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INFLUENCE OF RECREATIONAL TRAILS ON BREEDING BIRD COMMUNITIES

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Abstract. We investigated the influence of recreational trails on breeding bird communities in forest and mixed-grass prairie ecosystems in Boulder County, Colorado, United States, during 1994 and 1995. Species composition, nest predation, and brood parasitism by Brown-headed Cowbirds (*Molothrus ater*) were examined near and away from existing recreational trails. Bird species composition was altered adjacent to trails in both ecosystems. Generalist species were more abundant near trails, whereas specialist species were less common. Within the grassland ecosystem, birds were less likely to nest near trails. Within both ecosystems, nest predation was greater near trails. In forests, the rate of brood parasitism was not influenced by trails. No brood parasitism was found in the grassland ecosystem. Our results may be useful to natural-lands managers who must implement management policies regarding the spatial arrangement of trails and trail-use restrictions.

Key words: bird communities; Brown-headed Cowbird; Colorado; edge effects; *Molothrus ater*; nest parasitism; nest predation; recreation; recreational trails.

INTRODUCTION

Outdoor recreational activities are increasing in popularity throughout the United States (Flather and Cordell 1995). Results from a national survey indicate that the number of individuals participating in nonconsumptive wildlife-oriented activities nearly doubled between 1980 and 1990 (U.S. Department of the Interior, Fish and Wildlife Service and U.S. Department of Commerce, Bureau of the Census 1993). Heretofore, some have thought that nonconsumptive outdoor recreation was an environmentally benign activity. Increasing evidence, however, indicates that these activities can affect individuals, populations, and wildlife communities (Knight and Cole 1995). For example, Boyle and Samson (1985) reported that, in 81% of studies reviewed, nonconsumptive outdoor recreation had negative effects on wildlife.

Coinciding with rising levels of recreational activities is an increase in the number of trails crossing natural areas. Because trails bisect forest and grassland habitats, they may create habitat edges. Brood parasitism by Brown-headed Cowbirds (*Molothrus ater*) and nest predation typically increase in association with habitat edges (Whitcomb et al. 1981, Brittingham and Temple 1983, Paton 1994), which may, in turn,

alter bird species diversity and composition (Ambuel and Temple 1983). Most studies of habitat edge have been conducted in deciduous forests of the eastern United States, in small, isolated forest fragments surrounded by agricultural fields (Paton 1994). Fewer studies have examined how landscape modifications resulting in the development of internal edges (e.g., roads, utility right-of-ways, recreational trails), rather than external edges (e.g., habitat islands), affect bird communities.

Our study investigated the influence of recreational trails on breeding bird communities in forest and grassland ecosystems along the Front Range of Colorado. We addressed two null hypotheses: (1) species diversity, composition, and abundance do not differ near trails compared to away from trails; and (2) rates of nest predation and Brown-headed Cowbird brood parasitism are independent of the distance from trails.

STUDY AREA AND METHODS

We conducted our study on City of Boulder Open Space and Mountain Parks properties, an area encompassing ~11 000 ha in and around the city of Boulder, Colorado, United States (40°00' N, 105°15' E). Part of this land is in agricultural production and other parcels are reserved for outdoor recreation and wildlife. Elevation within the study area ranges from 1219 to 2438 m, encompassing forest, riparian, shrubland, and grassland habitats. Visitor use on the study area is almost 3.5×10^6 visits per year. Visitor intensities are highest during the spring, followed by summer, fall, and winter. Recreational activities include hiking, wildlife viewing, exercising pets, jogging, mountain biking, and horseback riding.

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Study sites were located in pine forest and mixed-grass prairie ecosystems. Forest ecosystems were dominated by ponderosa pine (*Pinus ponderosa*) associated with a mix of shrubs, grasses, and forbs. Mixed-grass prairie ecosystems contained a variety of tall, mid, and shortgrass species, including little bluestem (*Schizachyrium scoparium*), western wheat (*Agropyron smithii*), blue grama (*Bouteloua gracilis*), and side oats grama (*Bouteloua curtipendula*).

Bird communities

We examined breeding bird communities along recreational trails and control transects. Control transects (marked with small wooden stakes) were established to measure bird communities where no trails existed. All trails and control transects were located >800 m from urban development and ≥ 400 m from other trails and physiographic features such as forest edge, riparian areas, and ridge lines. Five and seven trails were monitored in the grassland and forest ecosystems, respectively. Seven trails and seven control transects were monitored in the forest ecosystem. Trail width was 1.25 ± 0.22 m (mean ± 1 SE) in the grasslands and 1.17 ± 0.20 m in the forests.

Bird communities were surveyed using fixed-distance line transects (Buckland et al. 1993) established parallel to trails at 0, 50, and 100 m from trail centers. On control transects, only the transect was surveyed. All transects (individual transect length ~ 350 m) were surveyed in a randomly assigned order once early (June) and once late (July) in the breeding season during 1994 and 1995. Transects were surveyed from 0.5 h before to 2 h after sunrise, and birds were recorded if detected within 25 m of the transect line. In the grassland ecosystem, we surveyed 10 transects at each distance (0, 50, and 100 m) away from trails and seven control transects. Because of the proximity of some trails in the forest ecosystem, uneven numbers of transects were established at each distance away from trail centers. In the forest ecosystem, we surveyed 13 transects at 0 m away from trails, nine transects at each 50 m and 100 m away from trails, and seven control transects.

Nest success

We located nests in the grasslands by dragging a heavy rope in 30 m wide swaths across the ground to flush birds from their nests during 23 May–30 July 1994 and 31 May–21 July 1995. Dragging was performed in a perpendicular direction to trails and control transects to maintain an equal sampling effort at all distances out to 200 m. Once located, a nest was identified to species, marked with a small stake located 10 m north of the nest, and its perpendicular distance to the trail or control transect was recorded. Nests in the forest were located by following adults carrying nesting material or food items, observing behavior such as nest defense, and searching trees and branches during

2 June–30 July 1994 and 25 May–31 July 1995. Once located, a nest was identified to species, marked with a small piece of flagging tape on a nearby tree, and the perpendicular distance to the trail or control transect was recorded. All nests in grasslands and forests were monitored every three days until the fledging of young or nest failure; evidence of brood parasitism, including the number of cowbird eggs or nestlings, was noted. Birds were not individually marked, so we did not know whether birds replaced nests following acts of predation. Because we consistently searched the same areas throughout the breeding season, nests in our sample were considered representative of the population. To reduce bias, all nests were monitored, using the same protocol, by a single observer (Martin and Geupel 1993). We observed no nest abandonments due to nest searching or monitoring activities.

Statistical analyses

Species diversity was evaluated using Simpson's Diversity Index (Begon et al. 1986). Because of small sample sizes, we were not able to compute density estimates of individual species using standard methods (Buckland et al. 1993). For each 0-m, 50-m, and 100-m trail transect and for control transects, we estimated an index of abundance for each species: mean number of observations/100 m (length) \times 50 m (width) for each species. This index of abundance for each transect was considered an independent sample for analysis. We used randomization tests (30 000 randomizations per test; Manly 1991, 1992) to compare abundance between transects within each ecosystem. We compared individual species abundance between 0-m transects and control transects to identify the effect of trail presence (trail effect). For each species, if a statistically significant trail effect was found, we then compared abundance between 0-, 50-, and 100-m transects to determine whether abundance significantly increased or decreased within 100 m of trails (distance effect). Data from each transect were pooled over the entire season within each year. Because overall bird abundance did not differ between years (grassland $P = 0.142$; forest $P = 0.369$), data were pooled across years within the grassland and forest ecosystems for analysis. Because we conducted multiple tests to ascertain trail and distance effects, we applied a sequential Bonferroni adjustment to α to control for Type I error (Rice 1990).

We collected nesting information only for open-cup nesting passerines. Within each ecosystem, species composition and the proportion of nests located of each species were similar between treatments. Because we had small sample sizes of nests for some species, analyses of individual species were not possible. Therefore, to avoid losing information from such species, to increase statistical power, and because open-cup nesting passerines in the same habitat type generally have the same nesting success, regardless of their own species

density (Chasko and Gates 1982), we pooled nest data across species for subsequent analyses.

In the grassland ecosystem, we maintained an equal search effort for nests at all distances within 200 m of trails and control transects. Thus, we assumed that the distribution of nests in our sample represented the true distribution of all nests (detected and undetected). Logistic regression (GENMOD procedure, SAS Institute 1993) was used to determine if distance from trails or control transects was correlated with nest occurrence. Because the nest-searching techniques employed in the forest ecosystem did not allow an equal sampling effort at all distances away from trails and control transects, forest nests were not used in this analysis.

Logistic regression was used to determine the relationship between nest predation and distance from trails and control transects for nests within grassland and forest ecosystems. Unless all nests in the analysis are observed from the day of nest initiation, biases may occur in estimation of survival rates (Mayfield 1975). Therefore, we analyzed nest predation data in a manner analogous to Mayfield's (1975) method, which provides unbiased estimates of survival rates (Bart and Robson 1982). Each individual day from the time a nest was located until the nesting attempt ended was considered an independent observation. When necessary, the end of a nest attempt was estimated as the midpoint between the last two visits.

Logistic regression was used to determine the relationship between brood parasitism and distance from forest trails (no brood parasitism was found in the grasslands). For this analysis, each nest was considered an independent observation. Because Solitary Vireos (*Vireo solitarius*) were heavily parasitized (11 of 15 nests; 73%), two analyses were performed: (1) for Solitary Vireo nests alone, and (2) for all other species pooled. For all analyses, we used an a priori $\alpha = 0.10$ to improve statistical power (see Gutzwiller et al. 1997).

RESULTS

Bird communities

We recorded 13 and 29 bird species in the grassland and forest ecosystems, respectively. Species diversity (Simpson's Diversity Index) was approximately four times greater in the forest ecosystem (9.55) than in the grassland ecosystem (2.50). Four species in the grassland ecosystem and 11 species in the forest ecosystem provided adequate sample sizes for statistical analyses. We observed trail effects for a variety of species in both grassland and forest ecosystems. Three grassland species were significantly more abundant along control transects than along trails (Western Meadowlark, *Sturnella neglecta*, $P < 0.001$; Vesper Sparrow, *Pooecetes gramineus*, $P = 0.006$; and Grasshopper Sparrow, *Ammodramus savannarum*, $P = 0.015$; Fig. 1). In the forests, five species were significantly more abundant

along control transects than along trails (Western Wood-pewee, *Contopus sordidulus*, $P < 0.001$; Chipping Sparrow, *Spizella passerina*, $P < 0.001$; Pygmy Nuthatch, *Sitta pygmaea*, $P < 0.001$; Solitary Vireo, $P = 0.002$; and Townsend's Solitaire, *Myadestes townsendi*, $P = 0.014$). Conversely, in the forest, American Robins (*Turdus migratorius*) were significantly more abundant along trails than along control transects ($F = 0.003$; Fig. 1).

In addition to showing trail effects, birds also exhibited distance effects. Two grassland species increased in abundance with increasing distance from trails (Western Meadowlark, $P = 0.001$; and Grasshopper Sparrow, $P = 0.041$; Fig. 1). The abundance of four forest species increased with increasing distance from trails (Western Wood-pewee, $P < 0.001$; Chipping Sparrow, $P = 0.013$; Pygmy Nuthatch, $P = 0.027$; and Solitary Vireo, $P = 0.081$). Conversely, American Robins were more abundant near forest trails than away from them ($P = 0.045$; Fig. 1). Although small sample sizes precluded statistical analysis, Black-billed Magpies (*Pica pica*) and House Finches (*Carpodacus mexicanus*) were detected only along grassland and forest trails, respectively.

Nest placement, predation, and brood parasitism

In the grassland ecosystem, nests were less likely to occur near trails than away from trails ($P = 0.005$, $n = 163$ nests; Fig. 2). No trend was found along control transects, because nests were evenly distributed ($P = 0.371$, $n = 97$ nests). Year was not a significant predictor of nest placement along trails ($P = 0.551$) or along control transects ($P = 0.167$).

Within both the grassland and forest ecosystems, we found a significant positive relationship between nest survival and distance from trails (grassland, $P = 0.003$, $n = 163$ nests, $n = 1954$ nest days; forest, $P = 0.049$, $n = 162$ nests, $n = 2040$ nest days; Fig. 3). Nest survival did not vary with distance from control transects in either grasslands ($P = 0.530$, $n = 97$ nests, $n = 965$ nest days) or forests ($P = 0.875$, $n = 92$ nests, $n = 1106$ nest days). Year was not a significant predictor of nest survival in grasslands (trails, $P = 0.680$; control transects, $P = 0.400$) or forests (trails, $P = 0.224$; control transects, $P = 0.950$).

No brood parasitism was found in the grassland ecosystem, either along trails or control transects. Within the forest ecosystem, there were no significant relationships between brood parasitism and distance from trails for Solitary Vireo nests ($P = 0.704$, $n = 15$ nests) or for nests of all other species pooled ($P = 0.278$, $n = 147$ nests). However, 95% confidence intervals around parameter estimates for the model variable "nest distance from trail" were relatively large [parameter estimate 0.004 (-0.017 , 0.025) for Solitary Vireo nests; parameter estimate -0.0065 (-0.019 , 0.006) for nests of all other species pooled], indicating that the results may be inconclusive. Year of study was

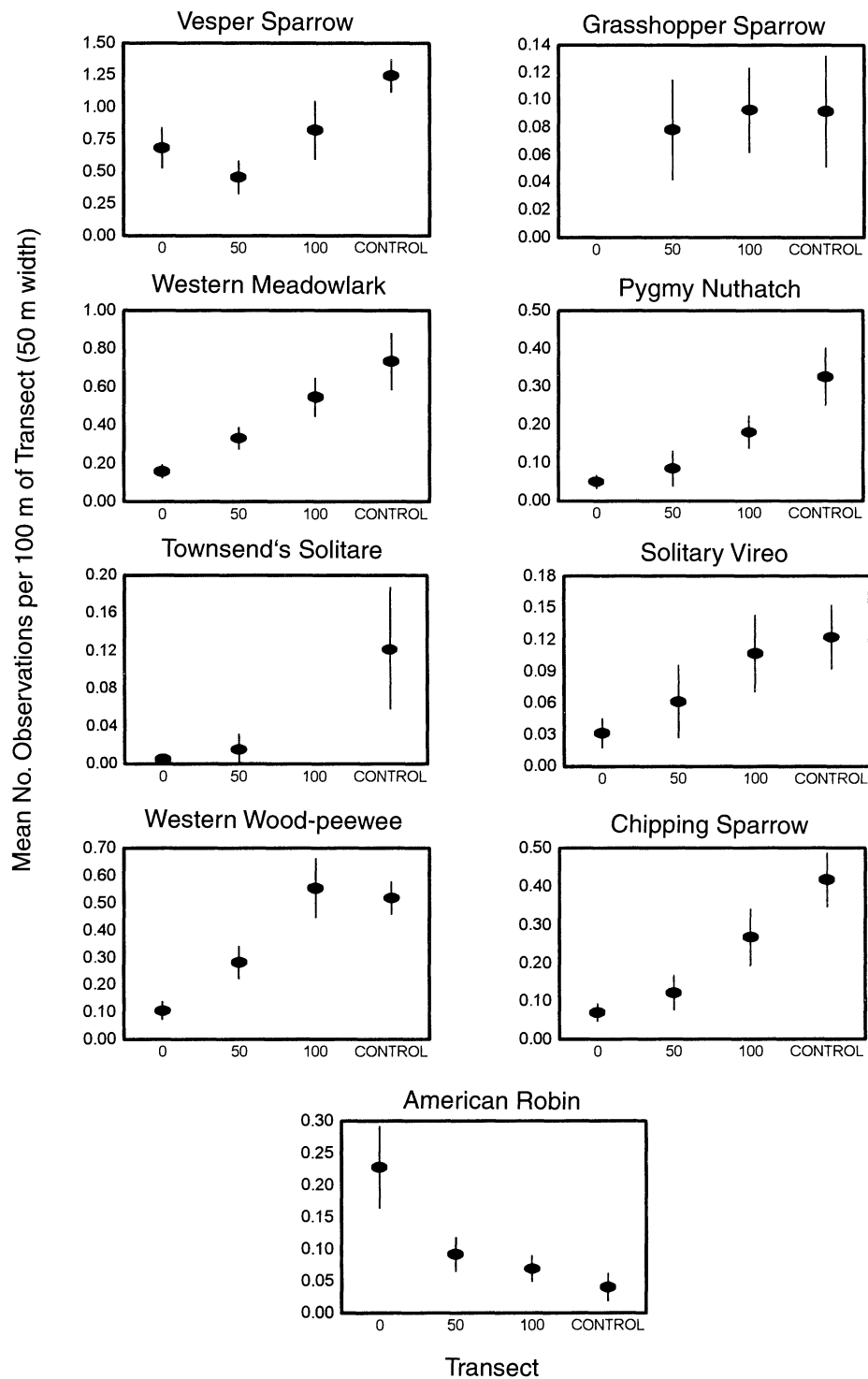


FIG. 1. Index of abundance of birds detected along transects at 0, 50, and 100 m away from trails, and control transects in the grassland and forest ecosystems during 1994 and 1995, City of Boulder Open Space and Mountain Parks, Boulder, Colorado, USA. Vertical lines denote one standard error.

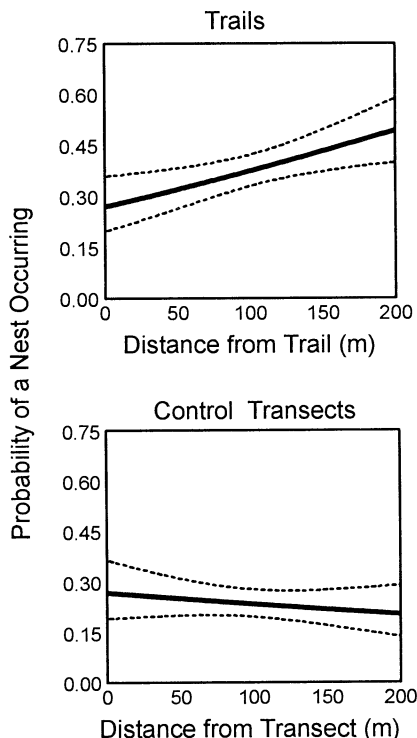


FIG. 2. Predicted probability that a nest will occur at a given distance from trails and control transects within the grassland ecosystem during 1994 and 1995, City of Boulder Open Space and Mountain Parks, Boulder, Colorado. Dotted lines denote 95% confidence interval.

not a significant predictor of brood parasitism for either Solitary Vireo nests ($P = 0.656$) or for nests of all other species pooled ($P = 0.202$).

DISCUSSION

Our results indicate that composition and abundance of birds were altered adjacent to trails in both grassland and forest ecosystems. In particular, some species did not occur, or occurred in lower densities, near trails than at greater distances from trails, whereas some species, mainly generalists, were more abundant near trails. For the majority of species found in reduced numbers near trails, the zone of influence of trails appears to be ~ 75 m, however, Townsend's Solitaires appear even more sensitive to trails; they exhibited reduced numbers as far as 100 m away from trails. Because survey protocol was the same for both trails and controls, alterations in species composition and distribution were due to the trails, rather than to the temporary presence of the surveyor.

Our results concur with those of Hickman (1990), who found that trails altered bird community composition. He reported that habitat edge species, such as Blue Jays (*Cyanocitta cristata*), American Robins, and Brown-headed Cowbirds, were more abundant on sites with trails than on sites without trails. Furthermore, fragmentation by other narrow corridors, such as roads

and utility right-of-ways, is sufficient to produce habitat edge effects. For example, Ferris (1979), Kroodsma (1982), Rich et al. (1994), and Hanowski and Niemi (1995) found that habitat interior species were less abundant and habitat edge species were more abundant near the corridors.

Another mechanism by which recreational trails may influence breeding bird communities is the associated human disturbance. Species sensitive to disturbance by humans may avoid areas where human activity is common, or may occur in reduced abundance. Van der Zande et al. (1984) reported a negative relationship between the intensity of recreation occurring on trails and the density for eight of 13 avian species, with some species being more sensitive than others. In another study, Van der Zande and Vos (1984) found that 11 of the 12 most common bird species exhibited lower numbers in areas where recreation use was common than in areas with fewer visitors.

We found fewer nests near trails in the grassland ecosystem, further indicating that some birds avoided trails. Reijnen and Foppen (1994) found that in areas where primary song was affected by disturbance, birds appeared reluctant to establish nesting territories. Gutzwiller et al. (1994) reported that even a single pedestrian moving through a bird's territory was sufficient to reduce the occurrence and consistency of primary song. Because song is an integral component of breeding behavior (e.g., territory defense and mate attraction), it is reasonable to believe that birds sensitive to human disturbance may be reluctant to establish nest sites where human activity is frequent, i.e., near trails (Gutzwiller et al. 1997). Nest site selection is also influenced by rates of nest predation, with a dispersion of nests away from areas of heavy predation pressure (Martin 1988). Therefore, fewer nests near trails may be, in part, a result of greater rates of nest predation in these areas.

We also found elevated rates of nest predation near trails. Paton (1994) reviewed studies investigating the influence of habitat edge on nest predation, and found that 71% and 57% of the studies reviewed showed elevated levels of predation on artificial and natural nests, respectively, near habitat edges. Hickman (1990) and Rich et al. (1994) found that avian nest predators were attracted to narrow, open corridors. Both authors suggested that this attraction could result in greater rates of nest predation near these corridors. Although we were unable to evaluate the assemblage of potential mammalian nest predators, raccoons (*Procyon lotor*), skunks (*Mephitis sp.*), and coyotes (*Canis latrans*) were common on our study site (S. G. Miller, *personal observation*) and are often associated with habitat edges and humans (Gates and Gysel 1978). Avian nest predators such as corvids typically concentrate activities near habitat edges (Whitcomb et al. 1981, Wilcove 1985, Møller 1989). Our observations that Black-billed Magpies were more abundant near trails, coupled with

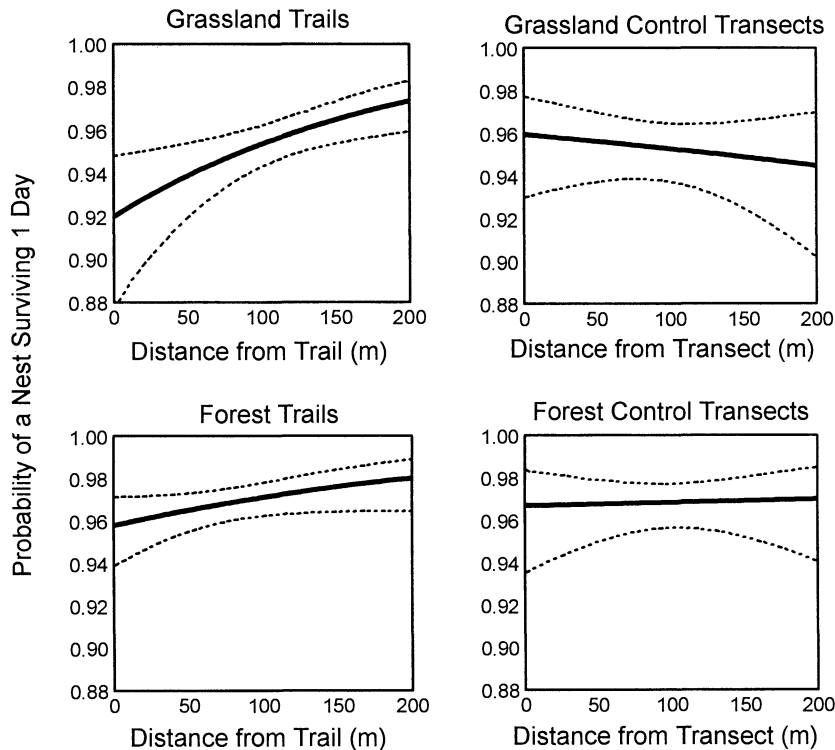


FIG. 3. Predicted probability that a nest will survive one day at a given distance from trails and control transects within the grassland and forest ecosystems during 1994 and 1995, City of Boulder Open Space and Mountain Parks, Boulder, Colorado. Dotted lines denote 95% confidence interval.

the possible attraction of mammalian nest predators, may explain the greater rates of nest predation near trails.

Brood parasitism by Brown-headed Cowbirds is considered an important element in reducing reproductive success of songbirds, especially near habitat edges (Brittingham and Temple 1983, Robinson 1988). Cowbirds are considered common on the plains and foothills of Colorado (Sclater 1912, Bailey and Niedrach 1965, Davis 1969) and are typically associated with cattle (Rothstein et al. 1980). We found no brood parasitism, nor did we detect cowbirds during our surveys in the grasslands, even though these sites were grazed by livestock during our study. Although we are unable to explain the absence of cowbirds on our grassland sites, others have found similarly unexpected results. For example, Hahn and Hatfield (1995) found higher brood parasitism rates in forest interior bird communities than on adjacent old fields and edges, where traditional host species were available. They suggested that cowbirds may switch habitats, either cyclically or opportunistically, to take advantage of nontraditional hosts (i.e., forest interior species) which lack adequate defense strategies.

It has been suggested that cowbirds are attracted to and use open corridors as access routes into forest interiors and, consequently, parasitize forest-interior species (Small and Hunter 1988, Askins 1994). For ex-

ample, cowbirds were attracted to nature trails (Hickman 1990) and open corridors as narrow as 2.5 m (Rich et al. 1994) in deciduous forests. We found no relationship between cowbird abundance or brood parasitism and distance from forest trails, suggesting that trails did not serve as access routes for cowbirds on our study area.

Because our study area was situated within an urban/suburban matrix, our results were no doubt influenced by the surrounding landscape (Engels and Sexton 1994). Furthermore, the intensity of recreational activities on our study area was extremely heavy. Therefore, caution should be used when extrapolating results obtained in our study to landscapes lacking either urban development, intense recreational pressure, or both. For example, Rocky Mountain National Park, located only 40 km from our study area, receives similar recreational pressure, yet is almost an order of magnitude larger in size and is more removed from urban development. It is plausible that recreational trails in landscapes different than ours (e.g., Rocky Mountain National Park) may not exert similar effects on bird communities.

Our results indicate that trails may serve as habitat edges for some, but not necessarily all, species. Additionally, the potential effect of recreational disturbance cannot be discounted. Thus, the question of whether the influence of recreational trails on bird communities is due to the physical presence of the trail, or

rather to the associated human disturbance remains, for the most part, unanswered. Both mechanisms may be acting in concert. Nonetheless, our results show that breeding bird communities are altered adjacent to trails in grassland and forest ecosystems, thereby creating an arduous dilemma for natural-lands managers.

Because both wildlife and humans are components of natural areas, the goal of natural-lands managers should be to develop methods to ensure their coexistence (Knight and Temple 1995). Management of natural areas must entail not only proper trail placement, but also recreationist management. Consolidation of trails to certain areas (e.g., edges of forests and grasslands) will reduce the fragmentation of large blocks of habitat, maintaining less-disturbed areas for species sensitive to fragmentation. Natural area personnel can inform recreationists of how their activities affect wildlife and how they can modify their regime of disturbance (e.g., remaining on trails and keeping pets leashed) to minimize impacts. Klein (1993) found that visitors who spoke to wildlife refuge personnel were less likely to disturb wildlife than were recreationists who did not.

The number of people participating in outdoor recreational activities is anticipated to increase in the future (Flather and Cordell 1995). As a result, the number of recreational trails crossing natural areas is also likely to increase. Our results indicate that trails affect the distribution and abundance, as well as the reproductive success, of bird species, suggesting the need for more thoughtful trail planning and management of recreationists in natural areas.

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LITERATURE CITED

- Ambuel, B., and S. A. Temple. 1983. Area-dependent changes in the bird communities and vegetation of southern Wisconsin forests. *Ecology* **64**:1057–1068.
- Askins, R. A. 1994. Open corridors in a heavily forested landscape: impact on shrubland and forest-interior birds. *Wildlife Society Bulletin* **22**:339–347.
- Bailey, A. M., and R. J. Niedrach. 1965. *Birds of Colorado*. Denver Museum of Natural History, Denver, Colorado, USA.
- Bart, J., and D. S. Robson. 1982. Estimating survivorship when the subjects are visited periodically. *Ecology* **63**:1078–1090.
- Begon, M., J. L. Harper, and C. R. Townsend. 1986. *Ecology: individuals, populations, and communities*. Sinauer Associates, Sunderland, Massachusetts, USA.
- Boyle, S. A., and F. B. Samson. 1985. Effects of nonconsumptive recreation on wildlife: a review. *Wildlife Society Bulletin* **13**:110–116.
- Brittingham, M. C., and S. A. Temple. 1983. Have cowbirds caused forest birds to decline? *BioScience* **33**:31–35.
- Buckland, S. T., D. R. Anderson, K. P. Burnham, and J. L. Laake. 1993. Distance sampling: estimating abundance of biological populations. Chapman and Hall, London, UK.
- Chasko, G. G., and J. E. Gates. 1982. Avian habitat suitability along a transmission-line corridor in an oak–hickory forest region. *Wildlife Monograph Number* 82.
- Davis, W. A. 1969. *Birds in western Colorado*. Colorado Field Ornithologist, Boulder, Colorado, USA.
- Engels, T. M., and C. W. Sexton. 1994. Negative correlation of Blue Jays and Golden-cheeked Warblers near an urbanizing area. *Conservation Biology* **8**:286–290.
- Ferris, C. R. 1979. Effects of Interstate 95 on breeding birds in northern Maine. *Journal of Wildlife Management* **43**:421–427.
- Flather, C. H., and H. K. Cordell. 1995. Outdoor recreation: historical and anticipated trends. Pages 3–16 in R. L. Knight and K. J. Gutzwiller, editors. *Wildlife and recreationists: coexistence through research and management*. Island Press, Covelo, California, USA.
- Gates, J. E., and L. W. Gysel. 1978. Avian nest dispersion and fledgling success in forest–field ecotones. *Ecology* **59**:871–883.
- Gutzwiller, K. J., R. T. Wiedenmann, K. L. Clements, and S. H. Anderson. 1994. Effects of human intrusion on song occurrence and singing consistency in subalpine birds. *Auk* **111**:28–37.
- Gutzwiller, K. J., E. A. Kroese, S. T. Anderson, and C. A. Wilkins. 1997. Does human intrusion alter the seasonal timing of avian song during breeding periods? *Auk* **114**:55–65.
- Hahn, D. C., and J. S. Hatfield. 1995. Parasitism at the landscape scale: cowbirds prefer forests. *Conservation Biology* **9**:1415–1424.
- Hanowski, J. M., and G. J. Niemi. 1995. A comparison of on- and off-road bird counts: do you need to go off road to count birds accurately? *Journal of Field Ornithology* **66**:469–483.
- Hickman, S. 1990. Evidence of edge species' attraction to nature trails within deciduous forest. *Natural Areas Journal* **10**:3–5.
- Klein, M. L. 1993. Waterbird behavioral responses to human disturbances. *Wildlife Society Bulletin* **21**:31–39.
- Knight, R. L., and D. N. Cole. 1995. Wildlife responses to recreationists. Pages 51–69 in A. L. Knight and K. Gutzwiller, editors. *Wildlife and recreationists: coexistence through research and management*. Island Press, Covelo, California, USA.
- Knight, R. L., and S. A. Temple. 1995. Wildlife and recreationists: coexistence through management. Pages 327–333 in R. L. Knight and K. Gutzwiller, editors. *Wildlife and recreationists: coexistence through research and management*. Island Press, Covelo, California, USA.
- Kroodsmas, R. L. 1982. Edge effect on breeding forest birds along a power line corridor. *Journal of Applied Ecology* **19**:361–370.
- Manly, B. F. J. 1991. *Randomization and Monte Carlo methods in biology*. Chapman and Hall, New York, New York, USA.
- . 1992. RT: a program for randomization testing. Version 1.02. West, Cheyenne, Wyoming, USA.
- Martin, T. E. 1988. Processes organizing open-nesting bird assemblages: competition or nest predation? *Evolutionary Ecology* **2**:37–50.
- Martin, T. E., and G. R. Geupel. 1993. Nest-monitoring plots: methods for locating nests and monitoring success. *Journal of Field Ornithology* **64**:507–519.
- Mayfield, H. F. 1975. Suggestions for calculating nest success. *Wilson Bulletin* **87**:456–466.
- Møller, A. P. 1989. Nest site selection across field–woodland ecotones: the effect of nest predation. *Oikos* **56**:240–246.
- Paton, P. W. C. 1994. The effect of edge on avian nest suc-

- cess: how strong is the evidence? *Conservation Biology* **8**: 17–26.
- Reijnen, R., and R. Foppen. 1994. The effects of car traffic on breeding bird populations in woodland. I. Evidence of reduced habitat quality for Willow Warbler (*Pyloscopus trochilus*) breeding close to a highway. *Journal of Applied Ecology* **31**:85–94.
- Rice, W. R. 1990. A consensus combined *P* value test and the family-wide significance of component tests. *Biometrics* **46**:303–308.
- Rich, A. C., D. S. Dobkin, and L. J. Niles. 1994. Defining forest fragmentation by corridor width: the influence of narrow, forest-dividing corridors on forest-nesting birds in southern New Jersey. *Conservation Biology* **8**:1109–1121.
- Robinson, S. K. 1988. Reappraisal of the costs and benefits of habitat heterogeneity for nongame wildlife. *Transactions of the North American Wildlife and Natural Resources Conference* **53**:145–155.
- Rothstein, S. I., J. Verner, and E. Stevens. 1980. Range expansion and diurnal changes in dispersion of the Brown-headed Cowbird in the Sierra Nevada. *Auk* **97**:253–267.
- SAS Institute. 1993. SAS Technical Report p-243, SAS/STAT Software: the GENMOD procedure. Release 6.09. SAS Institute, Cary, North Carolina, USA.
- Sclater, W. L. 1912. A history of the birds of Colorado. Witherby, London, UK.
- Small, M. F., and M. L. Hunter. 1988. Forest fragmentation and avian predation in forested landscapes. *Oecologia* **76**: 62–64.
- United States Department of the Interior, Fish and Wildlife Service, and U. S. Department of Commerce, Bureau of the Census. 1993. 1991 National survey of fishing, hunting, and wildlife-associated recreation. United States Government Printing Office, Washington, D.C., USA.
- Whitcomb, R. F., C. S. Robbins, J. F. Lynch, B. L. Whitcomb, M. K. Klimkiewicz, and D. Bystrak. 1981. Effects of forest fragmentation on avifauna of eastern deciduous forest. Pages 125–205 in R. L. Burgess and D. M. Sharp, editors. *Forest dynamics in man-dominated landscapes*. Springer-Verlag, New York, New York, USA.
- Wilcove, D. S. 1985. Nest predation in forest tracts and the decline of migratory songbirds. *Ecology* **66**:1211–1214.
- Zande, A. N. van der, J. C. Berkhuizen, H. C. van Latesteijn, W. J. ter Keurs, and A. J. Poppelaars. 1984. Impact of outdoor recreation on the density of a number of breeding bird species in woods adjacent to urban residential areas. *Biological Conservation* **30**:1–39.
- Zande, A. N. van der, and P. Vos. 1984. Impact of a semi-experimental increase in recreation intensity on the densities of birds in groves and hedges on a lake shore in The Netherlands. *Biological Conservation* **30**:237–259.