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Recreational Trail-Use Effects on American Robin
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RECREATIONAL TRAIL-USE EFFECTS ON

AMERICAN ROBIN (*Turdus migratorius*) AND YELLOW WARBLER (*Dendroica
petechia*) NESTING ECOLOGY AND BEHAVIOR

by

WILLIAM WESLEY MERKLE

B.A., Stanford University 1991

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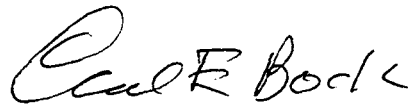
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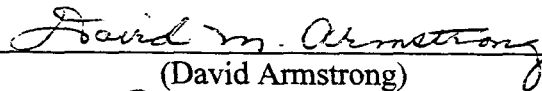
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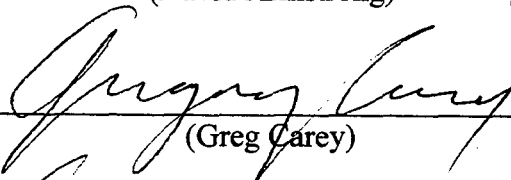
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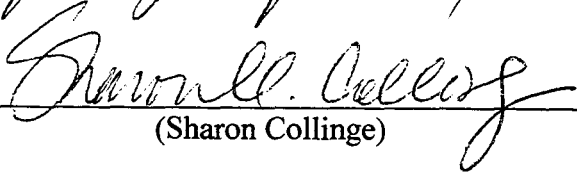
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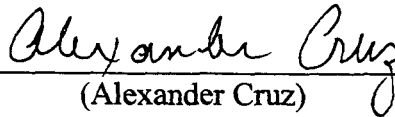
(David Armstrong)



(Greg Carey)



(Sharon Collinge)



(Alexander Cruz)

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Recreational trail-use effects on American robin (*Turdus migratorius*) and yellow warbler (*Dendroica petechia*) nesting ecology and behavior

Thesis directed by Professor Dr. Carl E. Bock

Abstract - I examined the effects of recreational trail-use on the nesting ecology and behavior of American robins (*Turdus migratorius*) and yellow warblers (*Dendroica petechia*) in willow (*Salix* spp.)/cottonwood (*Populus* spp.) riparian habitats located on public open space lands in Boulder County, Colorado. In 1999-2001, I located and monitored 319 robin and 113 warbler nests in riparian corridors with and without trails, to determine success. I conducted behavioral observations on pairs of birds associated with active nest-sites, and recorded frequencies of trail-use.

American robin nests were more abundant at medium and low-use trail study areas than at non-trail and high-use trail areas. Reproductive success was greatest at medium and high-use trail study areas and lowest at low-use trail areas. The weight of the heaviest nestling in each nest increased with recreational use at an area. Females incubated more, but fed nestlings less often with increasing trail-use, whereas males increased their food deliveries to nestlings as recreational use increased, compensating for the reduction in feedings by females. Although robins altered their behavior with increasing trail-use, no reproductive effects of these behavioral alterations were detected.

More yellow warbler nests than expected were located at study areas with intermediate levels of recreational use, whereas fewer nests than expected were located at non-trail study areas, and no warbler nests were located at the two study areas with the highest use. Reproductive success was greater at trail compared to non-trail study areas. Nest parasitism by brown-headed cowbirds (*Molothrus ater*) did not differ by recreational use-level. None of the behavioral measures varied with recreational use, possibly because warblers are active in the canopy and have small, well-concealed nests.

In conclusion, higher-use trail-sites for robins and trail-sites for warblers apparently provided refuges from nest predation that allowed for higher productivity, possibly due to the displacement of some nest predators by disturbance from recreational users. However, fewer robin nests than expected and no warbler nests were found at the two highest-use study areas, indicating that high levels of disturbance may have prevented some robins from nesting and a potential upper limit to this refuge effect for warblers.

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CHAPTER 1

IMPACTS OF PASSIVE RECREATION ON TERRESTRIAL LANDBIRDS

Abstract – I review the impacts of passive recreational activities on non-raptorial terrestrial landbirds, by addressing several topics of relevance to land managers, policy makers, and conservationists. Previous research suggests that generalist, and human and edge-associated landbirds, in addition to birds from the family Corvidae, sometimes increase in abundance with recreational activities, whereas specialist birds tend to decline. However, in some cases even common and generalized landbirds may decline in abundance with recreational use. Studies have associated passive recreation with the alteration of certain aspects of landbird behavior, including song occurrence, flushing response, nest defense, foraging, and activity and use of habitat. Results of studies examining reproductive success of landbirds have been equivocal. Some indicate increased nest predation risk with recreational activities, whereas others indicate a refuge effect due to the apparent displacement of nest predators. Future research should focus on determining whether alterations in landbird behavior with recreational activities are associated with declines in abundance and reductions in reproductive success, and on elucidating the direct and indirect mechanisms through which recreational activities affect landbirds. Researchers should measure frequencies of recreational use to test for threshold and non-linear responses. Finally, researchers should attempt to determine the factors that explain why landbirds in some areas may be subject to increased risk of nest predation with recreational activities, and in other areas benefit from a refuge effect.

In the United States, the number of people participating in passive recreational activities is increasing dramatically, a trend that is expected to continue (Flather and Cordell 1995, Cole 1996). Most land managers and scientists now recognize that recreational activities can have large impacts on wildlife populations. While the intensity of recreational use of public lands is clearly increasing, little is known about how these activities affect wildlife populations, including landbirds (van der Zande et al. 1984, Knight and Gutzwiller 1995, Gutzwiller et al. 1997). In most cases, land managers lack the information necessary to make informed decisions regarding potential trade-offs between recreational use of an area and its value for wildlife preservation.

Terrestrial landbirds have been selected as the focus of this review for several reasons. They are observable, relatively easily censused by their songs, calls, and high visibility, and their nests can be located and monitored to determine reproductive success. Landbirds also are typically active during the day, when most recreational activities occur. Many aspects of landbird ecology have been thoroughly researched, including their responses to some forms of disturbance and environmental perturbations, providing a basis for comparisons. Landbirds can serve as indicators of environmental quality in areas subject to recreational activities (Bibby 1999, Canterbury et al. 2000). Breeding populations of many North American landbirds are in decline (Robinson and Wilcove 1994, Peterjohn et al. 1995). Recreational activities, by negatively impacting breeding habitat quality, may be a factor in some of these declines. Research on landbirds may illuminate the mechanisms by which recreation affects populations, possibly providing insights to reasons behind some landbird declines.

Recreational impacts on terrestrial landbirds probably are due to multiple, interacting factors. Recreational effects may be either direct or indirect (van der Zande et al. 1984). Direct impacts immediately affect landbird habitat selection, behavior, or reproductive success, whereas indirect effects work through intermediary factors such as vegetation, food resources, nest predators, cowbird parasitism, or other factors such as diseases and parasites (Figure 1). Disturbances from recreationists may alter behavior and affect the reproductive success of individual birds, and, thereby, influence population dynamics (Gutzwiller et al. 1997, Marzluff 1997). In addition, recreational activities may alter communities by shifting competitive relationships (Gutzwiller 1995). Effects of recreation may be cumulative (increasing in effect by successive addition) and synergistic (one factor exacerbates the effects of a different factor) (Gutzwiller 1995).

The primary objectives of this review are to synthesize what is known, seek emerging principles, reveal knowledge gaps, and indicate new directions for future research regarding recreational impacts on landbirds. I approached this process by addressing several topics of relevance to land managers, policy makers, and conservationists. For this review, I included studies of terrestrial landbirds excluding raptors. I considered only passive, non-consumptive, and non-motorized recreational activities such as hiking, mountain biking, jogging, camping, rock climbing, nature viewing, and exercising pets. Hunting, off-road vehicles, and snowmobiles were not included. I searched the literature using the Chinook online library database at the University of Colorado (Boulder, Colorado), and the Web of Science, Zoological Record, and Dissertation Abstracts online databases. Each of these databases was searched for literature containing the keywords

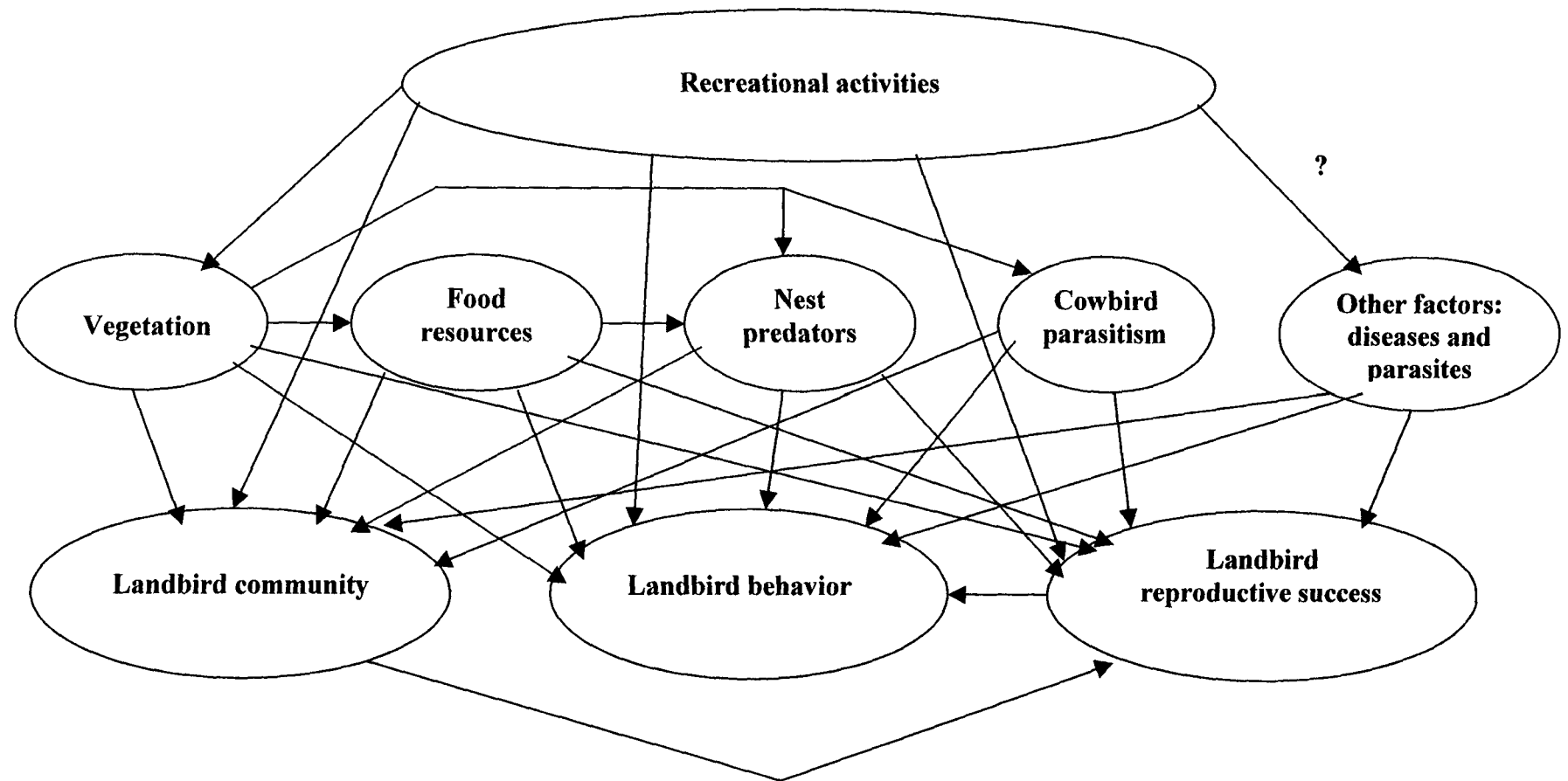


Figure 1. A schematic of how passive recreational activities can affect landbirds. Arrows indicate potential impacts.

recreation, human disturbance, trails, campsite, and campground, limiting searches to those dealing with birds or wildlife. Literature was restricted to documents printed in English, and only mainstream, national and international journals were considered (Table 1).

Major findings of my literature review are as follows:

Passive recreation can affect landbird abundance.

Several studies have found that generalist and edge-associated landbirds are attracted to trails and recreational activities, whereas specialist landbirds are displaced. American robins (*Turdus migratorius*), blue jays (*Cyanocitta cristata*), and brown-headed cowbirds (*Molothrus ater*) increased in abundance near recreational trails (Hickman 1990). Acadian flycatchers (*Empidonax viriscens*), which have been described as area-sensitive forest interior birds, also increased in abundance along trails, possibly because trails provided them open areas required for foraging. Only white-breasted nuthatches (*Sitta carolinensis*) were less abundant near trails, although no reason was given for their decline. Miller et al. (1998) also found that avian community composition was altered adjacent to recreational trails, with some generalist species more abundant near trails compared to lower abundance for more specialized landbirds. In grassland habitats, vesper sparrows (*Poocetes gramineus*), western meadowlarks (*Sturnella neglecta*), and grasshopper sparrows (*Ammodramus savannarum*) were more abundant on non-trail control transects compared to transects along trails. American robins were the only landbird to

Table 1. Studies of recreational impacts on terrestrial landbirds.

Study	Location	Habitat	Measure of recreational use	Type of study
Cooke 1980	Great Britain	Rural vs. suburban	Experimental human approaches	Landbird behavior
Knight 1984	Washington, U.S.	Shrub steppe grassland & agricultural fields	Experimental human approaches	Landbird behavior
van der Zande et al. 1984	Netherlands	Deciduous & coniferous woodlands	Recreational use (non-trail)	Landbird abundance
van der Zande and Vos 1984	Netherlands	Lake shore shrubs & woodlands	Recreational use (non-trail)	Landbird abundance
Blakesley and Reese 1988	Utah, U.S.	Riparian woodlands	Used vs. control areas	Landbird abundance
Hickman 1990	Illinois, U.S.	Deciduous riparian woodlands	Trail presence	Landbird abundance
Burger and Gochfeld 1991	India	Rural vs. suburban	Experimental human approaches	Landbird behavior
Gutzwiller et al. 1994, 1997, 1998a, 1998b	Wyoming, U.S.	Subalpine & mixed conifer forests	Experimental human intrusions & approaches	Landbird behavior
Ammon 1995	Colorado, U.S.	Subalpine wet meadows	Recreational use & used vs. control areas	Landbird nest success & nest predator abundance
Riffel et al. 1996 and Gutzwiller et al. 1999 and 2002	Wyoming, U.S.	Subalpine & mixed conifer forests	Experimental human intrusions	Landbird abundance
Saab 1996	Idaho, U.S.	Cottonwood riparian woodlands	Used vs. control areas	Landbird abundance
Camp and Knight 1998	California, U.S.	Cliffs	Climbed vs. unclimbed & type of use	Landbird abundance & behavior
Miller et al. 1998	Colorado, U.S.	Grasslands	Trail presence	Landbird abundance & nest success
		Ponderosa pine forests	Trail presence	Landbird abundance & nest success
Fernandez-Juricic and Telleria 1999	Madrid, Spain	Deciduous & coniferous woodlands in urban parks	Recreational use (non-trail)	Landbird nest success (recruitment)
Miller 1999	Colorado, U.S.	Willow/cottonwood riparian woodlands	Trail presence	Landbird nest success

Table 1 (continued)

Study	Location	Habitat	Measure of recreational use	Type of study
Fernandez-Juricic 2000a and 2000b	Madrid, Spain	Deciduous & coniferous woodlands in urban parks	Recreational use (non-trail)	Landbird abundance
Fernandez-Juricic and Telleria 2000	Madrid, Spain	Deciduous & coniferous woodlands in urban parks	Recreational use (non-trail)	Landbird behavior
Miller and Hobbs 2000	Colorado, U.S.	Willow/cottonwood riparian woodlands	Trail presence	Artificial nests & nest predator identification
Fernandez-Juricic et al. 2001	Madrid, Spain	Deciduous & coniferous woodlands in urban parks	Experimental human approaches	Landbird behavior
Miller et al. 2001	Colorado, U.S.	Grasslands	Experimental human approaches & type of use	Landbird behavior
		Ponderosa pine forests	Experimental human approaches & type of use	Landbird behavior

increase in abundance with proximity to recreational trails in forested habitats. Black-billed magpies (*Pica hudsonia*) in grasslands, and house finches (*Carpodacus mexicanus*) in forests, were detected only along trails, but in small numbers. Five landbirds described as habitat specialists, western wood peewees (*Contopus sordidulus*), pygmy nuthatches (*Sitta pygmaea*), Townsend's solitaires (*Myadestes townsendi*), plumbeous vireos (*Vireo plumbeus*), and chipping sparrows (*Spizella passerina*), decreased in abundance near trails in forests. Miller and Hobbs (2000) found that black-billed magpies (*P. hudsonia*) were more abundant along trail sites compared to control sites in riparian habitats.

The number of bird taxa did not differ with level of climbing activity at cliff sites (Camp and Knight 1998). However, generalist, and human and edge-associated species such as European starlings (*Sturnus vulgaris*) and brown-headed cowbirds were observed only at climbed cliffs, as were American robins (though only observed twice), and house finches were 69% more abundant at popular climbing cliffs compared to unclimbed cliffs. Of three landbirds seen only at unclimbed cliffs, two were observed only once, providing minimal evidence of displacement from climbed cliffs.

In contrast to the studies above, other work suggests that recreational activity can have negative effects on species richness or the abundance of common landbirds. In Madrid, Spain, the densities of four species of common ground foraging birds, blackbirds (*Turdus merula*), magpies (*P. pica*), starlings (*S. unicolor*), and woodpigeons (*Columba palumbus*) were reduced when pedestrians were near sampling plots compared to undisturbed plots, and breeding densities for each of these species decreased with increasing pedestrian use of urban parks (Fernandez-Juricic 2000a). Controlling for park area, pedestrian rate was positively associated with species turnover and negatively

associated with species richness and the probability of occurrence of 16 of 17 landbirds. Density estimates for 8 of 13 landbirds, many of which were common species, were negatively correlated with intensities of recreational use in deciduous and coniferous woodlands in the Netherlands (van der Zande et al. 1984). The richness and abundance of a set of common landbirds was reduced with experimental human intrusions in subalpine and mixed-conifer forests, but these effects were not cumulative over years (Riffell et al. 1996). The lack of a cumulative yearly effect may have been due to the replacement of displaced individuals or birds habituating to human intrusion in subsequent years of study (Riffell et al. 1996).

Other studies have found no effect of recreational activities on landbird abundance. In shrub and woodland habitats along a lake shore in the Netherlands, the densities of the 12 most abundant landbirds did not differ significantly between sites where recreational use increased significantly after a car park was developed and control sites with little recreational use (van der Zande and Vos 1984). Sauvajot et al. (1998) found no effect of human disturbance associated with roads and trails on the abundance of resident landbirds in chaparral habitats in California.

Recreational campsites can affect landbird abundance through the alteration of vegetation, attraction of human-associated species to food and garbage, and direct human disturbance (Cole and Landres 1995, Marzluff 1997). Saab (1996) found that overall landbird abundance was significantly reduced at campsites compared to unmanaged areas, even though vegetation was similar. Lower abundance at campsites was reported for eight landbirds. Only the warbling vireo (*Vireo gilvus*) increased in abundance at campsites. The warbling vireo may have been unaffected by recreational disturbance because it

occupies the upper canopy, but no reason was given for its increase in abundance at campsites. In another study, overall, the densities of 14 landbirds differed significantly between campground and control sites, with changes in bird communities associated with lower shrub, sapling, and tree densities, as well as reduced cover of deadwood and litter, in campgrounds (Blakesley and Reese 1988).

Passive recreation typically is associated with alterations of landbird behavior.

Changes in landbird behavior with recreational activities can be highly sensitive indicators of stress (Clemmons and Buchholz 1997). In one study, low-level experimental human intrusions reduced song occurrence for some species, although responses to intrusion were not consistent within species among sites and among years (Gutzwiller et al. 1994). In addition, low-level human intrusions did not strongly influence the seasonal timing of primary song of three landbirds (Gutzwiller et al. 1997). However, ruby-crowned kinglets (*Regulus calendula*) stopped singing earlier in the season at intruded compared to control sites in one year.

Landbirds in areas subject to passive recreational activities may alter how they respond to perceived threats from recreationists. For vesper sparrows and western meadowlarks in grasslands, and American robins in forests, the probability of flushing at a given distance from a trail (or the observers line of travel for off-trail observations), approach distance (how close a researcher could approach a bird before it flushed), and distance the bird traveled after flushing were almost always greater for off-trail observations compared to those conducted near trails (Miller et al. 2001). These differences were attributed to the habituation of birds in areas near trails to frequent and spatially predictable disturbance from recreational activities (Miller et al. 2001). Other

researchers also have found that landbirds allowed closer approach of humans in suburban areas or areas with higher human activity compared to rural areas and areas with less human activity (Cooke 1980, Burger and Gochfeld 1991). Alternatively, Fernandez-Juricic et al. (2001) found that alert distances (the distance at which a bird begins to exhibit alert behaviors in response to an approaching human) of house sparrows (*Passer domesticus*) increased near pathways in urban parks. They suggest that birds become more wary and less tolerant near areas with human activity.

Recreational activities may alter the nest defense behavior of landbirds. Intensity of female American robin and male and female red-winged blackbird (*Agelaius phoeniceus*) nest defense increased significantly at nests visited repeatedly during the nesting cycle, possibly due to a modification of parental nest defense behavior facilitated through positive reinforcement and loss of fear to human approach (Knight and Temple 1986b). Furthermore, male red-winged blackbirds were able to assess predatory risk, recognize previously encountered humans, and adjust their nest defense response accordingly (Knight and Temple 1986a). Knight (1984) found that ravens (*Corvus corax*) nesting in farmlands flew from nests at greater approach distances and remained farther from a researcher at the base of the nest than ravens nesting in rangelands. Also, ravens in rangelands more vigorously defended their nest sites by calling more frequently and diving more often at researchers compared to ravens in farmlands. Knight (1984) suggested that human persecution of ravens in farmlands may have made a less vigorous nest defense response beneficial, because ravens in these areas would avoid drawing attention to their nest sites.

Recreational activities can interrupt landbird foraging. Marzluff (1997) suggested that generalist foragers may be better able to tolerate recreational disturbances because they can switch to different types of food, whereas more specialized foragers may be more adversely affected. However, blackbirds, which are generalist foragers (Jonsson 1992), spent less time feeding, while increasing the amount of time they were vigilant and moving away from pedestrians, in response to recreationists in urban parks (Fernandez-Juricic and Telleria 2000).

Passive recreational activities also can alter the activity and positioning of landbirds. Landbirds were more likely to be perched at unclimbed cliff faces than at popular climbing cliffs (Camp and Knight 1998). Fernandez-Juricic and Telleria (2000) found that blackbirds foraged farther from pathways and closer to protective cover with increasing pedestrian use of urban parks. They suggested that blackbirds reacted to pedestrians as if they were potential predators. Conversely, Gutzwiller et al. (1998a) found that low-level human intrusions did not affect the vertical positioning of four landbirds: mountain chickadees (*Parus gambeli*), ruby-crowned kinglets, yellow-rumped warblers (*Dendroica coronata*), and dark-eyed juncos (*Junco hyemalis*).

Passive recreation can negatively or positively affect landbird nesting success.

High nest abandonment for three ground-nesting landbirds, Wilson's warblers (*Wilsonia pusilla*), Lincoln's sparrows (*Melospiza lincolnii*), and fox sparrows (*Passerella iliaca*), was significantly positively related to visitor numbers in one year (Ammon 1995). Yet, in the same study, nest predation rates were not higher in areas subject to recreational activities. Miller et al. (1998) found increased nest predation with proximity to recreational trails for a pooled sample of landbirds in grassland and forested habitats.

They suggest that edge-associated nest predators may have been attracted to trail corridors. No nest parasitism was detected in the grassland habitat, and nest parasitism did not vary with nest distance from trails in the forest plots. In another study, predation rates were higher on artificial nests in grassland fields located next to campgrounds (Rosenblatt et al. 2000).

Other studies have found that recreational activities may not affect reproductive success, or even that nest predation rates can decline with recreation and human disturbance. Pedestrian activity did not influence blackbird recruitment rates in urban parks (Fernandez-Juricic and Telleria 1999), even though blackbirds were shown to alter their foraging behavior and were found at reduced densities with pedestrian activity (Fernandez-Juricic 2000a, Fernandez-Juricic and Telleria 2000). Predation rates on artificial nests did not differ with distance from mowed trails, or between fields with and without mowed trails, in grasslands (Rosenblatt et al. 2000). Although these mowed trails may have resembled recreational trails structurally, they lacked recreational users. Miller and Hobbs (2000) found that predation rates on artificial nests increased with distance from trails along two riparian drainages, possibly due to the displacement of some nest predators by disturbance from recreational users. However, nesting success for American robins at the same sites did not differ between areas with and without trails, and predation rates on the artificial nests were an order of magnitude higher than for the natural nests (Miller 1999, Miller and Hobbs 2000). Ortega et al. (1997) found that American robin nests that were experimentally touched had higher success rates than control nests that were untouched; however, differences in nest height may have confounded the results.

Ortega et al. (1997) hypothesized that some predators may have avoided the human scent at touched nests.

Passive recreation can alter nest predator communities.

Some nest predators appear to be attracted to areas subject to recreational activities, whereas others appear to be repelled. Predators may be attracted to human refuse at picnic tables, garbage cans, and left along recreational trails (Miller 1994, Marzluff 1997). Corvid abundance increased with recreational activities and along recreational trails (Hickman 1990, Miller and Hobbs 2000, Gutzwiller et al. 2002), and Miller and Hobbs (2000) found that avian nest predators depredated more artificial nests than expected near trails in riparian habitats. However, Fernandez-Juricic (2000a) found that magpie (*P. pica*) abundance declined with increasing pedestrian use of urban parks. In subalpine meadows, short-tailed weasel (*Mustela erminea*) abundance was greater in areas with high compared to lower recreational use, although the nesting success of three ground-nesting landbirds did not vary with recreational use (Ammon 1995). Sauvajot et al. (1998) found reduced abundance of small mammals with human disturbance along roads and trails in chaparral habitats. Other researchers found that small mammals depredated more artificial nests than expected away from trails and fewer nests than expected near trails (Miller and Hobbs 2000). Rosenblatt et al. (2000) found no difference in mammal use of grassland fields with and without mowed trails. Finally, the diversity and abundance of diurnal raptors were lower along recreational trails compared to non-trail control sites in lowland riparian habitats (Fletcher et al. 1999).

Passive recreation can alter landbird nest placement

Landbirds may alter their nest placement apparently to avoid some disturbance from recreationists. Miller (1999) found that American robin nest height was negatively related to nest distance from a trail, and that nesting success increased with nest height. Black-billed magpies (*P. hudsonia*) that were experimentally disturbed nested higher in subsequent breeding seasons, presumably to avoid the risk of human disturbance (Knight and Fitzner 1985). However, Dhindsa et al. (1989) found that black-billed magpies (*P. hudsonia*) did not nest higher following human disturbance at nest sites, but human disturbance was associated with magpies changing trees for renesting in the same season.

Recreational impacts can depend on habitat type.

Research on plant communities has shown that passive recreational activities can alter plant communities, particularly low-standing vegetation subject to trampling, and dead wood that is harvested for campfires (Cole and Landres 1995, Marzluff 1997). Accordingly, landbirds dependent upon grassland, shrubby, or forest understory habitats, and those that are dependent on dead wood (e.g. secondary cavity nesters) are predicted to be most negatively affected by recreational activities (Marzluff 1997). Recreational activities may have pronounced impacts on landbirds in grasslands because these birds are ground nesters and foragers. Recreational activities and trails also may have large impacts on relatively uniform, less patchy habitats, such as forests in the midwest or eastern United States or grasslands, because landbirds in these habitats may be sensitive to habitat fragmentation and loss, edge effects, and human disturbance (Faaborg et al. 1995, Tewksbury et al. 1998). Naturally fragmented habitats, or those with large amounts of edge, such as riparian woodlands, may not be significantly affected by recreational

activities because landbirds in these systems may be adapted to edge and patchy environments (Berry and Bock 1998). Also, dense vegetation within some habitats can provide cover that allows landbirds to avoid some disturbance from recreationists (Fernandez-Juricic and Telleria 2000). Finally, recreational activities may have greater impacts at higher elevations compared to lower elevations due to the shorter breeding season, which provides less opportunity for renesting, and more extreme climatic conditions that may make extra energy expenditures (e.g. flushing) more costly (Badyaev and Ghalambor 2001).

Support for the above predicted habitat relationships is equivocal. Recreational effects in grasslands appear to be negative as predicted, with studies finding reduced landbird abundance and increased nest predation rates with recreational activities (Miller et al. 1998, Rosenblatt et al. 2001). In shrub habitats, recreational effects appear to be variable and not strongly negative as predicted (Ammon 1995, Sauvajot et al. 1998). Recreational effects in forests tend to be consistently negative, with studies indicating alteration of behavior, reduced landbird abundance, and increased nest predation rates (van der Zande et al. 1984, Gutzwiller et al. 1994, Riffel et al. 1996, Gutzwiller et al. 1997). However, recreational effects can be negative in anthropogenically and naturally fragmented habitats, providing no evidence that landbirds in these habitats are pre-adapted to recreational disturbance (Miller et al. 1998, Fernandez-Juricic 2000a). Some studies conducted in riparian habitats indicated that landbird communities were altered with recreational activities (Blakesley and Reese 1988, Hickman 1990, Saab 1996, Miller and Hobbs 2001), but other studies found no change in landbird communities and decreased nest predation rates with recreational activities (van der Zande and Vos 1984, Miller and

Hobbs 2001). Finally, although recreational effects on landbirds at high elevations appear to be negative, there is not enough evidence to suggest that the effects are stronger than at lower elevations (Gutzwiller et al. 1994, Ammon 1995, Riffel et al. 1996, Gutzwiller et al. 1997).

Recreational impacts on landbirds do not seem to differ between Europe and North America.

It is possible that landbirds in Europe might respond differently to recreational activities than closely related birds in North America as a result of the considerably longer history of dense human settlement and development in Europe (Martin and Clobert 1996). European species have had hundreds, and even thousands of years, to adapt to human disturbance. In comparison, North American landbirds have been subjected to much more recent and rapid increases in human disturbance, potentially allowing for habituation to disturbance and imprinting on certain habitats, but precluding genetic adaptation. For example, in Europe, most thrushes and many warblers forage and nest in urban areas. Comparatively, in North America, only the American robin among the thrushes occupies urban habitats, and most tree-nesting warblers (family Parulidae) typically do not nest in urban areas.

The prediction that European landbirds are better adapted to recreational disturbance than North American birds is not supported by the literature. Research suggests that European landbirds, even common species, can be affected negatively by recreational activities (van der Zande et al. 1984, Fernandez-Juricic 2000a, Fernandez-Juricic and Telleria 2000). In comparison, recreational effects on North American

landbirds seem to be variable and not consistently negative (Hickman 1990, Camp and Knight 1998, Miller et al 1998, Miller and Hobbs 2001).

Recreational impacts can depend upon the species or guild of bird.

Landbird characteristics can be associated with susceptibility to recreational impacts. It has been suggested that human-associated species, habitat generalists, edge-associated species, residents or short distance migrants, and species that nest and forage in the upper canopy may not be greatly effected or may even respond positively to recreational use (Marzluff 1997, Gutzwiller et al. 1998b). In contrast, habitat specialists, long distance migrants, and species that nest or forage on the ground are predicted to respond negatively to recreational use (Marzluff 1997, Gutzwiller et al. 1998b). There is some evidence to support these predictions.

Some researchers have found increases in the abundance of generalist and edge-associated landbirds and Corvidae with recreational activities (Hickman 1990, Miller et al. 1998, Miller and Hobbs 2000, Fernandez-Juricic 2001, Gutzwiller et al. 2002, but see Fernandez-Juricic 2000a). Other research has found decreased abundance of landbirds with more specialized habitat requirements along recreational trails (Miller et al. 1998). Fernandez-Juricic (2002) found that pedestrian use of urban parks was significantly related to the observed nested pattern of landbird communities: landbird communities in species-poor parks were subsets of those found in species-rich parks with lower use levels. He suggested that human disturbance served as an environmental filter, with landbirds distributing themselves in parks according to disturbance levels and species-specific sensitivity to disturbance.

In a study of the flush response of landbirds to approaching humans in relatively undisturbed areas, Gutzwiller et al. (1998b) found that approach distance was significantly greater for more conspicuous species and species that were active close to the ground, and that detectability period (amount of time a bird remained visible within 10 m of initial flush point) decreased when fewer conspecifics were nearby. Migratory status and body mass did not affect approach distance and detectability period. Other researchers found that alert distances differed among landbird species, with larger species less tolerant of human approach than smaller ones (Fernandez-Juricic et al. 2001). Riffel et al. (1996) found declines in relative richness and abundance of common landbirds with low intensity experimental intrusions; however, these effects were not due to migratory status (migrants versus residents), nest type (open-cup versus cavity), or nesting height (understory versus canopy). Resident landbirds were not affected by human disturbance associated with roads and trails in chaparral habitats in California (Sauvajot et al. 1998). Acadian flycatchers increased in abundance along recreational trails in deciduous riparian habitats, possibly because they used habitat openings along trails for foraging (Hickman 1990).

The type of recreational activity can affect recreational impacts on landbirds.

Knight and Cole (1995b) suggested that the type of recreational activity would influence recreational impacts on landbirds. Studies of flushing response indicate that some landbirds may have habituated (show reduced response) to recreationists in areas where recreational activities were frequent and predictable, such as along recreational trails, compared to areas where recreation was unpredictable and less frequent (Fernandez-Juricic et al. 2001, Miller et al. 2001, but see Fernandez-Juricic et al. 2001). Miller et al. (2001) found that landbirds responded similarly and at a greater distance to a pedestrian

alone and with a dog on leash than to a dog alone, possibly because dogs and other canids are not major predators of landbirds. The number of birds detected at different distance categories from cliffs did not differ based on type of recreational activity (climbing versus hiking) in the vicinity of the cliffs (Camp and Knight 1998).

Increasing numbers of recreationists typically negatively affect landbirds.

Landbirds can exhibit threshold responses to frequencies of recreational use (Knight and Cole 1995a), and increasing recreational use may magnify any recreational impacts (Marzluff 1997). However, even low levels of recreational activity (as low as 1 user per hour per ha per week) were associated with reduced landbird richness and abundance and some alterations of landbird behavior (Gutzwiller et al. 1994, Riffel et al. 1996, Gutzwiller et al. 1997). Other studies found that increasing numbers of recreationists were associated with reductions in landbird abundance and alteration of landbird foraging behavior (van der Zande et al. 1984, Fernandez-Juricic 2000a, Fernandez-Juricic and Telleria 2000). Ammon (1995) found that high nest abandonment rates in one year were associated with high numbers of recreationists in subalpine meadows. Much more research is needed in this area.

Passive recreational activities can fragment landscapes.

Studies of fragmented landscapes typically investigate species responses to habitat area and connectivity (Faaborg et al. 1995, Collinge and Forman 1998). Collinge and Forman (1998) identified four land conversion scenarios, representing common patterns of landscape change: shrinkage, bisection, fragmentation, and perforation. Passive recreational activities may be associated with some degree of habitat alteration due to the construction of trails, trampling, and campsites. On the other hand, the mere presence of

recreationists may alter the suitability or attractiveness of habitats without physically altering them. For example, the presence of recreationists may enhance habitat for disturbance-associated species and degrade habitats for disturbance-intolerant species. In terms of physical land conversion, recreational trails may bisect habitats by removing a central strip of the original habitat type, and trail networks may fragment landscapes by breaking intact habitats into smaller pieces, or habitat islands. In addition, campsites may perforate landscapes by creating small patches of altered habitat that gradually expand outwards. These patterns of landscape change all involve increases in the amount of habitat edge (Collinge and Forman 1998); edge effects will be covered in the following section.

Few studies have investigated how recreational activities, trails, and campsites alter effective habitat area or connectivity between habitats for landbirds. Fernandez-Juricic (2000b) found that the probability of occurrence of 16 landbirds in urban parks was negatively related to pedestrian rate after controlling for park size and isolation. He concluded that human disturbance apparently intensifies the effects of habitat fragmentation, similar to a reduction in habitat area or an increase in isolation. Thus, without physically altering habitats, disturbance from recreationists may reduce effective habitat area and increase the isolation between non-recreation areas, especially for disturbance-intolerant species.

Habitat area and isolation effects will depend on how far recreational impacts extend into surrounding areas. The physical break in habitat caused by most trails typically is only one or two meters wide and probably does not substantially change amounts of habitat area or restrict the movement of volant landbirds. Hickman

(1990) noted that recreational trails caused breaks in understory vegetation, but not in the canopy on study sites in deciduous forests. Also, for several species of landbird, observed median gap-crossing distance of inhospitable habitat exceeds 100 m (Grubb and Doherty 1999). Therefore, the physical alterations associated with recreational trails probably do not constitute habitat fragmentation and loss.

Passive recreation can cause both positive and negative edge effects.

Plant communities may be altered along recreational trails and in campsites by construction and maintenance activities, in addition to trampling by recreationists, creating habitat edges (Cole and Landres 1995). Changes in plant communities may affect landbird habitat selection either due to the changes in habitat structure, microclimate, or food availability (Cody 1985). For example, insect abundance can be reduced along habitat edges (Burke and Nol 1998). However, some aerial and ground foraging landbirds may benefit from habitat openings along recreational trails and in campsites (Blakesley and Reese 1988, Hickman 1990).

Generalist and edge-associated landbirds are predicted to increase in abundance with recreational activities and specialist landbirds are predicted to decline. In support, American robins increased in abundance along recreational trails (Hickman 1990, Miller et al. 1998), whereas landbirds with specialized habitat requirements declined (Miller et al. 1998). However, neither of these studies investigated factors associated with increased robin abundance along trails. Miller et al. (1998) suggested that increased nest predation rates along trails may have led to a reduction in the abundance of specialist landbirds, by altering their habitat selection preferences.

Recreational trails may function as corridors that facilitate the movements of nest predators and parasitic brown-headed cowbirds into habitat interiors (Chasko and Gates 1982, Askins 1994, Rich et al. 1994), potentially increasing nest predation and parasitism rates adjacent to trails. Researchers have found increases in the abundance of avian nest predators, black-billed magpies (*P. hudsonia*) and blue jays, and nest parasitic cowbirds along recreational trails (Hickman 1990, Miller and Hobbs 2000). Miller et al. (1998) found higher predation rates for a pooled sample of landbirds near trails, but did not find evidence that cowbird parasitism was higher near trails.

Alternatively, habitat edges associated with recreational activities may produce a refuge effect for landbirds capable of tolerating human disturbance, by displacing some nest predators (Osborne and Osborne 1980, Gering and Blair 1999). Researchers have found lower abundance of small mammals, and reduced predation rates on artificial nests by small mammals, in areas subject to recreational activities (Sauvajot et al. 1998, Miller and Hobbs 2000). Small mammals may decline in abundance because of reduced ground cover along trails and areas subject to recreational activities (Dickman and Doncaster 1987). Other research has shown lower raptor diversity and abundance along recreational trails (Fletcher et al. 1999). Raptors may avoid areas where small mammalian prey is scarce (Bock et al. In Press). Finally, Miller and Hobbs (2000) found that predation rates on artificial nests were lower near trails than farther from trails. Their results also suggest the displacement of some nest predators along recreational trails.

What is the spatial extent of recreational impacts?

Few studies have investigated the spatial extent of recreational impacts. Miller et al. (1998) found distance effects on landbird abundance extended about 75 m from

recreational trails. Although effects were infrequent, Gutzwiller and Anderson (1999) found that reductions in the abundance of some landbirds with experimental human intrusions did not extend beyond the perimeter of their 1-ha intruded study sites. More work in this area is needed to allow natural resource managers to better plan trail alignments and for determining possible habitat area effects.

CONCLUSIONS AND DIRECTIONS FOR FUTURE RESEARCH

Landbird responses to recreational activities will differ based upon natural history and species-specific tolerances to disturbance, and possibly even habitat type. Some general rules seem useful in predicting landbird responses to passive recreation. Generalist, edge, and human-associated landbirds, in addition to corvids, may be attracted to areas subject to recreational activities (although this generalization may not hold for areas subject to high recreational use). In comparison, landbirds with more specialized habitat requirements may decrease in abundance in areas subject to recreational activities. Recreational activities affect various aspects of landbird behavior. However, in areas that are subject to frequent and predictable recreational disturbance landbirds may be able to habituate. Ground nesters and foragers, and landbirds active closer to the ground may be more susceptible to recreational disturbance than birds that utilize the canopy. Although potentially useful, none of these general rules appear to be universally applicable.

The mechanisms of landbird attraction and avoidance of areas subject to recreational activities are not well understood. Future research should examine to what extent recreational activities directly affect landbirds, in addition to what roles indirect effects facilitated through changes in habitat vegetation, food resources, predator

communities, cowbird parasitism, or other factors contribute to recreational impacts (Figure 1). Studies examining where landbirds are nesting and foraging within habitats may help to uncover the relative importance of some of the above factors.

Research should focus upon frequency of recreational use, instead of just comparing areas subject to recreational activities with control areas. By examining frequency of use, researchers can determine whether there are threshold levels of use to which landbirds respond, and whether landbird responses vary consistently with use. Measures of intensity of recreational use also may provide researchers alternative ways to investigate non-linear responses, such as testing whether use is a limiting factor in landbird response patterns (Cade et al. 1999). In addition, differences in recreational use among studies may explain some inconsistencies in their results. For example, some landbirds may be attracted to study areas with low levels of recreational use, but decline in abundance in areas subject to higher levels of use. Furthermore, only a few studies have examined the effects of different types of recreational activities on landbirds. If types of recreationists have different impacts on landbirds, then use effects may be confounded.

Recreational activities usually alter various aspects of landbird behavior. However, in most cases it was unclear whether these behavioral alterations resulted in reductions in reproductive output or whether landbirds were able to compensate for these behavioral alterations. Thus, future research should examine potential links between behavioral alterations and landbird abundance and reproductive success.

Studies investigating landbird reproductive success with passive recreation, in addition to studies investigating potential nest predators, have produced equivocal results. Some research has indicated increased predation risk, whereas other research has indicated

a refuge effect, for nests in areas subject to recreational activities and along trails. What accounts for these inconsistencies? Is it related to differences among landbirds, habitat types, predator abundance and behavior, or intensity of recreational use? More research should focus on studying how recreational activities affect individual species of landbirds. In addition, researchers should attempt to identify nest predators and quantify how they respond to recreational activities.

LITERATURE CITED

- Ammon, E. M. 1995. Reproductive strategies and factors determining nest success in subalpine ground-nesting passerines. Ph.D. University of Colorado, Boulder, CO.
- Askins, R. A. 1994. Open corridors in a heavily forested landscape - impact on shrubland and forest-interior birds. *Wildlife Society Bulletin* 22:339-347.
- Badyaev, A. V., and C. K. Ghalambor. 2001. Evolution of life histories along elevational gradients: Trade-off between parental care and fecundity. *Ecology* 82:2948-2960.
- Berry, M. E., and C. E. Bock. 1998. Effects of habitat and landscape characteristics on avian breeding distributions in Colorado foothills shrub. *Southwestern Naturalist* 43:453-461.
- Bibby, C. J. 1999. Making the most of birds as environmental indicators. *Ostrich* 70:81-88.
- Blakesley, J. A., and K. P. Reese. 1988. Avian use of campground and noncampground sites in riparian zones. *Journal of Wildlife Management* 52:399-402.
- Bock, C.E., K.T. Vierling, S.L. Haire, J.D. Boone, and W.W. Merkle. In Press. Patterns of rodent abundance on open-space grasslands in relation to suburban edges. *Conservation Biology*.
- Burger, J., and M. Gochfeld. 1991. Human distance and birds - tolerance and response distances of resident and migrant species in India. *Environmental Conservation* 18:158-165.
- Burke, D. M., and E. Nol. 1998. Influence of food abundance, nest-site habitat, and forest fragmentation on breeding ovenbirds. *Auk* 115:96-104.
- Cade, B. S., J. W. Terrell, and R. L. Schroeder. 1999. Estimating effects of limiting factors with regression quantiles. *Ecology* 80:311-323.
- Camp, R. J., and R. L. Knight. 1998. Rock climbing and cliff bird communities at Joshua Tree National Park, California. *Wildlife Society Bulletin* 26:892-898.
- Canterbury, G. E., T. E. Martin, D. R. Petit, L. J. Petit, and D. F. Bradford. 2000. Bird communities and habitat as ecological indicators of forest condition in regional monitoring. *Conservation Biology* 14:544-558.

- Chasko, G. G., and J. E. Gates. 1982. Avian habitat suitability along a transmission-line corridor in an oak-hickory forest region. *Wildlife Monographs* 82:41.
- Clemmons, J. R., and R. Buchholz. 1997. Behavioral approaches to conservation in the wild. Cambridge University Press, Cambridge, England.
- Cody, M. L. 1985. Habitat selection in birds. Academic Press, Orlando, FL.
- Cole, D. N. 1996. Wilderness recreation use trends, 1965 through 1994. U.S.D.A., Forest Service, Intermountain Research Station, Ogden, UT.
- Cole, D. N., and P. B. Landres. 1995. Indirect effects of recreation on wildlife. Pages 183-201 *in* R. L. Knight and K. J. Gutzwiller, editors. *Wildlife and recreationists*. Island Press, Washington, D.C.
- Collinge, S. K., and R. T. T. Forman. 1998. A conceptual model of land conversion processes: predictions and evidence from a microlandscape experiment with grassland insects. *Oikos* 82:66-84.
- Cooke, A. S. 1980. Observations on how close certain passerine species will tolerate an approaching human in rural and suburban areas. *Biological Conservation* 18:85-88.
- Dhindsa, M. S., P. E. Komers, and D. A. Boag. 1989. Nest height of black-billed magpies - is it determined by human disturbance or habitat type. *Canadian Journal of Zoology* 67:228-232.
- Dickman, C. R., and C. P. Doncaster. 1987. The ecology of small mammals in urban habitats .I. Populations in a patchy environment. *Journal of Animal Ecology* 56:629-640.
- Faaborg, J., M. Brittingham, T. Donovan, and J. Blake. 1995. Habitat fragmentation in the temperate zone. Pages 357-380 *in* T. E. Martin and D. M. Finch, editors. *Ecology and management of Neotropical migratory birds*. Oxford University Press, New York, NY.
- Fernandez-Juricic, E. 2000b. Bird community composition patterns in urban parks of Madrid: The role of age, size and isolation. *Ecological Research* 15:373-383.
- Fernandez-Juricic, E. 2000a. Local and regional effects of pedestrians on forest birds in a fragmented landscape. *Condor* 102:247-255.
- Fernandez-Juricic, E. 2002. Can human disturbance promote nestedness? A case study with breeding birds in urban habitat fragments. *Oecologia* 131:269-278.

- Fernandez-Juricic, E. 2001. Avian spatial segregation at edges and interiors of urban parks in Madrid, Spain. *Biodiversity and Conservation* 10:1303-1316.
- Fernandez-Juricic, E., M. D. Jimenez, and E. Lucas. 2001. Alert distance as an alternative measure of bird tolerance to human disturbance: implications for park design. *Environmental Conservation* 28:263-269.
- Fernandez-Juricic, E., and J. L. Telleria. 1999. Recruitment patterns of blackbirds (*Turdus merula*) in urban fragmented populations. *Ardeola* 46:61-70.
- Fernandez-Juricic, E., and J. L. Telleria. 2000. Effects of human disturbance on spatial and temporal feeding patterns of blackbird *Turdus merula* in urban parks in Madrid, Spain. *Bird Study* 47:13-21.
- 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*. Island Press, Washington, D.C.
- Fletcher, R. J., S. T. McKinney, and C. E. Bock. 1999. Effects of recreational trails on wintering diurnal raptors along riparian corridors in a Colorado grassland. *Journal of Raptor Research* 33:233-239.
- Gering, J. C., and R. B. Blair. 1999. Predation on artificial bird nests along an urban gradient: predatory risk or relaxation in urban environments? *Ecography* 22:532-541.
- Grubb, T. C., and P. F. Doherty. 1999. On home-range gap-crossing. *Auk* 116:618-628.
- Gutzwiller, K. J. 1995. Recreational disturbance and wildlife communities. Pages 169-181 in R. L. Knight and K. J. Gutzwiller, editors. *Wildlife and recreationists*. Island Press, Washington, D.C.
- Gutzwiller, K. J., and S. H. Anderson. 1999. Spatial extent of human-intrusion effects on subalpine bird distributions. *Condor* 101:378-389.
- Gutzwiller, K. J., K. L. Clements, H. A. Marcum, C. A. Wilkins, and S. H. Anderson. 1998a. Vertical distributions of breeding-season birds: Is human intrusion influential? *Wilson Bulletin* 110:497-503.
- Gutzwiller, K. J., E. A. Kroese, S. H. Anderson, and C. A. Wilkins. 1997. Does human intrusion alter the seasonal timing of avian song during breeding periods? *Auk* 114:55-65.

- Gutzwiller, K. J., H. A. Marcum, H. B. Harvey, J. D. Roth, and S. H. Anderson. 1998b. Bird tolerance to human intrusion in Wyoming montane forests. *Condor* 100:519-527.
- Gutzwiller, K. J., S. K. Riffell, and S. H. Anderson. 2002. Repeated human intrusion and the potential for nest predation by gray jays. *Journal of Wildlife Management* 66:372-380.
- 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.
- Hickman, S. 1990. Evidence of edge species attraction to nature trails within deciduous forest. *Natural Areas Journal* 10:3-5.
- Jonsson, L. 1992. *Birds of Europe with North Africa and the Middle East*. Princeton University Press, Princeton, NJ.
- Knight, R. L. 1984. Responses of nesting ravens to people in areas of different human densities. *Condor* 86:345-346.
- Knight, R. L., and D. N. Cole. 1995a. Factors that influence wildlife responses to recreationists. Pages 71-79 in R. L. Knight and K. J. Gutzwiller, editors. *Wildlife and recreationists*. Island Press, Washington, D.C.
- Knight, R. L., and D. N. Cole. 1995b. Wildlife responses to recreationists. Pages 51-68 in R. L. Knight and K. J. Gutzwiller, editors. *Wildlife and recreationists*. Island Press, Washington, D.C.
- Knight, R. L., and R. E. Fitzner. 1985. Human disturbance and nest site placement in black-billed magpies. *Journal of Field Ornithology* 56:153-157.
- Knight, R. L., and K. J. Gutzwiller, editors. 1995. *Wildlife and recreationists*. Island Press, Washington, DC.
- Knight, R. L., and S. A. Temple. 1986a. Methodological problems in studies of avian nest defense. *Animal Behaviour* 34:561-566.
- Knight, R. L., and S. A. Temple. 1986b. Why does intensity of avian nest defense increase during the nesting cycle? *Auk* 103:318-327.
- Martin, T. E., and J. Clobert. 1996. Nest predation and avian life-history evolution in Europe versus North America: A possible role of humans? *American Naturalist* 147:1028-1046.

- Marzluff, J. M. 1997. Effects of urbanization and recreation on songbirds. Pages 89-102 in W. M. Block and D. M. Finch, editors. Songbird ecology in southwestern ponderosa pine forests: a literature review. Gen. Tech. Rep. RM-GTR-292. U.S.D.A., Forest Service, Rocky Mountain Forest and Range Experimental Station, Fort Collins, CO.
- Miller, J. R. 1999. The effect of human settlement on bird communities in lowland riparian areas. Ph.D. Thesis. Colorado State University, Fort Collins, CO.
- Miller, J. R., and N. T. Hobbs. 2000. Recreational trails, human activity, and nest predation in lowland riparian areas. *Landscape and Urban Planning* 50:227-236.
- Miller, S. G., R. L. Knight, and C. K. Miller. 1998. Influence of recreational trails on breeding bird communities. *Ecological Applications* 8:162-169.
- Miller, S. G., R. L. Knight, and C. K. Miller. 2001. Wildlife responses to pedestrians and dogs. *Wildlife Society Bulletin* 29:124-132.
- Ortega, C. P., J. C. Ortega, C. A. Rapp, S. Vorisek, S. A. Backensto, and D. W. Palmer. 1997. Effect of research activity on the success of American robin nests. *Journal of Wildlife Management* 61:948-952.
- Osborne, P., and L. Osborne. 1980. The contribution of nest site characteristics to breeding- success among blackbirds *Turdus merula*. *Ibis* 122:512-517.
- Peterjohn, B. G., J. R. Sauer, and C. S. Robbins. 1995. Population trends from the North American Breeding Bird Survey. Pages 3-39 in T. E. Martin and D. M. Finch, editors. *Ecology and management of Neotropical migratory birds*. Oxford University Press, New York, NY.
- 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.
- Riffell, S. K., K. J. Gutzwiller, and S. H. Anderson. 1996. Does repeated human intrusion cause cumulative declines in avian richness and abundance? *Ecological Applications* 6:492-505.
- Robinson, S. K., and D. S. Wilcove. 1994. Forest fragmentation in the temperate zone and its effects on migratory songbirds. *Bird Conservation International* 4:233-249.
- Rosenblatt, D. L., J. L. Newton, and E. J. Heske. 2000. Effects of mowed trails on depredation of artificial nests in grassland. *Prairie Naturalist* 32:29-41.

- Saab, V. A. 1996. Influences of spatial scale and land-use practices on habitat relationships of breeding birds in cottonwood riparian forests. Ph.D. Thesis. University of Colorado, Boulder, CO.
- Sauvajot, R. M., M. Buechner, D. A. Kamradt, and C. M. Schonewald. 1998. Patterns of human disturbance and response by small mammals and birds in chaparral near urban development. *Urban Ecosystems* 2:279-297.
- Tewksbury, J. J., S. J. Hejl, and T. E. Martin. 1998. Breeding productivity does not decline with increasing fragmentation in a western landscape. *Ecology* 79:2890-2903.
- van der Zande, A. N., 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.
- van der Zande, A. N., 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.

CHAPTER 2
RECREATIONAL TRAIL-USE EFFECTS ON AMERICAN ROBIN NESTING
ECOLOGY AND BEHAVIOR

Abstract - I examined the effects of recreational trail-use on the nesting abundance, reproductive success, and behavior of American robins (*Turdus migratorius*) in willow/cottonwood riparian habitats located on public open space lands in Boulder County, Colorado. In 1999-2001, I located and monitored 319 robin nests in riparian corridors with and without trails, and I conducted behavioral observations on pairs of birds associated with active nest sites. I quantified frequency of recreational use, and I classified each study area based on its average recreational use-level. Robin nests were more abundant at medium and low-use trail study areas than at non-trail and high-use trail areas. Reproductive success was greatest at medium and high-use trail study areas and lowest at low-use trail areas. The weight of the heaviest nestling in each nest increased with recreational use at an area. Females incubated more, but fed nestlings less often with increasing trail-use, whereas males increased their food deliveries to nestlings as recreational use increased, compensating for the reduction in female feeding. No reproductive effects of these behavioral alterations were detected. Higher-use trail study areas apparently provided refuges from nest predation that allowed for higher productivity, possibly due to the displacement of potential nest predators by disturbance from recreational users. However, fewer nests than expected were found at high-use study areas, indicating that high levels of disturbance may have prevented some robins from nesting. Although I cannot rule out the possibility that higher canopy cover at the two

highest-use study areas was related to high levels of nesting success in those areas, differences in nesting habitat selection and reproductive success were not associated with differences in vegetation among the other study areas. Results of this study suggest that trails and their use altered predator communities, with avian predators potentially driving nest site selection at trail study areas, and a more varied predator community, particularly ground predators, potentially driving nest site selection at non-trail areas.

INTRODUCTION

In the United States, the number of people participating in passive recreational activities is increasing dramatically, a trend that is expected to continue (Flather and Cordell 1995). Growing human populations increase both the intensity of recreational use of surrounding public lands (Flather and Cordell 1995) and demands for additional recreational opportunities. Most land managers and scientists now recognize that recreational activities can affect the distribution and abundance of songbird populations. Although several studies have investigated these relationships (van der Zande et al. 1984, Gutzwiller et al. 1997), our knowledge of the mechanisms driving species responses to recreational use remains rudimentary (Merkle, Chapter 1). Furthermore, only four studies of songbirds have specifically investigated recreational effects associated with trails (Hickman 1990, Miller et al. 1998, Miller and Hobbs 2000, Miller et al. 2001). Trail effects may differ from other forms of passive recreation because trails concentrate people along a specific corridor, and features associated with the physical structure of trails may attract or repel certain avian and non-avian species (Marzluff 1997, Miller et al. 1998).

Recreational trail-use may alter avian community structure, reproductive success, and behavior (van der Zande et al. 1984, Knight and Gutzwiller 1995). Some studies investigating avian community structure have found that generalist and edge-associated songbirds, including American robins (*Turdus migratorius*), can increase in abundance at areas with trails, whereas the abundance of specialists decreases (Hickman 1990, Miller et al. 1998). Furthermore, it has been suggested that human-associated predators may be attracted to trail areas due to picnic tables, garbage cans, and human litter associated with recreational users (Miller 1994). Avian nest predators and brood parasites can increase in abundance at areas developed with recreational trails (Hickman 1990, Miller and Hobbs 2000, Gutzwiller et al. 2002), potentially reducing the reproductive success of any open-cup nesting songbirds. Other research has indicated that non-trail recreation was negatively related to the abundance of even common and generalized birds such as European blackbirds (*Turdus merula*), which are the ecological equivalent of American robins, starlings (*Sturnus unicolor*), and magpies (*Pica pica*) (Fernandez-Juricic 2000).

Recreational trails and their use may reduce songbird reproductive success and potentially cause areas to function as population sinks (Pulliam 1988). Miller et al. (1998) found decreased nesting success for a pooled sample of songbirds near recreational trails in both mixed grassland and ponderosa pine (*Pinus ponderosa*) habitats. In contrast, Miller and Hobbs (2000) found lower predation rates on artificial nests near trails in lowland riparian habitats, possibly because of the displacement of some nest predators. Pooling data across species may obscure species specific relationships, and conclusions based on artificial nests often do not accurately reflect predation pressures on natural nests (Major and Kendal 1996, Ortega et al. 1998). For these reasons, and due to the equivocal

results of previous studies, more research investigating how individual species of songbirds respond to recreational trails clearly is needed. In addition, all of the above results from trail studies were based only upon trail presence and did not account for the potential effects of different numbers of trail-users. Measuring the frequency of recreational use is important because some effects only may be apparent above certain threshold levels (Knight and Cole 1995), and increased use may magnify recreational impacts (Marzluff 1997).

Disturbance from recreationists can alter the behavior of songbirds, potentially reducing reproductive success (Gutzwiller et al. 1997). Incubating songbirds may flush off nests and spend more time away from nests due to human disturbance (Gotmark 1992). Alternatively, human disturbance at nest sites may cause songbirds to increase vigilance and to defend nests more aggressively (Knight and Temple 1986, Ortega et al. 1997). Recreational trails may reduce food availability, affecting songbird foraging (Cole and Landres 1995, Burke and Nol 1998). In addition, human disturbance may interrupt the foraging of adults (Fernandez-Juricic and Telleria 2000) or food delivery to nestlings.

Trails and trail users also may indirectly affect songbirds through their impacts on vegetation (van der Zande et al. 1984, Cole and Landres 1995, Knight and Gutzwiller 1995). Trail construction and maintenance, in addition to trampling effects of users, can alter plant communities and vegetation structure along trails (Cole and Landres 1995). In addition, ground disturbance and trail-users may spread exotic invasive plants and noxious weeds along trail corridors (Cole and Landres 1995, Marzluff 1997). Changes in plant communities along trails may affect habitat selection and use by songbirds, as well as avian and non-avian nest predators (Cody 1985, Marzluff 1997).

This study was conducted in willow (*Salix* spp.)/cottonwood (*Populus* spp.) riparian habitats. Although they cover less than 1% of the semi-arid western United States landscape, riparian systems support high numbers of plant and animal species and may be critical in maintaining biodiversity on a regional scale (Knopf et al. 1988, Naimen et al. 1993, Rottenborn 1999, Collinge et al. 2001). Western riparian habitats support a greater diversity and higher abundances of breeding and migrating birds than the extensive surrounding upland habitats (Bottorff 1974, Knopf et al. 1988, Ohmart 1994). Despite their conservation value, riparian systems typically are subjected to high levels of human disturbance (Knopf et al. 1988, Ohmart 1994). Researchers have estimated that 95% of riparian habitats in the West have been severely degraded or destroyed (Ohmart 1994, Rottenborn 1999). The development and use of recreational trails may be a factor contributing to the degradation of riparian systems. Riparian habitats are preferentially selected as sites for greenway networks and development of recreational trails (Miller 1994, Miller and Hobbs 2000). For example, sections of most of the major riparian systems in Boulder County, Colorado, have been developed with recreational trails (Miller and Hobbs 2000; Merkle, personal observation).

To examine the ways that recreational trail-use affected an open-cup nesting songbird in riparian habitats, I located and monitored American robin nests, and observed the behavior of robins at their nest sites in riparian corridors with and without recreational trails. Specifically, I tested whether trails and intensities of trail-use affected robin nesting density and reproductive success, and whether robin behavior varied along a gradient of increasing recreational trail-use. Based upon previous studies of robins and other songbirds, I predicted that robin nesting density would increase with recreational trails and

use. I predicted that reproductive success of robins would decline with increasing recreational use. I also predicted that, with increasing recreational use, robins would: 1) decrease incubation due to females flushing off nests in response to recreationists, 2) decrease food deliveries to nestlings, and 3) increase vigilance. Finally, I tested whether vegetation differed among study areas, and whether vegetation affected robin habitat selection and nest success.

METHODS

Study area

I selected eleven study areas in lowland willow/cottonwood riparian woodlands (Andrews and Righter 1992) on four drainages on public open lands in Boulder County, Colorado (40°05' N, 105°15' W) (Appendixes 1 and 2). Boulder County is situated at the interface of the western Great Plains and the eastern edge of the Rocky Mountains. All study areas were at approximately 1,600 m elevation, and downstream of the point where a drainage exited the foothills of the Rocky Mountains onto the plains. Study areas were subject to a range of trail-use intensities, including a control area without trails on each of the four drainages surveyed. Study areas consisted of linear strands of riparian woodlands surrounded by grassland/agricultural fields. American robins are common breeders in these riparian habitats (Pantle 1998). I surveyed eight study areas in 1999, with one additional study area added in 2000 (n = 9 study areas), and two additional study areas added in 2001 (n = 11 study areas). Study areas were separated by at least 1 km, except for two areas with trails that were separated by a major road, and one non-trail and trail

area that were separated by two fences that precluded use. The border of the non-trail study area was at least 150 m from the trail in the adjacent area.

Tree communities were dominated by plains cottonwood (*Populus deltoides*), narrowleaf cottonwood (*Populus angustifolia*), a hybrid of the plains and narrowleaf cottonwood (*Populus x acuminata*), and crack willow (*Salix fragilis*). Other relatively common trees included Russian olive (*Elaeagnus angustifolia*), alder (*Alnus tenuifolia*), river birch (*Betula fontinalis*), and hawthorn (*Crataegus* spp.). Interspersed with the trees were thickets of shrubs, mostly sandbar willow (*Salix exigua*) and snowberry (*Symphoricarpos occidentalis*), with fewer patches of chokecherry (*Prunus virginiana*).

Nest searching and monitoring

During May through August of 1999-2001, I located and monitored a total of 319 American robin nests at all of my study areas. Because robin nests are fairly large and conspicuous, and robins are not overly secretive when approaching their nests, I am confident that I located almost every robin nest at each of the study areas. I checked each nest to determine its status when it was first discovered. Subsequently, I checked active nests every three to four days, recording the date and the number of eggs, nestlings, or fledglings observed. I considered a nest successful if it fledged at least one young, and I defined productivity as the number of young successfully fledging from a nest. If nest contents disappeared prior to fledging, I recorded a predation event. As an additional measure of nest success, I classified nests based on the final stage in the nesting cycle that was achieved (no eggs detected = 0, eggs = 1, nestlings = 2, or fledged = 3), referred to as the nest end stage. I did not detect any brown-headed cowbird (*Molothrus ater*) parasitism of active robin nests. Because individual robins were not color-banded, I

cannot be certain that birds did not renest after failed nesting attempts. Robins that nested early in the season may have renested after successfully fledging a brood (Sallabanks and James 1999; Merkle, unpublished data). Based upon examination of a frequency plot of the dates when all nests were located, I considered nests found prior to julian day 151 (31 May in 1999 and 2001, and 30 May in 2000) in each year as within the initial flush of nesting. I used only these nests in the analysis of nesting habitat selection to avoid most cases of renesting, minimizing pseudoreplication. Due to difficulty in determining the number of young in some nests, I was only able to assign productivity to 311 of the 319 total nests monitored until completion.

Nestling weight

In 2001, I measured nestling weights at twenty-five readily accessible nests. On the tenth day after hatching, I weighed nestlings to the nearest 0.1 g using a 100-g pesola scale and replaced them in the nest (based upon methods in Magrath 1991). Because American robin nestlings typically fledge between 12-15 days after hatching, weighing nestlings at ten days post-hatching provided an approximation of fledging weight without unduly influencing the timing of fledging (Sallabanks and James 1999; Merkle, unpublished data). All nestlings that were weighed remained in their nests after being replaced. I continued to monitor nests at which nestlings were weighed until completion, but I did not conduct additional behavioral observations at these nests.

For each nest, I tested whether average or heaviest nestling weight was correlated with the average number of recreational users per hour at a study area, because larger nestlings may be able to outcompete smaller nestlings for favorable central feeding locations (McRae et al. 1993). I was not able to make comparisons between nestling

weights at study areas with and without trails because I was only able to weigh nestlings at three nests at non-trail areas. Similarly, small sample size precluded comparing nestling weights among use-levels.

Behavioral observations

I selected pairs of American robins associated with active nest sites for behavioral observation using the focal sampling technique (Martin and Bateson 1993). Focal sampling involved watching the pair of birds associated with a nest site and recording all instances of several categories of behaviors. I watched nest sites continuously, and I recorded the frequencies (e.g. food deliveries or nest defense) and time spent performing various behaviors (e.g. incubation or vigilance), and the species and sex of the bird performing the behavior. I sexed robins by head and breast coloration (Pyle 1997, Slagsvold 1997a), as well as behavioral cues (e.g. only the female develops a brood patch for incubating eggs or brooding nestlings; Pyle 1997, Sallabanks and James 1999). I assumed that birds in the immediate vicinity of a nest site were the focal pair of birds associated with that nest. This assumption is reasonable because American robins typically are monogamous and defend territories around their nest sites (Sallabanks and James 1999). Individual observation periods lasted approximately 75 minutes and were conducted using binoculars from a position behind naturally-occurring vegetation at a distance of 15-30 m. I moved into viewing position, then waited 10-15 minutes before beginning the observation. Observations only proceeded when both of the focal birds were not obviously reacting to my presence. I attempted to watch each active nest at least once during the egg and nestling stages of the nesting cycle. After each nest observation, I

checked the nest for the number of eggs or nestlings, using the nest monitoring protocol described above.

I classified behaviors into categories based on Woodard and Murphy (1999) and preliminary observations of the study species (Merkle, unpublished data). Behavioral categories included the following: (1) *Absent*: neither of the focal pair of birds visible around the immediate nest site; (2) *Incubating* or *brooding*: female on the nest incubating eggs or brooding young; (3) *Vigilant*: bird perched near the nest with an alert posture; (4) *Nest guarding*: a male behavior in which the male bird moves to a perch close to the nest when the female leaves the nest after an incubation or brooding bout; (5) *Food deliveries*: the frequency of food deliveries; (6) *Response to recreational users*: any reaction to disturbance (e.g. flush from nest, alarm call, and nest defense behaviors) and the cause; (7) *Nest defense*: chasing or reacting to hetero- or con-specific animals identified to species near the nest. I observed a total of 109 robin nests in the egg stage of the nesting cycle, and 107 nests in the nestling stage of the nesting cycle (some nests were watched during both periods).

I converted all data for behavioral measures and recreational use to percentages of the total time a nest was observed, or as rates per unit time. Total female vigilance time was considered as the percentage of time that the female was incubating or brooding plus the percentage of time that the female was vigilant while off the nest. Total male vigilance time was the percentage of time the male was vigilant plus the percentage of time that the male was nest guarding. The total number of female and male defensive reactions to other animals near the nest was considered as the total nest defense rate.

I analyzed behavioral data separately between the egg and nestling stages of the nesting cycle. To avoid problems with pseudoreplication, I averaged data from different behavioral observations taken at the same nest during the same stage of the nesting cycle (Martin and Bateson 1993). Observation date, start time, and observation length did not vary among categories of trail presence or use-level for observations of nests with both eggs and nestlings, indicating that behavioral observations were conducted consistently across sampling categories.

Quantifying recreational disturbance

During behavioral observations, I recorded the frequency of recreational trail-users. I used the total number of people passing by a nest during an observation divided by observation time (referred to hereafter as the total recreational user rate) as an index of the intensity of recreational use at each nest. I classified study areas on the basis of average recreational use-level measured during nest observations, as follows: high-use > 60 users/hr, medium-use 20-60 users/hr, low-use 0-20 users/hr, and no use (based on approximately 31 hours of sampling per study area). Simultaneously recording bird behavior and recreational trail-use provided data that directly linked trail-use and the associated behavioral responses of focal pairs of birds. The total recreational user rate measured at each nest did not vary with year, observation date, temperature, observation time, or observation length.

Vegetation sampling—nest site characteristics

I measured the height and diameter at breast height (dbh) of the nest tree and the structure and composition of the surrounding vegetation based on the protocol of Martin et al. (1997). I estimated the percentage green ground cover less than 50 cm tall and counted

all shrub stems > 50 cm tall within five meters of the nest. In addition, I recorded the species and size class (dbh) of all tree stems within 11.3 m (~0.04 ha) of the nest. Trees were grouped in size classes as follows: sapling < 8 cm; 8 cm ≤ small trees < 23 cm; 23 ≤ medium trees ≤ 38 cm, and large trees > 38 cm. I summed the total number of saplings and the total number of tree stems in each size class across species. I measured the distance from the nest to the nearest point on a trail (Miller et al. 1998), and the width of riparian vegetation where the nest was located (Miller 1999). I quantified nest concealment from each of the four cardinal directions by estimating the percentage of a 25 cm circle centered at the nest that would be covered by vegetation at a distance of 5 m from the nest at a level horizontal to the nest (based on Martin et al. 1997). I measured percent canopy cover using a concave spherical densiometer. Four readings were taken from a point directly below each nest, turning 90° between readings. I measured nest tree and nest heights using a clinometer or a 2-meter measuring stick.

Nest sites versus non-nest sites

In 2001, to examine the microhabitats that robins selected as nest sites, I sampled a random non-nest site paired with each actual nest site. I located non-nest sites by randomly heading either 30 m upstream or downstream parallel to the creek from the nest (based on Ralph et al. 1993). I selected the first tree of the same species as the tree containing the nest encountered after 30 m as the non-nest tree, and it served as the center of the vegetation plot. I used the same sampling protocol as above for nest sites, excluding any measures specific to the actual nest.

Study area vegetation and habitat area

I sampled the vegetation at each study area using the same protocol as was employed for measuring the vegetation surrounding each nest site, not including any measures specific to quantifying the nest. I located four random points at least 200 m apart at each study area. I sampled each of these central points, as well as three surrounding satellite points 30 m away at 120 degree increments (total of 16 samples per study area). Because the satellite points likely were not independent, I averaged the data from each central point and surrounding three satellites before making vegetation comparisons (four points per study area). I determined the area searched for nests at each study area by estimating the length of riparian habitat from USGS 1:24,000 topographic maps and multiplying by the average of 16 riparian widths measured at each study area.

Data analyses

I treated each nest as a replicate. To increase statistical power, I pooled data from the three years of study for most analyses. Due to deviations from normality, unequal sample sizes, and unequal variances for many variables, I primarily used non-parametric statistics (Zar 1996). I used a critical *P*-value of 0.05 to determine significance for all statistical tests, and I reported tests with *P*-values between 0.05 and 0.10 as marginally significant.

The proportion of nests located while the female was building (37.0%, *n* = 118 nests), laying (11.6%, *n* = 37 nests) or incubating eggs (32.0%, *n* = 102 nests), or the parents were tending nestlings (19.4%, *n* = 62 nests), did not differ between trail and non-trail study areas (*n* = 319 nests, *df* = 1, $\chi^2 = 1.62$, *P* = 0.65), or among use-levels (*n* = 319 nests, *df* = 3, $\chi^2 = 10.70$, *P* = 0.30). Because there was no bias in the stage of the nesting

cycle when nests were initially located between trail and non-trail study areas or among use-levels, I did not utilize Mayfield (1975) type corrections for nesting success.

I used Chi-square tests to determine whether the number of robin nests found at study areas grouped by recreational use-level differed from what would be expected based on area alone, and whether the number of nests succeeding compared to failing and surviving to each nest end stage differed between trail and non-trail study areas and among recreational use levels. I used Mann-Whitney U and Kruskal-Wallis tests to examine whether nest end stage and productivity measures differed between trail and non-trail study areas and among recreational use-levels, and to test whether nest site characteristics differed between successful and unsuccessful nests and among nest end stages. I used Kruskal-Wallis tests to test whether vegetation differed among study areas by recreational use-level. For vegetation measures that differed significantly among recreational use-levels, I used Mann-Whitney U-tests to make post-hoc comparisons between all combinations of recreational use-levels. A Kruskal-Wallis test also was used to test whether habitat area differed among study areas grouped by recreational use-level. I used Spearman's rank correlation procedure to test for correlations of nestling weights with the average number of recreational users at a study area, to test for correlations between behavioral measures and the total recreational user rate, and to test for correlations between behavioral measures and nestling age and the number of nestlings. I tested whether nest site characteristics differed from paired non-nest sites using Wilcoxon signed-rank tests. I utilized SAS version 8.01 for Windows for all statistical tests (SAS Institute Inc. 1999).

RESULTS

Nest density

Nests were not distributed evenly by land area in study areas grouped by recreational use-level (Table 2). Considerably more nests than expected were found at medium-use study areas, and more nests than expected were found at low-use areas. In contrast, many fewer nests than expected were found at non-trail study areas, and fewer nests than expected were found at high-use areas. The habitat area searched for nests at each study area did not differ among recreational use-levels.

Reproductive success

Overall nesting success for robins in this study was 47.0 % ($n = 319$ nests). Predation accounted for 85.2% ($n = 169$ nests) of all nest failures. The number of nests succeeding compared to failing, and nest end stage, did not differ between study areas with and without trails (Table 3). However, the number of nests succeeding compared to failing and nest end stage differed significantly among recreational use-levels (Table 3). Both fledging success and nest end stage were greatest at medium-use study areas followed by high-use, no-use, and then low-use areas. Neither productivity per nest nor productivity per successful nest differed between study areas with and without trails (Table 3). However, both productivity per nest and productivity per successful nest were greatest at high-use study areas and smallest at low-use areas (Table 3).

Nestling weights

Because two nests with extremely low nestling weights may have been driving statistical relationships, I present results from analyses performed on the complete data set

Table 2. Expected vs. observed number of American robin nests based on habitat area in study areas grouped by recreational use-level in Boulder County, Colorado.

Use-level ^a	Area (km ²) ^b	Expected nests	Observed nests
Non-trail	0.132	72.4	46
Low	0.085	46.6	60
Medium	0.105	57.6	81
High	0.059	32.4	22
TOTAL	0.382	209	209

Notes: Chi-square test: $df = 3$, $\chi^2 = 13.51$, $P < 0.005$.

^a Non-trail = 0 users/hr; Low = 0-20 users/hr; Medium = 20-60 users/hr; High > 60 users/hr.

^b Average area searched per year.

Table 3. Reproductive parameters for American robins nesting at study areas with varying recreational use-levels in Boulder County, Colorado.

Variable	Study areas by recreational use-level				Combined trail study areas
	Non-trail	Low	Medium	High	
Fledging success (%) ^a (n = 319 nests)	45.3 (75)	32.1 (84)	56.1 (123)	54.0 (37)	47.5 (244)
Nest end stage ^{bc} (n = 319 nests)	1.97 ± 0.12 (75)	1.67 ± 0.12 (84)	2.21 ± 0.09 (123)	2.03 ± 0.19 (37)	2.00 ± 0.07 (244)
Productivity per nest ^d (n = 311 nests)	1.26 ± 0.18 (73)	0.84 ± 0.15 (83)	1.71 ± 0.15 (118)	1.78 ± 0.29 (37)	1.42 ± 0.10 (238)
Productivity per successful nest ^e (n = 143 nests)	2.87 ± 0.12 (32)	2.69 ± 0.17 (26)	3.11 ± 0.08 (65)	3.30 ± 0.19 (20)	3.04 ± 0.07 (111)

Notes: Nesting data were pooled over all use-levels from study areas with trails to produce the combined trail study areas column. Fledging success data are the percentage of nests that fledged at least one young. All other data are means ± SE. Sample sizes are in parentheses.

^a Chi-square test of number of nests succeeding compared to failing among study areas grouped by recreational use-level: df = 3, $\chi^2 = 12.35$, $P < 0.007$.

^b Nest end stage categories: 0 = no eggs; 1 = eggs; 2 = nestlings; 3 = fledged.

^c Kruskal-Wallis test: df = 3, $\chi^2 = 13.67$, $P < 0.004$.

^d Kruskal-Wallis test: df = 3, $\chi^2 = 17.58$, $P < 0.0006$.

^e Kruskal-Wallis test: df = 3, $\chi^2 = 9.68$, $P < 0.03$

($n = 25$ nests) and a reduced data set ($n = 23$ nests) in which the two "outlier" nests were removed. For the complete data set ($n = 25$ nests), the weight of the heaviest nestling in each nest was positively correlated with the average number of recreational users per hour at a study area ($r = 0.55$, $P < 0.005$). Average nestling weight was marginally positively correlated with the average number of recreational users per hour at a study area ($r = 0.34$, $P < 0.10$). For the reduced data set ($n = 23$ nests), heaviest nestling weight, but not average nestling weight, remained positively correlated with the average number of recreational users per hour at a study area ($r = 0.45$, $P < 0.05$).

Behavior

At nests observed with eggs, the percentage of time females spent incubating was significantly positively correlated with the total recreational user rate (Figure 1). Total female vigilance time also was significantly positively correlated with the total recreational user rate ($n = 109$, $r = 0.25$, $P < 0.05$) and highly positively correlated with the percentage of time spent incubating ($n = 109$, $r = 0.95$, $P < 0.001$). Total male vigilance time and the total nest defense rate were not correlated with the total recreational user rate.

For nests observed with nestlings, female food delivery rate was significantly negatively correlated with the total recreational user rate (Figure 2). In contrast, male and total food delivery rates were not significantly correlated with the total recreational user rate (Figures 3 and 4). Female percentage of total food deliveries was significantly negatively correlated with the total recreational user rate ($n = 107$, $r = -0.24$, $P < 0.02$). Total male vigilance time was negatively correlated with the total recreational user rate (Figure 5).

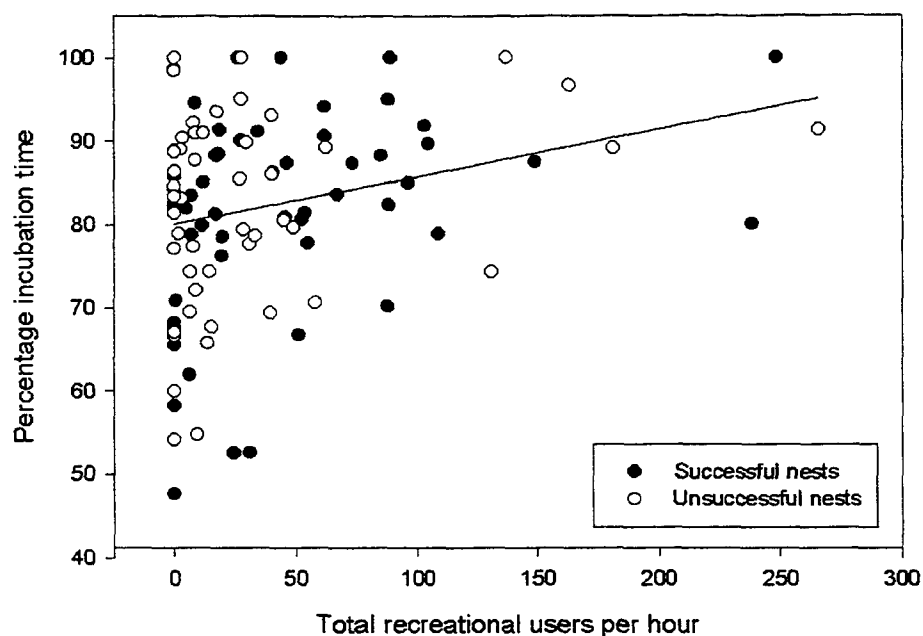


Figure 1. Percentage of time females spent incubating vs. total recreational users per hour for 109 American robin nests.
Spearman correlation procedure: $r = 0.23$, $P < 0.05$.
Regression line: $y = 80.09 + 0.06x$, $r^2 = 0.06$, $F = 7.31$, $P < 0.01$.

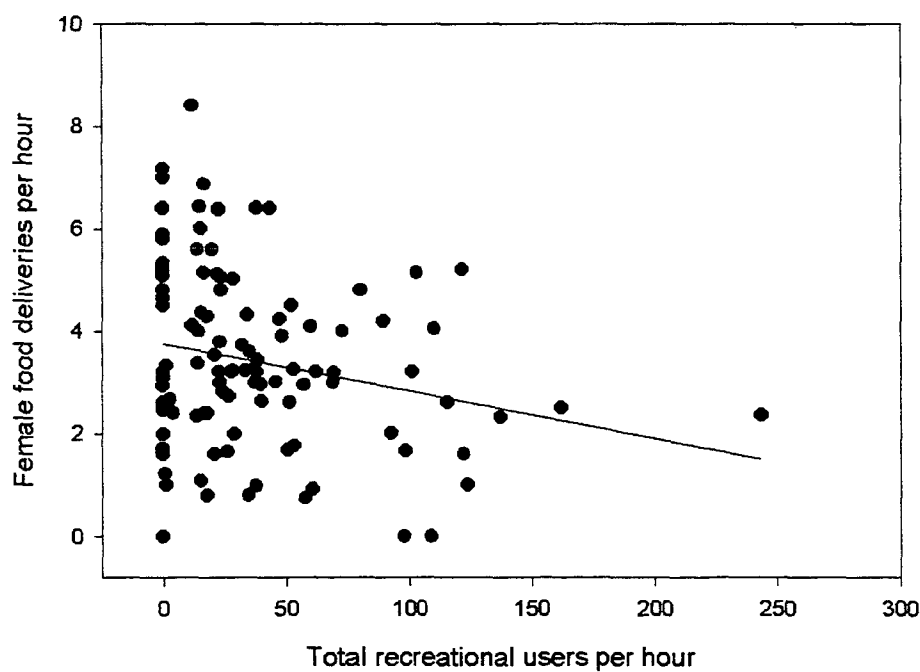


Figure 2. Female food deliveries per hour vs. total recreational users per hour for 107 American robin nests.
Spearman correlation procedure: $r = -0.19$, $P < 0.05$.
Regression line: $y = 3.76 - 0.009x$, $r^2 = 0.05$, $F = 5.50$, $P < 0.03$.

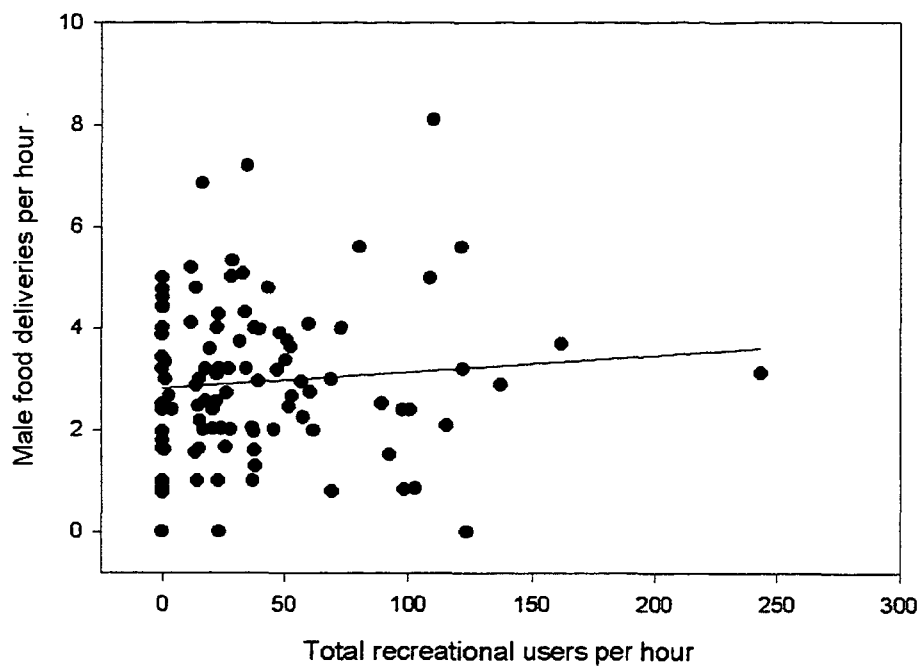


Figure 3. Male food deliveries per hour vs. total recreational users per hour for 107 American robin nests.

Spearman correlation procedure: $r = 0.10$, $P = 0.32$.

Regression line: $y = 2.82 + 0.003x$, $r^2 = 0.003$, $F = 0.78$, $P = 0.37$.

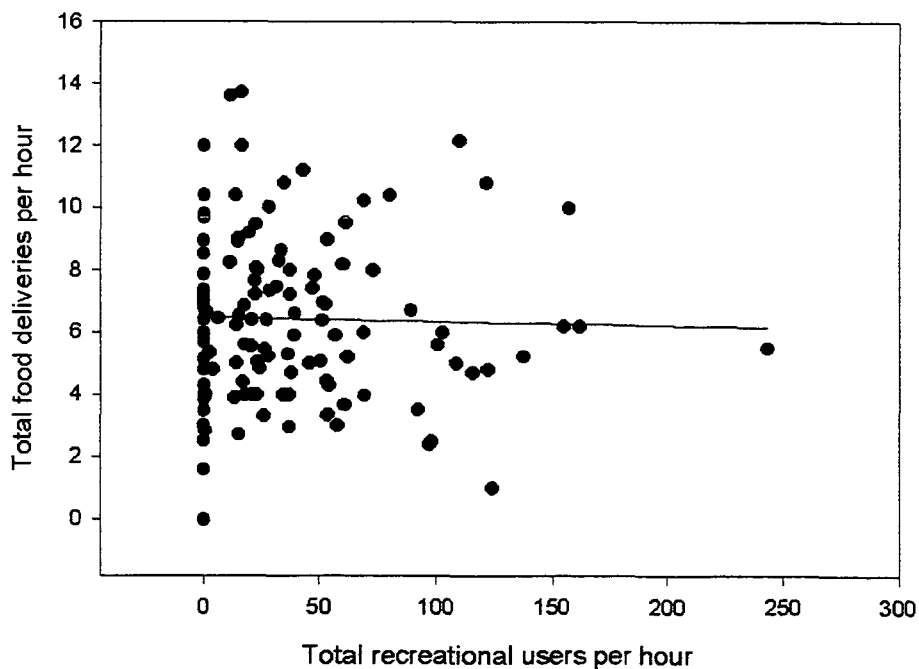


Figure 4. Total (female+male) food deliveries per hour vs. total recreational users per hour for 107 American robin nests.

Spearman correlation procedure: $r = -0.08$, $P = 0.41$.

Regression line: $y = 6.50 - 0.006x$, $r^2 = 0.009$, $F = 0.92$, $P = 0.81$.

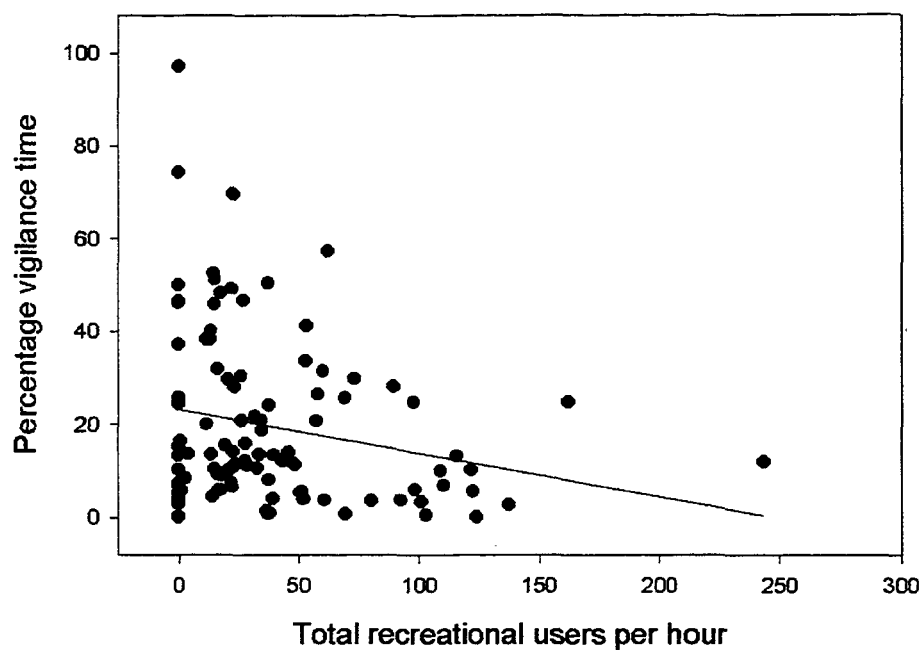


Figure 5. Percentage of time males spent vigilant vs. total recreational users per hour for 107 American robin nests. Spearman correlation procedure: $r = -0.19$, $P < 0.05$. Regression line: $y = 0.23 - 9.35 \times 10^{-4}x$, $r^2 = 0.05$, $F = 5.18$, $P < 0.03$.

Female and total food delivery rates were significantly positively correlated with nestling age (female: $n = 107$, $r = 0.34$, $P < 0.01$; total: $n = 107$, $r = 0.22$, $P < 0.05$). Additionally, percentage female brooding time and total female vigilance time were significantly negatively related to nestling age (brooding: $n = 107$, $r = -0.49$, $P < 0.001$; vigilance: $n = 107$, $r = -0.42$, $P < 0.001$). Female food delivery rate was not correlated with the number of nestlings, whereas total food delivery rate was significantly positively correlated with the number of nestlings ($n = 107$, $r = 0.22$, $P < 0.05$). Male food delivery rate and total vigilance time did not vary with either nestling age or number of nestlings. Nestling age did not vary with the total recreational user rate; however, the number of nestlings was weakly positively correlated with the total recreational user rate ($n = 107$, $r = 0.22$, $P < 0.05$). Because nestling age did not vary with the total recreational user rate, differences in provisioning rates were not due to differences in nestling age at observed nests. Total food delivery rate was not significantly related to the total recreational user rate.

Study area vegetation

High-use study areas had greater canopy cover and more total medium trees than other study areas grouped by recreational use-level (Table 4). Canopy cover and total medium trees did not differ among medium, low, and non-use study areas. Total shrub densities were lower at high-use study areas, but this result was only marginally significant (Table 4). None of the vegetation measures differed significantly between sampling points at combined trail and non-trail study areas (Table 4).

Table 4. Vegetation attributes (mean \pm SE) of study areas pooled by recreational use-level.

Variable	Study areas by recreational use-level				Combined trail study areas (n = 28 points) ¹
	Non-trail (n = 16 points) ¹	Low (n = 12 points) ¹	Medium (n = 8 points) ¹	High (n = 8 points) ¹	
Canopy cover (%) ²	34.43 \pm 5.63 ^a	34.50 \pm 6.92 ^a	28.12 \pm 5.82 ^a	61.58 \pm 4.00 ^b	40.42 \pm 4.35
Riparian width (m)	24.26 \pm 3.58	22.35 \pm 4.63	25.51 \pm 4.44	29.37 \pm 4.23	25.26 \pm 2.62
Green ground cover (%)	78.96 \pm 1.84	76.69 \pm 3.50	81.25 \pm 2.65	69.06 \pm 6.16	75.81 \pm 2.51
Total shrubs ³	20.44 \pm 4.83 ^a	24.29 \pm 4.22 ^{ab}	11.19 \pm 5.94 ^{ac}	4.81 \pm 1.42 ^c	14.98 \pm 2.91
Total saplings	43.89 \pm 7.76	30.19 \pm 8.44	24.22 \pm 6.73	49.22 \pm 8.83	33.92 \pm 5.03
Total small trees	7.27 \pm 1.41	6.62 \pm 2.07	5.53 \pm 1.48	13.31 \pm 2.45	8.22 \pm 1.32
Total medium trees ⁴	1.52 \pm 0.39 ^a	1.77 \pm 0.54 ^a	1.28 \pm 0.43 ^a	3.78 \pm 0.58 ^b	2.21 \pm 0.36
Total large trees	0.86 \pm 0.22	0.54 \pm 0.18	1.19 \pm 0.58	1.41 \pm 0.41	0.97 \pm 0.22

Notes: Vegetation data were pooled over all use-levels from study areas with trails to produce the combined trail study areas column. When Kruskal-Wallis tests among recreational use-levels were significant, individual pair-wise comparisons between use-levels were made using Mann-Whitney U-tests. Different letters indicate significant difference ($P < 0.05$, unless indicated) between use-levels.

¹ Each point is the average of the central sampling point and surrounding three satellite points (four points per study area).

² Kruskal-Wallis test among recreational use-levels: $df = 3$, $\chi^2 = 11.47$, $P < 0.01$.

³ Kruskal-Wallis test among recreational use-levels: $df = 3$, $\chi^2 = 7.76$, $P < 0.06$. Individual differences between use-levels were significant at $P < 0.10$ level.

⁴ Kruskal-Wallis test among recreational use-levels: $df = 3$, $\chi^2 = 9.63$, $P < 0.03$.

Nest sites versus non-nest sites

At non-trail study areas, nest sites had significantly less green ground cover, more total saplings, and occurred in marginally narrower riparian stands compared to non-nest sites (Table 5). At study areas with trails, nest tree dbh was marginally larger than random trees, and nest sites tended to have greater canopy cover than non-nest sites (Table 5).

Nest site characteristics and reproductive success

For nests at non-trail study areas, green ground cover, total medium trees, and riparian width were all significantly greater at fledged nests than at nests that failed (Table 6). Average nest concealment tended to be lower at fledged nests compared to nests that failed (Table 6). None of the variables tested differed among nest end stages.

For nests at study areas with trails, total saplings were fewer and canopy cover was greater at nests that fledged than at nests that failed (Table 6). Total small trees tended to be fewer at fledged nests compared to failed nests (Table 6). Canopy cover differed significantly among nest end stages, with higher canopy cover associated with a nest surviving to later nest end stages (Table 6). Nest height and green ground cover were marginally significantly different among nest end stages, with both variables tending to decrease for nests surviving until later nest end stages (Table 6). Nest distance to a trail did not differ between successful and unsuccessful nests. Nests ranged between 0-135 m from trails (average = 20.32 ± 1.32 m, $n = 242$ nests), however only 11 of the 242 nests (4.5%) were greater than 60 m from a trail.

Table 5. Vegetation characteristics (mean \pm SE) of American robin nest sites and paired non-nest sites from 2001 for trail and non-trail study areas.

Variable	Trail	n	Means for nests	Means for non-nests	S-value	P
Nest tree dbh (m)	Non-trail	24	1.16 \pm 0.21	0.75 \pm 0.17	53.5	0.13
	Trail	90	0.90 \pm 0.11	0.73 \pm 0.10	433.5	< 0.08
Green ground cover (%)	Non-trail	24	61.85 \pm 5.08	78.85 \pm 2.71	-96	<0.005
	Trail	92	65.90 \pm 2.63	69.86 \pm 2.59	-264	0.27
Total saplings	Non-trail	24	67.50 \pm 20.23	27.04 \pm 6.37	76	< 0.03
	Trail	92	37.22 \pm 4.85	31.07 \pm 3.96	265	0.24
Riparian width (m)	Non-trail	24	31.21 \pm 4.16	37.07 \pm 4.00	-61.5	< 0.08
	Trail	91	27.99 \pm 1.76	26.15 \pm 1.85	359.5	0.15
Canopy cover (%)	Non-trail	24	79.48 \pm 4.60	78.03 \pm 3.77	10	0.78
	Trail	91	82.60 \pm 1.82	77.28 \pm 2.22	421.5	< 0.10

Notes: S-value and P from Wilcoxon signed-rank test for paired samples.
Only variables with $P < 0.10$ for either non-trail or trail sites were listed.

Table 6. American robin nest site characteristics (mean \pm SE) by nest end stage and for all failed nests combined for study areas with and without recreational trails.

	Trail	Nest end stage				All failed nests Variable combined
		0 – No eggs detected	1 – Eggs	2 – Nestlings	3 – Fledged	
Nest height (m)	Non-trail	6.55 \pm 0.61 (5)	5.06 \pm 0.61 (26)	4.07 \pm 0.55 (10)	4.98 \pm 0.53 (34)	5.00 \pm 0.43 (41)
	Trail ^a	5.55 \pm 0.59 (23)	5.43 \pm 0.32 (70)	4.52 \pm 0.58 (34)	4.69 \pm 0.25 (115)	5.21 \pm 0.26 (127)
Nest concealment (%)	Non-trail ^b	56.00 \pm 7.98 (5)	56.30 \pm 3.58 (26)	51.00 \pm 7.56 (10)	45.40 \pm 4.19 (34)	54.97 \pm 3.02 (41)
	Trail	43.75 \pm 4.52 (21)	50.47 \pm 2.48 (69)	56.40 \pm 3.31 (33)	50.35 \pm 1.83 (115)	50.91 \pm 1.85 (123)
Green ground cover (%)	Non-trail ^c	59.25 \pm 14.25 (5)	57.43 \pm 5.41 (26)	57.38 \pm 9.19 (10)	69.71 \pm 4.14 (34)	57.64 \pm 4.33 (41)
	Trail ^d	52.23 \pm 6.48 (23)	69.45 \pm 2.99 (70)	68.45 \pm 3.92 (34)	64.60 \pm 2.25 (115)	66.04 \pm 2.34 (127)
Total saplings	Non-trail	22.20 \pm 19.23 (5)	65.58 \pm 16.39 (26)	51.10 \pm 26.54 (10)	58.03 \pm 16.27 (34)	56.76 \pm 12.44 (41)
	Trail ^e	39.96 \pm 6.86 (23)	28.90 \pm 3.67 (70)	36.91 \pm 10.12 (34)	24.26 \pm 2.69 (115)	33.05 \pm 3.59 (127)
Total small trees	Non-trail	8.40 \pm 4.57 (5)	9.58 \pm 1.58 (26)	6.60 \pm 2.79 (10)	9.71 \pm 1.44 (34)	8.71 \pm 1.31 (41)
	Trail ^f	6.00 \pm 1.18 (23)	9.93 \pm 1.20 (70)	8.50 \pm 1.80 (34)	7.61 \pm 1.08 (115)	8.83 \pm 0.85 (127)
Total medium trees	Non-trail ^g	3.00 \pm 2.53 (5)	3.27 \pm 1.07 (26)	1.50 \pm 0.90 (10)	4.12 \pm 0.77 (34)	2.80 \pm 0.77 (41)
	Trail	2.22 \pm 0.57 (23)	2.90 \pm 0.38 (70)	2.79 \pm 0.77 (34)	1.92 \pm 0.22 (115)	2.75 \pm 0.31 (127)
Riparian width (m)	Non-trail ^h	32.92 \pm 8.20 (5)	32.77 \pm 3.69 (26)	30.47 \pm 7.24 (10)	47.67 \pm 4.84 (34)	32.23 \pm 3.02 (41)
	Trail	29.99 \pm 6.41 (23)	29.18 \pm 2.17 (70)	23.10 \pm 2.87 (34)	23.63 \pm 1.33 (114)	27.70 \pm 1.83 (127)
Canopy cover (%)	Non-trail	82.47 \pm 5.69 (5)	77.41 \pm 4.51 (26)	82.97 \pm 9.51 (10)	82.24 \pm 2.64 (34)	79.38 \pm 3.68 (41)
	Trail ⁱ	75.13 \pm 4.19 (23)	74.58 \pm 2.40 (70)	83.09 \pm 2.37 (33)	84.42 \pm 1.15 (115)	76.91 \pm 1.68 (126)

Notes: Only variables with $P < 0.10$ for non-trail or trail study areas were listed. Sample sizes in parentheses.

^a Kruskal-Wallis test among nest end stages: $df = 3$, $\chi^2 = 6.92$, $P < 0.08$.

^b Mann-Whitney U-test between successful and unsuccessful nests: $Z = -1.74$, $P < 0.09$.

^c Mann-Whitney U-test between successful and unsuccessful nests: $Z = 1.98$, $P < 0.05$.

^d Kruskal-Wallis test among nest end stages: $df = 3$, $\chi^2 = 7.16$, $P < 0.07$.

^e Mann-Whitney U-test between successful and unsuccessful nests: $Z = -1.99$, $P < 0.05$.

^f Mann-Whitney U-test between successful and unsuccessful nests: $Z = -1.67$, $P < 0.10$.

^g Mann-Whitney U-test between successful and unsuccessful nests: $Z = 2.19$, $P < 0.03$.

^h Mann-Whitney U-test between successful and unsuccessful nests: $Z = 2.41$, $P < 0.02$.

ⁱ Mann-Whitney U-test between successful and unsuccessful nests: $Z = 3.02$, $P < 0.003$.

^j Kruskal-Wallis test among nest end stages: $df = 3$, $\chi^2 = 13.70$, $P < 0.004$.

DISCUSSION

Results of this study suggest that American robins nested preferentially along trails with medium and low recreational use compared to study areas without trails or trails with the heaviest recreational use. Other researchers have found increased robin abundance near trails (Hickman 1990, Miller et al. 1998). The opening of habitat surrounding trails and trampling associated with recreational use near trails may enhance foraging opportunities (Blakesley and Reese 1988) or reduce the risks from ground predators. Eiserer (1980) found that robins preferred short grass to taller grass for foraging. In addition, ground predators may be less abundant with lower ground cover surrounding trails (Dickman and Doncaster 1987), or these predators may be more exposed to robins foraging near trails. Robins frequently foraged on trails or immediately adjacent to trails during this study.

Although robins in my study clearly were attracted to trails with low to medium-use (Table 4), they fared the best reproductively at medium and high-use trail study areas (Table 3). These results indicate that low-use study areas possibly functioned as ecological traps (Gates and Gysel 1978, Misenhelter and Rotenberry 2000), and that robins failed to perceive the value of high-use study areas. Some robins may have avoided nesting at high-use study areas due to the high levels of human disturbance. Fernandez-Juricic (2000) found that the abundance of European blackbirds and starlings decreased with pedestrian use of urban parks. Although robins may have recognized the value of areas developed with trails as nesting habitat, either the relationship between use-rate and habitat quality (e.g. risk of predation) was not predictable based on area attributes, or the robin has not yet evolved a sensitivity to it (Martin 1993).

Increased reproductive success at medium and high-use study areas may have been due to a refuge effect resulting from a decline in predatory pressures in areas with relatively high recreational activity (Osborne and Osborne 1980, Gering and Blair 1999). Similarly, in lowland riparian habitats, Miller and Hobbs (2000) found that predation rates on artificial nests decreased with proximity to recreational trails. Other studies also have found decreased predation rates on both natural and artificial nests in areas with high human activity (Tomialojc and Profus 1977, Osborne and Osborne 1980, Tarvin and Smith 1995, Gering and Blair 1999). At study areas with higher intensities of recreational use, even some predatory species that are attracted to trails may have been displaced. For example, magpies decreased in abundance with increasing pedestrian use of urban parks (Fernandez-Juricic 2000). Another possibility is that even though human-associated predators may have increased with trails and use (Miller et al. 1998), at higher-use study areas these predators may have foraged primarily on human refuse from garbage cans, picnic areas, and littering, and spent less time searching out robin nests (Miller 1999). In my study, the reproductive success of robins was lowest at low-use study areas. Some avian nest predators have been found to increase in abundance near trails (Hickman 1990, Miller and Hobbs 2000), and low numbers of recreational users may not have been enough to displace them.

Overall nesting success for robins in this study was 47.0% ($n = 319$ nests). This value falls toward the lower end of the range of nesting success from the literature for American robins of 42.7% ($n = 122$ nests) in the Pacific Northwestern United States (Sallabanks and James 1999) to 90% ($n = 113$ nests) in suburban areas of Montreal, Quebec, Canada (Morneau et al. 1995). However, robin nesting success in this study was

consistent with an overall estimate of nesting success for robins and other studies that examined robin responses to aspects of human disturbance. Martin (1995) calculated average robin nesting success at 48.8% based on a review of the literature. In a study conducted in riparian habitat in southwestern Colorado in which the contents of some nests were experimentally touched, robin nesting success was 43.6% ($n = 156$ nests) (Ortega et al. 1997). McLean et al. (1986) found robin nesting success of 46.7% ($n = 122$ nests) for nests that were experimentally approached to study nest defense behavior on a university campus in Vancouver, British Columbia, Canada. Nesting success at my low-use study areas was 32.1% ($n = 84$), which is considerably below success values reported from other studies of robins.

Nestling weights clearly did not decrease with recreational use and, in fact, the weight of the heaviest nestling in each nest was positively correlated with the average rate of recreational use at each study area. However, the average weight of nestlings in each nest was not strongly related to recreational use level. Slagsvold (1997b) found that in American robin broods in which the male fed more than the female, the male predominantly fed the largest nestling, whereas the female predominantly fed the smallest nestling. I found that female percentage of total food deliveries was significantly negatively correlated with recreational use, with males tending to feed more than females at higher-use study areas. Thus, males may have been predominantly feeding the largest nestling in broods at higher-use study areas, potentially explaining why heaviest nestling weight increased with recreational use. Average nestling weight may not have been strongly related to recreational use because females may have been predominantly feeding the smallest nestling in broods at higher-use study areas.

Increased heaviest nestling weight with recreational use may also have been due to enhanced foraging opportunities due to trampling and reduced predator numbers at higher-use study areas (Dickman and Doncaster 1987, Blakesley and Reese 1988; but see Fernandez-Juricic and Telleria 2000). Higher fledging weights have been associated with increased fledgling survival (Magrath 1991, Both et al. 1999). Higher-use study areas not only had increased fledging success and productivity, but also the largest nestlings that fledged from nests at higher-use study areas were heavier and may have been more likely to survive than the largest nestlings that fledged from lower-use areas.

Contrary to my prediction, female robins spent greater percentages of time incubating with increasing recreational use (Figure 1). Total female vigilance time also increased with recreational use at nests observed with eggs, but this was due largely to increased incubation time. Increased incubation may have been a behavioral response that put females in a better position to defend the nest, or that made the nest more cryptic (Westmoreland and Best 1986, Martin 1992). On several occasions female robins were observed returning to incubate on the nest from the same direction as approaching recreational users, possibly to be in position on the nest as users passed. I never witnessed robins flushing off nests in response to recreational users. In contrast, Yalden and Yalden (1990) found that golden plovers (*Pluvialis apricaria*) flushed off nests and spent more time away from nests when recreationists were present, and Gotmark (1992) suggested that human disturbance at nest sites may cause birds to flush off nests, possibly making them more susceptible to predation. Many female songbirds do not flush until the nest is closely approached. Incubating robins probably did not flush off nests in response to users because most recreationists were unaware of and did not closely approach nests.

Female food deliveries to nests declined with increasing recreational use (Figure 2). This may have been due to increased disturbance from recreationists interrupting foraging or the delivery of food to nestlings. Fernandez-Juricic and Telleria (2000) found that European blackbirds decreased foraging time, and foraged farther from pathways and closer to protective cover with increasing pedestrian use of an urban park. Another possible explanation is that females at higher-use study areas that spent more time incubating eggs foraged more for themselves than for nestlings after eggs hatched to make up for energy deficits incurred during increased incubation bouts. The female percentage of total food deliveries to nests also declined with recreational use, indicating that males may have increased their food deliveries to compensate for reduced female food deliveries at nests located at high-use study areas. At these nests, male robins may have increased their food deliveries due to the begging of hungry nestlings (Whittingham and Robertson 1993). Increased male food deliveries probably explains why I found no difference in total food deliveries to nests with recreational use, and why nestling weights did not decrease with increasing use.

High-use study areas had higher canopy cover, more medium-sized trees, and tended to have fewer total shrubs compared to other study areas grouped by recreational use-level (Table 4). At study areas with trails, robins tended to select nest sites in trees larger in dbh and with higher canopy cover than random points, and nest site canopy cover was positively associated with increased nesting success. Accordingly, high rates of nest success at high-use areas may have been associated with the relatively closed canopies of these areas. Thus, high-use study areas potentially had more preferred, high quality nesting sites than other study areas. However, fewer nests than expected were located at

these high-use areas. This result may indicate that high levels of recreational disturbance may have prevented some robins from utilizing favorable nest sites at high-use study areas. Habitat characteristics apparently were not related to nesting habitat selection or nesting success at the other study areas. In addition, because habitat area did not differ among study areas by recreational use-level, habitat area effects were not associated with observed differences in nesting habitat selection and reproductive success.

My results suggest that different predator communities between study areas with and without trails may have exerted different selective pressures on nesting robins. Based upon observations made during this study, other studies conducted locally, and reports of known predators of robin nests, I developed a list of potential robin nest predators occurring on my study areas (Miller et al. 1998; Sallabanks and James 1999, Miller and Hobbs 2000; Merkle, personal observation). Avian nest predators included cooper's hawks (*Accipiter cooperii*), sharp-shinned hawks (*Accipiter striatus*), common ravens (*Corvus corax*), American crows (*Corvus brachyrhynchos*), black-billed magpies (*P. hudsonia*), blue jays (*Cyanocitta cristata*), house wrens (*Troglodytes aedon*), and common grackles (*Quiscalus quiscula*). Mammalian predators included fox squirrels (*Sciurus niger*), deer mice (*Peromyscus maniculatus*), coyotes (*Canis latrans*), red fox (*Vulpes vulpes*), raccoons (*Procyon lotor*), striped skunks (*Mephitis mephitis*), and domestic cats (*Felis catus*). Reptilian predators included bullsnakes (*Pituophis melanoleucus*) and, possibly, garter snakes (*Thamnophis* spp.). Avian nest predators may have been the primary selective force on robin nest site selection at study areas with trails, whereas a more varied predator community, particularly ground predators, may have driven nest site selection at non-trail study areas. Several studies have found increased corvid abundance,

including black-billed magpies (*P. hudsonia*) and blue jays, at trail areas (Hickman 1990, Miller and Hobbs 2000) and areas subject to recreational use (Gutzwiller et al. 2002). On the other hand, Sauvajot et al. (1998) found that small mammal abundance decreased with human disturbance associated with road and trail development. Supporting these studies, Miller and Hobbs (2000) found that corvids preyed upon more artificial nests than expected near trails, whereas mice depredated more artificial nests than expected away from trails. Finally, raptor diversity and abundance were lower, and raptor perch distance from riparian corridors was greater, at trail compared to non-trail control areas (Fletcher et al. 1999).

At study areas with trails, robin nest site selection and the factors associated with successful nests indicate that predation from avian predators, especially corvids, potentially was the primary threat to robin nests. In another study conducted locally, corvids accounted for the majority of marks left on clay eggs in artificial nests designed to resemble American robin nests in lowland riparian habitats (Miller and Hobbs 2000). In my study, robins tended to select trees larger in total dbh and higher in canopy cover for nesting compared to non-nest trees (Table 5), possibly to decrease nest visibility from above for foraging corvids. Consistent with this idea, greater canopy cover was associated with fledged nests and nests that survived to later nest end stages (Table 6). Successful robin nests also had significantly fewer total saplings and tended to have fewer small trees than failed nests, and nests succeeding to later nest end stages tended to have less green ground cover, all factors which may have been associated with increased canopy cover. In addition, saplings and small trees may have provided low perch sites that would allow corvids to view nests from within, or under, the nest tree canopy (Ratti and Reese 1988,

Paton 1994). Lower robin nests tended to have a greater chance of succeeding to later nest end stages, possibly because they were less visible and susceptible to avian nest predators (Yahner 1991). Other researchers have suggested that birds may place nests higher to avoid human disturbance (Knight and Fitzner 1985, Miller 1999), but my results suggest a potential trade-off between nest height and nest survival for robins.

Nest distance to a trail did not differ between successful and unsuccessful nests or among nest end stages. In contrast, Miller et al. (1998) found that nesting success increased with nest distance from a trail for a pooled sample of forest songbirds, including robins. However, due to the narrow, linear nature of riparian habitats (study areas averaged 50-60 m in total width), trail effects were likely to have permeated the entire system and nest distances from trails did not vary much, making it unlikely that I would detect distance effects.

At non-trail study areas, robin nest site selection may have been driven by threat of predation from ground predators, including small mammals. Robins selected nest sites that had lower green ground cover, more saplings, and narrower riparian widths than random points (Table 5). Lower ground cover may have provided favorable foraging areas immediately surrounding the nest (Eiserer 1980). However, robins can forage up to 300 m away from their nests (Sallabanks and James 1999). In fact, I rarely saw robins foraging within the 5 m of the nest that was sampled for ground vegetation cover (Merkle, unpublished data), making it unclear whether reduced ground cover surrounding the nest was selected for foraging. Other possible explanations are that ground predators may be less abundant with lower ground cover, or that these predators would be more exposed as they approached the nest tree with lower ground cover (Bekoff et al. 1987, Dickman and

Doncaster 1987, Gotmark et al. 1995). More saplings may have increased vertical structural complexity making it more difficult for predators that search vegetation randomly to locate nests (Martin 1993). Robins tended to select nest sites with narrower riparian widths at non-trail study areas, possibly to nest closer to habitat edges (Davidson and Knight 2001).

Factors associated with robin nesting success at non-trail study areas could not be attributed specifically to either ground or avian predators, possibly indicating a varied predator community. Greater numbers of medium sized trees and greater riparian width surrounding successful nests compared to nests that failed may have made locating nests more difficult for predators by increasing the potential area and number of possible nest trees to search, or by making it more difficult to detect nests while travelling along the edge of the woodland habitat (Gates and Gysel 1978, Martin 1993; Table 6). Greater green ground cover surrounding successful nest sites may have provided cover for fledglings immediately after they departed the nest.

Although robins at non-trail study areas seemed to prefer nest sites with less green ground cover and narrower riparian widths, nests with these surrounding characteristics were more likely to fail. Nest site preferences are innate, and, thus, should have remained consistent over the three years of this study (Cody 1985, Misenhelter and Rotenberry 2000). The apparent inconsistency of nest site preference with suitability for reproduction potentially indicates a recent shift in conditions to which robins have not yet adapted (Misenhelter and Rotenberry 2000). A possible explanation is that non-trail study areas may be subject to an influx of nest predators from areas developed with recreational trails,

similar to the "crowding effect" demonstrated in some studies of habitat fragmentation (Lovejoy et al. 1986, Foster and Gaines 1991, Collinge and Forman 1998).

MANAGEMENT IMPLICATIONS

Robin habitat selection, nesting success, and behavior all varied with recreational use and would not have been evident if I had only examined trail presence or absence. These results suggest that the intensity of human disturbance along trail corridors is an important factor that should be considered when assessing trail impacts on wildlife.

The apparent refuge effect for robins at medium and high-use trail study areas suggests that songbirds capable of tolerating human disturbance may fare well at areas with higher recreational use. Similarly, Sauvajot et al. (1998) found that resident birds showed little response to human disturbance associated with roads and trails. However, the refuge effect also potentially indicates alteration of the predator community, with evidence suggesting that native small mammals and raptors are likely to be displaced from these areas (Sauvajot et al. 1998, Fletcher et al. 1999, Miller and Hobbs 2000). Increasing recreational use was not universally good for robins. Nesting density of robins was lower than expected based on habitat area at high-use study areas, possibly indicating that high levels of recreational disturbance may have displaced some robins from nesting at these areas (Fernandez-Juricic 2000).

Trends of growth in recreational activities show increasing public demand for new trails and less crowded recreational experiences (Flather and Cordell 1995). New trails and established trails that are not well known to the public, difficult to

access, or in remote areas presumably will have lower use levels. Results of this study suggest that such low-use study areas may have the strongest negative impacts.

In planning trail placements in riparian habitats, areas with well-established vegetation and large trees should be preferentially selected because they provide nesting cover for open-cup nesting songbirds, potentially reducing their risks of predation from corvids. Management for songbirds at riparian areas without trails could include working to increase vegetation density and riparian width by precluding grazing and reducing water diversions (Ohmart 1994, Saab et al. 1995).

Caution should be used in extrapolating results of this study to other songbird species, because American robins are habitat generalists that often increase in abundance with human development and disturbance (Marzluff et al. 1998, Pantle 1998, Bock et al. 1999), and may even achieve higher nesting success in disturbed and edge habitats (Tewksbury et al. 1998, Davidson and Knight 2001). Species with more specialized habitat requirements and that are less disturbance-tolerant may respond quite differently. However, at the same study areas, I found that reproductive success of yellow warblers (*Dendroica petechia*) was greater at trail compared to non-trail study areas, though I did not find any warblers nesting at high-use areas (Merkle, unpublished data). On the other hand, I found that warbler behavior did not vary with increasing recreational use (Merkle, unpublished data), possibly because they have well concealed nests and forage in the canopy (Marzluff 1997, Lowther et al. 1999).

Given continued land development and increasing recreational use of remaining public open lands, it is important to investigate how recreational activities affect wildlife populations (Flather and Cordell 1995, Marzluff et al. 2001). In order to develop

management plans that balance songbird habitat requirements with the recreational demands of people, additional research on the impacts of trail-use on the reproductive success and behavior of other songbird species is needed. Studies should also investigate songbird responses in other habitat types and landscape settings. Based on this study, a promising direction for future inquiry would be identifying the predators responsible for depredating natural nests and learning how they respond to recreational trails and use.

LITERATURE CITED

- Andrews, R., and R. Righter. 1992. Colorado birds : a reference to their distribution and habitat. Denver Museum of Natural History, Denver, CO.
- Bekoff, M., A. C. Scott, and D. A. Conner. 1987. Nonrandom nest-site selection in evening grosbeaks. *Condor* 89:819-829.
- Blakesley, J. A., and K. P. Reese. 1988. Avian use of campground and noncampground sites in riparian zones. *Journal of Wildlife Management* 52:399-402.
- Bock, C. E., J. H. Bock, and B. C. Bennett. 1999. Songbird abundance in grasslands at a suburban interface on the Colorado High Plains. *Studies in Avian Biology* 19:131-136.
- Both, C., M. E. Visser, and N. Verboven. 1999. Density-dependent recruitment rates in great tits: the importance of being heavier. *Proceedings of the Royal Society of London Series B-Biological Sciences* 266:465-469.
- Bottorff, R. L. 1974. Cottonwood habitat for birds in Colorado. *American Birds* 28:975-979.
- Burke, D. M., and E. Nol. 1998. Influence of food abundance, nest-site habitat, and forest fragmentation on breeding ovenbirds. *Auk* 115:96-104.
- Cody, M. L. 1985. Habitat selection in birds. Academic Press, Orlando, FL.
- Cole, D. N., and P. B. Landres. 1995. Indirect effects of recreation on wildlife. Pages 183-201 in R. L. Knight and K. J. Gutzwiller, editors. *Wildlife and recreationists*. Island Press, Washington, D.C.
- Collinge, S. K., and R. T. T. Forman. 1998. A conceptual model of land conversion processes: predictions and evidence from a microlandscape experiment with grassland insects. *Oikos* 82:66-84.
- Collinge, S. K., M. Holyoak, C. B. Barr, and J. T. Marty. 2001. Riparian habitat fragmentation and population persistence of the threatened valley elderberry longhorn beetle in central California. *Biological Conservation* 100:103-113.
- Davidson, A. S., and R. L. Knight. 2001. Avian nest success and community composition in a western riparian forest. *Journal of Wildlife Management* 65:334-344.
- Dickman, C. R., and C. P. Doncaster. 1987. The ecology of small mammals in urban habitats .I. Populations in a patchy environment. *Journal of Animal Ecology* 56:629-640.

- Eiserer, L. A. 1980. Effects of grass length and mowing on foraging behavior of the American robin (*Turdus migratorius*). *Auk* 97:576-580.
- Fernandez-Juricic, E. 2000. Local and regional effects of pedestrians on forest birds in a fragmented landscape. *Condor* 102:247-255.
- Fernandez-Juricic, E., and J. L. Telleria. 2000. Effects of human disturbance on spatial and temporal feeding patterns of blackbird *Turdus merula* in urban parks in Madrid, Spain. *Bird Study* 47:13-21.
- 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*. Island Press, Washington, D.C.
- Fletcher, R. J., S. T. McKinney, and C. E. Bock. 1999. Effects of recreational trails on wintering diurnal raptors along riparian corridors in a Colorado grassland. *Journal of Raptor Research* 33:233-239.
- Foster, J., and M. S. Gaines. 1991. The effects of a successional habitat mosaic on a small mammal community. *Ecology* 72:1358-1373.
- Gates, J. E., and L. W. Gysel. 1978. Avian nest dispersion and fledging success in field-forest ecotones. *Ecology* 59:871-883.
- Gering, J. C., and R. B. Blair. 1999. Predation on artificial bird nests along an urban gradient: predatory risk or relaxation in urban environments? *Ecography* 22:532-541.
- Gotmark, F. 1992. The effects of investigator disturbance on nesting birds. Pages 63-104 in D. M. Power, editor. *Current Ornithology*, Vol. 9. Plenum Press, New York, NY.
- Gotmark, F., D. Blomqvist, O. C. Johansson, and J. Bergkvist. 1995. Nest site selection: A trade-off between concealment and view of the surroundings? *Journal of Avian Biology* 26:305-312.
- Gutzwiller, K. J., E. A. Kroese, S. H. Anderson, and C. A. Wilkins. 1997. Does human intrusion alter the seasonal timing of avian song during breeding periods? *Auk* 114:55-65.
- Gutzwiller, K. J., S. K. Riffell, and S. H. Anderson. 2002. Repeated human intrusion and the potential for nest predation by gray jays. *Journal of Wildlife Management* 66:372-380.
- Hickman, S. 1990. Evidence of edge species attraction to nature trails within deciduous forest. *Natural Areas Journal* 10:3-5.

- Knight, R. L., and R. E. Fitzner. 1985. Human disturbance and nest site placement in black-billed magpies. *Journal of Field Ornithology* 56:153-157.
- Knight, R. L., and K. J. Gutzwiller, editors. 1995. *Wildlife and recreationists*. Island Press, Washington, DC.
- Knight, R. L., and S. A. Temple. 1986. Methodological problems in studies of avian nest defense. *Animal Behaviour* 34:561-566.
- Knopf, F. L., R. R. Johnson, T. Rich, F. B. Samson, and R. C. Szaro. 1988. Conservation of riparian ecosystems in the United States. *Wilson Bulletin* 100:272-284.
- Lovejoy, T. E., J. Bierregaard, R.O., A. B. Rylands, J. R. Malcolm, C. E. Quintela, L. H. Harper, J. Brown, K.S., A. H. Powell, G. V. N. Powell, H. O. R. Schubart, and M. B. Hays. 1986. Edge and other effects of isolation on Amazon forest fragments. Pages 257-285 in M. E. Soulé, editor. *Conservation biology: the science of scarcity and diversity*. Sinauer Associates, Inc., Sunderland, MA.
- Lowther, P. E., C. Celada, N. K. Klein, C. C. Rimmer, and D. A. Spector. Yellow Warbler (*Dendroica petechia*). In *The Birds of North America*, no. 454 (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.
- Magrath, R. D. 1991. Nestling weight and juvenile survival in the blackbird, *Turdus merula*. *Journal of Animal Ecology* 60:335-351.
- Major, R. E., and C. E. Kendal. 1996. The contribution of artificial nest experiments to understanding avian reproductive success: a review of methods and conclusions. *Ibis* 138:298-307.
- Martin, P., and P. Bateson. 1993. *Measuring behaviour*, 2nd edition. Cambridge University Press, Cambridge.
- Martin, T. E. 1992. Interaction of nest predation and food limitation in reproductive strategies. Pages 163-197 in D. M. Power, editor. *Current Ornithology*, Vol. 9. Plenum Press, New York, NY.
- Martin, T. E. 1993. Nest predation and nest sites - new perspectives on old patterns. *Bioscience* 43:523-532.
- Martin, T. E. 1995. Avian life history evolution in relation to nest sites, nest predation, and food. *Ecological Monographs* 65:101-127.

- Martin, T.E., C.R. Paine, C.J. Conway, W.M. Hochachka, P. Allen, and W. Jenkins. 1997. BBIRD Field Protocol. Montana Cooperative Wildlife Research Unit, University of Montana, Missoula, MT.
<http://pica.wru.umt.edu/BBIRD/research.htm>.
- Marzluff, J. M. 1997. Effects of urbanization and recreation on songbirds. Pages 89-102 in W. M. Block and D. M. Finch, editors. Songbird ecology in Southwestern ponderosa pine forests: a literature review. Gen. Tech. Rep. RM-GTR-292. U.S.D.A., Forest Service, Rocky Mountain Forest and Range Experimental Station, Fort Collins, CO.
- Marzluff, J.M., R. Bowman, and R. Donnelly, editors. 2001. Urbanization, avian communities, and landscape ecology. Kluwer Academic Publishers, Norwell, MA.
- Marzluff, J. M., F. R. Gehlbach, and D. A. Manuwal. 1998. Urban environments: influences on avifauna and challenges for the avian conservationist. Pages 283-299 in J. M. Marzluff and R. Sallabanks, editors. Avian conservation. Island Press, Washington, D.C.
- Mayfield, H. F. 1975. Suggestions for calculating nest success. Wilson Bulletin 87:456-466.
- McLean, I. G., J. N. M. Smith, and K. G. Stewart. 1986. Mobbing behavior, nest exposure, and breeding success in the American robin. Behaviour 96:171-185.
- McRae, S. B., P. J. Weatherhead, and R. Montgomerie. 1993. American robin nestlings compete by jockeying for position. Behavioral Ecology and Sociobiology 33:101-106.
- Miller, C. K. 1994. Environmental impacts of passive recreational trails in riparian areas. Pages 96-105 in Proceedings of the 6th Annual Colorado Riparian Association Conference, Alamosa, CO.
- Miller, J. R. 1999. The effect of human settlement on bird communities in lowland riparian areas. Ph.D. Thesis. Colorado State University, Fort Collins, CO.
- Miller, J. R., and N. T. Hobbs. 2000. Recreational trails, human activity, and nest predation in lowland riparian areas. Landscape and Urban Planning 50:227-236.
- Miller, S. G., R. L. Knight, and C. K. Miller. 1998. Influence of recreational trails on breeding bird communities. Ecological Applications 8:162-169.
- Miller, S. G., R. L. Knight, and C. K. Miller. 2001. Wildlife responses to pedestrians and dogs. Wildlife Society Bulletin 29:124-132.

- Misenhelter, M. D., and J. T. Rotenberry. 2000. Choices and consequences of habitat occupancy and nest site selection in sage sparrows. *Ecology* 81:2892-2901.
- Morneau, F., C. Lepine, R. Decarie, M. A. Villard, and J. L. Desgranges. 1995. Reproduction of American robin (*Turdus migratorius*) in a suburban environment. *Landscape and Urban Planning* 32:55-62.
- Naiman, R. J., H. Decamps, and M. Pollock. 1993. The role of riparian corridors in maintaining regional biodiversity. *Ecology* 31:209-212.
- Ohmart, R. D. 1994. The effects of human induced changes on the avifauna of western riparian habitats. *Studies in Avian Biology* 15:273-285.
- Ortega, C. P., J. C. Ortega, C. A. Rapp, and S. A. Backensto. 1998. Validating the use of artificial nests in predation experiments. *Journal of Wildlife Management* 62:925-932.
- Ortega, C. P., J. C. Ortega, C. A. Rapp, S. Vorisek, S. A. Backensto, and D. W. Palmer. 1997. Effect of research activity on the success of American robin nests. *Journal of Wildlife Management* 61:948-952.
- Osborne, P., and L. Osborne. 1980. The contribution of nest site characteristics to breeding- success among blackbirds *Turdus merula*. *Ibis* 122:512-517.
- Pantle, D. 1998. American robin. Pages 396-397 in H. E. Kingery, editor. Colorado breeding bird atlas. Colorado Bird Atlas Partnership, Denver, CO.
- Paton, P. W. 1994. The effect of edge on avian nest success: how strong is the evidence? *Conservation Biology* 8:17-26.
- Pulliam, H. R. 1988. Sources, sinks, and population regulation. *American Naturalist* 132:652-661.
- Pyle, P. 1997. Identification guide to North American birds. Slate Creek Press, Bolinas, CA.
- Ralph, C. J., G. R. Geupel, P. Pyle, T. E. Martin, and D. F. DeSante. 1993. Handbook of field methods for monitoring landbirds. Gen. Tech. Rep. PSW-GTR-144. U.S.D.A., Forest Service, Pacific Southwest Research Center, Albany, CA.
- Ratti, J. T., and K. P. Reese. 1988. Preliminary test of the ecological trap hypothesis. *Journal of wildlife management* 52:484-491.
- Rottenborn, S. C. 1999. Predicting the impacts of urbanization on riparian bird communities. *Biological Conservation* 88:289-299.

- SAS Institute Inc. 1999. SAS/STAT user's guide. Version 8.0. SAS Institute Inc., Cary, NC.
- Saab, V. A., C. E. Bock, T. D. Rich, and D. S. Dobkin. 1995. Livestock grazing effects in western North America. Pages 311-353 in T. E. Martin and D. M. Finch, editors. Ecology and management of Neotropical migratory birds : a synthesis and review of critical issues. Oxford University Press, New York, NY.
- Sallabanks, R. and F.C. James. American Robin (*Turdus migratorius*). In The Birds of North America, no. 462 (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.
- Sauvajot, R. M., M. Buechner, D. A. Kamradt, and C. M. Schonewald. 1998. Patterns of human disturbance and response by small mammals and birds in chaparral near urban development. Urban Ecosystems 2:279-297.
- Slagsvold, T. 1997b. Brood division in birds in relation to offspring size: sibling rivalry and parental control. Animal Behavior 54:1357-1368.
- Slagsvold, T. 1997a. Is there a sexual conflict over hatching asynchrony in American robins? Auk 114:593-600.
- Tarvin, K. A., and K. G. Smith. 1995. Microhabitat factors influencing predation and success of suburban blue jay *Cyanocitta cristata* nests. Journal of Avian Biology 26:296-304.
- Tewksbury, J. J., S. J. Hejl, and T. E. Martin. 1998. Breeding productivity does not decline with increasing fragmentation in a western landscape. Ecology 79:2890-2903.
- Tomialojc, L., and P. Profus. 1977. Comparative analysis of breeding bird communities in two parks of Wroclaw and in an adjacent Querco-Carpinetum forest. Acta Ornithologica 16:117-177.
- van der Zande, A. N., 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.
- Westmoreland, D., and L. B. Best. 1986. Incubation continuity and the advantage of cryptic egg coloration to mourning doves. Wilson Bulletin 98:297-300.
- Whittingham, L. A., and R. J. Robertson. 1993. Nestling hunger and parental care in red-winged blackbirds. Auk 110:240-246.

- Woodard, J. D., and M. T. Murphy. 1999. Sex roles, parental experience and reproductive success of eastern kingbirds, *Tyrannus tyrannus*. *Animal Behaviour*, 57:105-115.
- Yahner, R. H. 1991. Avian nesting ecology in small even-aged aspen stands. *Journal of wildlife management* 55:155-159.
- Yalden, P. E., and D. W. Yalden. 1990. Recreational disturbance of breeding golden plovers *Pluvialis apricarius*. *Biological Conservation* 51:243-262.
- Zar, J. H. 1996. *Biostatistical analysis*, 3rd edition. Prentice Hall, Upper Saddle River, NJ.

CHAPTER 3
RECREATIONAL TRAIL-USE EFFECTS ON THE NESTING ECOLOGY
AND BEHAVIOR OF A RIPARIAN SPECIALIST,
THE YELLOW WARBLER

Abstract - I examined the effects of recreational trail-use on the reproductive success and behavior of yellow warblers (*Dendroica petechia*) in willow (*Salix* spp.)/cottonwood (*Populus* spp.) riparian habitats located on public open space lands in Boulder County, Colorado. In 1999-2001, I located and monitored 113 warbler nests in riparian corridors with and without trails, and I conducted behavioral observations on pairs of birds associated with active nest sites. More warbler nests than expected were located at study areas with intermediate levels of recreational use, whereas fewer nests than expected were located at non-trail study areas, and no warbler nests were located at the two study areas with the highest use. Reproductive success was greater at trail compared to non-trail study areas. Nest parasitism by brown-headed cowbirds (*Molothrus ater*) did not differ by recreational use-level. Successful nests that were parasitized were less productive than successful, unparasitized nests. None of the behavioral measures varied with recreational use. Although I cannot rule out the possibility that higher canopy cover at the two highest-use study areas made those areas unattractive to warblers, differences in nesting habitat selection and nesting success were not associated with differences in vegetation characteristics among study areas with nesting warblers. Warblers selected nest sites with more saplings than random points at both non-trail and trail

study areas. No vegetation measures were associated with successful nests at non-trail study areas, whereas higher nests, and nests with lower canopy cover, were more likely to fledge young at study areas with trails. Higher nests may have been less susceptible to ground predators, and trees with lower canopy cover may have had structural differences that made them more difficult or less attractive for ground predators to climb. Parasitized nests were lower in nesting substrates than unparasitized nests at study areas with and without trails. Study areas with trails apparently provided refuges from nest predation. This may have been the result of displacement of nest predators, most likely small mammals, due to disturbance by recreational users. However, recreational use may have reduced the availability of suitable riparian habitat for nesting warblers. No warbler nests were found at the two highest-use study areas, potentially indicating an upper limit to the refuge effect for warblers, and warbler nest density was lower at non-trail study areas than trail study areas with low and medium use.

INTRODUCTION

In the United States, public lands are being subjected to increasing levels of recreational use (Flather and Cordell 1995, Cole 1996). Although most land managers and scientists recognize that recreational activities may be impacting songbird populations, little is known about the mechanisms by which recreation may affect individual species (Merkle, Chapter 1). Few studies have investigated how recreational trails affect songbirds, and those that have did not account for the potential effects of different numbers of trail-users (Hickman 1990, Miller et al. 1998,

Miller and Hobbs 2000, Miller et al. 2001), which may magnify recreational impacts (Marzluff 1997) or produce threshold responses (Knight and Cole 1995).

Recreational trail-use may affect specialist songbirds more strongly than generalists (Knight and Cole 1995, Marzluff 1997). Researchers have found increases in the abundance of several generalist and edge-associated songbirds species along trails and decreases in the abundance of some specialists (Hickman 1990, Miller et al. 1998). Declines in the abundance of specialist songbirds along trails may be due to the attraction of nest predators, such as blue jays (*Cyanocitta cristata*) and black-billed magpies (*Pica hudsonia*), and parasitic brown-headed cowbirds (*Molothrus ater*), to trail corridors and areas used for recreational activities (Hickman 1990, Rich et al. 1994, Camp and Knight 1998, Miller and Hobbs 2000).

Increases in nest predators and parasitic cowbirds can reduce the reproductive success of songbirds along trails. Miller et al. (1998) found increased predation rates on a pooled sample of songbird nests with proximity to recreational trails in grassland and ponderosa pine (*Pinus ponderosa*) ecosystems, but did not find evidence of increased parasitism rates in either system. In contrast, Miller and Hobbs (2000) found reduced predation rates on artificial nests near trails in lowland riparian habitats, possibly because of the displacement of some nest predators by recreational activities. Pooling data across species may obscure species specific relationships, and conclusions based on artificial nests often do not accurately reflect predation pressures on natural nests (Major and Kendal 1996, Ortega et al. 1998). For these reasons, and due to the equivocal results of previous studies, more research is needed

to determine how individual species of songbirds respond to recreational users along trails.

Direct disturbance from recreationists can alter the behavior of songbirds, potentially reducing reproductive success (Gutzwiller et al. 1997). Disturbance from recreationists may decrease songbird nest attentiveness (Gotmark 1992), increase vigilance and nest defense (Knight and Temple 1986, Ortega et al. 1997), and interrupt adult foraging (Fernandez-Juricic and Telleria 2000) or food deliveries to nestlings. Trails and trail users also may indirectly affect songbirds through their impacts on vegetation (van der Zande et al. 1984, Cole and Landres 1995, Knight and Gutzwiller 1995). Changes in plant communities along trails may affect habitat selection and use by songbirds, as well as by avian and non-avian nest predators (Cody 1985, Marzluff 1997).

Riparian habitats are extremely important breeding sites and migration corridors for many songbird species, especially in arid parts of the western United States (Bottorff 1974, Knopf et al. 1988, Naiman et al. 1993, Ohmart 1994, Moore et al. 1995). However, riparian habitats are typically subjected to high levels of human disturbance and are often preferentially selected as sites for recreational trails (Miller 1994, Ohmart 1994). In the western U.S., the yellow warbler (*Dendroica petechia*) is a habitat specialist in riparian areas and wetlands (Bent 1953, Ehrlich et al. 1988, Knopf and Sedgwick 1992). Disturbance from recreational trail-use within riparian systems may have pronounced impacts on yellow warbler populations due to the importance of riparian habitats to breeding populations and the high degree of human alteration of these systems. Some populations of yellow warblers in the western U.S.

are declining apparently due to the degradation and loss of riparian woodlands and high levels of cowbird parasitism (Andrews and Righter 1992, Ehrlich et al. 1992, Lowther et al. 1999). Yellow warblers are frequently parasitized by brown-headed cowbirds, and parasitism reduces warbler productivity (Clark and Robertson 1981, Ortega and Ortega 2000). Additionally, cowbirds may be attracted to trails (Hickman 1990, Chace et al. In Press), subjecting warblers nesting in riparian habitats developed with trails to increased parasitism pressures.

The primary objectives of this study were to investigate how recreational trail-use affected yellow warblers. Specifically, I tested whether trails and intensities of trail-use affected nesting density and reproductive success of warblers, and whether warbler behavior varied along a gradient of increasing recreational trail-use. Based upon previous studies of other songbirds, I predicted that warbler nesting density would decline with recreational use. I predicted that warbler reproductive success would decrease and that cowbird parasitism rates of warbler nests would increase with increasing recreational trail-use. I also predicted that, with increasing recreational use, warblers would: 1) decrease incubation due to females flushing off nests in response to recreationists, 2) decrease food deliveries to nestlings, and 3) increase vigilance. Finally, I tested whether vegetation differed among study areas, and whether vegetation affected warbler habitat selection and reproductive success.

METHODS

Study area

I located eleven study areas in lowland willow/cottonwood riparian woodlands (Andrews and Richter 1992) on four riparian drainages on public open lands in Boulder County, Colorado (40°05' N, 105°15' W), which is situated at the interface of the western Great Plains and the eastern edge of the Rocky Mountains (Appendixes 1 and 2). All study areas were at approximately 1,600 m elevation, and downstream of the point where a drainage exited the foothills of the Rocky Mountains onto the plains. Study areas were subject to a range of trail-use intensities, including a control area without trails on each of the four drainages surveyed. Study areas consisted of linear strands of riparian woodlands surrounded by grassland/agricultural fields. Yellow warblers are relatively common breeders in these riparian habitats (Andrews and Richter 1992, Kuenning 1998). Eight study areas were surveyed in 1999, with one additional study area added in 2000 (n = 9 study areas), and two additional study areas added in 2001 (n = 11 study areas). Study areas were separated by at least 1 km, except for two areas with trails that were separated by a major road, and one non-trail and trail area that were separated by two fences that precluded use. The border of the non-trail study area was at least 150 m from the trail in the adjacent area.

Tree communities were dominated by plains cottonwood (*Populus deltoides*), narrowleaf cottonwood (*Populus angustifolia*), a hybrid of the plains and narrowleaf cottonwood (*Populus x acuminata*), and crack willow (*Salix fragilis*). Other relatively common trees included Russian olive (*Elaeagnus angustifolia*), alder (*Alnus tenuifolia*), river birch (*Betula fontinalis*), and hawthorn (*Crataegus* spp.). Interspersed with the trees

were thickets of shrubs, mostly sandbar willow (*Salix exigua*) and snowberry (*Symphoricarpos occidentalis*), with fewer patches of chokecherry (*Prunus virginiana*).

Nest searching and monitoring

During May through August of 1999-2001, I located and monitored a total of 113 yellow warbler nests. Although warbler nests are small and well concealed, I believe that most active nests were located at each study area. I checked each nest to determine its status when it was first discovered. Subsequently, I checked active nests every three to four days, recording the date and the number of warbler and cowbird eggs, nestlings, or fledglings observed. Nest parasitism was detected by the presence of cowbird eggs or nestlings in the nest. I considered a nest successful if it fledged at least one warbler, and I defined productivity as the number of warbler young successfully fledging from a nest (Goossen and Sealy 1982, Ortega and Ortega 2000). If nest contents disappeared prior to fledging, I recorded a predation event. As an additional measure of nest success, I classified nests based on the final stage in the nesting cycle that was achieved (e.g. no eggs detected = 0, eggs = 1, nestlings = 2, or fledged = 3), referred to as the nest end stage. Because individual warblers were not color banded, I cannot be certain that birds did not reneest after failed nesting attempts. However, warblers typically only rear one brood per season (Lowther et al. 1999). Based upon examination of a frequency plot of the dates when nests were located, I considered nests found prior to julian day 166 (15 June in 1999 and 2001 and 14 June in 2000) in each year as within the initial flush of nesting. I used only these nests in the analysis of nesting habitat selection to avoid most cases of renesting, minimizing pseudoreplication.

Behavioral observations

I selected pairs of warblers associated with active nest sites for behavioral observation using the focal sampling technique (Martin and Bateson 1993). Focal sampling involved watching the pair of birds associated with a nest site and recording all instances of several categories of behaviors. I watched nest sites continuously, recording the frequencies (e.g. food deliveries or nest defense) and time spent performing various behaviors (e.g. incubation or vigilance), and the species and sex of the bird performing the behavior. I sexed birds by plumage (Pyle 1997), as well as behavioral cues (e.g. only the female develops a brood patch for incubating eggs or brooding nestlings; Pyle 1997, Lowther et al. 1999). I assumed that birds in the immediate vicinity of a nest site were the focal pair of birds associated with that nest. This assumption is reasonable because yellow warblers typically are monogamous and defend territories around their nest sites (Lowther et al. 1999). Individual observation periods lasted approximately 75 minutes and were conducted using binoculars from a position behind naturally-occurring vegetation at a distance of 15-30 m from the nest. I moved into viewing position, then waited 10-15 minutes before beginning the observation. Observations only proceeded when both of the focal birds were not obviously reacting to my presence. I attempted to watch each active nest at least once during the egg and nestling stages of the nesting cycle. After each nest observation, I checked the nest for the number of eggs or nestlings, using the nest monitoring protocol described above.

I classified behaviors into categories based on Woodard and Murphy (1999) and preliminary observations of the study species (Merkle, unpublished data). Behavioral categories included the following: (1) *Absent*: neither of the focal pair of birds visible

around the immediate nest site; (2) *Incubating* or *brooding*: female on the nest incubating eggs or brooding young; (3) *Vigilant*: bird perched near the nest with an alert posture; (4) *Nest guarding*: a male behavior in which the male bird moves to a perch close to the nest when the female leaves the nest after an incubation or brooding bout; (5) *Food deliveries*: the frequency of food deliveries, including males feeding incubating females on the nest; (6) *Response to recreational users*: any reaction to disturbance (e.g. flush from nest, alarm call, and nest defense behaviors) and the cause; (7) *Nest defense*: chasing or reacting to hetero- or con-specific animals identified to species near the nest. I observed 45 warbler nests in the egg stage of the nesting cycle, and 33 warbler nests were observed during the nestling stage of the nesting cycle (some nests were watched during both periods).

I converted all data for behavioral measures and recreational use to percentages of the total time a nest was observed, or as rates per unit time. Total female vigilance time was considered as the percentage of time that the female was incubating or brooding plus the percentage of time that the female was vigilant while off the nest. Total male vigilance time was the percentage of time the male was vigilant plus the percentage of time that the male was nest guarding. The total number of female and male defensive reactions to other animals near the nest was considered as the total nest defense rate.

I analyzed behavioral data separately between the egg and nestling stages of the nesting cycle. I averaged data from different behavioral observations taken at the same nest during the same stage of the nesting cycle to avoid problems with pseudoreplication (Martin and Bateson 1993). Observation date, start time, and observation length did not vary among categories of trail presence or recreational use-level for observations of nests

with both eggs and nestlings, indicating that behavioral observations were conducted consistently across sampling categories.

Quantifying recreational disturbance

During behavioral observations, I recorded the frequency of recreational trail-users. I used the total number of people passing by a nest during an observation divided by observation time (referred to hereafter as the total recreational user rate) as an index of the intensity of recreational use at each nest. I classed study areas on the basis of average recreational use-level measured during nest observations, as follows: high-use > 60 users/hr, medium-use 20-60 users/hr, low-use 0-20 users/hr, and no use (based on approximately 31 hours of sampling per study area). Simultaneously recording bird behavior and recreational trail-use provided data that directly linked trail-use and the associated behavioral responses of focal pairs of birds. The total recreational user rate measured at each nest did not vary with year, observation date, temperature, observation time, or observation length.

Vegetation sampling--nest site characteristics

I measured the height and diameter at breast height (dbh) of the nest tree and the structure and composition of the surrounding vegetation based on the protocol of Martin et al. (1997). I estimated the percentage green ground cover less than 50 cm tall, and I counted all shrub stems > 50 cm tall within five meters of the nest. In addition, I recorded the species and size class (dbh) of all tree stems within 11.3 m (~0.04 ha) of the nest. I grouped trees in size classes as follows: sapling < 8 cm; 8 cm ≤ small trees < 23 cm; 23 ≤ medium trees ≤ 38 cm, and large trees > 38 cm. I summed the total number of saplings and the total number of tree stems in each size class across species. I measured the

distance from the nest to the nearest point on a trail (Miller et al. 1998), and the width of riparian vegetation where the nest was located (Miller 1999). I quantified nest concealment from each of the four cardinal directions by estimating the percentage of a 25 cm circle centered at the nest that would be covered by vegetation at a distance of 5 m from the nest at a level horizontal to the nest (based on Martin et al. 1997). I measured percent canopy cover using a concave spherical densiometer. Four readings were taken from a point directly below each nest, turning 90° between readings. I measured nest tree and nest heights using a clinometer or a 2-meter measuring stick.

Nest sites versus non-nest sites

In 2001, to examine the microhabitats that warblers selected as nest sites, I sampled a random non-nest site paired with each actual nest site. I located non-nest sites by randomly heading either 30 m upstream or downstream parallel to the creek from the nest (based on Ralph et al. 1993). I selected the first tree of the same species as the tree containing the nest encountered after 30 m as the non-nest tree, and it served as the center of the vegetation plot. I used the same sampling protocol as above for nest sites, excluding any measures specific to the actual nest.

Study area vegetation and habitat area

I sampled vegetation at each study area using the same protocol as was employed for measuring the vegetation surrounding each nest site, not including any measures specific to quantifying the nest. I located four random points at least 200 m apart at each study area. I sampled vegetation at each of these central points, as well as three surrounding satellite points 30 m away at 120 degree increments (total of 16 samples per study area). Because the satellite points likely were not independent, I averaged the data

from each central point and surrounding three satellites before making vegetation comparisons (four points per study area). I determined the total area searched for nests at each study area by estimating the length of riparian habitat from USGS 1:24,000 topographic maps and multiplying by the average of 16 riparian widths measured at each study area.

Data analyses

I treated each nest as a replicate. To increase statistical power, I pooled from the three years of study for most analyses. Due to deviations from normality, unequal sample sizes, and unequal variances for many variables, I primarily used non-parametric statistics (Zar 1996). I used a critical *P*-value of 0.05 to determine significance for all statistical tests, and I reported tests with *P*-values between 0.05 and 0.10 as marginally significant.

The proportion of nests located while the female was building (54.9%, *n* = 62 nests), laying (16.8%, *n* = 19 nests) or incubating eggs (23.0, *n* = 26 nests), or the parents were tending nestlings (5.3%, *n* = 6 nests) did not differ between trail and non-trail study areas (*n* = 113 nests, *df* = 1, Fisher's table probability 0.01, *p* = 0.80), or among study areas grouped by recreational use-level (*n* = 113 nests, *df* = 3, Fisher's table probability = 6.00×10^{-5} , *p* = 0.69). Because there was no bias in the stage of the nesting cycle when nests were initially located between trail and non-trail study areas or among groups of study areas by recreational use-level, I did not utilize Mayfield (1975) type corrections for nesting success. In addition, because most nests (94.7%) were found before hatching, the following analyses should have accurately estimated nesting success and rates of cowbird parasitism (Ortega and Ortega 2000).

Despite consistent search effort among study areas, I did not locate any warbler nests at the two high-use study areas. Due to the absence of nests from these areas, I only included high-use study areas in the following statistical analyses: 1) I used Chi-square tests to determine whether the number of warbler nests found at study areas grouped by recreational use-level differed from what would be expected based on area alone; 2) I used Kruskal-Wallis tests to test whether vegetation differed among study areas by recreational use-level. For vegetation measures that did differ significantly among recreational use-levels, I used Mann-Whitney U-tests to make post-hoc comparisons between all combinations of recreational use-levels; 3) I also used a Kruskal-Wallis test to test whether habitat area differed among study areas grouped by recreational use-level.

All of the following statistical analyses were based on the nine study areas where warbler nests were located. I used Mann-Whitney U and Kruskal-Wallis tests to test whether the number of nests succeeding compared to failing, surviving to each nest end stage, and parasitized versus unparasitized differed between trail and non-trail study areas and among recreational use-levels. I used Mann-Whitney U and Kruskal-Wallis tests to test whether nest end stage and productivity measures differed between trail and non-trail study areas and among recreational use-levels, and to test whether nest site characteristics differed between successful and unsuccessful nests, parasitized and unparasitized nests, and among nest end stages. I also used Mann-Whitney U tests to test for differences between average productivity per successful nest and average nest end stage at parasitized compared to unparasitized nests. I used Spearman's rank correlation to test for correlations between behavioral measures and the total recreational user rate and between behavioral measures and nestling age and the number of nestlings. I utilized Wilcoxon

signed-rank tests to test whether nest site characteristics differed from paired non-nest sites. I used SAS version 8.01 for Windows for all statistical tests (SAS Institute Inc. 1999).

RESULTS

Nest density

Nests were not distributed evenly by land area in study areas grouped by recreational use-level (Table 7). Considerably more nests than expected were found at medium-use study areas, and a few more nests than expected were found at low-use study areas. In comparison, fewer nests than expected were found at non-trail study areas, and no nests were found at high-use study areas. The habitat area searched for nests at each study area did not differ among recreational use-levels.

Reproductive success

Overall, nesting success for yellow warblers was 32.7% ($n = 113$ nests). Predation accounted for 92.1% ($n = 76$ nests) of all nest failures. The number of nests succeeding compared to failing (fledging success) was significantly greater at study areas with trails compared to non-trail study areas (Table 8). Additionally, productivity per nest was significantly higher, and average nest end stage was marginally higher at trail compared to non-trail study areas (Table 8). Productivity per successful nest did not differ between trail and non-trail study areas or among recreational use-levels (Table 8). Nest success, nest end stage, and productivity per nest did not differ significantly among recreational use-levels at study areas with trails (Table 8).

Table 7. Expected vs. observed number of yellow warbler nests based on habitat area in study areas grouped by recreational use-level in Boulder County, Colorado.

Use-level ^a	Area (km ²) ^b	Expected nests	Observed nests
Non-trail	0.132	22.9	15
Low	0.085	14.7	17
Medium	0.105	18.2	34
High	0.059	10.2	0
TOTAL	0.382	66	66

Notes: Chi-square test: $df = 3$, $\chi^2 = 16.80$, $P < 0.001$.

^a Non-trail = 0 users/hr; Low = 0-20 users/hr; Medium = 20-60 users/hr; High > 60 users/hr.

^b Average area searched per year.

Table 8. Reproductive parameters for yellow warblers nesting at study areas with varying recreational use-levels in Boulder County, Colorado.

Variable	Study areas by recreational use-level			Combined trail study areas
	Non-trail	Low	Medium	
Fledging success (%) ^a (n = 113 nests)	18.8 (32)	40.0 (25)	37.5 (56)	38.3 (81)
Nest end stage ^{bc} (n = 113 nests)	1.28 ± 0.17 (32)	1.60 ± 0.24 (25)	1.77 ± 0.14 (56)	1.72 ± 0.12 (81)
Productivity per nest ^d (n = 113 nests)	0.50 ± 0.20 (32)	1.24 ± 0.32 (25)	1.02 ± 0.19 (56)	1.09 ± 0.16 (81)
Productivity per successful nest (n = 37 nests)	2.67 ± 0.42 (6)	3.10 ± 0.18 (10)	2.71 ± 0.18 (21)	2.84 ± 0.14 (31)
Parasitism rates (%) (n = 113 nests)	15.6 (32)	12.0 (25)	28.6 (56)	23.5 (81)

Notes: Nesting data were pooled over all use-levels from study areas with trails to produce the combined trail study areas column. Fledging success data are the percentage of nests that fledged at least one warbler, and parasitism rates are the percentage of all nests at which parasitism was detected. All other data are means ± SE. Sample sizes are in parentheses.

^a Chi-square test of number of nests succeeding compared to failing at trail and non-trail study areas: $df = 1$, $\chi^2 = 3.97$, $P < 0.04$.

^b Nest end stage categories: 0 = no eggs; 1 = eggs; 2 = nestlings; 3 = fledged.

^c Mann-Whitney U-test between non-trail and trail parameter: $Z = -1.84$, $P < 0.07$.

^d Mann-Whitney U-test between non-trail and trail parameter: $Z = -2.01$, $P < 0.05$.

Whereas the percentage of parasitized nests was nearly twice as large at medium compared to low and non-use study areas, the number of parasitized compared to unparasitized nests was not significantly different between trail and non-trail study areas or among recreational use-levels (Table 8). Productivity per successful parasitized nest (2.37 ± 0.28 , $n = 11$ nests) was significantly less than at successful unparasitized nests (3.00 ± 0.14 , $n = 26$ nests; $Z = -1.99$, $P < 0.05$). Nest end stage was significantly greater at parasitized (2.04 ± 0.19 , $n = 24$ nests) compared to unparasitized nests (1.47 ± 0.12 , $n = 89$ nests; $Z = 2.35$, $P < 0.02$). However, when nests that were never observed with eggs (nest end stage = 0) were removed from the analysis, nest end stage did not differ between parasitized (2.04 ± 0.19 , $n = 24$ nests) and unparasitized nests (1.79 ± 0.11 , $n = 73$ nests; $Z = 1.13$, $P = 0.26$).

Behavior

None of the behavioral measures tested, including percentage time the female spent incubating, was significantly correlated with the total recreational user rate at nests observed during the egg stage of the nesting cycle (Figure 6). The percentage of time females spent incubating and total female vigilance time were significantly positively correlated with the number of male food deliveries to the incubating female (incubation: $n = 45$, $r = 0.34$, $P < 0.05$; vigilance: $n = 45$, $r = 0.38$, $P < 0.01$).

Food delivery rates (Figures 7, 8, and 9), percentage brooding time, and vigilance were not correlated with the total recreational user rate for nests observed with nestlings, whether parasitized nests were included or not. Female and total food delivery rates were not correlated with either the number of nestlings or nestling age. Male food delivery rate showed a trend of increasing with number of nestlings ($n = 33$ nests, $r = 0.33$, $P < 0.10$).

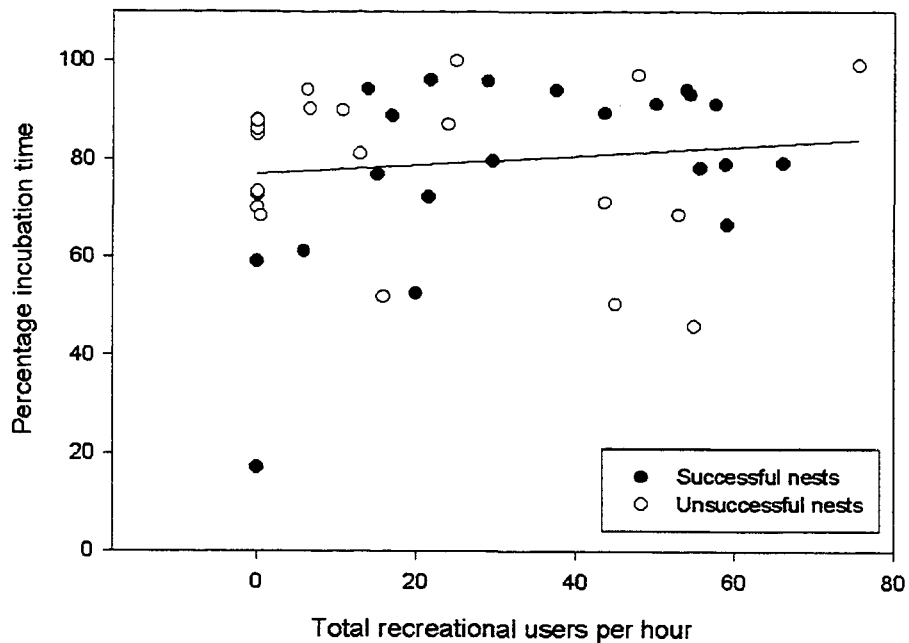


Figure 6. Percentage of time females spent incubating vs. total recreational users per hour for 45 yellow warbler nests.
Regression line: $y = 76.76 + 0.10x$; $r^2 = 0.02$; $F = 0.83$; $P = 0.37$.

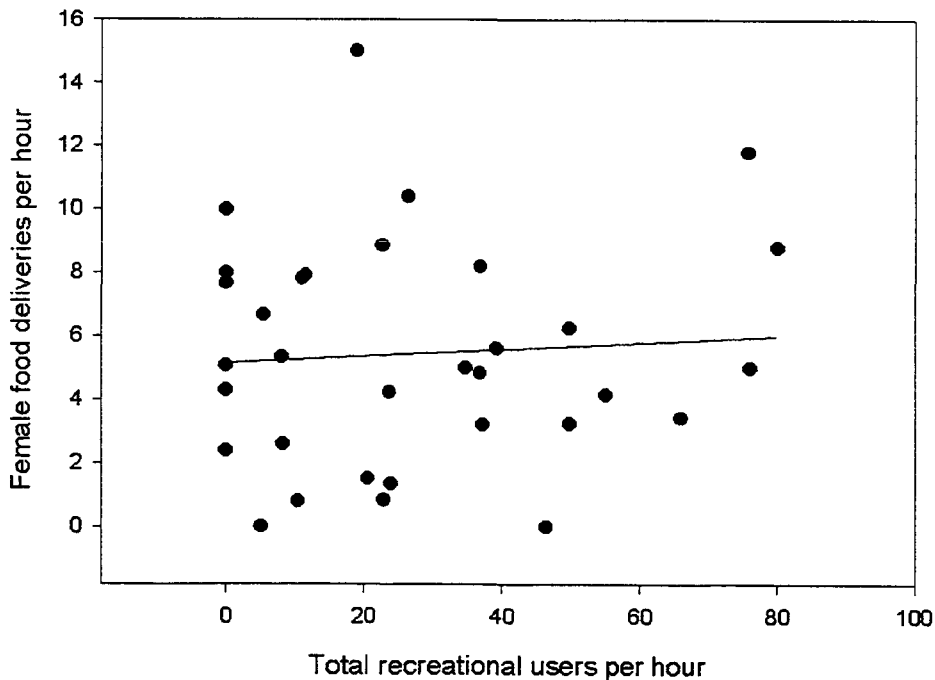


Figure 7. Female food deliveries per hour vs. total recreational users per hour for 33 yellow warbler nests.
Regression line: $y = 5.17 + 0.01x$; $r^2 = 0.005$; $F = 0.16$; $P = 0.69$.

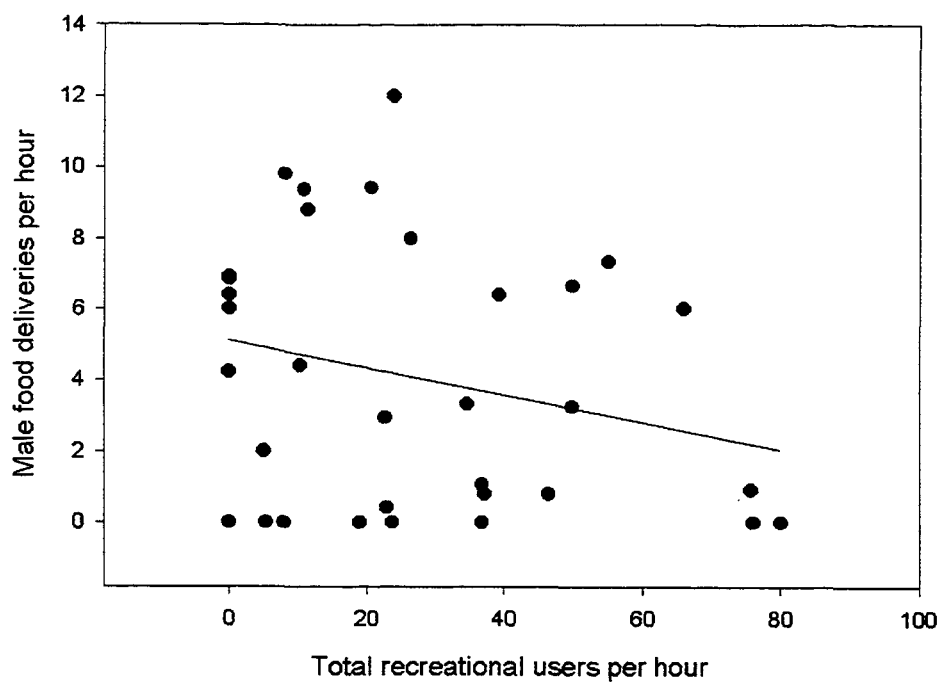


Figure 8. Male food deliveries per hour vs. total recreational users per hour for 33 yellow warblers nests.
Regression line: $y = 5.12 - 0.04x$; $r^2 = 0.06$; $F = 2.11$; $P = 0.16$.

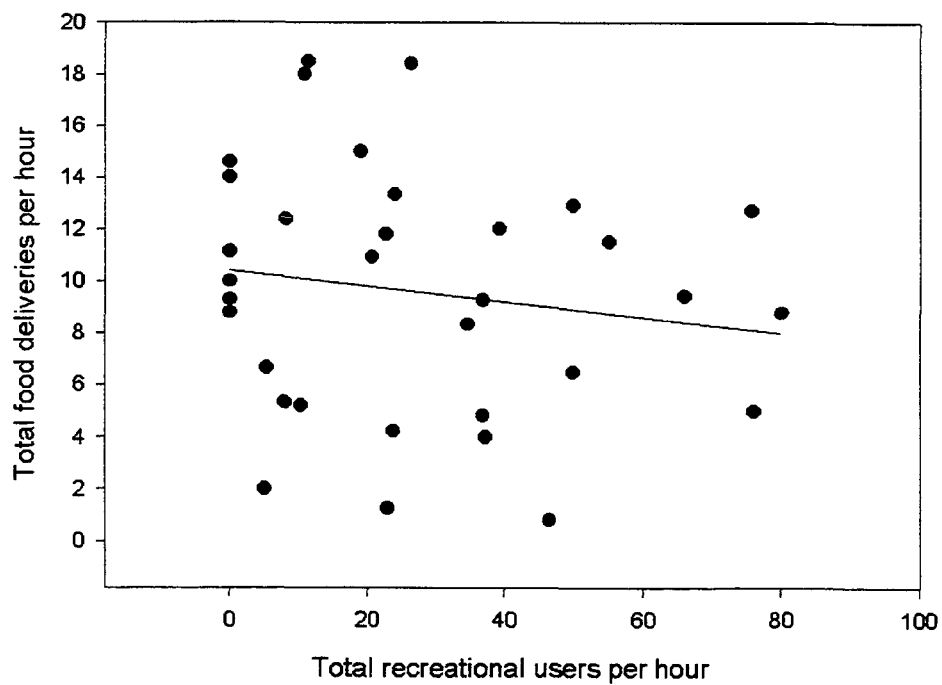


Figure 9. Total (female + male) food deliveries per hour vs. total recreational users per hour for 33 yellow warbler nests.
Regression line: $y = 10.43 - 0.03x$; $r^2 = 0.02$; $F = 0.74$; $P = 0.40$.

Percentage brooding time and total female vigilance time were significantly negatively correlated with nestling age (brooding: $n = 33$ nests, $r = -0.62$, $P < 0.001$; vigilance: $n = 33$ nests, $r = -0.52$, $P < 0.01$). Total nest defense rate tended to increase with the number of nestlings ($n = 33$ nests, $r = 0.34$, $P < 0.10$).

However, examining only unparasitized nests, female food delivery rate was significantly positively correlated with nestling age ($n = 25$ nests, $r = 0.51$, $P < 0.01$), and total food delivery rate tended to increase with nestling age ($n = 25$ nests, $r = 0.39$, $P < 0.06$). Male food delivery rate was not related to nestling age, but still showed a trend of increasing with number of nestlings ($n = 25$ nests, $r = 0.38$, $P < 0.07$).

Study area vegetation

High-use study areas had greater canopy cover and more total medium trees than other study areas grouped by recreational use-level (Table 9). Canopy cover and total medium trees did not differ among medium, low, and non-use study areas. Total shrub densities were lower at high-use study areas, but this result was only marginally significant (Table 9). None of the vegetation measures differed significantly between sampling points at combined trail and non-trail study areas (Table 9).

Nest sites versus non-nest sites

At non-trail study areas, nest sites had more total saplings and total small trees than non-nest sites (Table 10). At study areas with trails, nest sites had more total saplings and tended to have higher canopy cover than non-nest sites (Table 10).

Nest site characteristics and reproductive success

None of the variables tested differed significantly between successful and unsuccessful nests at non-trail study areas. Total shrubs tended to differ among nest

Table 9. Vegetation attributes (mean \pm SE) of study areas pooled by recreational use-level.

Variable	Study areas by recreational use-level				Combined trail study areas (n = 28 points) ¹
	Non-trail (n = 16 points) ¹	Low (n = 12 points) ¹	Medium (n = 8 points) ¹	High (n = 8 points) ¹	
Canopy cover (%) ²	34.43 \pm 5.63 ^a	34.50 \pm 6.92 ^a	28.12 \pm 5.82 ^a	61.58 \pm 4.00 ^b	40.42 \pm 4.35
Riparian width (m)	24.26 \pm 3.58	22.35 \pm 4.63	25.51 \pm 4.44	29.37 \pm 4.23	25.26 \pm 2.62
Green ground cover (%)	78.96 \pm 1.84	76.69 \pm 3.50	81.25 \pm 2.65	69.06 \pm 6.16	75.81 \pm 2.51
Total shrubs ³	20.44 \pm 4.83 ^a	24.29 \pm 4.22 ^{ab}	11.19 \pm 5.94 ^{ac}	4.81 \pm 1.42 ^c	14.98 \pm 2.91
Total saplings	43.89 \pm 7.76	30.19 \pm 8.44	24.22 \pm 6.73	49.22 \pm 8.83	33.92 \pm 5.03
Total small trees	7.27 \pm 1.41	6.62 \pm 2.07	5.53 \pm 1.48	13.31 \pm 2.45	8.22 \pm 1.32
Total medium trees ⁴	1.52 \pm 0.39 ^a	1.77 \pm 0.54 ^a	1.28 \pm 0.43 ^a	3.78 \pm 0.58 ^b	2.21 \pm 0.36
Total large trees	0.86 \pm 0.22	0.54 \pm 0.18	1.19 \pm 0.58	1.41 \pm 0.41	0.97 \pm 0.22

Notes: Vegetation data were pooled over all use-levels from study areas with trails to produce the combined trail study areas column. When Kruskal-Wallis tests among recreational use-levels were significant, individual pair-wise comparisons between use-levels were made using Mann-Whitney U-tests. Different letters indicate significant difference ($P < 0.05$, unless indicated) between use-levels.

¹ Each point is the average of the central sampling point and surrounding three satellite points (four points per study area).

² Kruskal-Wallis test among recreational use-levels: $df = 3$, $\chi^2 = 11.47$, $P < 0.01$.

³ Kruskal-Wallis test among recreational use-levels: $df = 3$, $\chi^2 = 7.76$, $P < 0.06$. Individual differences between use-levels were significant at $P < 0.10$ level.

⁴ Kruskal-Wallis test among recreational use-levels: $df = 3$, $\chi^2 = 9.63$, $P < 0.03$.

Table 10. Vegetation characteristics of yellow warbler nest sites and paired non-nest sites from 2001 for trail and non-trail study areas (mean \pm SE).

Variable	Trail	n	Means for nests	Means for non-nests	S-value	P
Total saplings	Non-trail	14	72.07 \pm 15.24	44.50 \pm 15.04	33.5	<0.04
	Trail	35	30.46 \pm 5.24	24.86 \pm 5.26	119.5	<0.02
Total small trees	Non-trail	14	7.86 \pm 1.49	5.29 \pm 1.46	25.5	<0.05
	Trail	35	6.06 \pm 1.35	4.54 \pm 0.86	35	0.43
Canopy cover (%)	Non-trail	14	69.40 \pm 8.45	66.78 \pm 8.92	2	0.92
	Trail	35	82.69 \pm 2.85	74.26 \pm 3.61	106	< 0.09

Notes: S-value and P from Wilcoxon signed-rank test for paired samples. Only variables with $P < 0.10$ for either non-trail or trail study areas were listed.

end stages, but not in a consistent pattern related to nesting success (Table 11). At study areas with trails, successful nests were higher in nesting substrates, had lower canopy cover, and tended to have greater concealment than unsuccessful nests (Table 11). Nest height also tended to differ among nest end stages, although not in a pattern consistent with survival to later nest end stages (Table 11). Nest distance to a trail did not differ between successful and unsuccessful nests. Nests ranged between 0-134 m from trails (average = 24.61 ± 2.41 m, $n = 81$ nests). However, only 4 of 81 nests (4.9%) were greater than 60 m from a trail.

At study areas without trails, parasitized nests had lower concealment and tended to be lower in height than unparasitized nests (Table 12). For nests at study areas with trails, parasitized nests were located in trees smaller in dbh, were lower in height, and were surrounded by more total shrubs than unparasitized nests (Table 12). Nest distance to a trail did not differ between parasitized and unparasitized nests. Removing the nests classified as nest end stage 0 did not change the results of statistical tests at either study areas with or without trails, so only the results of the statistical tests analyzing all nests are presented.

DISCUSSION

Results of this study suggest that warblers nested preferentially at medium-use trail study areas compared to non-trail study areas. These results contradict the prediction that songbirds with specialized habitat requirements will decrease in abundance in areas with recreational trails. The preference for medium-use study areas may have been due to reduced predation pressures resulting from the

Table 11. Yellow warbler nest site characteristics (mean \pm SE) by nest end stage and for all failed nests combined for study areas with and without recreational trails.

Variable	Trail	Nest end stage				All failed nests combined
		0 – No eggs detected	1 – Eggs	2 – Nestlings	3 – Fledged	
Nest height (m)	Non-trail	6.17 \pm 1.36 (5)	6.24 \pm 0.73 (19)	5.80 \pm 3.10 (2)	4.27 \pm 1.14 (6)	6.20 \pm 0.61 (26)
	Trail ^{ab}	5.14 \pm 0.65 (11)	6.24 \pm 0.48 (32)	4.12 \pm 1.43 (7)	6.86 \pm 0.54 (31)	5.70 \pm 0.40 (50)
Nest concealment (%)	Non-trail	50.94 \pm 10.27 (4)	66.48 \pm 4.69 (16)	85.62 \pm 6.88 (2)	70.50 \pm 6.08 (5)	65.40 \pm 4.24 (22)
	Trail ^c	54.38 \pm 8.54 (8)	65.69 \pm 4.00 (27)	51.96 \pm 6.64 (7)	69.51 \pm 3.28 (28)	61.25 \pm 3.30 (42)
Total shrubs	Non-trail ^d	0.80 \pm 0.80 (5)	26.89 \pm 9.38 (19)	0 (2)	25.00 \pm 9.62 (6)	19.81 \pm 7.20 (26)
	Trail	14.27 \pm 9.46 (11)	42.38 \pm 15.09 (32)	59.14 \pm 37.38 (7)	52.23 \pm 25.60 (31)	38.54 \pm 11.15 (50)
Canopy cover (%)	Non-trail	80.13 \pm 7.89 (5)	71.50 \pm 7.12 (19)	73.19 \pm 6.37 (2)	74.88 \pm 9.54 (6)	73.29 \pm 5.40 (26)
	Trail ^e	79.02 \pm 5.54 (11)	81.14 \pm 2.78 (32)	79.30 \pm 7.36 (7)	73.34 \pm 2.93 (31)	80.41 \pm 2.33 (50)

Notes: Only variables with $P < 0.10$ for either non-trail or trail study areas were listed. Sample sizes in parentheses.

^a Mann-Whitney U-test between successful and unsuccessful nests: $Z = 2.01$, $P < 0.05$.

^b Kruskal-Wallis test among nest end stages: $df = 3$, $\chi^2 = 7.08$, $P < 0.07$.

^c Mann-Whitney U-test between successful and unsuccessful nests: $Z = 1.70$, $P < 0.09$.

^d Kruskal-Wallis test among nest end stages: $df = 3$, $\chi^2 = 7.08$, $P < 0.07$.

^e Mann-Whitney U-test between successful and unsuccessful nests: $Z = -2.13$, $P < 0.0$

Table 12. Vegetation characteristics of parasitized and unparasitized yellow warbler nest sites for trail and non-trail study areas.

Variable	Trail	Parasitized nests	Unparasitized nests	Z-value	P
Plant dbh (m)	Non-trail	0.71 ± 0.30 (5)	0.74 ± 0.13 (25)	-0.28	0.78
	Trail	0.53 ± 0.20 (19)	0.98 ± 0.14 (60)	-2.77	<0.006
Nest height (m)	Non-trail	3.49 ± 1.17 (5)	6.27 ± 0.58 (27)	-1.92	<0.06
	Trail	4.50 ± 0.78 (19)	6.65 ± 0.33 (62)	-2.51	<0.02
Nest concealment (%)	Non-trail	47.25 ± 6.10 (5)	70.68 ± 3.65 (22)	-2.53	<0.02
	Trail	65.07 ± 3.76 (19)	64.36 ± 3.01 (51)	-0.14	0.89
Total shrubs	Non-trail	26.40 ± 14.61 (5)	19.74 ± 6.76 (27)	0.49	0.63
	Trail	80.32 ± 24.24 (19)	32.58 ± 13.44 (62)	2.35	<0.02

Notes: Values are mean ± SE with sample sizes in parentheses. Z-statistic and P-value from Mann-Whitney U-tests. Only variables with $P < 0.10$ for either non-trail or trail study areas were listed.

displacement of some nest predators (Osborne and Osborne 1980, Gering and Blair 1999). Warbler's aversion to non-trail study areas may have been due to higher risk of nest predation (Martin 1993). In studies of avian use of campgrounds in riparian areas, Saab (1996) found that yellow warblers decreased in abundance at campsites along the Snake River in Idaho, whereas Blakesley and Reese (1998) found no difference in yellow warbler abundance between campgrounds and non-campgrounds in northern Utah.

Warblers completely avoided nesting at the two highest-use study areas. This result may indicate a threshold level of recreational disturbance above which warblers will not nest. However, high-use study areas had higher canopy cover, more medium-sized trees, and tended to have fewer total shrubs compared to other study areas grouped by recreational use-level (Table 9). Higher canopy cover at nest sites was associated with reduced nesting success at study areas with trails. Thus, warblers may have avoided high-use study areas with their closed canopies because of reduced habitat quality. On the other hand, warblers tended to select nest sites with higher canopy cover than random points at study areas with trails. Nests in larger trees and with fewer surrounding shrubs were less likely to be parasitized at study areas with trails. Accordingly, high-use study areas with high numbers of medium-sized trees and low shrub density could have potentially provided warblers nest-sites that were safe from cowbird parasitism.

Casual observations at other riparian corridors in the region suggest that other factors, such as the loss of habitat along riparian migration corridors (Moore et al. 1995), in addition to recreational use rate may be affecting the presence of yellow

warblers (Merkle, personal observation). For example, I did observe several breeding pairs of warblers and one nest along two areas that would have been considered as high-use under my classification criteria, on a drainage in Denver, Denver County, Colorado (Merkle, personal observation). I also found only one potential breeding pair of warblers during casual surveys of two areas that would have been classified as medium-use, along a drainage in Fort Collins, Larimer County, Colorado (Merkle, personal observation).

Warbler reproductive success was greater at trail compared to non-trail study areas, and similar in magnitude between low and medium-use trail study areas (Table 8). Increased reproductive success at study areas with trails may have been due to a refuge effect due to the displacement of some potential nest predators by trail-users (Osborne and Osborne 1980, Gering and Blair 1999). Similarly, Miller and Hobbs (2000) found decreased predation rates on artificial nests with proximity to recreational trails in lowland riparian habitats. Other studies also have found reduced predation rates on both natural and artificial nests in areas associated with high human activity (Tomialojc and Profus 1977, Osborne and Osborne 1980, Tarvin and Smith 1995, Gering and Blair 1999). Warbler susceptibility to small mammalian nest predators, which may reach higher abundance at study areas without trails and avoid more heavily used trails, may explain the observed differences in nesting success. For example, Sauvajot et al. (1998) found that small mammal abundance decreased with human disturbance associated with road and trail development, and Miller and Hobbs (2000) found that mice depredated more nests than expected away from trails compared to near trails. These results are contrary to Miller et al.'s (1998) finding

that nest success for a pooled sample of songbirds decreased with proximity to recreational trails in both forested and grassland habitats.

Based upon observations made during this study, other studies conducted locally, and reports of known predators of warbler nests, I developed a list of potential warbler nest predators occurring on my study areas (Miller et al. 1998; Lowther et al. 1999, Miller and Hobbs 2000; Merkle, personal observation). Avian nest predators included cooper's hawks (*Accipiter cooperii*), sharp-shinned hawks (*Accipiter striatus*), common ravens (*Corvus corax*), American crows (*Corvus brachyrhynchos*), black-billed magpies, blue jays, house wrens (*Troglodytes aedon*), common grackles (*Quiscalus quiscula*), and brown-headed cowbirds. Mammalian predators included fox squirrels (*Sciurus niger*), deer mice (*Peromyscus maniculatus*), coyotes (*Canis latrans*), red fox (*Vulpes vulpes*), raccoons (*Procyon lotor*), striped skunks (*Mephitis mephitis*), and domestic cats (*Felis catus*). Reptilian predators included bullsnakes (*Pituophis melanoleucus*) and garter snakes (*Thamnophis* spp.).

Parasitism rates were nearly twice as high at medium compared to low and non-use study areas, suggesting an increase in parasitism pressure in areas subject to intermediate levels of recreational use. However, the data were not sufficient to support this claim. Other researchers have found that cowbirds increased in abundance along trails or with recreational activities (Hickman 1990, Camp and Knight 1998, Chace et al. In Press). In contrast, Miller et al. (1998) found that neither cowbird abundance nor parasitism rates increased with proximity to recreational trails. Another cost of cowbird parasitism was reduced productivity: mean warbler

productivity for successful nests was significantly lower for parasitized compared to unparasitized nests. Other studies have found similar results, possibly due to host egg removal at parasitized nests by female cowbirds (Burgham and Picman 1989, Sealy 1992, Ortega and Ortega 2000).

Overall, nesting success for yellow warblers in this study was 32.7% (n = 113 nests). This value is lower than nesting success reported from other studies of yellow warblers, which ranged from 42% (n = 74 nests) in British Columbia, Canada, to 72% (n = 72 nests) in James Bay, Canada (Lowther et al. 1999). Based on a review of the literature, Martin (1995) calculated average nesting success for yellow warblers to be 49.8%. In a study conducted regionally in riparian habitat in southwestern Colorado, yellow warbler nesting success was measured at 43.9% (n = 66 nests) (Ortega and Ortega 2000). In this study, nesting success at low and medium-use trail study was 38.3% (n = 81 nests), which was closer to, although still below, success values from other studies. Nesting success at non-trail study areas at 18.8% (n = 32 nests) was less than half the success values reported in other studies. Vierling (2000) suggested that the entire Boulder suburban area functioned as a regional sink for red-winged blackbirds (*Agelaius phoeniceus*), possibly because human activity attracted high densities of human-associated predators. Nest parasitism in this study was 21.2% (n = 113 nests). This value is towards the lower end of the range of nest parasitism rates for yellow warblers, ranging from 13.9% (n = 209 nests) in central Alberta, Canada, to 76.9% (n = 26 nests) in Ontario, Canada (Lowther et al. 1999). Ortega et al. found that 36.4% (n = 66 nests) were parasitized in southwestern Colorado (Ortega and Ortega 2000).

None of the behavioral measures examined varied with recreational trail-use. The lack of behavioral response may have been due to warblers foraging (primarily foliage gleaning) in the canopy, and their small, well-concealed nests (Lowther et al. 1999; Merkle, personal observation). Gutzwiller et al. (1998) found that songbirds active closer to the ground were more sensitive to the approach of experimental human intruders than songbirds active higher in the canopy. In addition, Saab (1996) found that warbling vireos (*Vireo gilvus*) increased in abundance at campsites versus non-campsites and suggested that their habit of nesting in the upper canopy allowed them to avoid ground-level disturbance from recreationists (although yellow warblers declined in abundance at campsites in the same study). Finally, other researchers have suggested that small birds may be more tolerant of human disturbance than larger birds because they are more difficult to detect, historically have not been persecuted, and have greater energetic demands (e.g. higher metabolic rates make flushing more costly) (Cooke 1980, Knight and Cole 1995, Marzluff 1997).

Although differences in vegetation cannot be ruled out as a factor in warbler avoidance of high-use study areas, habitat characteristics apparently were not related to nesting habitat selection or nesting success at the study areas where warbler nests were found. Parasitized nests at study areas with trails had more surrounding shrubs than unparasitized nests, but parasitism rates were not higher at low compared to medium-use study areas. Vegetation did not differ between study areas with and without recreational trails (Table 9). In addition, because habitat area did not differ among study areas grouped by recreational use-level, habitat area effects were not

associated with observed differences in nesting habitat selection and reproductive success.

Warblers selected nest sites with more saplings than random points at both non-trail and trail study areas (Table 10). At non-trail study areas, warblers also selected nest sites with more surrounding small trees than random points (Table 10). Increased vertical complexity of saplings and small trees may make detecting nests more difficult for randomly searching predators (Martin 1993). Knopf and Sedgwick (1992) also found that yellow warblers selected nest shrubs in areas of higher vegetation density, and Sanders and Edge (1998) found that yellow warbler abundance increased with willow volume. Warblers at study areas with trails also tended to select nest sites with higher canopy cover than random points, possibly in response to higher corvid abundance along recreational trails (Hickman 1990, Miller and Hobbs 2000; Table 10).

At non-trail areas, none of the nest site characteristics, including total saplings and total small trees, were significantly associated with nesting success. Although total shrubs did tend to differ among nest end stages, no pattern with nest survival was evident, possibly because the two nests that failed with nestlings both were located in areas with no surrounding shrubs (Table 11). Researchers have suggested that the lack of nest sites safe from predation may indicate a diverse predator community at these non-trail study areas (Dion et al. 2000, Budnik et al. 2002).

Successful warbler nests at study areas with trails were located higher in nest trees and tended to have greater concealment (Table 11). Other studies have found

increased nest success with nest height, possibly because higher nests were less susceptible to ground predators (Wilson and Cooper 1998, Burhans et al. 2002). Yahner (1991) also suggested that higher nests were more susceptible to avian nest predators, providing an additional indication that ground predators were the major threat to warbler nests in this study. Furthermore, nesting higher may be a way of avoiding ground-level disturbance from trail-users (Knight and Fitzner 1985, Miller 1999). Although warblers at study areas with trails tended to select nest sites with higher canopy cover than random points, nests with higher canopy cover were more likely to fail (Tables 10 and 11). This inconsistency between nest site selection and habitat quality may have been due to chance (e.g. Type II error). The trend for warblers to select nest sites with higher canopy cover was only marginally significant and based only on 35 nests found in 2001. Nest trees with lower canopy cover may have had structural differences that made them more difficult or less attractive for ground predators to climb.

Nest distance to a trail did not differ between successful and unsuccessful nests, or among nest end stages. In contrast, Miller et al. (1998) found that nesting success increased with nest distance from a trail for a pooled sample of songbirds in forested and grassland habitats. However, due to the narrow, linear nature of riparian habitats (study areas averaged 50-60 m in total width), trail effects were likely to have permeated the entire system, and nest distances from trails did not vary much, making it unlikely that I would detect distance effects.

Parasitized nests were located lower in nesting substrates compared to unparasitized nests at both non-trail and trail study areas. Other researchers have also

found higher parasitism rates of lower songbird nests, including yellow warblers, possibly because cowbirds are active and forage on or near the ground and may discover low nests from this vantage (Briskie et al. 1990, Hahn and Hatfield 1995, Chace et al. 2000). At non-trail study areas, lower concealment at parasitized versus unparasitized nests may have allowed cowbirds to locate nests by making them easier to see or by making it easier to follow warblers to their nests (Burhans 1997, Budnik et al. 2002). Nest concealment may have also increased for nests placed higher in plant crowns (Wilson and Cooper 1998, Budnik et al. 2002). At study areas with trails, parasitized nests were located in trees smaller in dbh and in areas surrounded by greater number of total shrubs than unparasitized nests. Smaller trees may have provided fewer suitable higher nesting locations. Greater total shrubs surrounding nests at study areas with trails may have provided low perches that provided cowbirds better vantage points to search for nests and observe warbler activity (Budnik et al. 2002).

MANAGEMENT IMPLICATIONS

Warblers apparently achieved higher reproductive success at trail compared to non-trail study areas and preferred nesting at medium-use trail study areas. Furthermore, warbler nesting behavior did not vary with recreational trail-use. These results indicate that songbirds capable of tolerating human disturbance, even those with fairly specialized habitat requirements, may fare well in some areas developed with recreational trails due to an apparent refuge effect. Similarly, Sauvajot et al.

(1998) found that resident songbirds showed little response to human disturbance associated with roads and trails.

However, even though all study areas had what appeared to be suitable vegetation structure for nesting, recreational use may have compressed the realized niche for warblers (Vanvalkenburgh and Wayne 1994, Ilse and Hellgren 1995). Warblers were not found nesting at high-use study areas, potentially indicating an upper limit to the refuge effect in association with high levels of human disturbance. The refuge effect also potentially indicated shifts in the predator community, with evidence suggesting that small mammals were likely to have been displaced from study areas with trails (Sauvajot et al. 1998, Miller and Hobbs 2000). Lower warbler nesting density at non-trail areas was associated with a higher risk of nest predation, possibly due to an influx of small mammalian predators from areas developed with trails. Thus, recreational use may have reduced the availability of suitable riparian habitat for nesting warblers. Accordingly, recreational use may be an additional factor contributing to the degradation of western riparian habitats, and may lead to further declines, and possible local extirpations, for some populations of warblers (Andrews and Righter 1992, Ehrlich et al. 1992, Lowther et al. 1999).

Sections of most major riparian systems in Boulder County, Colorado, have been developed with recreational trails (Miller and Hobbs 2000; Merkle, personal observation). Evidence from this study suggests that recreational trails and users may alter predator communities, potentially increase nest parasitism, and displace some breeding populations from high-use trail areas. Thus, the need for additional trails in riparian habitats in this area should be thoroughly and thoughtfully examined based

on the potential for negative effects on overall riparian biodiversity. For example, even at low and medium-use study areas where warblers did relatively well reproductively, this higher level of nesting success probably was due to the displacement of some species of nest predators.

At both trail and non-trail study areas, nest concealment and nest height were consistently positively associated with nest site selection and reproductive success. These results suggest that management for songbirds in riparian habitats should include increasing vegetation density possibly by precluding grazing and reducing water diversions (Ohmart 1994, Saab et al. 1995). In addition, fostering the growth of larger trees will provide nest sites that may be less susceptible to ground predators and cowbird parasitism. Accordingly, trails should be aligned to take advantage of areas with dense, well-established vegetation, including larger trees. Also, dense vegetation within some habitats may provide cover that allows songbirds to avoid some disturbance from recreationists (Fernandez-Juricic and Telleria 2000).

Songbird responses to recreational trail-use are most likely species specific, and accordingly, extrapolating results of this study to other species in other localities should be done conservatively. For example, warblers are frequent cowbird hosts and may be able to avoid some aspects of recreational disturbance because they are active in the canopy and build small, well-concealed nests. Other species with different natural histories may respond quite differently to recreational trail-use. However, at the same study areas, I found that American robins (*Turdus migratorius*) also may have benefited from a refuge effect, although only at medium and high-use study areas (Merkle, unpublished data). Robin nesting success was lowest at low-use study

areas, which may indicate that different predators were primarily responsible for nest failures of robins compared to yellow warblers. Evidence suggested that robins were mainly susceptible to avian nest predators, whereas warblers were primarily susceptible to small mammals. Robin behavior also varied with recreational use, possibly because they forage on the ground; though, robins were apparently able to compensate behaviorally to nest successfully near recreational trails.

LITERATURE CITED

- Andrews, R., and R. Righter. 1992. Colorado birds : a reference to their distribution and habitat. Denver Museum of Natural History, Denver, CO.
- Bent, A. C. 1953. Life histories of North American wood warblers. United States National Museum Bulletin 203:1-734.
- Blakesley, J. A., and K. P. Reese. 1988. Avian use of campground and noncampground sites in riparian zones. *Journal of Wildlife Management* 52:399-402.
- Bottorff, R. L. 1974. Cottonwood habitat for birds in Colorado. *American Birds* 28:975-979.
- Briskie, J. V., S. G. Sealy, and K. A. Hobson. 1990. Differential parasitism of least flycatchers and yellow warblers by the brown-headed cowbird. *Behavioral Ecology and Sociobiology* 27:403-410.
- Budnik, J. M., F. R. Thompson, and M. R. Ryan. 2002. Effect of habitat characteristics on the probability of parasitism and predation of Bell's vireo nests. *Journal of Wildlife Management* 66:232-239.
- Burgham, M. C. J., and J. Picman. 1989. Effect of brown-headed cowbirds on the evolution of yellow warbler anti-parasite strategies. *Animal Behaviour* 38:298-308.
- Burhans, D. E. 1997. Habitat and microhabitat features associated with cowbird parasitism in two forest edge cowbird hosts. *Condor* 99:866-872.
- Burhans, D. E., D. Dearborn, F. R. Thompson, and J. Faaborg. 2002. Factors affecting predation at songbird nests in old fields. *Journal of Wildlife Management* 66:240-249.
- Camp, R. J., and R. L. Knight. 1998. Rock climbing and cliff bird communities at Joshua Tree National Park, California. *Wildlife Society Bulletin* 26:892-898.
- Chace, J. F., J. J. Walsh, A. Cruz, J. W. Prather, and H. M. Swanson. In Press. Spatial and temporal activity patterns of the brood parasitic brown-headed cowbird at an urban/wildland interface. *Landscape and Urban Planning*.
- Chace, J. F., S. T. McKinney, and A. Cruz. 2000. Nest-site characteristics and nesting success of the greater pewee in Arizona. *Southwestern Naturalist* 45:169-175.
- Clark, K. L., and R. J. Robertson. 1981. Cowbird parasitism and evolution of anti-parasite strategies in the yellow warbler. *Wilson Bulletin* 93:249-258.

- Cody, M. L. 1985. Habitat selection in birds. Academic Press, Orlando, FL.
- Cole, D. N. 1996. Wilderness recreation use trends, 1965 through 1994. Research paper INT-RP-488. U.S.D.A., Forest Service, Intermountain Research Station, Ogden, UT.
- Cole, D. N., and P. B. Landres. 1995. Indirect effects of recreation on wildlife. Pages 183-201 in R. L. Knight and K. J. Gutzwiller, editors. Wildlife and recreationists. Island Press, Washington, D.C.
- Cooke, A. S. 1980. Observations on how close certain passerine species will tolerate an approaching human in rural and suburban areas. Biological Conservation 18:85-88.
- Dion, N., K. A. Hobson, and S. Larviere. 2000. Interactive effects of vegetation and predators on the success of natural and simulated nests of grassland songbirds. Condor 102:629-634.
- Ehrlich, P. R., D. S. Dobkin, and D. Wheye. 1988. The birder's handbook : a field guide to the natural history of North American birds. Simon and Schuster, New York, NY.
- Ehrlich, P. R., D. S. Dobkin, and D. Wheye. 1992. Birds in jeopardy. Stanford University Press, Stanford, CA.
- Fernandez-Juricic, E., and J. L. Telleria. 2000. Effects of human disturbance on spatial and temporal feeding patterns of blackbird *Turdus merula* in urban parks in Madrid, Spain. Bird Study 47:13-21.
- 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. Island Press, Washington, D.C.
- Gering, J. C., and R. B. Blair. 1999. Predation on artificial bird nests along an urban gradient: predatory risk or relaxation in urban environments? Ecography 22:532-541.
- Goossen, J. P., and S. G. Sealy. 1982. Production of young in a dense nesting population of yellow warblers, *Dendroica petechia*, in Manitoba. Canadian Field-Naturalist 96:189-199.
- Gotmark, F. 1992. The effects of investigator disturbance on nesting birds. Pages 63-104 in D. M. Power, editor. Current Ornithology, Vol. 9. Plenum Press, New York, NY.

- Gutzwiller, K. J., E. A. Kroese, S. H. Anderson, and C. A. Wilkins. 1997. Does human intrusion alter the seasonal timing of avian song during breeding periods? *Auk* 114:55-65.
- Gutzwiller, K. J., H. A. Marcum, H. B. Harvey, J. D. Roth, and S. H. Anderson. 1998. Bird tolerance to human intrusion in Wyoming montane forests. *Condor* 100:519-527.
- Hahn, D. C., and J. S. Hatfield. 1995. Parasitism at the landscape scale: cowbirds prefer forests. *Conservation Biology* 9:1415-1424.
- Hickman, S. 1990. Evidence of edge species attraction to nature trails within deciduous forest. *Natural Areas Journal* 10:3-5.
- Ilse, L. M., and E. C. Hellgren. 1995. Resource partitioning in sympatric populations of collared peccaries and feral hogs in southern Texas. *Journal of Mammalogy* 76:784-799.
- Knight, R. L., and D. N. Cole. 1995. Factors that influence wildlife responses to recreationists. Pages 71-79 in R. L. Knight and K. J. Gutzwiller, editors. *Wildlife and recreationists*. Island Press, Washington, D.C.
- Knight, R. L., and R. E. Fitzner. 1985. Human disturbance and nest site placement in black-billed magpies. *Journal of Field Ornithology* 56:153-157.
- Knight, R. L., and K. J. Gutzwiller, editors. 1995. *Wildlife and recreationists*. Island Press, Washington, DC.
- Knight, R. L., and S. A. Temple. 1986. Methodological problems in studies of avian nest defense. *Animal Behaviour* 34:561-566.
- Knopf, F. L., R. R. Johnson, T. Rich, F. B. Samson, and R. C. Szaro. 1988. Conservation of riparian ecosystems in the United States. *Wilson Bulletin* 100:272-284.
- Knopf, F. L., and J. A. Sedgwick. 1992. An experimental study of nest-site selection by yellow warblers. *Condor* 94:734-742.
- Kuenning, R. R. 1998. Yellow warbler. Pages 418-419 in H. E. Kingery, editor. *Colorado breeding bird atlas*. Colorado Breeding Bird Atlas Partnership, Denver, CO.
- Lowther, P. E., C. Celada, N. K. Klein, C. C. Rimmer, and D. A. Spector. Yellow Warbler (*Dendroica petechia*). In *The Birds of North America*, no. 454 (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.

- Major, R. E., and C. E. Kendal. 1996. The contribution of artificial nest experiments to understanding avian reproductive success: a review of methods and conclusions. *Ibis* 138:298-307.
- Martin, P., and P. Bateson. 1993. *Measuring behaviour*, 2nd edition. Cambridge University Press, Cambridge.
- Martin, T. E. 1993. Nest predation and nest sites - new perspectives on old patterns. *Bioscience* 43:523-532.
- Martin, T. E. 1995. Avian life history evolution in relation to nest sites, nest predation, and food. *Ecological Monographs* 65:101-127.
- Martin, T.E., C.R. Paine, C.J. Conway, W.M. Hochachka, P. Allen, and W. Jenkins. 1997. BBIRD Field Protocol. Montana Cooperative Wildlife Research Unit, University of Montana, Missoula, MT.
<http://pica.wru.umt.edu/BBIRD/research.htm>.
- Marzluff, J. M. 1997. Effects of urbanization and recreation on songbirds. Pages 89-102 in W. M. Block and D. M. Finch, editors. *Songbird ecology in Southwestern ponderosa pine forests: a literature review*. Gen. Tech. Rep. RM-GTR-292. U.S.D.A., Forest Service, Rocky Mountain Forest and Range Experimental Station, Fort Collins, CO.
- Mayfield, H. F. 1975. Suggestions for calculating nest success. *Wilson Bulletin* 87:456-466.
- Miller, C. K. 1994. Environmental impacts of passive recreational trails in riparian areas. Pages 96-105 in *Proceedings of the 6th Annual Colorado Riparian Association Conference*, Alamosa, CO.
- Miller, J. R. 1999. The effect of human settlement on bird communities in lowland riparian areas. Ph.D. Thesis. Colorado State University, Fort Collins, CO.
- Miller, J. R., and N. T. Hobbs. 2000. Recreational trails, human activity, and nest predation in lowland riparian areas. *Landscape and Urban Planning* 50:227-236.
- Miller, S. G., R. L. Knight, and C. K. Miller. 1998. Influence of recreational trails on breeding bird communities. *Ecological Applications* 8:162-169.
- Miller, S. G., R. L. Knight, and C. K. Miller. 2001. Wildlife responses to pedestrians and dogs. *Wildlife Society Bulletin* 29:124-132.

- Moore, F. R., J. Gathreaux, S.A., P. Kerlinger, and T. R. Simons. 1995. Habitat requirements during migration: important link in conservation. Pages 121-144 in T. E. Martin and D. M. Finch, editors. Ecology and management of Neotropical migratory birds. Oxford University Press, New York, NY.
- Naiman, R. J., H. Decamps, and M. Pollock. 1993. The role of riparian corridors in maintaining regional biodiversity. *Ecology* 31:209-212.
- Ohmart, R. D. 1994. The effects of human induced changes on the avifauna of western riparian habitats. *Studies in Avian Biology* 15:273-285.
- Ortega, C. P., J. C. Ortega, C. A. Rapp, and S. A. Backensto. 1998. Validating the use of artificial nests in predation experiments. *Journal of Wildlife Management* 62:925-932.
- Ortega, C. P., J. C. Ortega, C. A. Rapp, S. Vorisek, S. A. Backensto, and D. W. Palmer. 1997. Effect of research activity on the success of American robin nests. *Journal of Wildlife Management* 61:948-952.
- Ortega, J. C., and C. P. Ortega. 2000. Effects of brown-headed cowbirds and predators on the nesting success of yellow warblers in southwest Colorado. *Journal of Field Ornithology* 71:516-524.
- Osborne, P., and L. Osborne. 1980. The contribution of nest site characteristics to breeding- success among blackbirds *Turdus merula*. *Ibis* 122:512-517.
- Pyle, P. 1997. Identification guide to North American birds. Slate Creek Press, Bolinas, CA.
- Ralph, C. J., G. R. Geupel, P. Pyle, T. E. Martin, and D. F. DeSante. 1993. Handbook of field methods for monitoring landbirds. Gen. Tech. Rep. PSW-GTR-144. Forest Service, U.S.D.A., Forest Service, Pacific Southwest Research Center, Albany, CA.
- 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.
- SAS Institute Inc. 1999. SAS/STAT user's guide. Version 8.0. SAS Institute Inc., Cary, NC.
- Saab, V. A. 1996. Influences of spatial scale and land-use practices on habitat relationships of breeding birds in cottonwood riparian forests. Ph.D. thesis. University of Colorado, Boulder, CO.

- Saab, V. A., C. E. Bock, T. D. Rich, and D. S. Dobkin. 1995. Livestock grazing effects in western North America. Pages 311-353 in T. E. Martin and D. M. Finch, editors. Ecology and management of Neotropical migratory birds: a synthesis and review of critical issues. Oxford University Press, New York, NY.
- Sanders, T. A., and W. D. Edge. 1998. Breeding bird community composition in relation to riparian vegetation structure in the western United States. *Journal of Wildlife Management* 62:461-473.
- Sauvajot, R. M., M. Buechner, D. A. Kamradt, and C. M. Schonewald. 1998. Patterns of human disturbance and response by small mammals and birds in chaparral near urban development. *Urban Ecosystems* 2:279-297.
- Sealy, S. G. 1992. Removal of yellow warbler eggs in association with cowbird parasitism. *Condor* 94:40-54.
- Tarvin, K. A., and K. G. Smith. 1995. Microhabitat factors influencing predation and success of suburban blue jay *Cyanocitta cristata* nests. *Journal of Avian Biology* 26:296-304.
- Tomialojc, L., and P. Profus. 1977. Comparative analysis of breeding bird communities in two parks of Wroclaw and in an adjacent Querco-Carpinetum forest. *Acta Ornithologica* 16:117-177.
- van der Zande, A. N., 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.
- Vanvalkenburgh, B., and R. K. Wayne. 1994. Shape divergence associated with size convergence in sympatric East-African jackals. *Ecology* 75:1567-1581.
- Vierling, K. T. 2000. Source and sink habitats of Red-winged Blackbirds in a rural/suburban landscape. *Ecological Applications* 10:1211-1218.
- Wilson, R. R., and R. J. Cooper. 1998. Acadian flycatcher nest placement: does placement influence reproductive success? *Condor* 100:673-679.
- Woodard, J. D., and M. T. Murphy. 1999. Sex roles, parental experience and reproductive success of eastern kingbirds, *Tyrannus tyrannus*. *Animal Behaviour*, 57:105-115.
- Yahner, R. H. 1991. Avian nesting ecology in small even-aged aspen stands. *Journal of wildlife management* 55:155-159.

Zar, J. H. 1996. Biostatistical analysis, 3rd edition. Prentice Hall, Upper Saddle River, NJ.

LITERATURE CITED

- Ammon, E. M. 1995. Reproductive strategies and factors determining nest success in subalpine ground-nesting passerines. Ph.D. University of Colorado, Boulder, CO.
- Andrews, R., and R. Righter. 1992. Colorado birds : a reference to their distribution and habitat. Denver Museum of Natural History, Denver, CO.
- Askins, R. A. 1994. Open corridors in a heavily forested landscape - impact on shrubland and forest-interior birds. *Wildlife Society Bulletin* 22:339-347.
- Badyaev, A. V., and C. K. Ghalambor. 2001. Evolution of life histories along elevational gradients: Trade- off between parental care and fecundity. *Ecology* 82:2948-2960.
- Bekoff, M., A. C. Scott, and D. A. Conner. 1987. Nonrandom nest-site selection in evening grosbeaks. *Condor* 89:819-829.
- Bent, A. C. 1953. Life histories of North American wood warblers. United States National Museum Bulletin 203:1-734.
- Berry, M. E., and C. E. Bock. 1998. Effects of habitat and landscape characteristics on avian breeding distributions in Colorado foothills shrub. *Southwestern Naturalist* 43:453-461.
- Bibby, C. J. 1999. Making the most of birds as environmental indicators. *Ostrich* 70:81-88.
- Blakesley, J. A., and K. P. Reese. 1988. Avian use of campground and noncampground sites in riparian zones. *Journal of Wildlife Management* 52:399-402.
- Bock, C. E., J. H. Bock, and B. C. Bennett. 1999. Songbird abundance in grasslands at a suburban interface on the Colorado High Plains. *Studies in Avian Biology* 19:131-136.
- Bock, C.E., K.T. Vierling, S.L. Haire, J.D. Boone, and W.W. Merkle. In Press. Patterns of rodent abundance on open-space grasslands in relation to suburban edges. *Conservation Biology*.
- Both, C., M. E. Visser, and N. Verboven. 1999. Density-dependent recruitment rates in great tits: the importance of being heavier. *Proceedings of the Royal Society of London Series B-Biological Sciences* 266:465-469.

- Bottorff, R. L. 1974. Cottonwood habitat for birds in Colorado. *American Birds* 28:975-979.
- Briskie, J. V., S. G. Sealy, and K. A. Hobson. 1990. Differential parasitism of least flycatchers and yellow warblers by the brown-headed cowbird. *Behavioral Ecology and Sociobiology* 27:403-410.
- Budnik, J. M., F. R. Thompson, and M. R. Ryan. 2002. Effect of habitat characteristics on the probability of parasitism and predation of Bell's vireo nests. *Journal of Wildlife Management* 66:232-239.
- Burger, J., and M. Gochfeld. 1991. Human distance and birds - tolerance and response distances of resident and migrant species in India. *Environmental Conservation* 18:158-165.
- Burgham, M. C. J., and J. Picman. 1989. Effect of brown-headed cowbirds on the evolution of yellow warbler anti-parasite strategies. *Animal Behaviour* 38:298-308.
- Burhans, D. E. 1997. Habitat and microhabitat features associated with cowbird parasitism in two forest edge cowbird hosts. *Condor* 99:866-872.
- Burhans, D. E., D. Dearborn, F. R. Thompson, and J. Faaborg. 2002. Factors affecting predation at songbird nests in old fields. *Journal of Wildlife Management* 66:240-249.
- Burke, D. M., and E. Nol. 1998. Influence of food abundance, nest-site habitat, and forest fragmentation on breeding ovenbirds. *Auk* 115:96-104.
- Cade, B. S., J. W. Terrell, and R. L. Schroeder. 1999. Estimating effects of limiting factors with regression quantiles. *Ecology* 80:311-323.
- Camp, R. J., and R. L. Knight. 1998. Rock climbing and cliff bird communities at Joshua Tree National Park, California. *Wildlife Society Bulletin* 26:892-898.
- Canterbury, G. E., T. E. Martin, D. R. Petit, L. J. Petit, and D. F. Bradford. 2000. Bird communities and habitat as ecological indicators of forest condition in regional monitoring. *Conservation Biology* 14:544-558.
- Chace, J. F., J. J. Walsh, A. Cruz, J. W. Prather, and H. M. Swanson. In Press. Spatial and temporal activity patterns of the brood parasitic brown-headed cowbird at an urban/wildland interface. *Landscape and Urban Planning*.
- Chace, J. F., S. T. McKinney, and A. Cruz. 2000. Nest-site characteristics and nesting success of the greater pewee in Arizona. *Southwestern Naturalist* 45:169-175.

- Chasko, G. G., and J. E. Gates. 1982. Avian habitat suitability along a transmission-line corridor in an oak-hickory forest region. *Wildlife Monographs* 82:41.
- Clark, K. L., and R. J. Robertson. 1981. Cowbird parasitism and evolution of anti-parasite strategies in the yellow warbler. *Wilson Bulletin* 93:249-258.
- Clemmons, J. R., and R. Buchholz. 1997. Behavioral approaches to conservation in the wild. Cambridge University Press, Cambridge, England.
- Cody, M. L. 1985. Habitat selection in birds. Academic Press, Orlando, FL.
- Cole, D. N. 1996. Wilderness recreation use trends, 1965 through 1994. U.S.D.A., Forest Service, Intermountain Research Station, Ogden, UT.
- Cole, D. N., and P. B. Landres. 1995. Indirect effects of recreation on wildlife. Pages 183-201 in R. L. Knight and K. J. Gutzwiller, editors. *Wildlife and recreationists*. Island Press, Washington, D.C.
- Collinge, S. K., and R. T. T. Forman. 1998. A conceptual model of land conversion processes: predictions and evidence from a microlandscape experiment with grassland insects. *Oikos* 82:66-84.
- Collinge, S. K., M. Holyoak, C. B. Barr, and J. T. Marty. 2001. Riparian habitat fragmentation and population persistence of the threatened valley elderberry longhorn beetle in central California. *Biological Conservation* 100:103-113.
- Cooke, A. S. 1980. Observations on how close certain passerine species will tolerate an approaching human in rural and suburban areas. *Biological Conservation* 18:85-88.
- Davidson, A. S., and R. L. Knight. 2001. Avian nest success and community composition in a western riparian forest. *Journal of Wildlife Management* 65:334-344.
- Dhindsa, M. S., P. E. Komers, and D. A. Boag. 1989. Nest height of black-billed magpies - is it determined by human disturbance or habitat type. *Canadian Journal of Zoology* 67:228-232.
- Dickman, C. R., and C. P. Doncaster. 1987. The ecology of small mammals in urban habitats .I. Populations in a patchy environment. *Journal of Animal Ecology* 56:629-640.
- Dion, N., K. A. Hobson, and S. Larviere. 2000. Interactive effects of vegetation and predators on the success of natural and simulated nests of grassland songbirds. *Condor* 102:629-634.

- Ehrlich, P. R., D. S. Dobkin, and D. Wheye. 1988. The birder's handbook : a field guide to the natural history of North American birds. Simon and Schuster, New York, NY.
- Ehrlich, P. R., D. S. Dobkin, and D. Wheye. 1992. Birds in jeopardy. Stanford University Press, Stanford, CA.
- Eiserer, L. A. 1980. Effects of grass length and mowing on foraging behavior of the American robin (*Turdus migratorius*). Auk 97:576-580.
- Faaborg, J., M. Brittingham, T. Donovan, and J. Blake. 1995. Habitat fragmentation in the temperate zone. Pages 357-380 in T. E. Martin and D. M. Finch, editors. Ecology and management of Neotropical migratory birds. Oxford University Press, New York, NY.
- Fernandez-Juricic, E. 2000a. Bird community composition patterns in urban parks of Madrid: The role of age, size and isolation. Ecological Research 15:373-383.
- Fernandez-Juricic, E. 2000b. Local and regional effects of pedestrians on forest birds in a fragmented landscape. Condor 102:247-255.
- Fernandez-Juricic, E. 2002. Can human disturbance promote nestedness? A case study with breeding birds in urban habitat fragments. Oecologia 131:269-278.
- Fernandez-Juricic, E. 2001. Avian spatial segregation at edges and interiors of urban parks in Madrid, Spain. Biodiversity and Conservation 10:1303-1316.
- Fernandez-Juricic, E., M. D. Jimenez, and E. Lucas. 2001. Alert distance as an alternative measure of bird tolerance to human disturbance: implications for park design. Environmental Conservation 28:263-269.
- Fernandez-Juricic, E., and J. L. Telleria. 1999. Recruitment patterns of blackbirds (*Turdus merula*) in urban fragmented populations. Ardeola 46:61-70.
- Fernandez-Juricic, E., and J. L. Telleria. 2000. Effects of human disturbance on spatial and temporal feeding patterns of blackbird *Turdus merula* in urban parks in Madrid, Spain. Bird Study 47:13-21.
- 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. Island Press, Washington, D.C.
- Fletcher, R. J., S. T. McKinney, and C. E. Bock. 1999. Effects of recreational trails on wintering diurnal raptors along riparian corridors in a Colorado grassland. Journal of Raptor Research 33:233-239.

- Foster, J., and M. S. Gaines. 1991. The effects of a successional habitat mosaic on a small mammal community. *Ecology* 72:1358-1373.
- Gates, J. E., and L. W. Gysel. 1978. Avian nest dispersion and fledging success in field-forest ecotones. *Ecology* 59:871-883.
- Gering, J. C., and R. B. Blair. 1999. Predation on artificial bird nests along an urban gradient: predatory risk or relaxation in urban environments? *Ecography* 22:532-541.
- Goossen, J. P., and S. G. Sealy. 1982. Production of young in a dense nesting population of yellow warblers, *Dendroica petechia*, in Manitoba. *Canadian Field-Naturalist* 96:189-199.
- Gotmark, F. 1992. The effects of investigator disturbance on nesting birds. Pages 63-104 in D. M. Power, editor. *Current Ornithology*, Vol. 9. Plenum Press, New York, NY.
- Gotmark, F., D. Blomqvist, O. C. Johansson, and J. Bergkvist. 1995. Nest site selection: A trade-off between concealment and view of the surroundings? *Journal of Avian Biology* 26:305-312.
- Grubb, T. C., and P. F. Doherty. 1999. On home-range gap-crossing. *Auk* 116:618-628.
- Gutzwiller, K. J. 1995. Recreational disturbance and wildlife communities. Pages 169-181 in R. L. Knight and K. J. Gutzwiller, editors. *Wildlife and recreationists*. Island Press, Washington, D.C.
- Gutzwiller, K. J., and S. H. Anderson. 1999. Spatial extent of human-intrusion effects on subalpine bird distributions. *Condor* 101:378-389.
- Gutzwiller, K. J., K. L. Clements, H. A. Marcum, C. A. Wilkins, and S. H. Anderson. 1998a. Vertical distributions of breeding-season birds: Is human intrusion influential? *Wilson Bulletin* 110:497-503.
- Gutzwiller, K. J., E. A. Kroese, S. H. Anderson, and C. A. Wilkins. 1997. Does human intrusion alter the seasonal timing of avian song during breeding periods? *Auk* 114:55-65.
- Gutzwiller, K. J., H. A. Marcum, H. B. Harvey, J. D. Roth, and S. H. Anderson. 1998b. Bird tolerance to human intrusion in Wyoming montane forests. *Condor* 100:519-527.

- Gutzwiller, K. J., S. K. Riffell, and S. H. Anderson. 2002. Repeated human intrusion and the potential for nest predation by gray jays. *Journal of Wildlife Management* 66:372-380.
- 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.
- Hahn, D. C., and J. S. Hatfield. 1995. Parasitism at the landscape scale: cowbirds prefer forests. *Conservation Biology* 9:1415-1424.
- Hickman, S. 1990. Evidence of edge species attraction to nature trails within deciduous forest. *Natural Areas Journal* 10:3-5.
- Jonsson, L. 1992. *Birds of Europe with North Africa and the Middle East*. Princeton University Press, Princeton, NJ.
- Knight, R. L. 1984. Responses of nesting ravens to people in areas of different human densities. *Condor* 86:345-346.
- Knight, R. L., and D. N. Cole. 1995a. Factors that influence wildlife responses to recreationists. Pages 71-79 *in* R. L. Knight and K. J. Gutzwiller, editors. *Wildlife and recreationists*. Island Press, Washington, D.C.
- Knight, R. L., and D. N. Cole. 1995b. Wildlife responses to recreationists. Pages 51-68 *in* R. L. Knight and K. J. Gutzwiller, editors. *Wildlife and recreationists*. Island Press, Washington, D.C.
- Knight, R. L., and R. E. Fitzner. 1985. Human disturbance and nest site placement in black-billed magpies. *Journal of Field Ornithology* 56:153-157.
- Knight, R. L., and K. J. Gutzwiller, editors. 1995. *Wildlife and recreationists*. Island Press, Washington, DC.
- Knight, R. L., and S. A. Temple. 1986a. Methodological problems in studies of avian nest defense. *Animal Behaviour* 34:561-566.
- Knight, R. L., and S. A. Temple. 1986b. Why does intensity of avian nest defense increase during the nesting cycle. *Auk* 103:318-327.
- Knopf, F. L., R. R. Johnson, T. Rich, F. B. Samson, and R. C. Szaro. 1988. Conservation of riparian ecosystems in the United States. *Wilson Bulletin* 100:272-284.
- Knopf, F. L., and J. A. Sedgwick. 1992. An experimental study of nest-site selection by yellow warblers. *Condor* 94:734-742.

- Kuenning, R. R. 1998. Yellow warbler. Pages 418-419 in H. E. Kingery, editor. Colorado breeding bird atlas. Colorado Breeding Bird Atlas Partnership, Denver, CO.
- Lovejoy, T. E., J. Bierregaard, R.O., A. B. Rylands, J. R. Malcolm, C. E. Quintela, L. H. Harper, J. Brown, K.S., A. H. Powell, G. V. N. Powell, H. O. R. Schubart, and M. B. Hays. 1986. Edge and other effects of isolation on Amazon forest fragments. Pages 257-285 in M. E. Soule, editor. Conservation biology: the science of scarcity and diversity. Sinauer Associates, Inc., Sunderland, MA.
- Lowther, P. E., C. Celada, N. K. Klein, C. C. Rimmer, and D. A. Spector. Yellow Warbler (*Dendroica petechia*). In The Birds of North America, no. 454 (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.
- Magrath, R. D. 1991. Nestling weight and juvenile survival in the blackbird, *Turdus merula*. Journal of Animal Ecology 60:335-351.
- Major, R. E., and C. E. Kendal. 1996. The contribution of artificial nest experiments to understanding avian reproductive success: a review of methods and conclusions. Ibis 138:298-307.
- Martin, P., and P. Bateson. 1993. Measuring behaviour, 2nd edition. Cambridge University Press, Cambridge.
- Martin, T. E. 1992. Interaction of nest predation and food limitation in reproductive strategies. Pages 163-197 in D. M. Power, editor. Current Ornithology, Vol. 9. Plenum Press, New York, NY.
- Martin, T. E. 1993. Nest predation and nest sites - new perspectives on old patterns. Bioscience 43:523-532.
- Martin, T. E. 1995. Avian life history evolution in relation to nest sites, nest predation, and food. Ecological Monographs 65:101-127.
- Martin, T. E., and J. Clobert. 1996. Nest predation and avian life-history evolution in Europe versus North America: A possible role of humans? American Naturalist 147:1028-1046.
- Martin, T.E., C.R. Paine, C.J. Conway, W.M. Hochachka, P. Allen, and W. Jenkins. 1997. BBIRD Field Protocol. Montana Cooperative Wildlife Research Unit, University of Montana, Missoula, MT.
<http://pica.wru.umt.edu/BBIRD/research.htm>.

- Marzluff, J. M. 1997. Effects of urbanization and recreation on songbirds. Pages 89-102 *in* W. M. Block and D. M. Finch, editors. Songbird ecology in Southwestern ponderosa pine forests: a literature review. Gen. Tech. Rep. RM-GTR-292. U.S.D.A., Forest Service, Rocky Mountain Forest and Range Experimental Station, Fort Collins, CO.
- Marzluff, J., R. Bowman, and R. Donnelly, editors. 2001. Urbanization, avian communities, and landscape ecology. Kluwer Academic Publishers, Norwell, MA.
- Marzluff, J. M., F. R. Gehlbach, and D. A. Manuwal. 1998. Urban environments: influences on avifauna and challenges for the avian conservationist. Pages 283-299 *in* J. M. Marzluff and R. Sallabanks, editors. Avian conservation. Island Press, Washington, D.C.
- Mayfield, H. F. 1975. Suggestions for calculating nest success. *Wilson Bulletin* 87:456-466.
- McLean, I. G., J. N. M. Smith, and K. G. Stewart. 1986. Mobbing behavior, nest exposure, and breeding success in the American robin. *Behaviour* 96:171-185.
- McRae, S. B., P. J. Weatherhead, and R. Montgomerie. 1993. American robin nestlings compete by jockeying for position. *Behavioral Ecology and Sociobiology* 33:101-106.
- Miller, C. K. 1994. Environmental impacts of passive recreational trails in riparian areas. Pages 96-105 *in* Proceedings of the 6th Annual Colorado Riparian Association Conference, Alamosa, CO.
- Miller, J. R. 1999. The effect of human settlement on bird communities in lowland riparian areas. Ph.D. Thesis. Colorado State University, Fort Collins, CO.
- Miller, J. R., and N. T. Hobbs. 2000. Recreational trails, human activity, and nest predation in lowland riparian areas. *Landscape and Urban Planning* 50:227-236.
- Miller, S. G., R. L. Knight, and C. K. Miller. 1998. Influence of recreational trails on breeding bird communities. *Ecological Applications* 8:162-169.
- Miller, S. G., R. L. Knight, and C. K. Miller. 2001. Wildlife responses to pedestrians and dogs. *Wildlife Society Bulletin* 29:124-132.
- Misenhelter, M. D., and J. T. Rotenberry. 2000. Choices and consequences of habitat occupancy and nest site selection in sage sparrows. *Ecology* 81:2892-2901.

- Moore, F. R., J. Gathreaux, S.A., P. Kerlinger, and T. R. Simons. 1995. Habitat requirements during migration: important link in conservation. Pages 121-144 in T. E. Martin and D. M. Finch, editors. Ecology and management of Neotropical migratory birds. Oxford University Press, New York, NY.
- Morneau, F., C. Lepine, R. Decarie, M. A. Villard, and J. L. Desgranges. 1995. Reproduction of American robin (*Turdus migratorius*) in a suburban environment. Landscape and Urban Planning 32:55-62.
- Naiman, R. J., H. Decamps, and M. Pollock. 1993. The role of riparian corridors in maintaining regional biodiversity. Ecology 31:209-212.
- Ohmart, R. D. 1994. The effects of human induced changes on the avifauna of western riparian habitats. Studies in Avian Biology 15:273-285.
- Ortega, C. P., J. C. Ortega, C. A. Rapp, and S. A. Backensto. 1998. Validating the use of artificial nests in predation experiments. Journal of Wildlife Management 62:925-932.
- Ortega, C. P., J. C. Ortega, C. A. Rapp, S. Vorisek, S. A. Backensto, and D. W. Palmer. 1997. Effect of research activity on the success of American robin nests. Journal of Wildlife Management 61:948-952.
- Osborne, P., and L. Osborne. 1980. The contribution of nest site characteristics to breeding- success among blackbirds *Turdus merula*. Ibis 122:512-517.
- Pantle, D. 1998. American robin. Pages 396-397 in H. E. Kingery, editor. Colorado breeding bird atlas. Colorado Bird Atlas Partnership, Denver, CO.
- Paton, P. W. 1994. The effect of edge on avian nest success: how strong is the evidence? Conservation Biology 8:17-26.
- Peterjohn, B. G., J. R. Sauer, and C. S. Robbins. 1995. Population trends from the North American Breeding Bird Survey. Pages 3-39 in T. E. Martin and D. M. Finch, editors. Ecology and management of Neotropical migratory birds. Oxford University Press, New York, NY.
- Pulliam, H. R. 1988. Sources, sinks, and population regulation. American Naturalist 132:652-661.
- Pyle, P. 1997. Identification guide to North American birds. Slate Creek Press, Bolinas, CA.
- Ralph, C. J., G. R. Geupel, P. Pyle, T. E. Martin, and D. F. DeSante. 1993. Handbook of field methods for monitoring landbirds. Gen. Tech. Rep. PSW-GTR-144. U.S.D.A., Forest Service, Pacific Southwest Research Center, Albany, CA.

- Ratti, J. T., and K. P. Reese. 1988. Preliminary test of the ecological trap hypothesis. *Journal of wildlife management* 52:484-491.
- 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.
- Riffell, S. K., K. J. Gutzwiller, and S. H. Anderson. 1996. Does repeated human intrusion cause cumulative declines in avian richness and abundance? *Ecological Applications* 6:492-505.
- Robinson, S. K., and D. S. Wilcove. 1994. Forest fragmentation in the temperate zone and its effects on migratory songbirds. *Bird Conservation International* 4:233-249.
- Rosenblatt, D. L., J. L. Newton, and E. J. Heske. 2000. Effects of mowed trails on depredation of artificial nests in grassland. *Prairie Naturalist* 32:29-41.
- Rottenborn, S. C. 1999. Predicting the impacts of urbanization on riparian bird communities. *Biological Conservation* 88:289-299.
- SAS Institute Inc. 1999. SAS/STAT user's guide. Version 8.0. SAS Institute Inc., Cary, NC.
- Saab, V. A. 1996. Influences of spatial scale and land-use practices on habitat relationships of breeding birds in cottonwood riparian forests. Ph.D.thesis University of Colorado, Boulder.
- Saab, V. A., C. E. Bock, T. D. Rich, and D. S. Dobkin. 1995. Livestock grazing effects in western North America. Pages 311-353 in T. E. Martin and D. M. Finch, editors. *Ecology and management of Neotropical migratory birds : a synthesis and review of critical issues*. Oxford University Press, New York, NY.
- Sallabanks, R. and F.C. James. American Robin (*Turdus migratorius*). In *The Birds of North America*, no. 462 (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.
- Sanders, T. A., and W. D. Edge. 1998. Breeding bird community composition in relation to riparian vegetation structure in the western United States. *Journal of Wildlife Management* 62:461-473.
- Sauvajot, R. M., M. Buechner, D. A. Kamradt, and C. M. Schonewald. 1998. Patterns of human disturbance and response by small mammals and birds in chaparral near urban development. *Urban Ecosystems* 2:279-297.

- Sealy, S. G. 1992. Removal of yellow warbler eggs in association with cowbird parasitism. *Condor* 94:40-54.
- Slagsvold, T. 1997a. Brood division in birds in relation to offspring size: sibling rivalry and parental control. *Animal Behavior* 54:1357-1368.
- Slagsvold, T. 1997b. Is there a sexual conflict over hatching asynchrony in American robins? *Auk* 114:593-600.
- Tarvin, K. A., and K. G. Smith. 1995. Microhabitat factors influencing predation and success of suburban blue jay *Cyanocitta cristata* nests. *Journal of Avian Biology* 26:296-304.
- Tewksbury, J. J., S. J. Hejl, and T. E. Martin. 1998. Breeding productivity does not decline with increasing fragmentation in a western landscape. *Ecology* 79:2890-2903.
- Tomialojc, L., and P. Profus. 1977. Comparative analysis of breeding bird communities in two parks of Wroclaw and in an adjacent Querco-Carpinetum forest. *Acta Ornithologica* 16:117-177.
- van der Zande, A. N., 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.
- van der Zande, A. N., 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.
- Vanvalkenburgh, B., and R. K. Wayne. 1994. Shape divergence associated with size convergence in sympatric East-African jackals. *Ecology* 75:1567-1581.
- Vierling, K. T. 2000. Source and sink habitats of red-winged blackbirds in a rural/suburban landscape. *Ecological Applications* 10:1211-1218.
- Westmoreland, D., and L. B. Best. 1986. Incubation continuity and the advantage of cryptic egg coloration to mourning doves. *Wilson Bulletin* 98:297-300.
- Whittingham, L. A., and R. J. Robertson. 1993. Nestling hunger and parental care in red-winged blackbirds. *Auk* 110:240-246.
- Wilson, R. R., and R. J. Cooper. 1998. Acadian flycatcher nest placement: does placement influence reproductive success? *Condor* 100:673-679.

- Woodard, J. D., and M. T. Murphy. 1999. Sex roles, parental experience and reproductive success of eastern kingbirds, *Tyrannus tyrannus*. *Animal Behaviour*, 57:105-115.
- Yahner, R. H. 1991. Avian nesting ecology in small even-aged aspen stands. *Journal of wildlife management* 55:155-159.
- Yalden, P. E., and D. W. Yalden. 1990. Recreational disturbance of breeding golden plovers *Pluvialis apricarius*. *Biological Conservation* 51:243-262.
- Zar, J. H. 1996. *Biostatistical analysis*, 3rd edition. Prentice Hall, Upper Saddle River, NJ.

Appendix 1. Locations of study sites

Drainage	Trail	Use-level	Site Location
Boulder Creek	Yes	High	Eben Fine on Boulder Creek, Eben Fine Park and area to east along Boulder Creek to Sixth St.
Boulder Creek	Yes	High	Boulder Creek Trail, east of 30th street to Arapahoe Ave.
Boulder Creek	Yes	Low	White Rocks Trail, Valmont Rd. north along Dry Creek #3 to Boulder Creek
Boulder Creek	No	No	Kaufmann Property on Boulder Creek, east of 75th St. to start of White Rocks conservation easement
Coal Creek	Yes	Low	Coal Creek Lafayette, South Public Rd. west to subdivision at Centaur Village Ct.
Coal Creek	No	No	Coal Creek No Trail, ~1.4 km east of Hwy. 128 to conservation easement east of 66th St.
South Boulder Creek	Yes	Medium	Bobolink Trail on South Boulder Creek, Baseline Rd. south to South Boulder Rd.
South Boulder Creek	Yes	Medium	South Boulder Creek Trail on South Boulder Creek, South Boulder Rd. south to where trail veers to west to Marshall Rd.
South Boulder Creek	No	No	Fancher Property on South Boulder Creek, from fenceline where South Boulder Creek trail heads west, south to fenceline at end of Boulder Open Space and Mountain Parks property
St. Vrain Creek	Yes	Low	St. Vrain Greenway in Longmont, from Hover Rd. east to pond to east of Sunset St.
St. Vrain Creek	No	No	Marlatt property on St. Vrain Creek, southwest of Hygiene, from ~400 m west of 75th street to fenceline ~500 m to nw along river, and along ditch between ponds to Crane Hollow Rd.

STUDY AREAS

