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# SCALE DEPENDENCE IN THE EFFECTS OF FOREST COVERAGE ON PARASITIZATION BY BROWN-HEADED COWBIRDS

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*Abstract.* Previous work has shown that the rate at which Brown-headed Cowbirds (*Molothrus ater*) parasitize forest nesting birds is affected by the proportion of a local landscape that is forested. However, much of the previous work has been restricted to a relatively small part of the cowbird's range, and has looked at forest coverage in very restricted areas around study plots. We used data from a wider geographical area, the entire width of the United States, and examined forest coverage in relatively large areas (10-km and 50-km radii) around study plots to determine if forest coverage is a generally useful statistic for predicting rates of brood parasitization. As was found in previous studies, we showed that increased amounts of forest coverage within 10 km of an area resulted in lower rates of parasitization by cowbirds. This pattern held not only among widely separated sites, but also within local clusters of study plots. However, we found that increased amounts of forest within 50 km of a study site resulted in slightly increased rates of parasitization in sites west of the Great Plains, contrary to previous research findings. Forest structure, as indicated by the relationship between forest coverage and other measures of forest distribution and abundance, differed across the United States. However, differences in forest structure were not obviously related to differences in the manner that parasitization and forest coverage covaried from east to west across the continent. Even given the variable patterns found, management for higher proportions of forest within 10-km radius areas should result in decreased rates of parasitization of host species; however, the impact of such a management strategy will vary across the continent.

*Key Words:* Brown-headed Cowbird, forest coverage, geographical variation, landscape structure, *Molothrus ater,* parasitization rate, scale.

Areas containing a greater proportion of forest have a lower abundance of Brown-headed Cowbirds (*Molothrus ater*) (Donovan et al. 1997, Donovan et al. in press, Tewksbury et al. 1998), and show a lower rate of parasitization of the nests of host species (Robinson et al. 1995b, Thompson et al. in press). The conclusion of this previous research is that larger proportions of forest, relative to all terrestrial habitats (the landscape), will result in a lower impact of Brown-headed Cowbirds on their hosts.

However, the majority of work relating forest coverage to rates of parasitization is from the eastern edge of the Great Plains (e.g., Robinson et al. 1995b, Donovan et al. 1997, Donovan et al. in press, Thompson et al. in press; but see Coker and Capen 1995, Tewksbury et al. 1998 for exceptions). We might expect the relationship between forest coverage and parasitization to differ away from the Midwest for a number of reasons. Variation in cowbird abundance may not only affect absolute rates of parasitization (Thompson et al. in press), but also the pattern of variation in parasitization rate with varying forest coverage. Cowbirds in different parts of the continent encounter communities of hosts with different lengths of exposure (e.g., Mayfield 1965) and responses (e.g., Briskie et al. 1992) to parasitization, and host species with longer exposure to cowbirds may be resistant to parasitization regardless of the proportion of forest in a landscape.

Geographical variation in the relationship between forest coverage and parasitization rate also may result because of geographical differences in the pattern of forest in a landscape. Cowbirds may respond to the amount of edge (Gates and Gysel 1978, Brittingham and Temple 1983, Thompson et al. in press), distance from foraging sites (Donovan et al. in press), or other features correlated with forest coverage. Within a region, the proportion of forest in a landscape may correlate well with measures such as the amount of edge (Robinson et al. 1995b). However, land-use practices and topography vary across the continent, such that the relationship between forest coverage and features such as edge may vary across the continent.

The relationship between cowbird parasitiza-

* Ordering of names of authors subsequent to T. E. Martin determined using a random number generator.

tion and forest coverage may vary as a function of the local area over which forests were measured, in addition to varying among widely separate regions of the continent. Research relating forest coverage to rates of cowbird parasitization initially examined effects of variation in the size of individual forest patches and distance from forest edges (e.g., Paton 1994), and only recently has looked at local landscapes around individual forest patches (e.g. Robinson et al, 1995b, Donovan et al. in press, Tewksbury et al. 1998). Within these local areas, forest coverage varied in its power to predict parasitization, depending on the size of the area over which forest coverage was measured (Donovan et al. in press, Tewksbury et al. 1998). However, it is still not clear whether the range of areas measured (up to 10-km radius) encompass those that give the best predictions of the rate of parasitization. Local variation in forest coverage may only affect the movements of individual cowbirds (functional responses). Better predictions of the rate of cowbird parasitization may be provided by measuring forest coverage over larger areas than previously considered, if forest coverage over larger regions predict the abundance of cowbirds (a numeric response) and rates of parasitization are better predicted by cowbird abundance than the behavior of individual cowbirds. Knowledge of the most appropriate scale on which to manage forest coverage is essential for informed decisions about land management.

Differences in forest coverage may not predict the same change in the rate of parasitization depending on whether the sites being compared are widely separated. To date, studies have looked at variation in cowbird abundance or parasitization in relation to either local (e.g., Tewksbury et al. 1998) or regional (e.g., Robinson et al. 1995b, Thompson et al. in press) variation in forest coverage, but not both simultaneously. It is still unclear whether parasitization rates vary with local differences in forest coverage in the same manner as they respond to differences in forest coverage among more widely spaced sites, because the proportion of forest in a local landscape may be highly correlated with the proportion of forest within a far wider region.

This paper examines four questions: (1) does the relationship between forest coverage and other measures of landscape structure (e.g., amount of edge, size of forest patches) vary across the continent? (2) do changes in forest coverage over small distances predict the same variation in parasitization rates as changes in forest coverage among sites more widely separated? (3) does the relationship between forest coverage and cowbird parasitization vary with the size of the region over which forest coverage is measured? and (4) does the relationship between forest coverage and parasitization differ among the eastern, central, and western United States? In conducting our analyses, we had no prior expectations of the patterns that would emerge. Our goal was to document patterns that could affect the way land managers use the previously described pattern of lower cowbird parasitization in areas containing a higher proportion of forested land.

## METHODS

The data on parasitization rates of forest birds come from the Breeding Biology Research and Monitoring Database (BBIRD), with data from 23,448 individual nests being represented in our analyses. BBIRD is a collaborative project in which researchers across the United States have monitored nests and recorded data following a standardized protocol (Martin et al. 1997). There were 26 study sites (Fig. 1) on which the nesting success of forest-nesting birds was monitored. Data from five sites were previously used in the analyses of Robinson et al. (1995b). Each study site included 2 to 31 separate study plots (median = 9), with a total of 366 study plots in the data set. The spatial arrangement of study plots into local groups (termed "study sites") allowed us to contrast the effects of local (within tens of kilometers), and large-scale (across hundreds of kilometers) variation in forest coverage. This comparison was made by examining the relationship between forest coverage and the rate of parasitization both within study sites and among study sites.

The data obtained from each study plot were the proportion of nests containing cowbird eggs or young; potential hosts were only included when at least one nest of a species was recorded as having been parasitized in our database. Proportions were calculated across all species of hosts combined. Roughly 75% of all variance in the rate of parasitization occurred among plots within individual study sites (calculated following Sokal and Rohlf [1981:216]; we excluded data from sites on which cowbirds were not present). Given the high proportion of variance in parasitization rate that occurred within individual sites, we treated each of the study plots as an independent data point; i.e., we treated the data from each study plot as independent estimates of the rate of parasitization within the area that encompassed the separate study plots that compose a site.

The data on landscape structure came from an ARC/INFO GIS layer that was produced for the USDA Forest Service's Forest and Rangeland Renewable Resources Planning Act (RPA) 1993 Assessment Update (Anonymous no date). Data

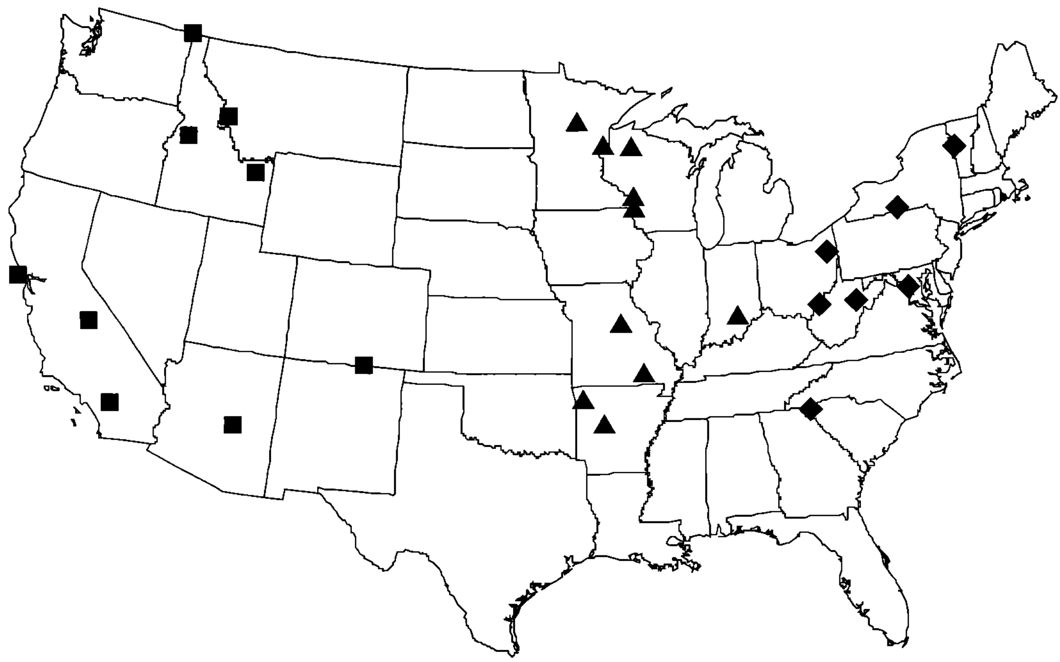

FIGURE 1. Locations of study sites. Diamond-shaped points indicate sites designated as "eastern", triangles as "Midwestern", and squares as "western". Each site plotted on this map is composed of several independent study plots.

were derived from NOAA satellite images (AVHRR data), with the Forest Service project being completed at the end of 1992. The finest resolution of the GIS layer is a 1 km square that is classified as either water, non-forest, or forest; within forested areas the type of forest was specified as one of 22 types (e.g., oak-hickory, pinyon-juniper). The relatively coarse resolution of the GIS layer placed constraints on our use and interpretation of the data on forest coverage. Each one of the 1-km squares could easily represent multiple patches of forest, detail that would be lost from our analyses. Additionally, our circles were approximate, with edge pixels from the GIS layer being included within a "circle" if >50% of that pixel was included within the circle. Because of the coarse resolution of the GIS layer, we used circles of 10-km radius (over 300 $km^2$) as the minimum area in which forest coverage was measured. We made this decision in order to average measurement errors caused by individual pixels in the GIS layer containing fractions of both forested and non-forested land. However, in interpreting our results, we do not know what fraction of the unexplained variance in parasitization rates was caused by variation in the spatial arrangement of forest at a resolution finer than was provided by our GIS layer.

Statistics describing landscape structure were obtained using FRAGSTATS (McGarigal and Marks 1995). The areas in which landscape structure was described were circles of 10-km and 50-km radius surrounding each study plot. The 10-km radius, chosen to allow comparison with Robinson et al. (1995b), was based on observations of distances that female cowbirds fly between feeding and nesting areas in the Midwest (Thompson 1994). Although female cowbirds have also been found flying distances of under 10 km in California (Rothstein et al. 1984), work in New Mexico (C. B. Goguen and D. R. Curson, unpubl. data) has found female cowbirds flying in excess of 10 km between foraging and nesting sites. Thus landscape structure further than 10 km from study plots can potentially affect cowbirds' presence and abundance. Fifty km was arbitrarily chosen to represent larger spatial scales. The circles of 50-km radius contain 25 times the surface area as the 10-km circles and roughly 9 times greater area than was used in any previous study examining effects of forest coverage on cowbird abundance (Donovan et al. 1997). We did not use data from 50-km circles in comparisons of the rate of parasitization within study sites, because within individual study sites the study plots were often so closely spaced that 50-km forest coverage were essentially identical among the plots within a single study site. In analyses examining presence and absence of parasitization among study sites, forest coverage for each site was calculated as the weighted average forest coverage around each study plot. Forest coverages were weighted by the proportion of a site's potential hosts that were found on each plot.

The proportion of a landscape in forest was used as the primary measure of landscape structure in this paper following the conventions of previous studies (e.g., Robinson et al. 1995b). However, other metrics generated by FRAGSTATS were also collated for each study plot: size of largest patch (as a proportion of the landscape), number of forest patches, mean size of forest patches, standard deviation in patch size, edge density (m/ha of edge), and the number of types of forest. Some of these metrics require further explanation because our FRAGSTATS calculations were done separately for each of the types of forest recognized in the original data set. As a result, we calculated edge density as the amount of non-forest edge, assuming that most non-forest edges were with forest. Additionally, the largest patch of forest in a landscape may be contiguous with other areas of forest of a different type, and the number of patches may not represent the actual number of discrete units of forest because patches of one type of forest may be nested within another type of forest. Still, these metrics represent some aspects of the spatial complexity of a landscape. Mean and standard deviation of patch size were calculated by decomposing the mean and SD for each forest type into sums and sums of squares and then calculating an overall mean and SD by combining this information across forest types.

Analyses relating parasitization rates to forest coverage were of two types: those examining whether variation in forest coverage affected whether any nests were parasitized, and those examining variation in the rate of parasitization given that at least some nests were parasitized. The former analyses concerned the presence or absence of parasitization, and we tested for patterns using logistic regression. For the latter analyses we used generalized linear models, and excluded sites on which no parasitization was found. Plots varied in the number of nests monitored, and thus the accuracy of our estimates of parasitization rates also varied. This varying accuracy was taken into account in our analyses by weighting each data point by 1/SE of the estimated rate of parasitization, which resulted in greater importance being placed on those data that were estimated with the greatest accuracy. In all analyses, continent-wide geographical variation in patterns were examined by dividing study sites into three regions (Fig. 1): west of the Great Plains, Midwest (eastern edge of the Great Plains), and east. Data were also divided into two categories, east or west of the Great Plains, to test if better predictions were made when two or three regions were used in analyses.

Data from all sites were used simultaneously in analyses that tested for variation in parasitization rate within individual sites. To use data from all sites in a single analysis, we standardized forest coverages and rates of parasitization to have a mean value of zero within each group of study plots. This standardizing eliminated overall differences in forest coverage and rate of parasitization among these sites, and thus analyses of within-site variation exclusively examine variation relative to the average parasitization rate and forest coverage for a site. Forest coverages used in this analysis were within a 10-km radius of each study.

All statistical analyses were conducted using SPSS 7 (SPSS 1996). We refer to results from statistical tests as being "statistically significant" when $P \leq 0.05$. However, because statistical significance is not necessarily an indication of biological reality or importance (e.g., Thomas 1997), we have also noted instances in which the results of statistical tests approached but did not meet the arbitrary criterion of $P = 0.05$. In these instances, we have presented confidence limits (e.g., Greenland 1988, Steidl et al 1997, Thomas 1997) around parameters estimated in the analyses as a more refined indication of the potential biological significance of results.

## RESULTS

Our results are divided into three sections. First, we examined landscape structure to show that landscape structure differed across the continent. These differences could provide a biological explanation for differences in the relationship between forest coverage and rates of cowbird parasitization across the continent. The second set of analyses examined whether variation in forest coverage was associated with the presence or absence of cowbird parasitization in a study area. Finally, where cowbirds were present, we show how the rate at which nests were parasitized was associated with forest coverage. These last two sets of analyses tested for geographical variation in parasitization rates, as well as for differences in the predicted effects of forest coverage that resulted from varying the area over which forest coverage was measured.

We examined the relationship between forest coverage and parasitization rates, both within local clusters of study plots and among widely separated study areas. The within-site analyses

TABLE 1. VARIATION IN LANDSCAPE STRUCTURE ALONG A GRADIENT OF FOREST COVER (10 KM SCALE). RESULTS ARE FROM GENERALIZED LINEAR MODELS

| Forest metric | % Forest (10 km) | | | Region | | | Interaction[c] | | | $R^2$ |
|---|---|---|---|---|---|---|---|---|---|---|
| | β | SE | P | β | SE | P | β | SE | P | |
| % Forest (50 km) | 0.630 | 0.046 | <0.001 | 6.736[a]<br>−17.068[b] | 5.860<br>4.358 | <0.001 | −0.096[a]<br>0.217[b] | 0.075<br>0.059 | <0.001 | 0.74 |
| # Forest Types | 0.028 | 0.004 | <0.001 | −1.703[a]<br>1.185[b] | 0.451<br>0.335 | <0.001 | 0.00915[a]<br>−0.0230[b] | 0.006<br>0.005 | <0.001 | 0.35 |
| # Forest Patches | 0.196 | 0.038 | <0.001 | −4.775[a]<br>19.971[b] | 4.732<br>3.513 | <0.001 | −0.00219[a]<br>−0.262[b] | 0.061<br>0.048 | <0.001 | 0.18 |
| Mean Patch Size (ha) | 12.131 | 13.713 | 0.001 | −36.895[a]<br>−521.68[b] | 1687.8<br>1253.1 | 0.899 | 31.379[a]<br>11.016[b] | 21.795<br>17.212 | 0.354 | 0.12 |
| SD Patch Size (ha) | 30.978 | 7.721 | <0.001 | 640.56[a]<br>−1547.6[b] | 950.3<br>705.6 | 0.014 | 8.117[a]<br>30.363[b] | 12.272<br>9.691 | 0.005 | 0.38 |
| Edge Density (m/ha) | 0.121<br>−0.001[d] | 0.012<br>0.000 | <0.001<br><0.001 | 4.496[a]<br>3.588[b] | 0.447<br>0.335 | <0.001 | −0.0467[a]<br>−0.0473[b] | 0.006<br>0.005 | <0.001 | 0.73 |
| Max. Patch Size (%) | 0.450 | 0.055 | <0.001 | −8.296[a]<br>−16.447[b] | 6.553<br>4.866 | 0.003 | 0.330[a]<br>0.328[b] | 0.085<br>0.067 | <0.001 | 0.71 |

[a] Regression coefficients for eastern sites (see Fig. 1).
[b] Regression coefficients for sites from the Midwest. Coefficients for western sites were set to zero in the analysis.
[c] Statistical interaction between % Forest and Region.
[d] Coefficient for quadratic term of the regression.

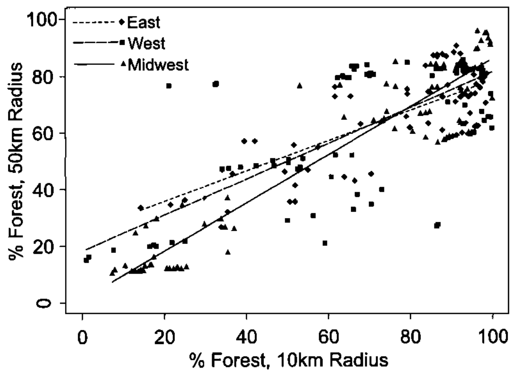


FIGURE 2. Relationship of forest coverage measured on different scales for the same study plots. Regression coefficients are given in Table 1. Regions noted in the legend correspond to those shown in Fig. 1.

were used to determine whether parasitization varied with local variation in landscape structure, whereas the among-site analyses show whether parasitization rates varied with differences in average forest coverage among widely separated regions.

## RELATIONSHIPS AMONG FOREST METRICS

Measuring forest coverage at one scale predicts forest coverage at other scales, but the statistical relationships differed among geographical regions across the continent (Table 1). Low forest coverages, measured within 10-km radii of study plots, indicated even lower proportions of forest within 50 km in the Midwest than in either eastern or western landscapes (Fig. 2).

The relationship between forest coverage and most of the other measures of landscape structure that we compiled also differed across the United States. The only exception was mean size of forest patches; as the proportion of forest in the landscape increased, the mean size of forest patches increased consistently across the United States. Edge density was always highest at intermediate levels of forest coverage, and for a given amount of forest cover the amount of edge was highest in eastern forests and lowest in western forests (Fig. 3).

All other forest metrics varied linearly with increasing forest coverage, and the patterns were typically that landscapes with greater forest coverage also contained a larger number of forest types, larger size for the biggest forest patch, greater variation in patch size, and greater number of forest patches (Table 1). The one exception was for numbers of forest patches; in eastern and western sites greater forest coverage meant a larger number of patches, but in the Midwest greater forest coverage meant fewer

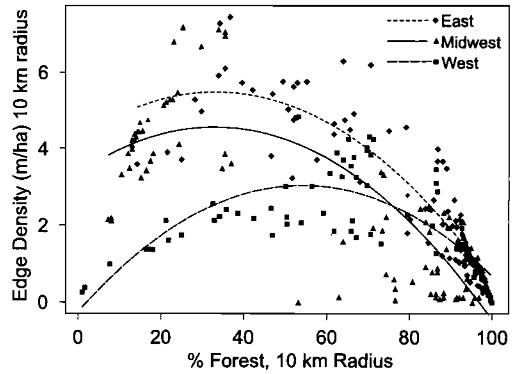


FIGURE 3. Relationship between forest coverage and edge density in different regions. Regions noted in the legend correspond to those shown in Fig. 1.

patches. This relationship at least partially resulted from different types of forest being treated as separate patches, in combination with the number of forest types remaining relatively unchanged with increased forest coverage in the Midwest (Table 1).

### Forest Coverage and Presence of Cowbird Parasitization

We found no indication that local variation in forest coverage affected the presence or absence of cowbird parasitization on a given study plot. Twelve of 26 sites had plots both with and without detected cowbird parasitization. For each of these 12 sites, we determined whether increased forest coverage (measured within a 10-km radius of each study plot) resulted in a change in the probability of finding cowbird eggs or nestlings. No single regression was statistically significant (range $P = 0.11$ to $P = 0.99$), which may reflect the low statistical power resulting from the small number ($N = 5$–$31$) of data points in each analysis.

Further, we also found no indication of an effect even when results from individual analyses were combined in a meta-analysis. The meta-analysis used the regression coefficients from the individual logistic regressions as data points. Each regression coefficient was weighted by 1/SE of the coefficient, meaning that the coefficients that were estimated more precisely were given greater importance in the analysis. These weighted regression coefficients were used in a 1-sample t-test to determine if on average greater forest coverage lead to a greater or lower probability of detection of parasitization on study plots. The results of the meta-analysis were not significant ($P = 0.64$, df = 11, weighted mean regression coefficient = $-0.0121 \pm 0.025$ SE), again indicating that when cowbirds were present in a region (i.e., at least one nest was parasitized on a study plot within a site) they did not avoid parasitizing nests on specific study plots in relation to local variation in forest coverage.

Sites with greater forest coverage tended to have a lower chance of cowbird parasitization, although the pattern only approached statistical significance (Table 2). For this analysis each of the separate study sites was treated as a single data point. The probability of detecting cowbird parasitization was not significantly affected by forest coverage on either scale of measurement (10-km or 50-km radii; Table 2). However, confidence limits around the regression coefficients showed a 95.3% probability that increased forest coverage within 10 km of study plots resulted in a decreased likelihood of cowbird parasitization at that site. Confidence limits also indicated a 92.7% probability that sites east of the Great Plains were less likely to have any cowbird parasitization.

### Forest Coverage and the Rate of Parasitization

Although we found some evidence that forest coverage affected the presence or absence of cowbird parasitization (above), we found more consistent evidence that the proportion of nests that were parasitized was related to forest coverage. Hosts were parasitized at lower rates when there was greater forest coverage, in comparisons both among study plots within the same study site and among widely separate study sites.

We examined the effects of local variation in forest coverage on the rate of brood parasitiza-

TABLE 2. Variation in Forest Coverage, and Presence or Absence of Cowbird Parasitization. Results Are From Logistic Regressions

| | % Forest | | | Region[a] | | |
|---|---|---|---|---|---|---|
| Scale, forest coverage | β | SE | P | β | SE | P |
| 10-km radius | −0.055 | 0.033 | 0.09 | 1.55 | 1.07 | 0.15 |
| 50-km radius | −0.0088 | 0.019 | 0.64 | 1.33 | 0.93 | 0.64 |

[a] Denotes whether sites were east or west of the Great Plains; results were similarly non-significant when data were divided into east, Midwest, and west. Regression coefficient is for data east of Great Plains; regression coefficient for west of Great Plains is zero.

TABLE 3. VARIATION IN FOREST COVERAGE AND THE PROPORTION OF NESTS PARASITIZED. RESULTS ARE FROM GENERALIZED LINEAR MODELS

| | % Forest | | | Region | | | Interaction[c] | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Test | β | SE | P | β | SE | P | β | SE | P | $R^2$ |
| Within Site (10 km) | −0.00099 | 0.0003 | <0.001 | −0.011[a]<br>−0.004[b] | 0.013<br>0.010 | 0.71 | | | | 0.08 |
| Among Site (10 km) | −0.00054 | 0.0003 | 0.001 | 0.235[a]<br>−0.004[b] | 0.070<br>0.038 | 0.003 | −0.0020[a]<br>0.0004[b] | 0.001<br>0.001 | 0.031 | 0.13 |
| Among Site (50 km) | 0.0014 | 0.0005 | 0.082 | 0.317[a]<br>0.103[b] | 0.079<br>0.036 | <0.001 | −0.0046[a]<br>−0.0019[b] | 0.001<br>0.0007 | <0.001 | 0.16 |

[a] Regression coefficients for eastern sites (see Fig. 1).
[b] Regression coefficients for sites from the Midwest. Coefficients for western sites were set to zero in the analysis.
[c] Statistical interaction between % Forest and Region.

tion by comparing forest coverage and the rate of parasitization among study plots within the same study site. A 10% increase in forest coverage was predicted to result in a roughly 1% decrease in the proportion of nests that were parasitized (Table 3). This effect did not vary across the continent, either when sites were divided as east or west of the Great Plains, or east, Midwest, and west. We added forest coverage as a quadratic term to the statistical model to test for non-linear relationships between forest coverage and parasitization rate. No quadratic effect approached statistical significance, and we conclude that non-linearity in the relationship was minimal.

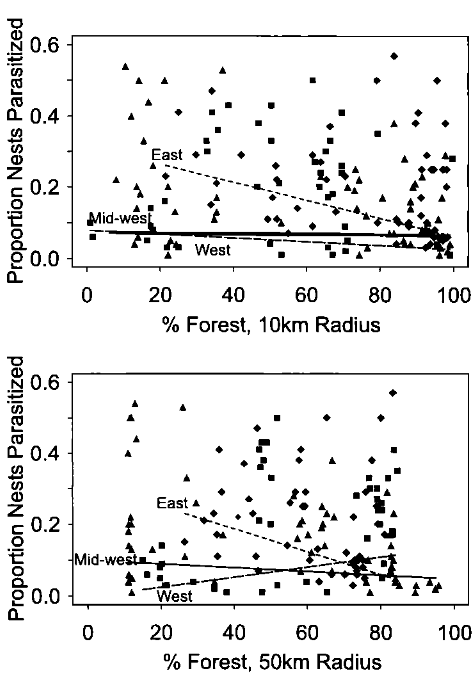


FIGURE 4. Variation in the rate of parasitization of nests as a function of forest coverage. Different point and line styles correspond to the legends in Figs. 2, 3.

Both forest coverage and geographical location affected the rate of parasitization in comparisons among widely separate regions; additionally, the effect of forest coverage varied with the scale at which forest coverage was measured (Table 3). The typical pattern was as expected: the rate of parasitization was lower with increased forest coverage. However, an increase in parasitization with increased forest coverage was found from sites west of the Great Plains, but only when forest coverages were measured within 50-km radii of study plots (Table 3, Fig. 4). Confidence intervals around this regression coefficient indicate that there was only a 0.4% chance that the true pattern was for parasitization to be lower in areas of higher forest coverage. Regression models better fit the data when study sites were divided into 3 regions than when only categorized as being either east or west of the Great Plains. When forest coverage was added as a quadratic term to the models, the goodness of fit of regressions was identical or improved over the relationships given in Table 3. However, the qualitative patterns shown in Fig. 4 remained unchanged.

The magnitude of the effect of forest coverage on parasitization rate (i.e., slope of the regression) was greater when differences in forest coverage were measured among widely separated sites; however, this result was not robust. Within a given geographical region, the slopes of the within- and among-site regressions were within 2 SE (a roughly 95% confidence interval) of each other, with confidence intervals calculated assuming that the main and interaction effects in the among-site analyses were independent. To further test for differences within and among sites, we calculated separate regressions for each geographic region, both within and among sites; in this case, regression coefficients within a region all overlapped in confidence limits of 1 SE (roughly 68% confidence limits).

## DISCUSSION

Generally, we found that rates of parasitization were lower in areas of greater forest coverage (Fig. 4), as previously described (Robinson et al. 1995b, Donovan et al. in press, Tewksbury et al. 1998). This pattern was perhaps minimally due to increased forest coverage tending to result in a lower probability of any cowbird parasitization (Table 2). However, the clearer effect was a statistically significant decrease in the proportion of nests parasitized with increasing forest coverage (Table 3, Fig. 4). The relationship between greater forest coverage and lower rates of parasitization held regardless of whether we examined variation in forest coverage among plots within a local area or among widely separated study sites (Table 3). The presence of a relationship between forest coverage and parasitization rate, even within single study sites, suggests that behavioral decisions of individual cowbirds were at least partially responsible for the larger-scale variation in parasitization rate previously found (e.g., Robinson et al. 1995b).

However, the generalization that lower rates of parasitization are associated with a greater proportion of forest is not universal; greater rates of parasitization were found in areas of greater forest coverage in sites west of the Great Plains (Fig. 4, bottom panel) when forest coverage was measured within a 50-km radius of study plots. We suspect that traits other than landscape structure, such as human land-use practices (e.g., Tewksbury et al. 1998) may be responsible for our findings (Fig. 4, bottom panel). This result was not an artifact of a narrower range of forest coverages from the western sites (Fig. 4), nor did data from a single site create the pattern. Although landscape structure varied with changes in forest coverage across the continent (Table 1; Figs. 2, 3), we found no traits for which western forests differed qualitatively from both eastern and mid-western forests. Hence, we do not think that our results (Fig. 4) were due to differences in landscape structure east and west of the Great Plains. Neither are we aware of any substantial differences in the behavior and habitat requirements among the races of Brown-headed Cowbird (Lowther 1993). We also do not think that our results (Fig. 4) were an artifact of combining data from all host species into a single measure of parasitization, because an artifact of differing species composition would be manifested at both scales of measurement of forest coverage (top and bottom panels of Fig. 4). Finally, although cowbird abundance declined westward, away from the center of the cowbird's range (Thompson et al. in press), the lower abundance of cowbirds in the west should simply lower the rate of parasitization but not cause a completely opposite response of parasitization rate to variation in forest coverage.

Our results indicate that the predicted rate of parasitization can be affected by the area over which forest coverage is measured (Table 3; Fig. 4, compare top and bottom panels). Previous work (Donovan et al. in press, Tewksbury et al. 1998) has shown that some scales of measuring forest coverage provide better predictions of the rate of parasitization than other scales. Our results indicate that not only the goodness of fit (measured as a correlation), but the actual predicted rates of parasitization (regression intercept and slope) were dependent on the scale at which forest coverage was measured (Table 3). However, we were not able to estimate the effects of variation in forest coverage on parasitization with great accuracy. The 95% confidence limits around the effect of forest coverage (10-km radius) in the eastern U.S. (Table 3) showed that the estimated effect could be somewhere within a 35-fold range of values! If this variation is due to insufficient sampling, the variation is probably sufficiently large to make the current estimates unsuitable for attempts to model (i.e., Hilborn and Mangel 1997, Starfield 1997) the demographic consequences to host species of modifying forest coverage. If the variation is biologically real, then our results indicate that relying on measurement of forest coverage to accurately predict rates of parasitization is probably not a fruitful endeavor.

The low accuracy of estimates is an indication that forest coverage explains only a small fraction of variation in the rate of parasitization (Table 3). As noted above, roughly 75% of all variance in the rate of parasitization was within local clusters of study plots, even though less than 23% of all variance in forest coverage was found among study plots within these same local clusters. While some of the within-site variance in the rate of parasitization was due to sampling error, variation in species composition of hosts among plots, and other random effects, we feel that the importance of non-forest landscape features (e.g., Tewksbury et al. 1998) should not be underestimated. One known reason is the need by female cowbirds to have both feeding sites and breeding areas in close proximity (Rothstein et al 1984, Thompson 1994, Donovan et al. in press), and feeding sites are often human-related features of landscapes (Verner and Ritter 1983, Airola 1986).

The one consistent finding of this study was that lower rates of parasitization of host species occurred with greater forest coverage within 10 km of a location, a result that held in spite of the different communities of hosts and their histories of exposure to cowbirds (Mayfield 1965) from east to west across the continent. This consistent result suggests that management for greater forest coverage even over relatively small spatial extents can decrease rates of brood parasitization. However, managers should realize that variation in forest coverage may show qualitatively different relationships with the rate of parasitization across the continent (Table 3, Fig. 4). The most extreme case was the sites from west of the Great Plains (Fig. 4), but we feel that data from additional sites are needed to substantiate the relationship between larger scale (50-km radius) forest coverage and rates of parasitization that we have found.

Nevertheless, it is clear that patterns found in one part of the continent should not be blindly extrapolated to other regions. Managers should also be aware that non-forest features such as feeding sites can play an important role in determining the rate of parasitization by cowbirds in a region (e.g., Airola 1986, Tewksbury et al. 1998, Thompson et al. in press). The effects of non-forest features should be carefully examined if demographic modeling is to be a useful part of a research and management strategy (e.g., Starfield 1997), because the effects of forest coverage alone on rates of parasitization are variable enough that accurate predictions of parasitization rate were not possible, even with a data set as large as was available for this study.

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