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Recreational trails, human activity, and nest predation in lowland riparian areas

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Abstract

In areas of human settlement, greenways and open-space land are often intended to serve recreational purposes as well as provide wildlife habitat, but the compatibility of these goals is uncertain. We examined the effect of recreational trails on the risk of nest predation and nest predator activity at four lowland riparian sites along the Front Range of Colorado. At one site on each of two streams, we placed a transect of artificial nests near a recreational trail and another transect on the opposite side of the stream. We also placed another transect of nests at a second site on each stream that was not associated with a recreational trail. In 1995, nests were baited with quail eggs; in 1996 a clay egg was also added to nests to aid us in nest predator identification. Artificial nests are not perfect surrogates for natural nests, but are useful in generating hypotheses about causes of nest failure and for detecting changes in predator assemblages.

Overall, predation rates were high (94%). There were significant differences in vulnerability to predation on the different transect types, with a tendency for predation rates to increase with distance from trails. There was a significant effect of time with a greater risk of predation in 1996. In 1996, 83% of the clay eggs that were recovered showed signs of predation. House Wrens destroyed 11% of the clay eggs; impressions from Black-billed Magpies, Blue Jays, and Common Grackles were found on 69%; mice preyed on 25%; and squirrels on 12% of the eggs. Birds attacked more nests near trails than away from trails, whereas mammals appeared to avoid nests near trails to some extent. These results support the contention that recreational trails and human activity may affect nesting success for some species, and suggest that patterns of nest predation reflect the unique, and sometimes, counter-intuitive responses of individual predator species. Rather than relying on simplistic assumptions about the compatibility of recreation and wildlife, it is important to consider how individual species respond to the habitat alteration and human activity associated with trails when deciding where trails should be located and in developing overall conservation strategies in human-dominated areas.

Keywords: Birds; Trail; Predation

1. Introduction

In landscapes dominated by human settlement, remnants of semi-natural vegetation are often set aside as parks or greenways. Much of the appeal of greenways for urban planners stems from the notion that these areas can simultaneously provide numerous

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recreational opportunities — hiking, biking, jogging, wildlife viewing — and a means to conserve biological diversity (Little, 1990; Smith and Hellmund, 1993). Indeed, these parcels of open space may represent the only locally available habitat for some native species.

Although both recreation and wildlife conservation are commonly emphasized in greenway management plans (Adams and Dove, 1989; Schiller and Horn, 1997; Miller et al., 1998; Lindsey, 1999), the compatibility of these two activities remains poorly understood. Outdoor recreation has been shown to harm most native species that have been studied (Boyle and Samson, 1985), suggesting that a dual emphasis on conservation and recreation may be more a marriage of convenience. Still, data are few and our understanding of the effects of recreational activities on native species remains quite limited (Knight and Cole, 1995). This lack of data undermines attempts to devise effective conservation strategies and fosters resentment in a public that is asked to curtail recreational activities in the name of species preservation (Zaslowsky, 1995).

Riparian corridors often serve as the backbone for local and regional greenway networks (Hay, 1991; Mankin and Warner, 1997). This is partly the result of a deep-rooted affinity that people have for watercourses, but also because lands bordering creeks and rivers are usually among the last available for conservation in settled landscapes. Floodplains are unsuitable for most other types of development. Riparian areas are also important sources of biological diversity (Naiman et al., 1993), particularly in arid and semi-arid environments. In the western United States, lowland riparian areas provide critical habitat for migrating and breeding birds (Johnson et al., 1977; Knopf, 1985; Ohmart, 1994; Skagen et al., 1998), but the extent to which the ecological integrity of these habitats is compromised by human activity is relatively unexplored.

Lowland riparian areas in semi-arid regions tend to be narrow and linear, rendering them vulnerable to disturbance (Backhouse, 1987). Recreational trails may disturb nesting birds in two ways. First, habitat is removed during trail construction and is altered along its margins as the result of trail maintenance, weed invasion, or changes in microclimate (Liddle, 1975; Cole, 1981; Benninger-Truax et al., 1992; Tyser and Worley, 1992). Second, human activity associated with trails may directly affect habitat use by breeding birds and by nest predators (Knight and Gutzwiller, 1995). Nest predation is the primary cause of nest mortality for land birds (Ricklefs, 1969; Skutch, 1985; Martin, 1992) and is thought to influence both habitat selection and community structure (Sieving and Willson, 1998). Nesting birds might be indirectly affected if trails influence habitat use by predators and, as a result, predation pressure varies as a function of proximity to trails.

We studied the effect of recreational trails on rates of nest loss and on nest predator activity in lowland riparian areas along the Front Range of Colorado. Specifically, we investigated the relationship between predation rates on artificial nests and proximity to recreational trails. We also examined changes in the intensity of predation, exerted by different predator species as distance from trails increased, to identify potential mechanisms underlying overall patterns of nest loss.

2. Study sites and methods

We worked at four lowland riparian sites in eastern Boulder County, Colorado. The sites were comprised of woodlands dominated by plains cottonwood (*Populus deltoides*), crack willow (*Salix fragilis*), and hybrids (*Populus*×*acuminata*) of plains cottonwood and narrow-leaf cottonwood (*Populus angustifolia*). Typical understory species included snowberry (*Symphoricarpos occidentalis*), chokecherry (*Prunus virginiana*), and sandbar willow (*Salix exigua*). These riparian woodlands were bordered by mixed-grass prairie and had an average total width of ≈60 m.

In order to examine the influence of recreational trails on nest loss, we selected a study site on each of two streams (South Boulder Creek and Coal Creek) that had a 2.5-m wide paved recreational trail in the riparian zone; we also selected a site on each stream that was not associated with a recreational trail. Sites on a given stream were ≥3 km apart and chosen to be as similar as possible with regard to width and vegetative structure. At the trail site on Coal Creek, suburban development bordered riparian woodlands on the same side of the stream as the trail, whereas development occurred on the streamside opposite

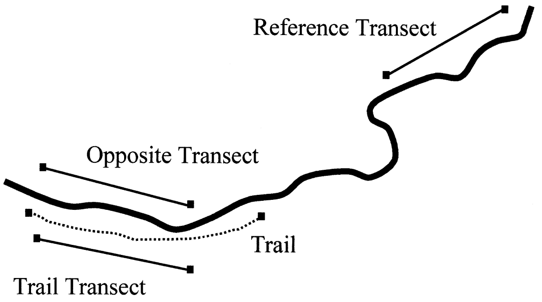

Fig. 1. Characterization of the study design indicating the placement of three artificial-nest transects relative to a recreational trail and stream.

the trail on South Boulder Creek and was located several hundred meters away from the study area. Otherwise, all sites were surrounded by a mosaic of mixed-grass prairie, agricultural land, and low-density rural housing.

Between the first week of June and the first week of July in 1995 and 1996, we placed one transect of artificial nests (n=20) at each trail site on the trail side of the stream (hereinafter, Trail) and a second transect of nests on the opposite side (hereinafter, Opposite). A third transect of nests was placed on a randomly chosen side of the stream at each non-trail site (Fig. 1). Because of differences in the level of development in the landscapes surrounding trail and non-trail sites, we do not regard the latter as true controls, but use these transects (hereinafter, Reference) for purposes of comparison with Trail and Opposite transects.

Artificial nests were placed 0.5–2 m aboveground in trees and shrubs in locations similar to those in which natural bird nests were found. Each nest was baited with two Japanese quail (*Coturnix coturnix*) eggs; in 1996, each nest received an additional egg made of modeling clay (Plastaline Modeling Clay; Van Aken International, Rancho Cucamonga, CA 1729). The clay egg was tethered to the nest with heavy-duty thread, enabling us to obtain tooth or bill impressions of nest predators (Möller, 1988; Major, 1991; Nour et al., 1993). Several workers have asserted that predation experiments relying on quail eggs alone may be biased against some nest predators because quail eggs are larger than typical songbird eggs (Roper, 1992; Haskell, 1995; DeGraaf and Maier, 1996; Bayne and Hobson, 1999, but see Craig, 1998). To avoid biases deriving from egg size, the clay models approximated the dimensions of a typical songbird egg (20 mm×15 mm, see Harrison, 1978).

We used commercially-available wicker canary nests modified with grass and mud in order to resemble American Robin (*Turdus migratorius*) nests, thus providing an appropriate search image for potential nest predators (Martin, 1987; Sieving, 1992). Because individual predator species may respond to human scent in different ways (Whelan et al., 1995), rubber gloves were worn while preparing nests and clay eggs, and rubber boots and gloves were worn when placing and checking the nests (Willebrand and Marcstrom, 1988). In order to avoid repeated predation by a predator traveling along a linear course, or ‘traplining’, nests were alternately placed 10–15 m on either side of the transect at 30-m intervals. This arrangement resulted in a between-nest distance of about 40 m. Nest-check routes were varied to prevent the creation of well-worn paths that might provide cues to predators regarding nest locations.

Nests were checked every third day for 15 days, simulating the combined egg-laying and incubation periods representative of most songbirds (Martin, 1987). When checking nests, the number of eggs remaining and nest condition were noted. A nest was considered depredated when one or more eggs was punctured or removed. When eggs were found to be missing, we searched the surrounding area within 10 m for any eggshell fragments.

We quantified predation pressure at each site using the methods of Mayfield (1961) as modified by Johnson (1979). A daily mortality rate (DMR) was calculated as the total number of predated nests divided by the total number of days that the nests were exposed to predation; the DMR is thus the probability of predation per day (Mayfield, 1961). DMRs were transformed using standard arcsine square-root transformations to stabilize variances and normalize data. Because the experiment was conducted at the same sites in subsequent years, a repeated measures analysis was used to test for heterogeneity among DMRs with transect (i.e. Trail, Opposite, Reference) as the main effect. For post hoc comparisons of DMRs between sites on a stream, we used χ^2-analyses (Sauer and Williams, 1989) and applied a sequential Bonferroni adjustment to α to control for Type I error (Rice, 1989).

In 1996, we identified nest predators by comparing impressions on clay eggs with a reference collection made from museum specimens and comprised of tooth and bill marks of predator species known to occur in the area. Impressions were also compared to marks on clay eggs recovered from artificial nests in nearby riparian areas in 1996 and 1997 where nest predators were positively identified using automatic cameras (Miller, 1999). Associations between predators and transect types were assessed using likelihood ratio tests. We used a significance level of 0.10 for all analyses to achieve a reasonable compromise between the probability of a Type I error and the power of our tests. However, we report the calculated significance of individual test statistics to allow the reader to use an alternative significance level if desired.

3. Results

Of the 240 nests used in this study, 226 were depredated. For three missing nests, we suspected causes other than predation and excluded them from all analyses. In 1996, 115 clay eggs were recovered, of which 96 showed signs of predation.

There were significant differences in vulnerability to predation across transect types ($F=22.06$, df=2, $p<0.02$) and a consistent trend for predation rates to increase with distance from trails (Fig. 2). In 1995, predation rates on the opposite side of the stream were higher than those on the Trail transect for South Boulder Creek ($X^2=3.88$, df=1, $p=0.049$) and for Coal Creek ($X^2=2.71$, df=1, $p=0.099$). Reference transects also had significantly greater predation rates compared to Trail transects in 1995 (South Boulder Creek: $X^{2=}11.55$, df=1, $p<0.001$; Coal Creek: $X^{2=}14.47$, df=1, $p<0.001$). The overall pattern in predation rates was similar in 1996 (Fig. 2) and the predation rates on the Reference transects were significantly higher than those on the Trail transects (South Boulder Creek: $X^{2=}15.27$, df=1, $p<0.001$; Coal Creek: $X^{2=}3.20$, df=1, $p=0.074$). There were, however, no significant differences between predation rates on the Trail and Opposite transects in 1996 (South Boulder Creek: $X^{2=}1.14$, df=1, $p=0.285$; Coal Creek: $X^2=1.34$, df=1, $P=0.247$).

The repeated measure (time) was significant ($F=18.69$, df=1, $p<0.03$), but the effect of time did not influence the treatment effect ($F=0.047$, df=2, $p>0.95$). Predation rates were higher in 1996 versus 1995 on South Boulder Creek for the Trail ($X^2=5.71$, df=1, $p<0.02$) and Reference transects ($X^2=6.85$, df=1, $p<0.01$), and on Coal Creek for the Trail ($X^2=9.72$, df=1, $p<0.002$) and Opposite ($X^2=7.92$, df=1, $p<0.005$) transects.

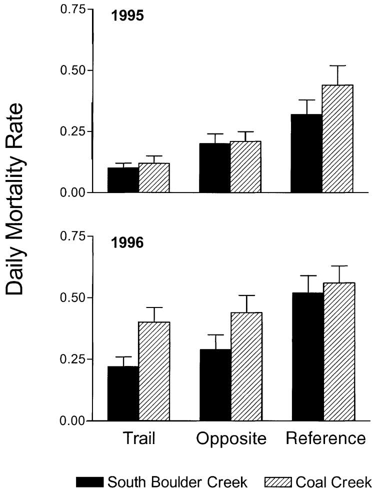

Fig. 2. Daily mortality rates (+1s.e.) for artificial nest transects near recreational trails, on the opposite side of the stream from trails, and at reference sites without trails) on South Boulder Creek and Coal Creek in Boulder County, CO.

Impressions on clay eggs resulting from egg destruction or predation were assigned to 1 of 6 categories, some of which included more than one species if their respective tooth or bill marks could not be reliably differentiated (Fig. 3). Some eggs had impressions belonging to more than one category. We surmised that House Wrens (*Troglodytes aedon*) were responsible for impressions on 11% of the 96 eggs that were destroyed. House Wrens are not nest predators in that they do not consume egg contents, but their propensity for destroying eggs in the nests of other birds is well-documented (Belles-Isles and Picman, 1986; Quinn and Holroyd, 1989; Pribil and Picman, 1991). The Common Grackle (*Quisculus quiscula*) and two corvids, the Blue Jay (*Cyanocitta cristata*) and the Black-billed Magpie (*Pica pica*), are reputed nest predators and were common in our study areas. Similar bill size, partial impressions, and variation in the angle of attack made it difficult to differentiate impressions left by these species, so we

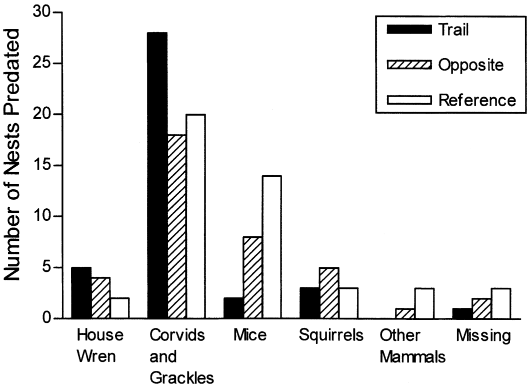

Fig. 3. Frequency distribution of artificial nests preyed upon in two lowland riparian areas, based on tooth and bill impressions on clay eggs. Tooth or bill impressions were assigned to 1 of 6 categories: House Wrens, Corvids and Grackles (Blues Jay, Black-billed Magpie, and Common Grackle), Mice, Squirrels (fox squirrel), Other Mammals (raccoon, red fox), and Missing (nests that were knocked down or stolen, or had clay eggs removed).

combined them in a single category. We attributed 69% of the impressions on the clay eggs to this group. Evidence collected in 1997 using artificial nests and automatic cameras at some of these same sites and in nearby riparian habitats (Miller, 1999) suggests that Common Grackles may play a relatively minor role in this group (21 photos of Black-billed Magpies and 14 of Blue Jays vs. 3 of Common Grackles). This observation is supported by Chase (1998) who reports that eggs and nestlings comprise a relatively small portion of the Common Grackle's diet.

Twenty-five percent of the destroyed eggs showed signs of predation by mice. Based on trapping data from some of these same study sites and other nearby riparian areas (D. Armstrong, University of Colorado, personal communication), we surmise that these predation events can most likely be attributed to the deer mouse (*Peromyscus maniculatus*). Squirrels accounted for marks on 11.5% of the eggs. Known habitat associations of squirrels in Colorado (Fitzgerald et al., 1994) and photos at artificial nests (Miller, 1999) indicate that the fox squirrel (*Scuirus niger*) is the likely predator. Several eggs had impressions of other mammals, including the raccoon (*Procyon lotor*) and red fox (*Vulpes vulpes*; Fig. 3). Nests that were knocked down or stolen, or had clay eggs removed, were all considered to be missing data.

Patterns in nest attacks differed between birds and mammals across transect types ($p<0.02$, df=1). Birds attacked more nests than expected near trails and overall, mammals preyed more on nests away from trails (df=2, $p<0.001$; Fig. 3). This pattern largely resulted from a tendency for Corvids and Grackles to prey on nests near trails (df=1, $p<0.01$), whereas mice avoided trails (df=1, $p<0.002$; Fig. 3).

4. Discussion

Overall, the risk of predation was quite high in this study, with >94% of the nests being depredated. These narrow riparian woodlands consisted entirely of 'edge' habitat (Paton, 1994) and contrasted sharply with the adjacent uplands; increased rates of nest loss are typical near high-contrast habitat edges in human-dominated landscapes (Brittingham and Temple, 1983; Angelstam, 1986; Andrén and Angelstam, 1988; Paton, 1994, but see Yahner et al., 1989).

The risk of predation tended to increase with distance from trails in this study. These results are consistent with those of Boag et al. (1984), who found that predation on artificial nests was lower near trails in coniferous forests and that mammalian predators tended to avoid these areas. Conversely, Miller et al. (1998) reported greater predation pressure on natural nests near trails in forested and grassland habitats that were also located in Boulder County. Miller and his colleagues suggested that this pattern could be attributed to greater numbers of avian nest predators near trail edges, as has been observed for other narrow corridors in woodland habitats (Hickman, 1990; Recher and Serventy, 1991, but see Rich et al., 1994). Our data are consistent with this scenario in that we found predation pressure by birds to be greater near trails. Clearly, the effect of trails and other narrow corridors on nesting success in wooded areas depends on more than the mere presence of a human-induced edge. Rates of nest loss reflect the cumulative pressure exerted by a suite of predator species, each exhibiting unique responses to the presence of recreational trails and people.

Human activity has been linked to reduced nest mortality for some species. Osborne and Osborne (1980) found that Blackbirds (*Turdus merula*) nesting near busy sidewalks or buildings on a university campus not only enjoyed significantly higher breeding success, but were much less discriminating with regard to nest-site characteristics than were birds in more remote locations. Likewise, nest predation pressure for birds breeding in two urban parks in Poland was negatively correlated with the frequency of human visits (Tomialojć and Profus, 1977), and similar results were reported for breeding birds in London's parks (Tomialojć, 1979). Both trails in the present study received substantial human visitation, averaging over 22 persons/h on the trail at South Boulder Creek and over 16 persons/h on the trail at Coal Creek during the 1997 avian breeding season (Miller, 1999). In fact, the trail at South Boulder Creek is the most heavily used in the entire City of Boulder Open Space system (C. Miller, City of Boulder Parks and Open Space Department, personal communication).

We assume that most human activity occurs during daylight hours, but diurnal predators in our study did not appear to be greatly affected by it. There was no evidence for trail avoidance in fox squirrels, the only diurnal mammalian predator that we identified. These animals are ubiquitous in riparian and urban areas along Colorado's Front Range and are well-habituated to humans (Fitzgerald et al., 1994). Nor did avian predators — all diurnal species — show signs of avoiding trails; nests near trails were actually more vulnerable to destruction by birds than were nests farther away. Corvids, in particular, are known to habituate to a human presence (Knight et al., 1987) and this appears to be the case in our study. Point count data showed that Black-billed Magpies were more numerous at both treatment sites in 1995 and at the treatment site on South Boulder Creek in 1996 when compared with the reference sites (Miller, 1999).

Mice and some larger mammals, such as raccoons and foxes, avoided trails. These animals are all nocturnal, however, making it unlikely that human activity was directly responsible for the observed patterns. It is possible that trail construction or heavy use of riparian areas by humans resulted in habitat alteration to an extent that made it less suitable for some species. Human activity might also have affected mammalian predators indirectly because people on trails were often accompanied by domestic dogs (Miller, 1999) and canine scent could cause some mammals to avoid these areas (Forman, 1995). Wild mammalian canines, such as coyotes (*Canis latrans*), are known to have an affinity for linear habitat features (Bider, 1968; Harris and Gallagher, 1989) and use trails at night (Forman, 1995; D. Armstrong, University of Colorado, personal communication). Indeed, we found coyote scat on or near trails on numerous occasions. In addition to leaving scent trails, these predators may also suppress populations of smaller mammals, particularly mice.

We saw an increase in predation rates in the second year, a phenomenon that has been reported by other workers conducting multi-year studies (Willebrand and Marcstrom, 1988; Cresswell, 1997; Marini, 1997; Hannon and Cotterill, 1998), but not in others (Storaas, 1988; Burger et al., 1994; Bayne et al., 1997; Danielson et al., 1997). The clay eggs that were added to nests in 1996 were more conspicuous than the quail eggs, but studies specifically designed to examine predation rates on different-colored eggs do not support the contention that this led to increased predation (Janzen, 1978; Slagsvold, 1980; Yahner and DeLong, 1992). Nest predators may have habituated to artificial nests. It is also possible that the increases we observed reflected fluctuations in local populations or changes in habitat use between years for some predator species. Such variability is common in many habitats, but is especially likely in riparian zones, given the unpredictable nature of disturbance in these areas. Indeed, higher-than-average rainfall in the spring of 1995 resulted in extensive flooding along the Front Range of Colorado.

Our data support the contention that in some cases a reproductive advantage may be conferred on birds that are able to nest in close proximity to trails or areas of human activity because of reduced nest losses. Not all species are equally prone to do so, however (Sodhi et al., 1999). Cooke (1980) observed that suburban birds were more tolerant of people than were birds in rural areas and resident species may be more tolerant than migrants (Burger and Gochfeld, 1991). Several studies have reported a negative relationship between the density of nesting birds and trails or areas of intense recreational use — again, some species exhibited greater sensitivity than others (van der Zande et al., 1984; van der Zande and Vos, 1984; Miller et al., 1998).

Our results should be interpreted with a measure of caution. It is important to remember that artificial nests are not perfect surrogates for natural nests.

We recognize the biases associated with artificial nests as well as the advantages they confer, such as the ability to control for nest appearance and location (Major and Kendal, 1996). These nests clearly lack certain cues that predators may use to locate natural nests, such as the scent of live birds or parental activity. Rather than dismiss the use of artificial nests because of these differences, we view them as null models that can be used to generate hypotheses about causes of nest failure and changes in predator assemblages. For example, predation rates on artificial nests were found to be an order of magnitude higher than rates on active American Robin nests (Miller, 1999). American Robins are vigorous defenders of their nests (Gottfried, 1979; Morneau et al., 1995), suggesting that a comparative study between species that differ in their intensity of nest defense might prove fruitful.

The sample size in this study was small and our reference sites differed from our treatment sites with regard to the surrounding landscape, although it should be noted that the same predators were identified on all transect types with the exception of medium-sized mammals, such as raccoons. The extent to which our results are representative of trail effects in other riparian habitats is unknown. Still, the patterns that we observed — a consistent tendency for predation rates to be lower near trails than on the streamside opposite trails or at reference sites and changes in predator identity with distance from trails — suggest that the relationship between recreational activity and habitat quality is not a simple one, and that native species may respond in different and sometimes unexpected ways. Our results may have especially important implications for efforts to protect the meadow jumping mouse (*Zapus hudsonius*), a species with strong affinities for lowland riparian habitats in this region, where the local subspecies (*Z.h. preblei*) has been listed as threatened. This is particularly true given the fact that most riparian areas along Colorado's Front Range either contain trails or are slated to have one constructed in the near future (D. Weber, Colorado Division of Wildlife, personal communication).

The situation along the Front Range of Colorado is not unique — outdoor recreational activity is predicted to increase nationally (Flather and Cordell, 1995) with a concomitant increase in the construction and use of recreational trails. There is increasing evidence that trails and human activity do affect wildlife and that different species exhibit responses that are unique and sometimes counter-intuitive. Until a better understanding of these phenomena is achieved, we recommend a cautious approach in deciding where trails should be located and in managing the human activities that occur there.

For lowland riparian habitats, decisions on locations for new trails should be based on available information regarding the habitat requirements of sensitive species. In the absence of such information, we offer a few general guidelines that also apply to established trails. To minimize adverse impacts on wildlife, trails should be located on one side of the stream only and human activity should be restricted to a well-defined corridor. Fences will help to accomplish the latter and there are designs (e.g., split-rail) that do not seem wholly out of place in semi-natural areas. It is also crucial that dogs be prohibited from ranging freely. The rationale underlying various restrictions should be made clear to the public via signs at entry points in the hope that greater understanding will foster greater cooperation. Periodic wildlife surveys are highly desirable in order to detect adverse impacts over time and the ability to interpret survey data is greatly enhanced if parallel studies are also conducted in riparian areas kept free of human activities. Such monitoring, in conjunction with more rigorous scientific investigations, will better enable us to assess the compatibility of recreation and nature conservation in greenways, and ultimately to devise more effective strategies for maintaining native species in human-dominated areas.

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