha (TREES). Slope (SLOPE) of the nest site was measured with a clinometer. All variables were continuous.

Data were pooled across years for analysis after testing for significant differences in site characteristics revealed no differences between years. Since variables were not normally distributed all nest site variables were log-transformed. Comparisons of unparasitized and parasitized nest sites were made with equal sample size Student's t-tests. Because data were not normally distributed, median tests (Wilcoxon two-sample test) were employed to compare shapes of frequency distributions of mean clutch size and mean number of fledglings per nest. Goodness-of-fit tests (G-tests with William's correction; Sokal and Rohlf 1981) were used to compare hatching and fledging success between unparasitized and parasitized nests. Means ± SE are reported for descriptive statistics. Results are reported as significant when $P < 0.05$.

A stepwise logistic regression was used to test for landscape differences between parasitized and unparasitized nests. Variables were log-transformed. Because of the high amount of variability in analyses of many factors, and to reduce the possibility of type II statistical errors, the values with $P < 0.2$ were allowed to enter the regression model, but allowed to remain only when $P < 0.1$.

## RESULTS

Brown-headed Cowbirds parasitized 51.9% of 185 Plumbeous Vireo nests (Table 1). Parasitized nests ($N = 81$) had significantly smaller mean clutch sizes (3.3 ± 0.10) than unparasitized nests ($N = 80$, mean = 3.8 ± 0.06, $z = 3.4284$, $P < 0.001$). Parasitized nests also had significantly lower hatching success ($P < 0.001$), fledging success ($P < 0.001$), and mean number of young to fledge ($P < 0.001$) than unparasitized nests (Table 2). Nest predation was monitored in 1993–1994, and 49.4% of Plumbeous Vireo nests ($N = 81$) were preyed upon with predation independent of parasitism ($G = 0.1056$, df = 1, $P > 0.75$). Of forty nests that were preyed upon, three were only partially depredated, and two of those fledged at least one vireo.

Nest success was not significantly different between 1993 and 1994, and therefore the data were combined ($G = 0.1128$, df = 1, $P > 0.05$). The probability of a Plumbeous Vireo clutch

TABLE 1. FREQUENCY OF PARASITISM OF PLUMBEOUS VIREO NESTS IN BOULDER COUNTY, COLORADO[a]

| | Year | | | | | | | Total |
|---|---|---|---|---|---|---|---|---|
| | 1984 | 1985 | 1986 | 1992 | 1993 | 1994 | 1997 | |
| Unparasitized | 11 | 12 | 17 | 5 | 25 | 12 | 7 | 89 |
| Parasitized | 9 | 12 | 17 | 3 | 21 | 23 | 11 | 96 |
| % Parasitism | 45.0% | 50.0% | 50.0% | 37.5% | 45.6% | 65.7% | 61.1% | 51.9% |

[a] Frequency of parasitism is independent of year ($G_{ADJ}$ = 3.5658, df = 6, P > 0.05).

surviving 30 days to fledge at least one young was 0.27, with egg success greater than nestling success. Furthermore, parasitized nests had a significantly lower probability of success than unparasitized nests (Table 3).

The majority of vireo nests were in ponderosa pine. In 1993–1994, 92.6% (N = 81) of vireo nests were built in ponderosa pine trees, while 5 nests in 1993 (10.9%) and 1 nest in 1994 (2.8%) were built in shrubs. Parasitized nests were significantly closer to openings in the forest canopy (OPEN) and nests with lower canopy cover (CANOPY) (Table 4). Distance to opening was the best predictor of whether a Plumbeous Vireo nest was parasitized in 1993–1994, and a stepwise logistic regression correctly classified 61.9% of 68 nests based on that criteria alone (criteria for model fit, $\chi^2$ = 5.483, df = 1, P = 0.019).

## DISCUSSION

Brown-headed Cowbirds typically parasitized 50% of Plumbeous Vireo nests we observed in each of the seven years of the study (Marvil and Cruz 1989, Chace et al. *in press*, Table 1). Cowbirds had a significant, negative impact on the Plumbeous Vireo nests they parasitized (Table 2). In the Colorado Front Range, Plumbeous Vireos nested in mature park-like stands of ponderosa pine, with low canopy cover and well spaced trees lacking any significant shrub or sapling layer. Cowbirds used canopy openings as small as 0.04 ha, and reduced canopy cover to search for nests to parasitize. Plumbeous Vireos nesting near such openings were significantly more likely to be parasitized (Table 4). Roads, trails, and residential areas also created openings in the canopy, but only natural openings showed any trend towards increased parasitism.

In an exploratory analysis based on the 1992 and 1993 data we lumped 55 vireo nests into one discrete landscape group (e.g., near road, near residence, in lower foothills, etc.), and found that parasitized vireo nests were strongly associated with roads and residential areas (Chace et al. *in press*). In that initial analysis we documented that anthropogenic factors of the landscape have an influence on Plumbeous Vireos reproductive success. However, here we illustrate the importance of finer scale canopy openings and the impacts they may have on the parasitism probability of vireo nests. The earlier analysis did not separate openings created by natural processes from anthropogenic openings, and while the few vireos that nest near roads and residential areas are very likely to fail due to both parasitism and predation, the majority of vireos nesting in more natural conditions are greatly affected by small changes in canopy density and distances to openings. This analysis is also more robust with larger, equal, sample sizes

TABLE 2. REPRODUCTIVE SUCCESS IN UNPARASITIZED AND PARASITIZED NESTS OF PLUMBEOUS VIREOS, BOULDER COUNTY, COLORADO, 1984–1986, 1992–1994, AND 1997

| | Vireo nests[a] | | | Cowbird |
|---|---|---|---|---|
| | Unparasitized | Parasitized | All | |
| No. active nests | 80 | 81 | 162 | — |
| Total eggs | 309 | 246 | 555 | 111 |
| Total hatched | 227 | 108 | 355 | 67 |
| Total fledged | 168 | 36 | 204 | 41 |
| Hatching success (%) | 73.5[b] | 43.9 | 60.4 | 60.4 |
| Fledgling success (%) | 54.4[b] | 14.6 | 36.8 | 36.9 |
| Fledge/egg hatch (%) | 74.0[b] | 33.3 | 61.0 | 61.2 |
| Mean fledge/active nest | 2.1[c] | 0.5 | 1.3 | 0.5 |

[a] Includes only nests found during incubation and followed to fledging or failure.
[b] Differences in fledgling success between unparasitized and parasitized nests are significant for hatching success ($G_{ADJ}$ = 12.8689, df = 1, P < 0.001), fledgling success ($G_{ADJ}$ = 49.0334, df = 1, P < 0.001), and fledgling/egg hatched ($G_{ADJ}$ = 14.2999, df = 1, P < 0.001).
[c] Differences between unparasitized and parasitized nests are significant (Wilcoxon two-sample test, Z = 6.24, P < 0.001).

TABLE 3. MAYFIELD'S NESTING SUCCESS[a] CALCULATED FOR PARASITIZED AND UNPARASITIZED PLUMBEOUS VIREO NESTS, 1993–1994

| | Probability of survival | | |
|---|---|---|---|
| | Egg stage | Nestling stage | Overall |
| Parasitized | 0.48 | 0.21 | 0.17 |
| Unparasitized | 0.66 | 0.59 | 0.40 |
| Overall | 0.55 | 0.43 | 0.27 |

[a] Probabilities based on survival of at least one offspring for duration of 16 day incubation period and 14 day nestling period.

and univariate parametric and multivariate statistics.

Cowbird abundance and parasitism have been shown to decrease with distance from the edge to the forest interior (Gates and Gysel 1978, Brittingham and Temple 1983, Temple and Cary 1988, Yahner and DeLong 1991, O'Conner and Faaborg 1992). Furthermore, cowbird abundance and parasitism increase when openings are created in an otherwise contiguous forest canopy (Brittingham and Temple 1983, Evans and Gates 1997). In the ponderosa pine forests of Boulder County, Plumbeous Vireos nested in a naturally discontinuous forest landscape with large openings and consequent edge effects. When observed in the ponderosa pine, female cowbirds have been found perched on the tops of trees. Plumbeous Vireo nests that are closer to openings and under lower canopy cover would be easier for cowbirds to locate, and parasitism reduces the reproductive success of vireos placing their nest in such locations.

Many of the bird species that breed in the ponderosa pine forests of the Colorado Front Range are sensitive across their southwestern range. In Arizona, Colorado, and New Mexico, the Plumbeous Vireo is designated as a high priority species, and it is of special concern in Arizona and Colorado (Winternitz and Crumpacker 1985, Hall et al. 1997). However, Breeding Bird Survey results (1966–1994) show that Plumbeous Vireo populations are increasing or are stable across their range. Plumbeous Vireos are an ideal species to study the impacts of cowbird parasitism, compare the frequency of parasitism across the Southwest, and determine habitat features that influence cowbird parasitism because they have low nests that are relatively easy to find, and they are a principal host of cowbirds in ponderosa pine and pinyon-juniper forests (Curson 1996). Land managers interested in evaluating the effects of landscape or habitat changes on a sensitive local migratory songbird in ponderosa pine or pinyon-juniper forests could get a reasonable estimation from examining Plumbeous Vireo reproductive success.

ACKNOWLEDGMENTS

We greatly appreciate R. E. Marvil for sharing her field notes and data (1984–1986) with us. D. Bennet, S. Severs, C. Bechtoldt, D. Evans, and J. Walsh provided invaluable field assistance. This manuscript greatly benefited from the comments of two anonymous reviewers. Funding for this study has been provided by the Boulder County Nature Association, City of Boulder Open Space, and the University of Colorado Graduate School and Department of E.P.O. Biology.

TABLE 4. MEAN VALUES (± SE) OF LANDSCAPE VARIABLES AT UNPARASITIZED AND PARASITIZED PLUMBEOUS VIREO NEST SITES, 1993–1994

| Variables | Unparasitized | Parasitized | n | P[a] |
|---|---|---|---|---|
| SLOPE (°) | 15.5 (1.25) | 16.7 (1.51) | 74 | 0.949 |
| TREES (#/ha) | 321.3 (33.84) | 296.3 (47.62) | 78 | 0.387 |
| GROUND (%) | 37.0 (3.40) | 41.3 (34.10) | 78 | 0.339 |
| CANOPY (%) | 69.0 (2.47) | 61.1 (3.18) | 78 | *0.045* |
| ROAD (m) | 904 (90.59) | 752 (91.11) | 78 | 0.269 |
| TRAIL (m) | 251 (81.03) | 282 (100.04) | 72 | 0.562 |
| OPEN (m) | 60.6 (14.21) | 25.8 (4.67) | 62 | *0.007* |
| RIPAR (m) | 363 (66.42) | 247 (59.23) | 78 | 0.123 |
| RESID (m) | 1119 (116.62) | 1108 (148.67) | 78 | 0.506 |
| TOWN (m) | 2094 (231.37) | 1706 (245.79) | 78 | 0.136 |
| NRHUMAN (m) | 169 (38.70) | 166 (40.77) | 72 | 0.591 |

[a] Result of Student t-test conducted on log-transformed variables.