

Modeling the effects of forest harvesting on landscape structure and the spatial distribution of cowbird brood parasitism

Eric J. Gustafson¹ and Thomas R. Crow²

¹ North Central Forest Experiment Station, 1158 Entomology Building Room 220, Purdue University, W. Lafayette, IN 47907-1158, USA; ² North Central Forest Experiment Station, P.O. Box 898, Rhinelander, WI 54501, USA

Keywords: Spatial pattern, timber harvest, clearcutting, GIS model, habitat fragmentation, forest interior, forest edge, brown-headed cowbird, brood parasitism, neotropical migratory birds

Abstract

Timber harvesting affects both composition and structure of the landscape and has important consequences for organisms using forest habitats. A timber harvest allocation model was constructed that allows the input of specific rules to allocate forest stands for clearcutting to generate landscape patterns reflecting the "look and feel" of managed landscapes. Various harvest strategies were simulated on four 237 km² study areas in Indiana, USA. For each study area, the model was applied to simulate 80 years of management activity. The resulting landscape spatial patterns were quantified using a suite of landscape pattern metrics and plotted as a function of mean harvest size and total area of forest harvested per decade to produce response surfaces. When the mean clearcut size was 1 ha, the area of forest interior remaining on the landscape was dramatically reduced and the amount of forest edge on the landscape increased dramatically. The potential consequences of the patterns produced by the model were assessed for a generalized neotropical migrant forest bird using a GIS model that generates maps showing the spatial distribution of the relative vulnerability of forest birds to brood parasitism by brown-headed cowbirds. The model incorporates the location and relative quality of cowbird feeding sites, and the relation between parasitism rates and distance of forest from edge. The response surface relating mean harvest size and total area harvested to the mean value of vulnerability to cowbird brood parasitism had a shape similar to the response surfaces showing forest edge. The results of our study suggest that it is more difficult to maintain large contiguous blocks of undisturbed forest interior when harvests are small and dispersed, especially when producing high timber volumes is a management goal. The application of the cowbird model to landscapes managed under different strategies could help managers in deciding where harvest activity will produce the least negative impact on breeding forest birds.

Introduction

Timber harvesting affects both composition and structure of the landscape and thus it has important consequences for organisms using forest habitats (Thompson *et al.* 1993). For example, forest interior conditions are thought to be important for many forest interior species (Karr 1982; Askins *et al.* 1987; Temple and Cary 1988), and the distribution,

size and shape of harvest operations such as clearcutting obviously impact the amount and location of the remaining forest interior (Franklin and Forman 1987; Ripple *et al.* 1991; Pearson *et al. in press*). Openings created by clearcutting produce edge conditions within the forest, producing a disruption in the continuity of forest interior habitat (*sensu* Lord and Norton 1990). Internal edges may have negative impacts on interior species by frag-

menting forest interior habitat and by providing improved habitat for generalist predators and brood parasites (Gates and Gysel 1978; Brittingham and Temple 1983; Kroodsma 1984; Small and Hunter 1988; Temple and Cary 1988). Fragmentation also has a temporal component. Sequential clearcutting in a landscape produces a mosaic of successional stages that may impact the development and persistence of avian communities (Freemark 1988; Crawford *et al.* 1981; Thompson *et al.* 1992).

Resource planners and managers rarely examine the long-term ecological consequences of specific management actions or compare the impacts of alternative management approaches in both a spatial and temporal context because they lack the analytical tools and basic scientific information to do so. Spatially-explicit models that incorporate change with time can help meet this challenge. We present such a model in this paper.

Recent studies of brood parasitism by brown-headed cowbirds (*Molothrus ater*) provide the information necessary to simulate the impacts of an "edge effect" under a variety of landscape conditions. The specific objectives of our study were: (1) to develop a model that simulates a range of forest harvest strategies in a spatially explicit way; (2) to examine the impact of variation in clearcut allocation rules on forest spatial structure over an extended time period; and (3) to assess the impacts of the simulated management strategies on the vulnerability of a generalized forest bird to brood parasitism by brown-headed cowbirds.

Methods

Timber harvest allocation model

A timber harvest allocation model was constructed that allows the input of specific rules to allocate forest stands for clearcutting to generate landscape patterns reflecting the "look and feel" of managed landscapes. The model is simplistic in that it does not attempt to optimize timber production or quality, nor does it predict the specific locations of future harvest activity. Instead, the model produces a stochastic implementation of broad management

strategies, and incorporates a number of features that allow simulation of decisions typically made by resource managers. In our study, we considered only harvests that produce openings within the forest. Harvest by single-tree selection was not modeled since such methods usually maintain an essentially closed canopy, and have been shown to produce little change in breeding bird populations (Crawford *et al.* 1981; Medin and Booth 1989).

The model was constructed to run within ERDAS (Erdas, Inc.) Geographic Information System (GIS) software using ERDAS Toolkit routines for input and output. ERDAS is a grid-cell (raster) GIS that allows flexible display and manipulation of digital maps. Timber harvest allocations are made by the model using a digital stand map, where grid-cell values reflect the age (in years) of each timber stand. The model allows control of the distribution of harvest sizes, where each clearcut has a size randomly drawn from a normal distribution whose mean and standard deviation are provided as input to the model. Other inputs to the model are the total area of forest to be harvested and the rotation length (as given by the minimum age on the input stand map where harvests may be allocated). The two algorithms included in the model for determining the spatial dispersion of allocations are random and clustered, where the number of allocations in a cluster is drawn from a normal distribution whose mean and standard deviation are provided by the user. The location of individual harvests are determined by randomly generating x and y coordinates and determining if that location is in a stand of an appropriate age for harvest. Clusters are allocated by generating the location of the first harvest, and then for subsequent harvests in the cluster, an x,y offset from the location of the first harvest in the cluster is randomly generated. The model also allows control of buffers to be left between harvests and between harvests and non-forest habitats. The model allocates pixels to a harvest by expanding in concentric layers from the single, randomly located pixel until the randomly generated size is achieved. The model prevents pixels from being allocated where the stand age is too young, or within buffer zones.

Table 1. Indices of pre-simulation landscape structure calculated for each study area. LRIV refers to the Lost River Unit, PRUN the Pleasant Run Unit, TELL, the Tell City Unit, and PARK, the Parke Co. study area.

Index	LRIV	PRUN	TELL	PARK
% forest	86.81	77.31	72.97	45.47
% short grasses	1.90	5.42	1.37	2.4
% tall grasses	3.16	6.57	9.10	14.33
% row crop	7.25	8.00	10.02	37.70
Linear forest edge (km)	1014.33	1078.35	1132.80	869.76
GISfrag (km) ^a	0.1755	0.1487	0.1254	0.0746
Total forest interior (ha) ^b	7470.63	5964.03	4773.78	2516.94
Mean interior block (ha) ^c	84.88	75.49	46.35	43.40
Vulnerability to cowbirds ^d	15.98	31.93	46.68	43.44

^a GISfrag (Ripple *et al.* 1991) is the mean distance of all pixels to the nearest forest opening.

^b Forest interior is here defined as forest pixels >210 m from the nearest forest edge.

^c Mean size of contiguous blocks of forest interior pixels.

^d Mean cowbird vulnerability value of all forest pixels on maps produced by the cowbird model.

Study areas and experimental design

Various harvest strategies were simulated on four 237 km² study areas, one in each of the Pleasant Run (PRUN), Lost River (LRIV), and Tell City (TELL) planning units, randomly selected from within 2 Ranger Districts of the Hoosier National Forest (HNF) in southern Indiana, USA, and one in a more agricultural landscape in Parke Co. (PARK), in west central Indiana. These study areas provided variation in proportion of forest, an important factor in determining landscape spatial pattern (Gustafson and Parker 1992). Digital land cover maps were produced from 2 Thematic Mapper images (April 12, 1986; April 26, 1988) classified with PC-ERDAS image processing software using supervised classification techniques (Lillesand and Kieffer 1987). Polygons were digitized at randomly selected locations on the HNF classification map (7966 points) and compared to reference data derived from color infra-red aerial photographs (1:40,000) taken in 1989. The overall classification accuracy was 92.0%, and the classification accuracy for forest was 97.4%. The Parke Co. map was evaluated using similar techniques (Gustafson *et al.* 1994), and had an overall classification accuracy of 96.0% and the classification accuracy for forest was 99.4%. Each study area contained varying proportions of forest and agricultur-

al land uses, and the spatial structure of the land cover in the study areas is summarized in Table 1.

The study areas were used as samples of existing landscapes within the region. Actual ownership boundaries were ignored, and the model was applied to these landscapes assuming that all forest was under single ownership and management, and that it consisted of a single, mature age class. For each study area, the model was applied to simulate 80 years of management activity. Each model run represented one decade of management activity, and after each model run the stand ages in the resulting stand age map were incremented by 10, simulating 10 years of forest growth. The process was repeated to simulate 80 years of forest growth and management (*i.e.*, a management run). Land use change (*i.e.*, conversion of forest to cropland) was not included in our simulations.

To determine the effect of variation in harvest size and total area harvested on the structure of the forest landscape, model parameters were varied as follows: (1) mean harvest size ranged from 1 and 100 ha, in 10 ha increments, with a standard deviation of 10% of the mean; and (2) total area harvested per decade varied between 0 and 8% of the forest area within each study area, in 1% increments. The rotation length was fixed at 70 years, so that only sites harvested in the first decade could be harvested again within a management run. These simulations

were conducted using the random dispersion and cluster dispersion algorithms, with a mean number of harvests per cluster of 7.0, and a standard deviation of 1.0. To avoid correlation among model runs, the random number generator was seeded using the computer system clock for each model run. Three replicates were simulated for each combination of harvest size and total area of forest harvested per decade.

The resulting landscape spatial structure was quantified using a suite of landscape pattern metrics. (1) The total area of forest interior was calculated for each management run by tabulating the total number of pixels >210 m from edge (Della-Salla and Rabe 1987; Andren and Angelstam 1988). Clearcuts > 50 years of age were considered to have returned to a closed-canopy condition that would support populations of most forest interior birds, and were not considered openings (Yahner and Wright 1985; Ratti and Reese 1988). Many forest interior bird densities reach normal densities in much younger stands (Thompson *et al.* 1992), but we used this conservative estimate in this study. (2) The total amount of forest edge was calculated by tabulating the number of forest pixels adjacent to an opening and multiplying by the width of a pixel. (3) The level of fragmentation and the production of forest edge was measured using the GIS-frag index of Ripple *et al.* (1991), which is the mean distance of all pixels to the nearest forest opening. Contagion (O'Neill *et al.* 1988), another commonly used index of spatial pattern, was not used because it did not satisfactorily quantify the interspersion of stand ages since each clearcut allocated was surrounded by a buffer of uncut forest, preventing clearcut pixels representing different ages from being adjacent to each other.

GIS model of vulnerability of forest birds to cowbird brood parasitism

The potential consequences of the patterns produced by the model were assessed for a generalized neotropical migrant forest bird (NTMB) using a GIS generated map showing the spatial distribution of the relative vulnerability of forest birds to

brood parasitism by brown-headed cowbirds. Rates of cowbird brood parasitism of forest bird nests are primarily influenced by the amount and type of open land habitats in the vicinity of the nest site (Brittingham and Temple 1983; Robinson 1992), and the distance of the nest site from the nearest forest edge (Brittingham and Temple 1983; Yahner and Scott 1988). The model was developed to predict the spatial distribution of cowbird parasitism rates from a land cover map.

The model incorporates two facets of cowbird biology. (1) Cowbird nest parasitism is generally limited to areas within up to 7 km of feeding sites (Rothstein *et al.* 1984), although average commuting distances are usually much less (Thompson *in press*; Robinson *et al.* 1993). (2) Cowbirds tend to search for host nests near the edges of forests, and often use openings within the forest as focal points to begin searches (Brittingham and Temple 1983). Since female cowbirds are territorial (Dufty 1982), sub-dominant females are driven further into the forest when cowbird population densities are relatively high (Robinson 1992).

Cowbird population densities are thought to be primarily limited by food resources, obtained mainly in agricultural and short vegetation (<15 cm) habitats. Thompson (*in press*) observed approximately 80% of feeding activity by radio-collared cowbirds in short-grass (grazed or mowed) habitats, 10% in tall grass and old field habitats, and 10% in row crops. To estimate a measure of relative cowbird density within commuting distance of each pixel on the land cover map, a circular moving window (radius = 2.5 km) was passed over each land cover map, and a weighted total of feeding habitat pixels within the window (f) was tabulated for each cell of the map, where the weights represent the relative value of each land cover as feeding habitat for cowbirds (short grass = 8, long grass = 1, row crop = 1). The value of f for each pixel was used as a surrogate for relative cowbird population density within 2.5 km of the pixel.

Also used was a GIS layer representing the distance of each forest pixel from the nearest forest edge. In the analyses of potential cowbird parasitism, only clearcuts ≤ 20 years old were assumed to function as openings for cowbirds searching for

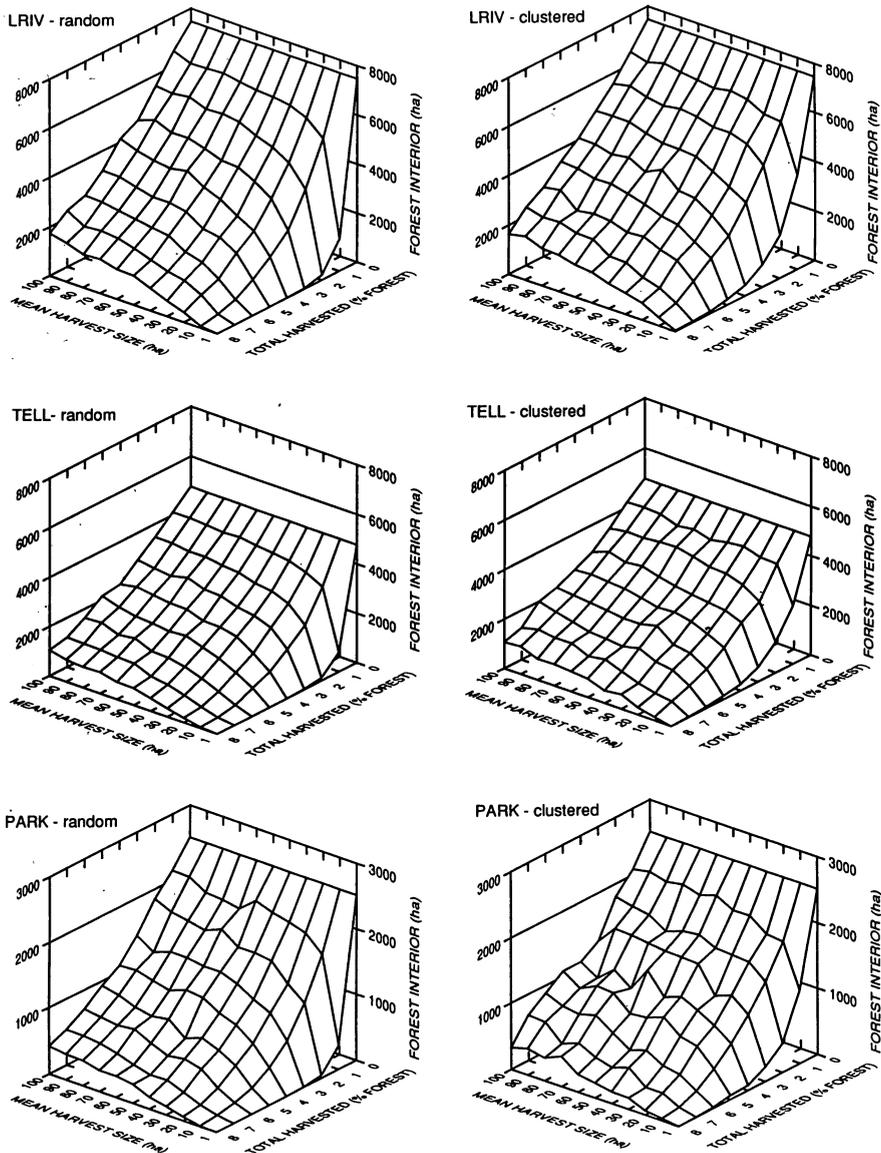


Fig. 1. Response surface showing the area of forest interior (> 210 m from an opening or forest stand < 50 years of age) as a function of mean clearcut size and total area of forest harvested per decade. The PRUN results are not shown, but were very similar to LRIV and TELL. Annotation indicates the study area and the spatial dispersion algorithm used.

host nests (F. Thompson, J. Probst *pers. comm*). A negative exponential function was derived from data collected in southern Wisconsin, USA, by Brittingham and Temple (1983) that measured the percent of forest bird nests parasitized by cowbirds as a function of the distance of the nests from the nearest forest edge. Maps whose pixel values represent the relative vulnerability (v) of forest birds to cowbird parasitism were produced by ap-

plying a function relating cowbird parasitism rates to the values in the 2 input layers. This value was calculated for each pixel by relating the weighted-total of feeding habitat value (f) and the distance (in meters) of the pixel from forest edge (d) by the following relationship:

$$v = f/f_{max} \cdot 10^{-0.00138(d)}$$

where f_{max} = the maximum possible weighted to-

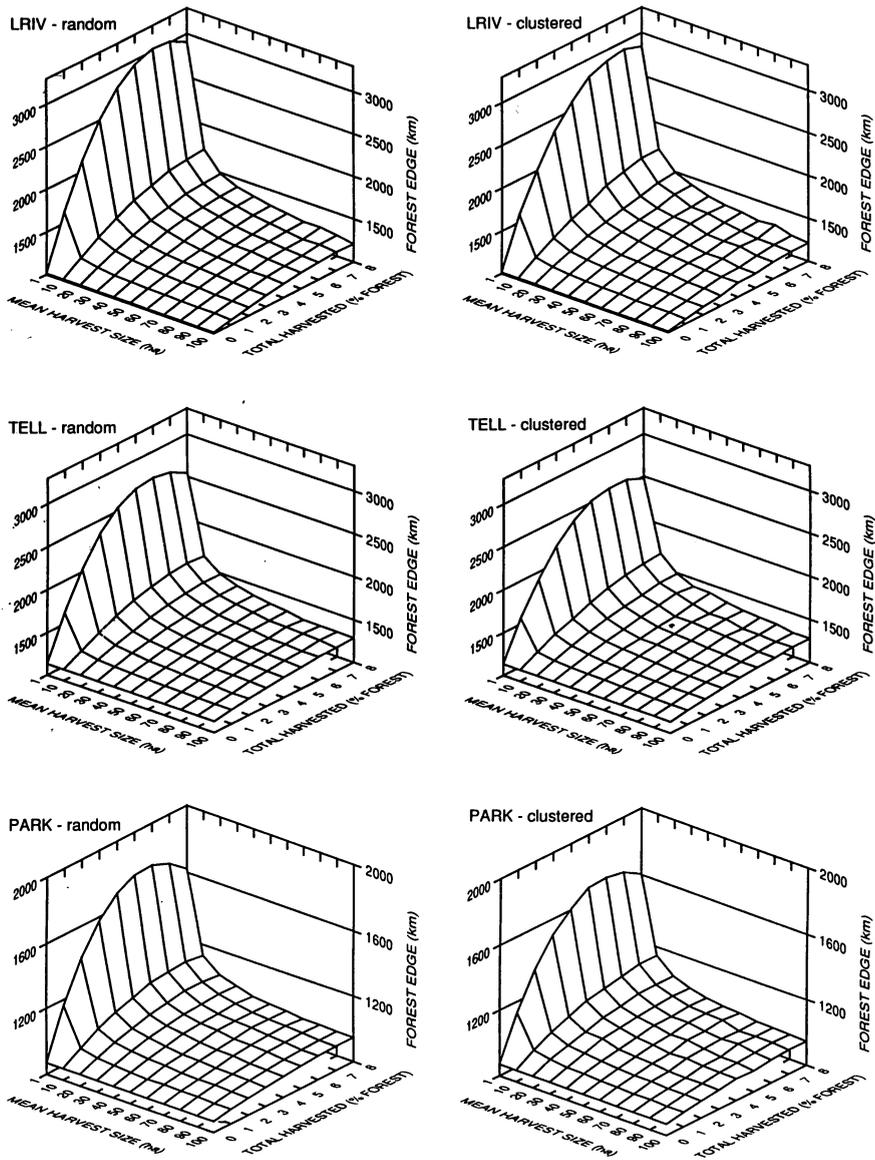


Fig. 2. Response surface showing the total length of forest edge (forest adjacent to an opening or forest stand < 50 years of age) as a function of mean clearcut size and total area of forest harvested per decade. The PRUN results are not shown, but were very similar to LRIV and TELL. Annotation indicates the study area and the spatial dispersion algorithm used.

tal (when all pixels within the window = 8,) and the constant was derived from Brittingham and Temple's (1983) data.

In forested landscapes, cowbirds are almost certainly limited by availability of feeding areas in agricultural habitats, and their numbers do not change in response to timber harvest (Thompson *et al.* 1992; Robinson *et al.* 1993). The model as formulated here assumes that cowbirds can respond in

an unlimited way to increases in edge. The model was used to assess changes in the spatial distribution of relative vulnerability to cowbird parasitism values produced by different patterns of openings.

The metrics of landscape spatial pattern were plotted against the harvest management parameters to produce response surfaces showing the effects of variation in management strategies. The maps of vulnerability of NTMBs to cowbird parasitism were

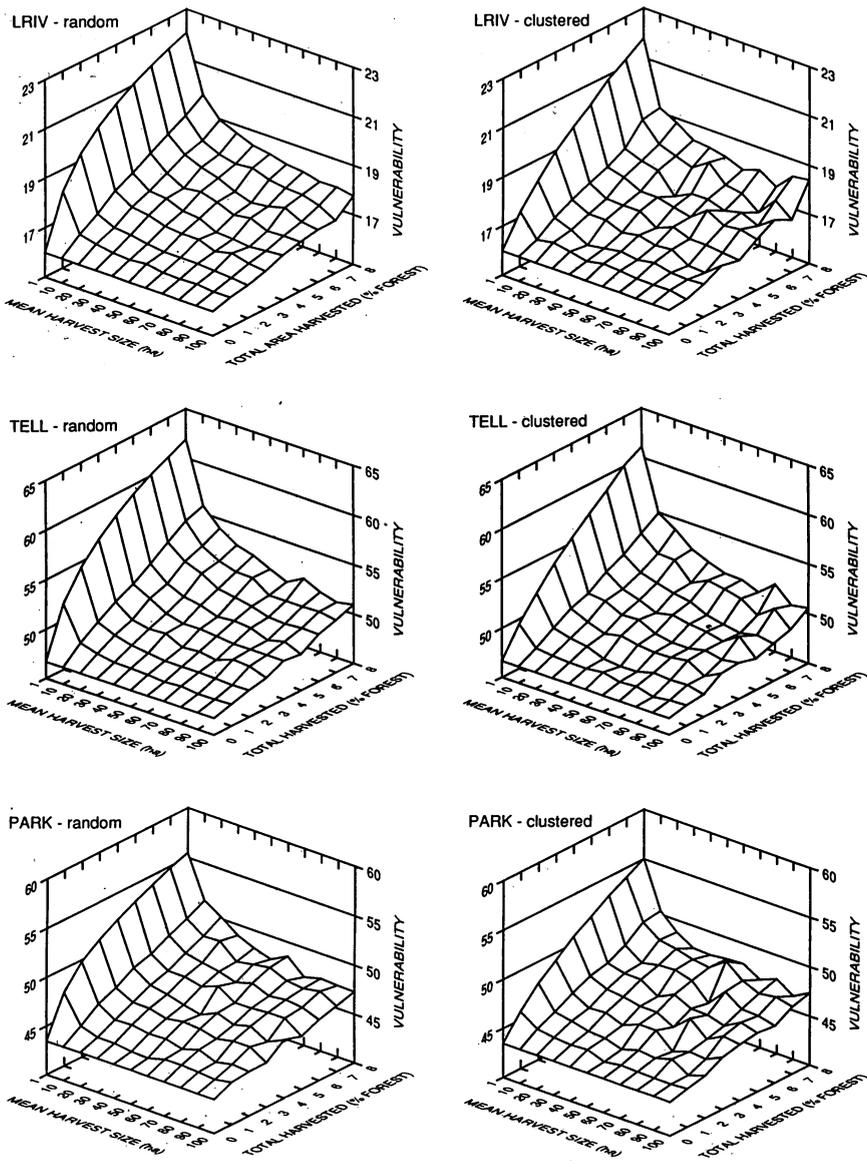


Fig. 3. Response surface showing the relative vulnerability of forest birds to cowbird brood parasitism as a function of mean clearcut size and total area of forest harvested per decade. Vulnerability is expressed as the mean value of all forest pixels on maps produced by the cowbird model. Higher values reflect a prediction by the model that cowbirds will parasitize a relatively higher proportion of forest bird nests across the landscape. The PRUN results are not shown, but were intermediate between LRIV and TELL. Annotation indicates the study area and the spatial dispersion algorithm used.

quantified by calculating the mean vulnerability value (\bar{v}) of all the forest pixels on each map and plotted to produce response surfaces.

Results

The area of forest interior remaining on the land-

scape was dramatically reduced when the mean clearcut size was 1 ha, even with low amounts of total harvest (Fig 1). Aggregating clearcuts produced a less marked decrease in forest interior when compared to a random dispersion of 1 ha cuts, but the difference became negligible as harvest size increased. Increased total area harvested produced

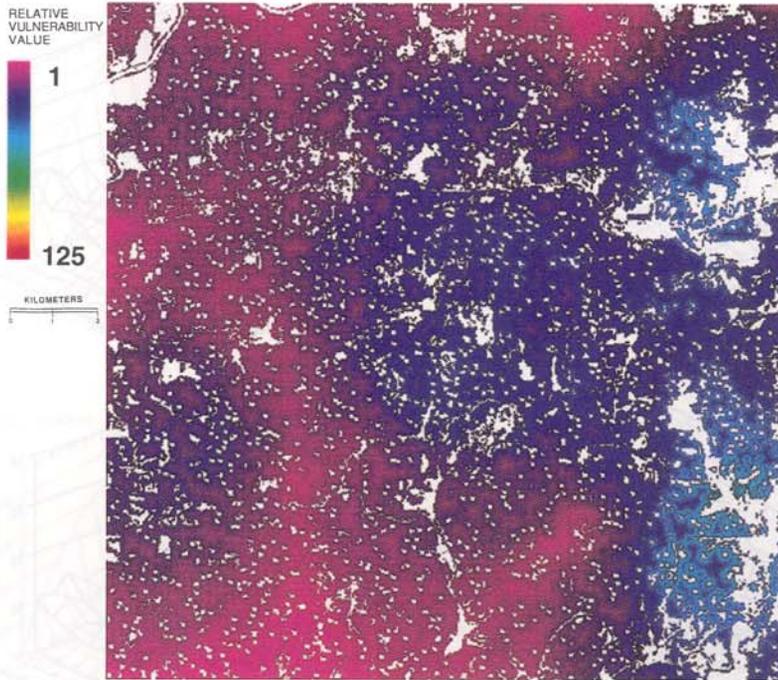


Fig. 4. Map of the spatial distribution of vulnerability to cowbird parasitism values in the Lost River Unit, when 3% of the forest was harvested per decade, using a mean harvest size of 1 ha and a random dispersion of clearcuts.

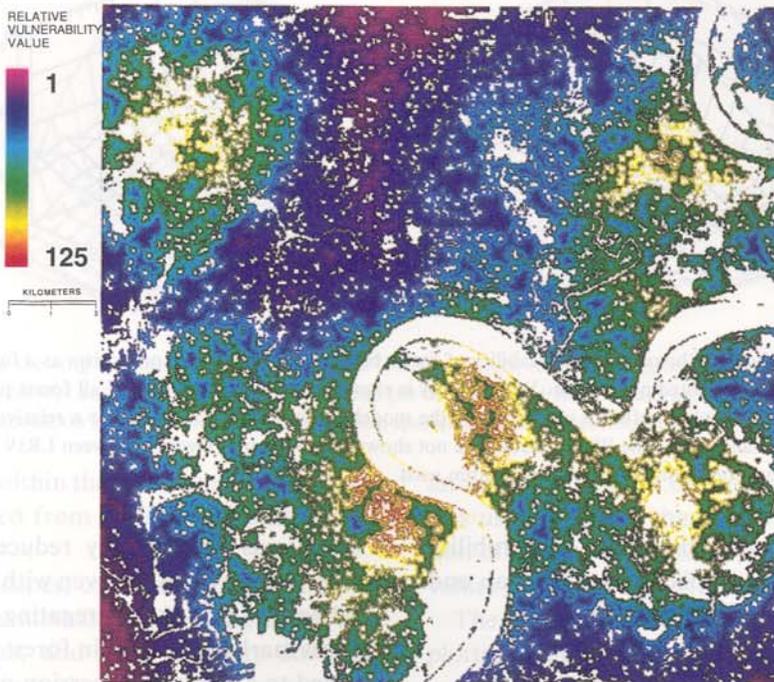


Fig. 5. Map of the spatial distribution of vulnerability to cowbird parasitism values in the Tell City Unit, when 3% of the forest was harvested per decade, using a mean harvest size of 1 ha and a random dispersion of clearcuts.

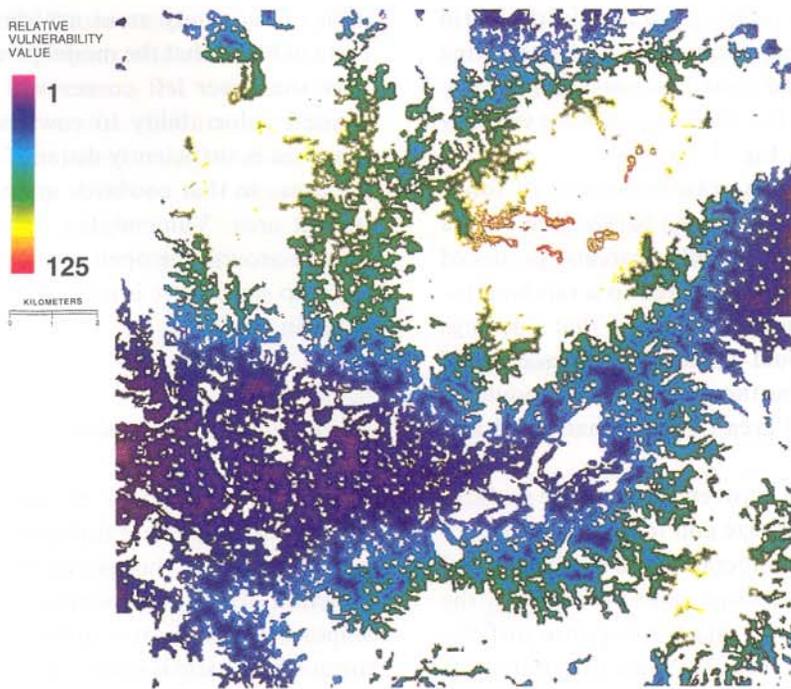


Fig. 6. Map of the spatial distribution of vulnerability to cowbird parasitism values in Parke Co., IN, when 3% of the forest was harvested per decade, using a mean harvest size of 1 ha and a random dispersion of clearcuts.

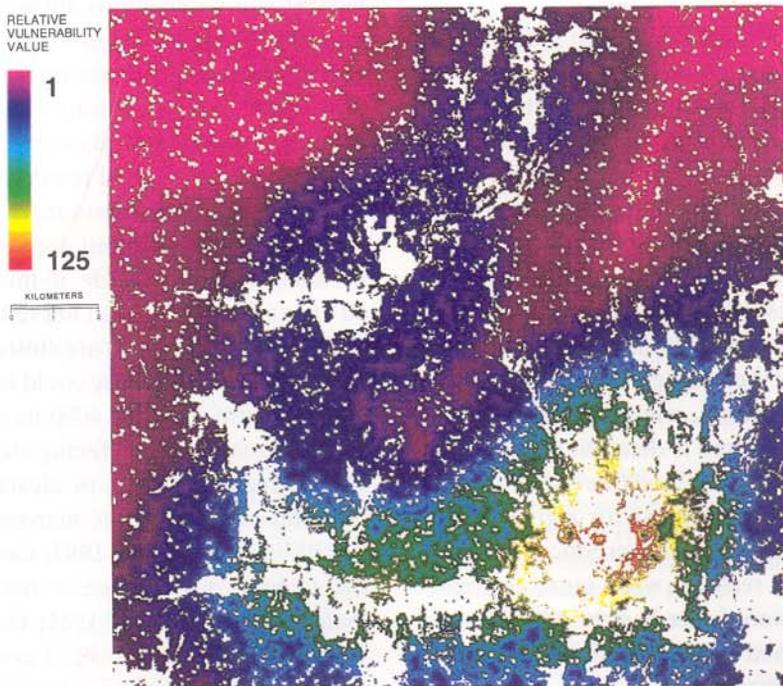


Fig. 7. Map of the spatial distribution of vulnerability to cowbird parasitism values in the Pleasant Run Unit, when 3% of the forest was harvested per decade, using a mean harvest size of 1 ha and a random dispersion of clearcuts.

what appears to be a negative exponential decline in area of forest interior. Response surfaces relating mean harvest size and total area harvested to GIS-frag are not shown, but their shapes were virtually identical to those in Fig. 1.

The most dramatic increase in amount of forest edge were produced when mean harvest size = 1 ha (Fig. 2). Aggregating small clearcuts produced slightly less edge when compared to a random dispersion due to a higher likelihood that openings < 50 years old would coalesce. Coalescence of openings also explains the decline in the amount of edge when the total area of forest harvested was > 7% per decade.

Note the similarity between the response surfaces relating mean harvest size and total area harvested to the mean value of vulnerability to cowbird brood parasitism on the landscape maps produced by the cowbird model (Fig. 3), and the response surfaces showing forest edge (Fig. 2). Since the amount of cowbird feeding habitat remained constant on each study area among harvest treatments, the differences in cowbird response to the spatial patterns produced by harvesting were related to the introduction of edge within the forest.

The variability of the spatial pattern indices was not constant throughout each response surface. Although the variability is not shown on the plots, relative amounts of variability can be inferred from the smoothness or roughness of the response surfaces, in that smooth portions of a response surface reflect low variability, and rough portions reflect higher variability. The variability of the spatial pattern indices was lowest when harvest were allocated randomly. In random dispersions, the spatial pattern is determined by the independent placement of a large number of openings, while in clustered dispersions, the spatial pattern is determined more by the placement of each cluster, and there are far fewer clusters than random openings for a given total harvest level. Large harvests also produced greater variability for similar reasons; when mean clearcut size was high there were fewer harvest allocations, and each allocation had a greater individual impact on the resulting pattern.

Examples of the spatial distribution of relative levels of vulnerability to cowbird parasitism for

each of the study areas are shown in Figs. 4–7. Note in Fig. 4 that the model predicts that clearcuts near the lower left corner will produce little increased vulnerability to cowbird parasitism since that area is sufficiently distant from cowbird feeding areas so that cowbirds are not likely to search in that area. Vulnerability to cowbird values are highest around the open areas on the right edge of the map since there is more habitat with high food value in that area.

Discussion and conclusion

An interesting finding of our study is that the shapes of the response surfaces were similar among study areas, even though the pre-simulation spatial structure of these landscapes differ (Table 1). The slopes of the response surfaces are steepest when mean harvest size is relatively small, indicating that the most significant gains in forest interior can be achieved by eliminating clearcuts < 10 ha, and to a lesser extent, by aggregating clearcuts. These response surfaces also provide insight into the mean harvest size necessary to allow harvesting of a certain percentage of the timber base and still retain a specific amount of forest interior. For example, if a goal were to retain at least 4000 ha of forest interior in the Lost River study area, < 1% of the timber base could be harvested per decade if mean harvest size = 1 ha and if harvests are distributed randomly across the landscape, but approximately 3% could be harvested per decade if mean harvest size = 30 ha, and > 4% if mean harvest size = 100 ha (see Fig. 1). If 1 ha harvests are clustered, approximately 1% of the timber base could be harvested per decade and still preserve 4000 ha of forest interior.

Forest managers are facing increased public pressure to reduce the size of clearcuts and to reduce the total area of forest managed by clearcutting (Franklin and Forman 1987; Crow 1989). Some of the impetus for change is for aesthetic reasons (Schroeder and Daniel 1981; Gobster and Chenoweth 1989), but much of it comes from the perception that clearcutting degrades wildlife habitat and that it enhances few resource values (Franklin and Forman 1987; Vinning 1991). Declining popu-

lations of many NTMBs are a cause of concern for both professional biologists and the public (Terborgh 1992), and since many NTMBs as well as other species require undisturbed, interior forest habitats, reducing the application of clearcutting has been advocated as a means to reduce forest fragmentation and to maintain large blocks of contiguous forest (Solheim *et al.* 1987; Alverson *et al.* 1988).

The results of our study suggest that it is more difficult to maintain large contiguous blocks of undisturbed forest interior when harvests are small and dispersed, especially when producing high timber volumes is a management goal. This argues against a strategy of dispersing large numbers of small cutting units (*e.g.*, group selection) throughout the forest. If the rate of harvest is rapid compared to the rate of recovery, these small openings "perforate" the landscape with high contrast patches embedded within a largely homogeneous forested matrix. Forest openings as small as 1 or 2 ha can provide loci for cowbird invasion, especially when they are close to open habitats such as agriculture fields or pastures (Brittingham and Temple 1983). It is theoretically possible to maintain specific levels of timber volume production and maintain certain amounts of undisturbed forest interior habitat simply by harvesting large blocks, and clustering those blocks in a portion of the landscape. Our results support a strategy of designing landscapes to provide a mix of commodity and non-commodity outputs by clustering or zoning management activities (Solheim *et al.* 1987; Probst and Crow 1991; Thompson *et al.* 1993).

The application of the cowbird model to landscapes managed under different strategies could help managers in deciding where harvest activity will produce the least negative impact on breeding forest birds (see discussion in Robinson *et al.* 1993; Thompson *et al.* 1993). Mathematical models that produce visual outputs such as the maps in Figs. 4–7 provide a valuable tool to planners and managers for evaluating alternative management strategies. For example, the question whether it is better to harvest in areas where cowbird impacts are high and breeding bird success is already low, or to concentrate harvests in areas out of range of cow-

bird populations (but resulting in less forest interior habitat) can be addressed with the cowbird model. Likewise, the importance of landscape context (*i.e.*, the composition and structure of the matrix) when evaluating "edge effect" can be easily visualized under a range of conditions (*e.g.*, different relative amounts and configurations of forest and farm lands) using this model.

Acknowledgments

Thanks to S.M. Pearson and F.R. Thompson, III for their critical reviews of earlier drafts of the manuscript.

References

- Alverson, W.S., Waller, D.M. and Solheim, S.L. 1988. Forest too deer: edge effects in northern Wisconsin. *Conserv. Biol.* 2: 348–358.
- Andren, H. and Angelstam, P. 1988. Elevated predation rates as an edge effect in habitat islands: experimental evidence. *Ecol.* 69: 544–547.
- Askins, R.A., Philbrick, M.J. and Sugeno, D.S. 1987. Relationship between the regional abundance of forest and the composition of forest bird communities. *Biol. Conserv.* 39: 129–152.
- Brittingham, M.C. and Temple, S.A. 1983. Have cowbirds caused forest songbirds to decline? *BioScience* 33: 31–35.
- Crawford, H.S., Hooper, R.G. and Titterton, R.W. 1981. Songbird population response to silvicultural practices in central Appalachian hardwoods. *J. Wildl. Manage.* 45: 680–692.
- Crow, T.R. 1989. Biological diversity and silvicultural systems. *In* Proceedings of the National Silviculture Workshop, Petersburg, Alaska. USDA Forest Service, Timber Management, Washington, DC.
- DellaSalla, D.A. and Rabe, D.L. 1987. Response of least flycatchers *Empidonax minimus* to forest disturbances. *Biol. Conserv.* 41: 291–299.
- Duffy, A.M. Jr. 1982. Movements and activities of radio-tracked brown-headed cowbirds. *Auk* 9: 316–327.
- Franklin, J.F. and Forman, R.T.T. 1987. Creating landscape patterns by forest cutting: ecological consequences and principles. *Landscape Ecol.* 1: 5–18.
- Freemark, K.E. 1988. Landscape ecology of forest birds in the northeast. *In* Healthy forests, healthy world: Proceedings of the 1988 Society of American Foresters National Convention, Rochester, NY.
- Gates, J.E. and Gysel, L.W. 1978. Avian nest dispersion and fledgling success in field-forest ecotones. *Ecol.* 59: 871–883.

- Gobster, P.H. and Chenoweth, R.E. 1989. The dimensions of aesthetic preference: a quantitative analysis. *J. Environ. Manage.* 29: 47-72.
- Gustafson, E.J. and Parker, G.R. 1992. Relationships between landcover proportion and indices of landscape spatial pattern. *Landscape Ecol.* 7: 101-110.
- Gustafson, E.J., Parker, G.R. and Backs, S.E. 1994. Evaluating spatial pattern of wildlife habitat: a case study of the Wild Turkey (*Meleagris gallopavo*). *Am. Midl. Nat.* 131: 24-33.
- Karr, J.R. 1982. Avian extinctions on Barro Colorado Island, Panama: a reassessment. *Am. Nat.* 119: 220-239.
- Kroodsmas, R.L. 1984. Effect of edge on breeding forest bird species. *Wilson Bull.* 96: 426-436.
- Lillesand, T.M. and Kiefer, R.W. 1987. Remote sensing and image interpretation. John Wiley and Sons, New York.
- Lord, J.M. and Norton, D.A. 1990. Scale and the spatial concept of fragmentation. *Conserv. Biol.* 4: 197-202.
- Medin, D.E. and Booth, G.D. 1989. Responses of birds and small mammals to single-tree selection logging in Idaho. Res. Pap. INT-408. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station.
- O'Neill, R.V., Krummel, J.R., Gardner, R.H., Sugihara, G., Jackson, B., DeAngelis, D.L., Milne, B.T., Turner, M.G., Zygmunt, B., Christensen, S.W., Dale, V.H. and Graham, R.L. 1988. Indices of landscape pattern. *Landscape Ecol.* 1: 153-162.
- Pearson, S.M., Turner, M.G., Gardner, R.H. and O'Neill, R.V. *in press*. An organism-based perspective of habitat fragmentation. *In Biodiversity in managed landscapes: theory and practise*. Edited by R.C. Szaro. Oxford University Press, Cary, NC.
- Probst, J.R. and Crow, T.R. 1991. Integrating biological diversity and resource management. *J. Forestry* 89: 12-17.
- Ratti, J.T. and Reese, K.P. 1988. Preliminary test of the ecological trap hypothesis. *J. Wildl. Manage.* 52: 484-491.
- Ripple, W.J., Bradshaw, G.A. and Spies, T.A. 1991. Measuring forest landscape patterns in the Cascade Range of Oregon, USA. *Biol. Conserv.* 57: 73-88.
- Robinson, S.K. 1992. Population dynamics of breeding Neotropical migrants in a fragmented Illinois landscape. *In Ecology and conservation of neotropical migrant landbirds*. pp. 408-418. Edited by J.M. Hagen and D.W. Johnston. Manomet Bird Observatory, Manomet, Mass.
- Robinson, S.K., Grzybowski, J.A., Rothstein, S.I., Brittingham, M.C., Petit, L.J. and Thompson, F.R. 1993. Management implications of cowbird parasitism on neotropical migrant songbirds. *In Status and management of neotropical migratory birds*. pp. 93-102. Edited by D.M. Finch and P.W. Stangel. Gen. Tech. Rep., RM-229, Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station.
- Rothstein, S.I., Verner, J. and Stevens, E. 1984. Radio-tracking confirms a unique diurnal pattern of spatial occurrence in the parasitic brown-headed cowbird. *Ecol.* 65: 77-88.
- Schroeder, H.W. and Daniel, T.C. 1981. Progress in predicting the perceived scenic beauty of forest landscapes. *Forest Science* 27: 71-80.
- Small, M.F. and Hunter, M.L. 1988. Forest fragmentation and avian nest predation in forested landscapes. *Oecologia* 76: 62-64.
- Solheim, S.L., Alverson, W.S. and Waller, D.M. 1987. Maintaining biotic diversity in National Forests: the necessity for large blocks of mature forests. *Endangered Species: Technical Bulletin Report* 4:1-3, The School of Natural Resources, University of Michigan, Ann Arbor, MI.
- Terborgh, J. 1992. Perspectives on the conservation of Neotropical migrant landbirds. *In Ecology and conservation of neotropical migrant landbirds*. pp. 7-12. Edited by J.M. Hagen and D.W. Johnston. Manomet Bird Observatory, Manomet, Mass.
- Temple, S.A. and Cary, J.R. 1988. Modeling dynamics of habitat-interior bird populations in fragmented landscapes. *Conserv. Biol.* 2: 340-347.
- Thompson, F.R. III, Djak, W.D., Kulowiec, T.G. and Hamilton, D.A. 1992. Breeding bird populations in Missouri Ozark forests with and without clearcutting. *J. Wildl. Manage.* 56: 23-30.
- Thompson, F.R. III, Probst J.R. and Raphael, M.G. 1993. Silvicultural options for neotropical migratory birds. *In Status and management of neotropical migratory birds*. pp. 353-362. Edited by D.M. Finch and P.W. Stangel. Gen. Tech. Rep., RM-229, Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station.
- Thompson, F.R. III 1993. Simulated responses of a forest interior bird population to forest management options in central hardwood forests of the United States. *Conserv. Biol.* 7: 325-333.
- Thompson, F.R. III. *in press*. Temporal and spatial patterns of breeding brown-headed cowbirds in the midwestern United States. *Auk*.
- Vinning, J. 1991. Environmental values, emotions, and public involvement. *In Ecosystem management in a dynamic society*. pp. 26-35. Edited by D.C. Le Master and G.R. Parker. Department of Forestry and Natural Resources, Purdue University, West Lafayette, IN.
- Yahner, R.H. and Scott, D.P. 1988. Effects of forest fragmentation on depredation of artificial nests. *J. Wildl. Manage.* 52: 158-161.
- Yahner, R.H. and Wright, A.L. 1985. Depredation of artificial ground nests: effects of edge and plot age. *J. Wildl. Manage.* 49: 508-513.