Local Gradients of Cowbird Abundance and Parasitism Relative to Livestock Grazing in a Western Landscape

CHRISTOPHER B. GOGUEN* AND NANCY E. MATHEWS

Department of Wildlife Ecology, University of Wisconsin, 1630 Linden Drive, Madison, WI 53706-1598, U.S.A.

Abstract: *We studied local patterns of Brown-headed Cowbird (*Molothrus ater*) abundance, parasitism rates, and nest success of a common host, the Plumbeous Vireo (*Vireo plumbeus*), in relation to the distribution of livestock grazing in an undeveloped region of northeastern New Mexico, 1992–1997. We predicted that both cowbird abundance and parasitism rates of vireo nests would decrease with increasing distance from active livestock grazing, and that the nesting success of vireos would increase. We measured cowbird abundance and host density and located and monitored vireo nests in pinyon-juniper and mixed-conifer habitats that ranged from actively grazed to isolated from livestock grazing by up to 12 km. Cowbird abundance declined with distance from active livestock grazing and was not related to host density or habitat type. Brood parasitism levels of vireo nests (*n = 182*) decreased from >80% in actively grazed habitats to 33% in habitats that were 8–12 km from active grazing but did not vary by habitat type or distance to forest edge. Vireo nesting success was higher in mixed-conifer habitat than in pinyon-juniper but was unrelated to distance from active livestock grazing. Nest losses due to parasitism declined with distance from active livestock grazing. Our results suggest that cowbird abundance and parasitism rates of hosts may be distributed as a declining gradient based on distance from cowbird feeding sites and that isolation from feeding sites can reduce the effects of parasitism on host populations. These findings provide support for management techniques that propose to reduce local cowbird numbers and parasitism levels by manipulating the distribution of cowbird feeding sites. The presence of parasitized nests >8 km from active livestock grazing suggests that, in some regions, management efforts may need to occur at larger scales than previously realized.*

Gradientes de Abundancia Locales de Tordos y Parasitismo Relativo al Pastoreo de Ganado en un Paisaje Occidental

Resumen: *Estudiamos patrones locales de abundancia del tordo cabeza café (*Molothrus ater*), las tasas de parasitismo y el éxito de nidada de un hospedero común, el vireo (*Vireo plumbeus*), en relación con la distribución del pastoreo en una región poco desarrollada del noreste de Nuevo México, entre 1992 y 1997. Pronosticamos que tanto la abundancia del tordo, como las tasas de parasitismo de nidos de vireo disminuirían con un incremento en la distancia a las zonas de pastoreo activo de ganado y el éxito de nidada de vireos incrementaría. Medimos la abundancia de tordos y la densidad de hospederos y localizamos y monitoreamos los nidos de vireos en hábitats de pino-cedro y de coníferas mixtas que variaron desde activamente pastoreadas hasta sitios distanciados del pastoreo hasta por 12 km. La abundancia de los tordos disminuyó con la distancia de las zonas de pastoreo activo de ganado y no estuvo relacionada con la densidad de hospederos o el tipo de hábitat. Los niveles de parasitismo de las nidadas del vireo (*n = 182*) disminuyeron de >80% en hábitats activamente pastoreados a 33% en hábitats que estuvieron de 8 a 12 km de distancia de los sitios de pastoreo activo, pero no variaron con el tipo de hábitat ni la distancia al borde del bosque. El éxito de nidada de vireos fue mayor en el hábitat mixto de coníferas que en el hábitat de pino-cedro, pero no estuvo relacionado con la distancia al sitio de pastoreo. Las pérdidas debidas al parasitismo disminuyeron con la distancia al sitio activo de pastoreo. Nuestros resultados sugieren que la abundancia de tordos y las tasas de parasitismo de hospederos podría estar distribuida en forma de un gradiente en descenso basado en la distancia a los sitios de alimentación de los tordos y a que el aislamiento de los sitios de*

*Current address: Department of Entomology and Applied Ecology, University of Delaware, Newark, DE 19717-1303, U.S.A., email goguen@udel.edu

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alimentación puede reducir los efectos del parasitismo de las poblaciones de hospederos. Estos resultados apoyan las técnicas de manejo que proponen la reducción local de números de tordos y los niveles de parasitismo al manipular la distribución de sitios de alimentación de tordos. La presencia de nidos parasitados >8 km de sitios con pastoreo activo sugiere que, en algunas regiones, los esfuerzos de manejo deben ocurrir a escalas mayores a lo que anteriormente se pensaba.

Introduction

The remarkable range expansion of the brood-parasitic Brown-headed Cowbird (*Molothrus ater*) over the past century, and concurrent declines in many songbird species used as hosts, has inspired considerable interest in discerning factors that limit cowbird abundance and distribution (Mayfield 1965; Brittingham & Temple 1983; Rothstein 1994). Historically, the geographic distribution of cowbirds appears to have been limited by the availability of feeding rather than breeding resources (Hamilton & Orians 1965; Mayfield 1965). Cowbirds typically feed in open habitats with short vegetation, such as those created and maintained by grazing ungulates (Lowther 1993). For breeding, however, the cowbird requires only the presence of host nests and is capable of reproducing successfully in a variety of forested and nonforested habitats (Mayfield 1965; Robinson et al. 1995*a*). Prior to European settlement, cowbirds were limited largely to the grasslands of central North America by what appears to have been a nearly obligate commensalistic foraging relationship with bison (*Bison bison*; Friedmann 1929; Mayfield 1965). But subsequent human activities associated with settlement, (such as forest clearing, livestock grazing, and agriculture), have provided cowbirds with alternative feeding habitats and resources, and at present cowbirds have colonized most of the United States and southern Canada (Lowther 1993).

Current research examining patterns of cowbird abundance has tended to emphasize a landscape scale. This is because the parasitic breeding strategy of cowbirds allows them to uncouple their breeding and feeding activities such that individual cowbirds often commute among several habitats during the span of a single day's activities (Rothstein et al. 1984; Thompson 1994). At the landscape level, patterns of cowbird abundance remain closely tied to the availability of feeding habitats (Verner & Ritter 1983; Airola 1986; Coker & Capen 1995; Robinson et al. 1995*b*). In the central United States, for example, cowbird abundance and parasitism rates experienced by forest songbirds are negatively correlated with the proportion of forest cover within a 10-km radius (Robinson et al. 1995*b*; Thompson et al. 2000). Although all forested habitats provide potential breeding resources, the number of cowbirds able to access these resources appears limited by the availability of nonforested habitats, which provide feeding resources.

At a more local scale, general conclusions concerning patterns of abundance of breeding cowbirds have been more difficult to reach (Donovan et al. 1997; Thompson et al. 2000). Nevertheless, in some forested habitats, particularly in landscapes where cowbird feeding habitat is localized, it appears that cowbird abundance and parasitism rates decline with increasing distance from forest edge and, ultimately, from feeding habitat (Brittingham & Temple 1983; Verner & Ritter 1983; Donovan et al. 1997, 2000; Morse & Robinson 1999). Thus, cowbird breeding distributions and rates of parasitism may occur as gradients based on distance from feeding habitat.

Livestock grazing is a dominant land use in the western United States (Holechek et al. 1989) and in many landscapes may provide the primary foraging opportunities for breeding cowbirds. Consequently, it is possible that the distribution of livestock may broadly determine the abundance and distribution of cowbirds within these landscapes. Management implications of this relationship are currently being evaluated in the context of livestock removals to protect endangered species (Goguen & Mathews 1999). Livestock removals entail the rotation of livestock away from host breeding habitat, at least during the songbird breeding season, in an effort to reduce or eliminate parasitism by eliminating cowbird feeding sites. Obviously, this technique depends on the assumption that local breeding distributions of cowbirds are constrained by the distribution of feeding habitats. Thus, knowledge of the generality and scale of cowbird gradients would help managers evaluate the broad applicability of this technique and would provide information useful in prescribing effective livestock removal distances.

We studied local patterns of cowbird abundance and parasitism rates of a common host, the Plumbeous Vireo (*Vireo plumbeus*), along a natural prairie-forest edge in northeastern New Mexico. Livestock grazing is the primary land use in the prairies of this undeveloped region. Some forested areas are not grazed during the songbird breeding season, however, and provide breeding habitat for cowbirds and hosts that is isolated by up to 12 km from active livestock grazing. Radiotelemetry studies indicate that cowbirds feed almost exclusively in association with livestock in this region (Goguen & Mathews 1999; Curson et al. 2000). Thus, we hypothesized that if proximity to feeding habitat is an important component of breeding habitat selection by female cowbirds, then

ı cowbird abundance and rates of parasitism on nbeous Vireo nests should decline in these forests ı increasing distance from active livestock grazing. :her, because parasitism often causes the failure of nbeous Vireo nests (Marvil & Cruz 1989; Goguen & hews 1998), we predicted that the nesting success ireos should increase with increasing distance from :ing.

hods

ly Area

conducted this research on the 13,350-ha NRA Whitton Center (WC) and the adjacent 8,090-ha V-7 Ranch R) in Colfax County, northeastern New Mexico (lat 45′N, long 104°30′W). These sites lie on the eastern ıe of the foothills of the Sangre de Cristo Mountains ıg the interface between the prairies of the Great ns and the forested mountains. Within the region, er elevations (<1990 m) are occupied by shortgrass rie dominated by blue grama (*Bouteloua gracilis*). ron pine (*Pinus edulis*) and one-seed juniper (*Juniperus monosperma*) woodlands occupy a narrow zone the lower mountain slopes (1990–2130 m). Mixed ifer forests of ponderosa pine (*Pinus ponderosa*) Douglas-fir (*Pseudotsuga menziesii*) dominate at ıer elevations.

ɔth the WC and V7R have a long history of native domestic grazing, with cattle grazing remaining the nary land use in the region. On the V7R, cattle are :ed seasonally (November–June) at a moderate stock-rate (approximately 45% annual forage removal) ıin the lower-elevation pinyon-juniper and prairie itats. Livestock grazing was halted at the WC in 1973 was reintroduced seasonally (late summer to au-n) to some mixed-conifer habitats in 1995. No live-:k are grazed on the WC during the primary songbird :ding period of mid-May through June, however.

ı 1992 we established eight 35-ha (700 × 500 m) ly plots within pinyon-juniper habitats: four on the vely grazed V7R and four on the ungrazed WC. Plots he WC ranged from 0.05 to 4.2 km away from the in-ace with active cattle grazing. We were unable to es-ish any pinyon-juniper plots in areas more distant ı active livestock grazing because of the distribution ·inyon-juniper habitat on the WC. In 1994 we estab-:d three additional study plots within mixed-conifer itats of the WC and added a fourth in 1996. These s were not grazed by domestic livestock during the gbird breeding season and during that period ranged ı 0.1 to 10.3 km away from the interface with active ing. We were unable to establish any actively grazed ed-conifer plots because all mixed-conifer habitat ıin the study sites was ungrazed during the songbird breeding season. Overall, all 12 plots were located within a 10-km radius region of the study area.

Host and Cowbird Abundance

We conducted morning point-count surveys to estimate the relative abundance of breeding cowbirds and their hosts on the study plots annually. Survey points were arranged on each plot in a 12-point grid, with points separated by 200 m. This systematically arranged grid of points ensured complete coverage of each plot and minimized double counting of individual birds. Each year, we surveyed each plot three times between 15 May and 15 June. Counts began 15 minutes before sunrise and were completed within 3 hours, between approximately 0530 and 0830 hours. We used 10-minute point counts and recorded, by species, all birds of both sexes observed or heard within 50 m of the point center. Surveys were not conducted on mixed-conifer plots in 1995 because unusually intense spring rains washed out access roads.

Nest Searches and Monitoring

We located and monitored Plumbeous Vireo nests in pinyon-juniper and mixed-conifer habitats, centered around the survey plots, to evaluate the effect of distance from livestock on parasitism and nesting success rates. We selected the Plumbeous Vireo as the focal species because it occurred at similar abundance in both habitat types and was a common cowbird host (Goguen & Mathews 1999). Upon locating a nest, we made an initial check to determine nest status and contents. Nests were rechecked every 2–4 days to monitor their status and fate. We classified nests as parasitized if a cowbird egg or young was observed in an active nest. The parasitism status of nests found with only vireo young >3 days old was classified conservatively as unknown because cowbird eggs could have been laid and failed prior to our discovery of the nest. We considered a nest successful if it fledged at least one vireo. We considered a nest failed due to cowbird parasitism if it was abandoned within 3 days of the parasitism event or if the presence of a cowbird nestling caused the death of all host eggs. To estimate general failure rates of vireo nests due to causes other than parasitism, we considered all nests that failed to fledge either a vireo or cowbird young, excluding nests abandoned due to parasitism, as depredated. Most of these nests were truly depredated, but this classification also included the few nests that failed due to weather or starvation. Because depredation status simply indicated whether a nest fledged at least one young, regardless of species, it was possible for a nest to fail first due to parasitism because all vireo young perish in competition with a cowbird and then to be depredated of the remaining cowbird nestling.

Analyses

We plotted each study plot and vireo nest on the WC on topographic maps for distance estimates. We estimated the distance from active grazing for each study plot on the WC as the minimum distance between the plot edge and the nearest fence line separating the WC from active cattle grazing during the summer songbird breeding season. We estimated the distance from active grazing of each vireo nest on the WC in a similar manner. All plots and nests on the V7R were assigned a distance from active grazing of 0 m.

We also estimated an approximate distance from forest edge for all nests because many past studies have suggested that proximity to forest edge influences nest fate and parasitism. For this variable, we estimated the distance from the nest to the nearest border between the forested nesting habitat and any nonforested habitat patch of at least 0.2 ha (45-m radius; Brittingham & Temple 1983). Nonforested habitats included either grassland or open oak shrubland. We did not consider the single-lane dirt roads that transect the forests as potential edges because most were covered by the forest canopy.

We calculated a mean abundance estimate for cowbirds and host species from survey data for each plot in each year. This estimate was calculated as the average number of detections of a species across the three surveys of a plot within a given year. Mean host abundance was calculated by summing on a plot the mean abundance estimates of each potential host species. We considered a species a potential host if it built an open-cup nest and bred during the period when our surveys were conducted (May–June). We included one known rejector species, the American Robin (*Turdus migratorius*), because cowbirds will lay eggs in their nests.

We used multiple linear regression to assess the importance of habitat type, distance from active grazing, and host abundance in predicting cowbird abundance. We used surveys only from 1994, 1996, and 1997 because they were the only years during which both pinyon-juniper and mixed-conifer plots were surveyed. To determine the best regression model, we used a forward stepwise selection procedure with a threshold value for variable entry of $p = 0.05$. Initially, we conducted separate analyses for each year to evaluate year effects. Because all three analyses resulted in the same model with a similar slope, we conducted a final summary analysis using the 3-year average as the estimate of cowbird and host abundance for each plot.

We analyzed nest data in two ways. First, we examined parasitism and nest fates with distance from grazing as a continuous variable. Using multiple logistic regression, we simultaneously examined the influence of year, habitat (pinyon-juniper or mixed-conifer), distance from forest edge, and distance from active livestock grazing on the likelihood of parasitism, nesting success, or nest depredation. We also examined interaction terms. We used a forward stepwise selection procedure with a threshold value for entry of $p = 0.05$. In each model the outcome variable was the logit transformation of the probability of a nest being parasitized, successful, or depredated, respectively (Hosmer & Lemeshow 1989). To examine parasitism intensity (i.e., cowbird eggs per parasitized nests), we used multiple linear regression to assess the importance of habitat and distance from grazing on the number of cowbird eggs laid per parasitized nest. For this analysis, we first square-root transformed the number of cowbird eggs per nest to better equalize the variance across the range of distances from grazing.

Second, we summarized and compared parasitism rates and nest fates according to habitat and distance from grazing categories. Each nest, regardless of the year when it was active, was placed into one of five categories according to dominant vegetation type and distance from active grazing. Nests located in pinyon-juniper habitat were divided into categories of "Grazed PJ" for nests in actively grazed habitats and "<4 km PJ" for nests in ungrazed habitats that were <4 km from active livestock grazing. Nests within mixed-conifer habitats were divided into <4 km MC, 4–8 km MC, and 8–12 km MC according to their distance from active livestock grazing. We used log-likelihood tests to assess whether the proportions of nests that were parasitized, successful, depredated, or failed due to parasitism differed among the five categories. We used Kruskal-Wallis one-way analysis of variance to test whether the mean number of cowbird eggs laid per parasitized nest differed among the five habitat-distance categories. We performed all statistical analyses using SYSTAT software (version 7.0, SPSS, Chicago). Statistical tests were considered significant at $p \leq 0.05$.

Results

Cowbird and Host Abundance

Mean abundance of cowbird hosts was higher in mixed-conifer habitats (mean = 31.14 ± 2.34) than in pinyon-juniper habitats (mean = 25.25 ± 1.30; $F = 5.77$; df = 1,10; $p = 0.04$) but was not related to distance from active livestock grazing. Cowbird abundance was predicted best by the distance of a plot from grazing ($r^2 = 0.68$; $F = 21.13$; df = 1, 10; $p = 0.001$), and it declined as distance from grazing increased (Fig. 1).

Cowbird Parasitism Rates and Vireo Nesting Success

We located and monitored 212 vireo nests: 105 in pinyon-juniper and 107 in mixed-conifer. Nests in pinyon-juniper habitat ranged from 0 to 4.3 km from active livestock grazing, but 62% were located in actively grazed

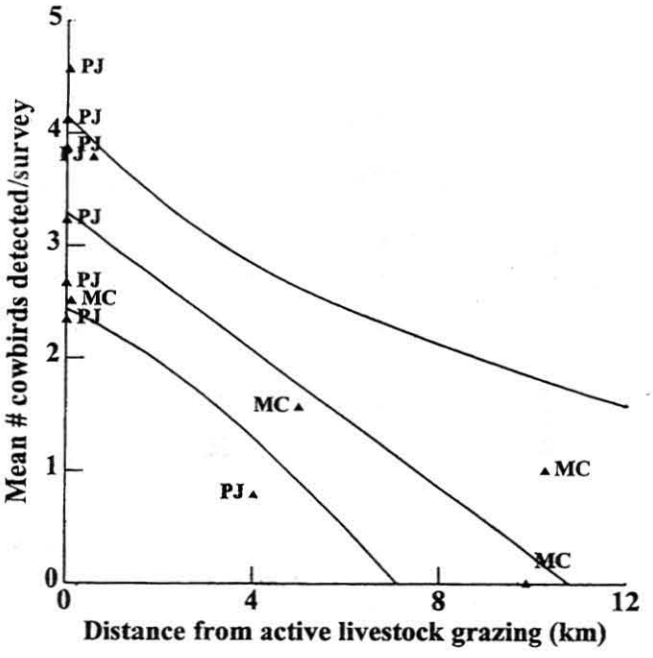

Figure 1. Cowbird abundance in pinyon-juniper (PJ) and mixed-conifer (MC) habitats relative to distance from active livestock grazing. Graph reports trendline and 95% confidence interval from simple linear regression analysis.

habitat, 36% within 1 km from grazing, and 4% over 1 km from grazing. Nests in mixed-conifer habitat ranged from 0 to 11.2 km from grazing and were relatively evenly distributed across that distance. Because of the natural interspersion of grass- and shrubland habitats within the forests, all nests, regardless of habitat type, were located within 640 m of a forest edge, and 81% were located ≤100 m from an edge (pinyon-juniper nests, mean = 74 m from edge, range, 0–350 m; mixed-conifer nests, mean = 85 m, range, 0–640 m).

Proportions of nests parasitized differed among the five habitat-distance categories. Over 70% were parasitized in habitats close to grazing, whereas only 33% were parasitized in mixed-conifer habitat 8-12 km from grazing (Table 1). The proportion of nests parasitized varied independently of habitat, year, or distance from edge and was best predicted by the logistic regression model including only the distance from active grazing. This model was used to predict the probability that a nest was parasitized based on distance from livestock using the logistic response function:

$$\text{probability}\{\text{parasitized}\} = \frac{\exp(1.39 - 0.25 \times \text{distance})}{1 + \exp(1.39 - 0.25 \times \text{distance})},$$

where 1.39 is the regression intercept, −0.25 is the regression slope, and "distance" is the distance of a nest from active livestock grazing in kilometers (Fig. 2).

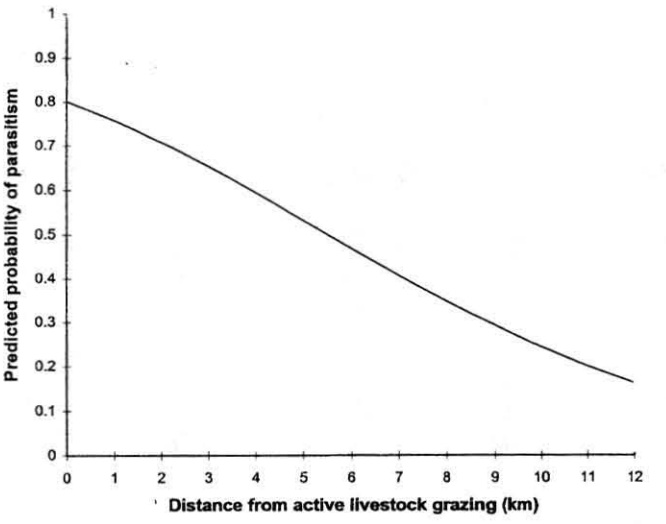

Figure 2. Probability of cowbird parasitism in relation to distance from active livestock grazing, as predicted by a logistic regression model, for Plumbeous Vireo nests in pinyon-juniper and mixed-conifer habitats in northeastern New Mexico.

Intensity of parasitism was negatively related to distance from grazing ($r^2 = 0.05$; $F = 5.39$; df = 1, 118; $p = 0.02$; Table 1). Multiple parasitism, with up to four cowbird eggs per nest, occurred often in habitats that were <4 km from grazing, but it was rare, with never more than two eggs per nest, in habitats further from grazing. Habitat type may also have influenced the intensity of parasitism: the mean number of cowbird eggs per parasitized nest tended to be greater in <4 km PJ habitats than in <4 km MC ($U = 272$, $p = 0.08$; Table 1).

Despite our observation that parasitism declined with distance from grazing, the probability of vireo nest success was best predicted by a logistic regression model containing only habitat type. Vireos in mixed-conifer habitat had higher nesting success than those in pinyon-juniper, regardless of distance from grazing. This occurred even though the proportion of nests that failed because of cowbird parasitism was positively related to the rate of parasitism ($r^2 = 0.94$, $F = 45.50$, df = 1, 3; $p = 0.007$; Table 1). Neither the log-likelihood comparisons of predation rates among habitat-distance categories (Table 1) nor logistic regression analyses of the likelihood of predation indicated any relationship between nest predation and habitat or distance to grazing. The predation rate of vireo nests in the <4 km MC category was only about half as large as rates in all other categories, however.

Discussion

Our study clearly documents a decrease in cowbird abundance with increasing distance from cowbird feed-

Table 1. Parasitism and nest fate characteristics of Plumbeous Vireo nests grouped by habitat type and distance from active livestock grazing.[a]

			Fate of nest (%)[e]		
Category[b]	*Parasitism rate (%)*[c]	*BHCO egg/para nest*[d]	*successful*[f]	*failed due to parasitism*[g]	*depredated*[h]
Grazed PJ	81.0 ± 5.2 (58)a	1.64 ± 0.12 (47)a	20.0 ± 5.2 (60)a	41.7 ± 6.4 (60)a	45.0 ± 6.4 (60)a
<4 km PJ	83.3 ± 6.2 (36)a	1.77 ± 0.17 (30)a	17.5 ± 6.0 (40)a	40.0 ± 7.7 (40)a	42.5 ± 7.8 (40)a
<4 km MC	70.6 ± 7.8 (34)a	1.38 ± 0.13 (24)ab	48.8 ± 7.8 (41)b	26.8 ± 6.9 (41)ab	24.4 ± 6.7 (41)a
4–8 km MC	40.0 ± 8.9 (30)b	1.09 ± 0.09 (11)b	45.7 ± 8.4 (35)b	14.3 ± 5.9 (35)b	42.9 ± 8.4 (35)a
8–12 km MC	33.3 ± 9.6 (24)b	1.13 ± 0.13 (8)b	43.3 ± 9.0 (30)b	13.3 ± 6.2 (30)b	46.7 ± 9.1 (30)a

[a] *Results reported as estimate ±1 SE (number of nests). Within columns, estimates followed by different letters were significantly different* ($p < 0.05$).
[b] *Habitat types: PJ, pinyon-juniper and MC, mixed-conifer.*
[c] *Proportion of nests parasitized differed among categories* ($G = 32.62$; $df = 4$; $p < 0.001$).
[d] *Mean number of Brown-headed Cowbird (BHCO) eggs per parasitized nest differed among categories* ($H = 11.31$; $p = 0.023$).
[e] *Nest fate percentages add up to >100% because "depredated" nests included nests in which the cowbird nestling was depredated after all vireo eggs had already failed due to parasitism.*
[f] *Proportion of nests that were successful differed among categories* ($G = 18.03$; $df = 4$; $p = 0.001$),
[g] *Proportion of nests that failed due to cowbird parasitism differed among categories* ($G = 15.01$; $df = 4$; $p = 0.005$).
[h] *Proportion of nests that were depredated did not differ among categories* ($G = 5.82$; $df = 4$; $p = 0.21$).

ing habitat, in this case livestock pasture, and demonstrates a concomitant decline in the rate of brood parasitism experienced by a common host. This declining gradient of parasitism in relation to cowbird feeding habitat is similar to the pattern observed recently within nests of the Kentucky Warbler (*Oporornis formosus*) in Illinois (Morse & Robinson 1999). Gradients in cowbird parasitism may result because female cowbirds face trade-offs when selecting where to feed and breed. The energetic costs of flight may constrain resources available for reproduction and favor birds that minimize the distance between their breeding and feeding sites. In contrast, territorial behavior in cowbirds (Rothstein et al. 1986), declines in reproductive success with increasing density, or increased rates of nest predation close to forest edges (Yahner 1988; Paton 1994) may favor birds that fly further.

Although parasitism rates declined with increasing distance from grazing and the proportion of Plumbeous Vireo nests that failed because of parasitism decreased with decreasing parasitism rate, nest success did not increase with distance from grazing as predicted. Instead, habitat appeared to be more important as vireos achieved higher success in mixed-conifer habitat regardless of distance from grazing. Differences in nest predation rates could mask possible distance-related effects of parasitism on nesting success, if, for example, predation and parasitism rates were negatively correlated. Yet statistical evaluations failed to indicate any patterns of nest predation. Among the habitat-distance categories the <4 km MC category was responsible for disrupting the pattern of nest success we predicted. Success for this category was higher than expected given its high parasitism rate, whereas its depredation rate was unusually low. These results could reflect a real effect of the habitat. Uneven sampling of nests among years and an undetected year effect may also be responsible, however. Unlike the other categories, a large proportion (68%) of the <4 km MC nests were located in a single year of the study. A low predation rate during that year may have inflated the success estimate for this category, whereas modest annual sample sizes of nests prevented a powerful test of year effects. Additional data are needed to better evaluate these relationships.

Perhaps the most unexpected result of our study was the scale over which the parasitism gradient occurred. Some researchers have found that cowbirds commute up to 7 km between breeding and feeding ranges, with most commuting substantially shorter distances (Rothstein et al. 1984; Thompson 1994; Gates & Evans 1998). In our landscape, cowbirds bred across the entire 12-km range we studied. Furthermore, we confirmed with radiotelemetry that the female cowbirds that breed in habitats >10 km from active livestock grazing were commuting 10-15 km daily to feed with livestock on the prairies (Curson et al. 2000). Given the gradual nature of the parasitism gradient on our site, it is doubtful that the declining pattern would have been apparent had we limited our research to only the first kilometer away from cowbird feeding habitat as other researchers have done (e.g., Hahn & Hatfield 1995; Donovan et al. 1997). The generality of our observations of long-distance commuting, however, needs to be evaluated in other regions with large blocks of contiguous forest.

Many previous studies have investigated the prevalence and importance of edge effects—higher nest predation or parasitism rates near habitat edges—as a mechanism to explain observations of poor reproductive success among songbirds within fragmented habitats (reviewed by Yahner 1988; Paton 1994). These studies typically focused on a narrow zone, usually <500 m wide, along the habitat edge, under the assumption that predators or parasites respond to structural or ecological features of the edge. Within grasslands near forests, there is strong evidence that parasitism increases close to the forest edge, perhaps because forests provide nest-

searching perches that are unavailable in the grassland (Best 1978; Johnson & Temple 1990). Within forests, results have been more equivocal. At a fine scale, cowbirds may respond numerically to higher host densities along a forest edge (Gates & Gysel 1978). At a broader scale, however, we suggest that proximity to feeding habitat drives local patterns of cowbird settlement. For example, in our study area all forests were naturally interrupted by narrow, grassy meadows along valley bottoms or large patches of oak shrubland on south-facing slopes. All of these open habitats lacked livestock during the songbird breeding season, however, and were not used as feeding sites by radio-tagged cowbirds that we monitored (Curson et al. 2000). Because of the regular distribution of nonforested habitats, most nests in our study were located within 300 m of a forest edge. Yet, given the patterns of cowbird abundance and parasitism observed, it was clear that distance to feeding habitat rather than distance to forest edge was the broader-scale constraint on local cowbird distributions in this landscape.

Conservation Implications

Reduction of cowbird parasitism is an important management objective in recovery efforts for several endangered and threatened songbird species in the United States (Robinson et al. 1995*a*). Cowbird control via trapping is a common and effective management technique, but its high cost and open-ended nature have caused managers to seek alternative solutions (Rothstein & Cook 2000). The apparent link between the distribution of cowbirds and their feeding habitats has generated interest in habitat-based management techniques, such as livestock removals or rotations, that may be incorporated into local grazing strategies on public lands (Goguen & Mathews 1999). At a landscape scale, it is apparent that cowbird abundance is influenced strongly by the availability of feeding habitat (Verner & Ritter 1983; Rothstein et al. 1984; Robinson et al. 1993, 1995*b*; Coker & Capen 1995; Thompson et al. 2000). As a result, most recommendations for regional cowbird management strategies have focused on concentrating or minimizing the availability of feeding habitats. Our results support the premise that local distributions of breeding cowbirds are also linked to the distribution of feeding habitat, and they suggest that localized livestock removals may be useful in managing cowbird distributions in areas where alternative feeding habitats are rare. In areas where alternative cowbird feeding sites (e.g., agricultural lands, human settlements) are common and difficult to eliminate, other, more traditional management options (e.g., cowbird trapping) may still be more appropriate.

We did not find an increase in Plumbeous Vireo nesting success with increasing distance from active livestock grazing, even though the proportion of vireo nests that failed due to parasitism were substantially lower in more distant sites. Although the explanation for this finding remains unclear, the possibility that it was due to undetected patterns of nest predation raises an important management concern: because nest predation is also an important cause of nesting failure for most songbird species (Martin 1992), managers need to consider the relative importance of nest predation when estimating how cowbird management techniques will affect host nesting success. For example, high parasitism rates may minimally influence host nesting success in areas where nest predation rates are also high, because most parasitized nests ultimately fail because of predation (e.g., Robinson 1992). Thus, efforts to reduce only parasitism rates in these sites may have little effect on host nesting success.

A key result of our research is to illustrate the potential extent of the gradient. Cowbird parasitism rates did not decline over hundreds of meters but rather over kilometers. This finding demonstrates that breeding cowbirds can access habitats at considerable distances from feeding sites, and it suggests that in some regions cowbird management efforts may need to occur at larger scales than previously proposed. For example, based on past radiotelemetry data, 7 km has often been used as an estimate of the maximum commuting distance of cowbirds (e.g., Gustafson & Crow 1994; Coker & Capen 1995). Yet, in our study area, predicted parasitism levels of vireo nests remained above 20% even when they occurred 10 km from active livestock grazing. Although it is unlikely that cowbirds commute these long distances in all regions, managers need to be aware of the potential commuting range of cowbirds. Further work is needed to verify the generality of parasitism gradients. Also, a better understanding of fine-scale factors, such as edge effects, breeding habitat preferences, and the influence of host densities, that may influence the form of these gradients is needed to help in the design of effective management strategies based on the manipulation of cowbird feeding habitats. This study should serve as a catalyst for more intensive investigations.

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