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DISSERTATION

THE EFFECT OF HUMAN SETTLEMENT ON BIRD COMMUNITIES IN LOWLAND RIPARIAN AREAS

Submitted by

James R. Miller

Graduate Degree Program in Ecology

In partial fulfillment of the requirements
for the Degree of Doctor of Philosophy
Colorado State University
Fort Collins, Colorado
Fall, 1999

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WE HERBY RECOMMEND THAT THE DISSERTATION PREPARED UNDER OUR SUPERVISION BY JAMES R. MILLER ENTITLED THE EFFECT OF HUMAN SETTLEMENT ON BIRD COMMUNITIES IN LOWLAND RIPARIAN AREAS BE ACCEPTED AS FULFILLING IN PART REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY.

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ABSTRACT OF DISSERTATION

THE EFFECT OF HUMAN SETTLEMENT ON BIRD COMMUNITIES IN LOWLAND RIPARIAN AREAS

I studied the ways that lowland riparian habitats and the bird species that use them change along a gradient of human settlement that proceeds from rural to urban areas on four drainages near the Front Range of Colorado. I examined correlations between settlement intensity, characteristics of riparian woodlands, and the structure and composition of bird communities. In addition, I investigated the effect of development on predation risk in riparian areas using natural and artificial nests. The effect of human activity and recreational trails on predation levels was also examined. The results of these studies demonstrate that avian communities in these riparian woodlands are influenced by a combination of local habitat features and by the level of development in the surrounding landscape.

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CHAPTER I

INTRODUCTION

In the western United States, the importance of lowland riparian areas is far greater than one might believe based on the amount of land surface that they occupy. These habitats provide numerous ecological services (Naiman and Decamps 1997) and are centers for biodiversity (Naiman *et al.* 1993). Intensive human use of riparian areas, however, may compromise their conservation value.

Lowland riparian systems receive the heaviest human use of any vegetation communities in the western U.S. (Thomas *et al.* 1979). Human activities that impact riparian areas include water development, agriculture, domestic livestock grazing, timber harvest, and recreation. Because western riparian areas at lower elevations exist primarily as narrow, linear strips of vegetation along water courses (Knopf *et al.* 1988), they are also likely to be affected substantially by activities that occur in the surrounding landscape matrix. As a result of both direct and indirect impacts, Ohmart (1994, p. 273) reported that over 95% of riparian habitats in western North America "...have been lost, altered, or degraded by human-induced change." One potential source of human-induced change is human settlement. For thousands of years, people have tended to settle near watercourses, and the situation is no different today. The extent to which people modify environments where they live and work, however, is unprecedented. Colorado, like many western states, is experiencing rapid population growth and much of this growth is occurring in a narrow belt along the Front Range of the Rocky Mountains, where approximately 80% of Colorado s population lives. This situation motivated me to focus my research on the effects of settlement on native diversity in riparian zones in this region. I specifically chose to work with avian communities because lowland riparian habitats are particularly important during breeding and migration, especially in the western U.S. (Stevens *et al.* 1977, Knopf and Samson 1994, Skagen *et al.* 1998).

I begin with a general discussion of conservation in areas where people live and work, focusing on the relationship between human settlement and both ecology and conservation biology (Chapter 2, with Richard Hobbs). I then present preliminary results of the project and provide background material in Chapter 3 (with John Wiens and Tom Hobbs), which was initially presented at a meeting held in Taupo, New Zealand, and serves as the basis for a chapter in the forthcoming book titled Nature Conservation 5: Managing the Matrix .

There are two important questions that must be asked regarding birds and the impact of humans on riparian areas. The first question is what birds are found in these habitats? and the second is are they reproducing successfully? . I address the first question in the first of three empirical chapters by examining the impact of development in the surrounding landscape on riparian bird community structure and composition (Chapter 4, with John Wiens and Tom Hobbs). In Chapter 5, I report the results of a study on nest predation in lowland riparian habitats (with Tom Hobbs). Although rates of nest loss are usually considered to increase with increasing development, largely on the basis of a study by Wilcove (1985), this supposition has not been subjected to many empirical tests. We used artificial nests in conjunction with monitoring natural nests to quantify the relationship between nest predation and development along a gradient of human settlement. This chapter is followed by work intended to examine the effect of an important feature of many riparian areas near towns or suburbs — recreational trails - on the risk of predation and on predation pressure by various nest predators (Chapter 6, with Tom Hobbs).

Chapter 7 consists of a general discussion of the importance of taking a landscape perspective when studying the effects of human settlement on avian assemblages (with Jennifer Fraterrigo, Tom Hobbs, Dave Theobald, and John Wiens). The various topics covered in this chapter are illustrated with examples drawn from the research conducted as part of this dissertation and from work conducted by others. This chapter ends with a proposed methodology for future research on birds in human-dominated areas. Finally, the important points from the preceding chapters are summarized and discussed relative to one another in the concluding, synthetic chapter.

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CHAPTER II

CITIES: THE FINAL FRONTIER FOR CONSERVATION BIOLOGY?

ABSTRACT

Nearly half the world s population and 70-80% of the people in many developed countries live in cities. We argue that the urbanization of humanity is resulting in increased isolation of people from nature. This, coupled with the conservation ideal of maintaining natural systems free of human intervention, is leading to a general lack of appreciation for biodiversity and its services, as reflected in political and legislative apathy towards the world s biota. We suggest that the conservation ideal based on balanced natural systems, untouched by man, is outdated and does not stand the scrutiny of modern ecology. Ecologists now recognize that natural systems are rarely static or in balance , but rather are dynamic, changing entities. Most landscapes in the world bear the imprint of long periods of human habitation and management, and even remote areas are now subject to human impacts. Despite growing awareness of the role of humans in ecosystems, however, relatively little attention has been paid to the ecology and conservation of systems where the bulk of humanity lives — i.e., cities. Although cities are unlikely to house large tracts of pristine nature, they are capable of retaining significant biological resources. In order to retain these resources and to foster a greater appreciation for biodiversity in urban dwellers, recent successes in rural community

based conservation and restoration schemes need to be repeated in cities. Local projects of this sort are a key way of engaging urban populations in conservation activities and hence of ensuring that broader biodiversity issues receive the attention they need and deserve. For such projects to happen, more conservation biologists and ecologists need to turn their attention to the urban environment.

INTRODUCTION

We live in an increasingly urbanized world. The shift from agrarian- to city-based societies has largely occurred over the last 100 years in industrialized nations and is now transpiring in developing nations, projected to peak during the first half of the next century (Berry 1991). Urbanites currently comprise nearly half of the global population and account for 70-80% of the citizens in North America, Europe, and some Pacific rim nations (United Nations Centre for Human Settlements 1996). A United Nations (1989) report estimated that by 2025 at least 60% of the world s population will live in cities and that this figure will likely reach 80% in developed countries. Soul (1995) has noted that now ...most politicians and bureaucrats are city people. The influence of city people will increase as the world becomes more urban. This is one of the quietest and most profound changes of consciousness that has occurred in the twentieth century. It does not portend well for informed, compassionate decisions about the future of wild nature.

The attitudes of politicians and bureaucrats, however, merely reflect those of society as a whole. In many ways, the role of nature in our lives is shrinking. Ever-increasing numbers of people are spending more and more time in built environments, often experiencing nature second-hand (if at all). Commercialization and globalized economies are far-reaching, and even cultures far-removed from large population centers are experiencing some erosion of their connections to the natural world (e.g., Nelson 1993). Nonetheless, estrangement from nature is most pronounced in urban and suburban areas, and it manifests itself in numerous ways: schoolchildren not knowing that milk comes from a cow or that the cotton in their clothes comes from plants; the upsurge in video games and computer pets ; a general lack of appreciation for natural systems that provide, for example, clean water; a steady decline in expectations regarding environmental quality (despite regulatory measures to improve this quality).

Estrangement from nature is a very real and important phenomenon, notwithstanding the assertion that biophilia is a deep-seated human attribute (Wilson 1984, Kellert & Wilson 1993). If people fail to recognize the origin of basic goods and services, if they have only limited contact with nature, how much value are they likely to attach to biological diversity? Certainly, the fundamental importance of biological diversity is unaffected by the degree to which it is appreciated by humankind. We suggest, however, that support for conservation and for ecological research depends in large measure on the value that the general public places on it. Keeley (1993) argues that An unfortunate feature of modern life is that many [people] have lost touch with our environment The natural environment is an important part of [our] heritage, and a citizenry with a broader aesthetic appreciation of the riches of that natural environment is badly needed if we are to live in harmony with the remnants of what is left. We believe that such a citizenry can only come to pass with a greater focus on biodiversity, conservation, and ecological research in human-dominated areas - i.e., the urban and production landscapes *where the bulk of the human population lives.*

We firstly examine the historical roots of conservation and discuss how this has influenced current attitudes and inadvertently contributed to the estrangement of people from nature. We then discuss the biological resources that remain in urban areas and the recognition that urban biodiversity has received from conservation biologists and ecologists. Finally, we explore the role of human communities and local involvement in urban conservation, and consider the benefits of a greater emphasis on conservation and ecological research in human-dominated areas.

HISTORICAL BASIS

The philosophical unpinnings of modern conservation have been strongly influenced by the writings of George Perkins Marsh (Botkin 1990). Marsh (1864) held people as separate from nature and viewed natural systems, undisturbed by humans, as balanced. Conservation action has thus tended to focus on protection from human activities and the preservation of nature s intrinsic balance. It follows that conservation value, when measured from this perspective, is directly proportional to the perceived absence of anthropogenic influences. It is not surprising, then, that the concept of wilderness has been central to the development of both land-use legislation and the general ethos of conservation, particularly in North America (Nash 1973). Conservation efforts have historically been directed to remote areas, far from the places where people live and work.

The more we learn, however, the more we realize that there is no place on earth that is remote enough to escape the influence of humans. Scientists worldwide are continually adding to the list of unintended but deleterious anthropogenic impacts on natural systems. These range from the direct consequences of human action — the death of plants and animals that results from dumping toxic waste into a river, for example — to indirect and subtle effects (McDonnell and Pickett 1993*a*), such as DDT-caused declines in raptor populations. Other indirect effects include the repercussions of action-at-a distance (Russell 1993), exemplified by the deposition of sulfur and nitrogen originating in Midwestern factories on forests and lakes in New England or by the annual declines in stratospheric ozone over Antarctica resulting from the use of air-conditioners in the northern hemisphere. Vitousek (1994) asserts that the pervasiveness of global change, especially regarding biogeochemical cycles, renders the use of the term pristine absurd.

No one seriously doubts that the impacts of modern humans on this planet are unprecedented in both scope and scale (Goudie 1990, Turner *et al.* 1991; Vitousek *et al.* 1997), but we are also gaining a greater appreciation for the extent to which indigenous peoples altered the virgin landscapes that first greeted European explorers. In fact, there is evidence to suggest that pre-colonial societies changed their world in ways that had profound consequences (Denevan 1992, Flannery 1994, Kohen 1995, Simmons 1996, Delcourt & Delcourt 1997, Langton 1998). Because human beings have been interacting with and modifying their environment for millions of years, that which we view as nature is in many ways a product of history (Worster 1996). It may therefore be more appropriate to view the world in terms of cultural landscapes (Birks *et al.* 1988), with contemporary land uses layered upon those of the past and both existing along a gradient of human impact.

Given the above, it becomes difficult to make a clear distinction between wilderness and non-wilderness. Similarly, the task of describing the natural condition of a given system is likely to be wrought with controversy (Maser 1990, Gunn 1991, Cowell 1993, Elliot 1994,1998). Our concepts of how ecosystems work have changed over the last few decades as we have begun to realize and accept that they are much more dynamic, spatially heterogeneous, and less predictable than we either thought or wished they were (Pahl-Wostl 1995, Fiedler *et al.* 1997, Hobbs & Morton 1999).

Marsh s conception of the relationship between humans and nature was flawed. Ecologists increasingly believe that most systems, even those with relatively little human disturbance, are quite variable and may exhibit alternative (meta-)stable states. Scientists have demonstrated convincingly that the balance of nature is largely a myth and that a non-equilibrium paradigm is more appropriate in most cases (Wiens 1984, Botkin 1990, Pickett *et al.* 1992). A natural ecosystem in any given area may thus be difficult if not impossible to define (Sprugel 1991). It follows that an insistence on conserving only natural ecosystems or on striving to restore ecosystems to a natural state (Elliot 1998) will likely lead to unachievable goals being set (Hobbs & Norton 1996, Hobbs 1999). Furthermore, concentration on wilderness and natural systems carries with it a tacit or explicit devaluation of other less wild or less natural systems.

Just as a focus on wilderness tends to devalue less wild areas, the focus in conservation circles on large reserves has led to the mindset that small reserves are of little value (Shafer 1995; Schwartz & van Mantgem 1997). The rationale for conserving large areas is straightforward: the larger the reserve, the more species it is likely to harbor and the better it is able to buffer native plants and animals from adverse human impacts. Some species, such as large predators, are especially in need of such protection. Schwartz and van Mantgem (1997) have observed that in recent years there has been an increased emphasis on maximizing reserve size in hopes that conservation in such reserves will prove sustainable over time. As an illustration of the bias toward large reserves, the 1993 United Nations List of National Parks and Protected Areas only included areas more than 10 km^2 (IUCN 1994).

Set against this, however, is the recognition that opportunities for setting aside or acquiring large tracts of land are rapidly diminishing. Indeed, McNeely *et al.* (1994) present data indicating that the growth rate of the global protected-areas network has slowed significantly over the past two decades, following a period of rapid growth in the 1960s and 1970s. Of the major biome types, none has more than 10% protection, and many have considerably less. Temperate grasslands, for example, have only 0.8% of their area protected in some way (IUCN 1994). Given the pace of land transformation and land-use change, it seems unlikely that calls for greatly expanded conservation networks (e.g., Soul & Sanjayan 1998) are realistic.

The acquisition of large tracts of land without prominent or marked evidence of significant human impact is simply not an option in many places. In a study of the largest undeveloped area in the New York Metropolitan region, the NewYork-New Jersey Highlands, Zipperer (1993) reported that over 77% (1,176) of the land parcels remaining undeveloped were between 2 and 120 ha in size and only three parcels were over 25,000 ha. This undeveloped area was in fact fragmented by roads, power-line corridors, etc. In some regions, such as the Midwestern U.S.A. or the wheatbelt of Western Australia, large reserves are measured in hundreds, not thousands, of hectares and the species in need of large tracts of wilderness have long since disappeared. Even our largest national parks are not likely to maintain their biological diversity in isolation (Newmark 1985, Janzen 1986, Noss & Cooperrider 1994), and large-scale wilderness preserves that today are well-buffered from human activities may not remain so in perpetuity. In the first few decades of this century, for example, who would have envisioned Yellowstone or Rocky Mountain National Parks as islands surrounded by residential development and production landscapes?

It is rapidly becoming apparent that new strategies are needed if we are to preserve the biological diversity that remains. We now realize that effective conservation will increasingly depend on networks of large reserves, smaller reserves, and effective management of the intervening, human-dominated matrix (Hobbs *et al.* 1993, Noss *et al.* 1997, Peck 1998). Conservation must be centered on landscapes, not habitat islands (Wiens 1997), and people must be part of the equation.

BIODIVERSITY AND CONSERVATION IN URBAN AREAS

Many conservationists tend to think of human settlement as synonymous with exotic species and habitat fragmentation, deterioration, or loss. Indeed, numerous studies have documented declines in species number and abundance for a variety of taxa in urban habitat fragments (Soul *et al.* 1988; Bolger *et al.* 1991; Recher & Serventy 1991; Bolger *et al.* 1997*a*; Drayton & Primack 1996; Bolger *et al.* 1997*b*). These semi-natural remnants are stereotyped as artificial and requiring intensive management to ensure their existence. There is, however, mounting evidence to the contrary. Urban forests, for example, such as the New York City Botanical Gardens, have surprised scientists by exhibiting remarkable resilience and unique adaptations to the many stresses inherent in urban environments (Wade *et al.* 1994, McDonnell *et al.* 1997). In fact, urban areas often retain substantial biological resources.

Jonsson (1995) reviewed evidence suggesting that important components of biological diversity remained in many cities, and that diverse plant and animal assemblages could persist even in highly populated areas. Documented examples include some of the world s largest cities; for instance, remnants of Mata Atlantica forests in Rio de Janeiro (Monteiro & Kaz 1992), the Singapore Botanic Garden (Tinsley 1983), the Ridge Forest in New Delhi (Kalpavriksh 1991), and urban green space in Calcutta (Ghosh 1989). New York City contains over 10,000 ha of municipal parkland, representing 13% of the city area — a third of which is natural area (Sauer 1998). And although we tend to associate cities with rock doves (*Columbia livia*), house sparrows (*Passer domesticus*), and European starlings (*Sturnus vulgaris*), studies in urban areas frequently report diverse avifaunas of predominantly native species (Gotfryd & Hansell 1986; Recher & Serventy 1991; Wood 1993; Danaid 1994, Hadidian *et al.* 1997, Briffett *et al.* 1999). What is remarkable about urban areas is not what has been lost, but rather what remains.

Conservation biologists have paid relatively little attention to cities, despite the biological resources found there. An index of the consideration that urban areas receive can be obtained from an examination of the coverage given to them in recent books on conservation biology. Table 1 indicates the number of index entries referring to city or urban in a selection of such books, and illustrates the almost complete lack of coverage. Most of the references that were found enumerated the threats to biodiversity posed by urbanization, rather than any consideration of biodiversity conservation within cities. Even Jacobson (1995), whose topic was education and communication, made no reference to cities or the people who live in them. Similarly, in the 1140 pages comprising the Global Biodiversity Assessment (Heywood 1995), discussion of urban areas takes up about 3 pages.

Whereas conservation biologists have tended to ignore cities, ecologists have tried to avoid them. The same ideas that led to a preservationist approach in conservation — that nature free from human-caused perturbation is constant and stable — also motivated many ecologists to conduct research in remote areas in order to understand the structure and function of undisturbed ecosystems (Botkin 1990, Pickett *et al.* 1992, Pickett & McDonnell 1993). Consequently, our understanding of the ecology of settled areas remains in its infancy (McDonnell and Pickett 1993*b*, Botkin & Beveridge 1997, Rees 1997). Until ecologists direct greater effort toward research in areas dominated by human land use, we will be constrained in our ability to conserve or restore biological diversity there (McDonnell 1997).

Although there has been a general lack of interest in urban conservation and ecology, there have been some notable exceptions. The importance of nature in the city was well-recognized in early American conservation writings. Worster (1973) includes articles written by Frederick Law Olmsted in 1871, stressing the importance of retaining nature within urban areas and emphasizing its psychological benefits and restorative powers, and by Charles W. Eliot in 1914, articulating the idea of the garden city (which already had a rich tradition in parts of Europe) as a means of extending nature into the city by means of low-density housing, private gardens, and parks or nature reserves close-at-hand. Harshberger (1923) advocated a new branch of ecology, hemerecology , meant to address cultivated parks and gardens. Adams (1935, 1938) urged ecologists to apply their research methods in urban settings and to include the human dimension in their research. Stearns and Montag (1974) echoed these sentiments, suggesting that the city should be studied in the same manner as any other ecosystem and that urban natural areas were undervalued in terms of the benefits they provide. In his landmark book, *Designing with Nature*, Ian McHarg (1967) advocated the incorporation of ecological considerations into urban planning. It is ironic that during the rise of the modern environmental movement in the 1960s and 1970s, a shift in conciousness clearly reflected in McHarg s writings, it became fashionable to disdain cities; urban areas were relegated to the backwaters of conservation. This is also ironic in that most scientists and environmentalists live in cities (Botkin & Beveridge 1997).

There are encouraging signs that attitudes about urban areas are changing. McDonnell and Pickett (1993) have argued convincingly for increased attention to human-dominated environments on the part of ecologists. Others are once again calling for a greater integration of nature with settled areas, not only so that people can find relief from the tension and stress of city life, but also in order to restore ecological function (Nassauer 1997). The National Science Foundation recently committed funding to two urban Long-Term Ecological Research (LTER) sites - one in Baltimore, Maryland, and the other in Tempe, Arizona (Parlange 1998). Tools with which to achieve effective conservation in human-dominated areas are being developed, such as habitat conservation planning (Beatley 1994).

Urban conservation holds promise far beyond protecting habitats and preserving species. There is the potential to change attitudes. The ecological footprint of a modern city extends far beyond the town s borders. Either directly or indirectly, most of our environmental problems stem from cities and from the attitudes and lifestlyes of the people who live there. It seems logical, then, that conservation efforts meant to redress such problems include a greater focus on urban dwellers. As Box and Harrison (1994) have noted, If the contribution of urban green spaces to future generations is to be justified solely in terms of their contribution to the stock of environmental assets, then urban environmental assets will always be deemed to be poor substitutes for their rural counterparts. On the other hand, if urban green space policies acknowledge the social and educational assets of accessible natural green spaces, then the inheritance value of these areas is unrivaled.

CONSERVATION AND HUMAN COMMUNITIES

There is ample and increasing evidence that local human communities have a key role to play in the conservation of biodiversity (Western *et al.* 1994; Saunders *et al.* 1995). Indeed, recent commentaries point to the folly of trying to separate wildlife conservation from the welfare of local peoples (Adams & McShane 1992). The paradigm shift from top-down control to bottom-up conservation is reflected in the efforts of an increasing number of organizations. The Nature Conservancy, for example, is moving away from simply acquiring and protecting reserves to community-based conservation built on cooperation and partnerships (Low 1998). Still, virtually all of the case studies presented in these volumes come from rural areas. Although the trend toward increased recognition of the importance of involving rural communities in conservation is commendable, this remains only a partial solution to a wider problem.

Urban communities can and should have a major role to play in the conservation of biodiversity. Given that the majority of people in many countries now or soon will live in cities, it is imperative that they be given a stake in the conservation of the planet s biota. A clear way to facilitate this is to start at the local level, where these people can actually experience nature first-hand. By actively engaging people directly in local conservation issues and activities, a greater appreciation for the value of biological diversity can be engendered.

There is still a strong emphasis in conservation on faraway places and the species that occur there, and this is reflected in a variety of television nature programs, books, and interactive computer software. These products open a window on the natural world for many people, enhance ecological understanding, and generate excitement and enthusiasm for conservation. Nevertheless, even the best merchandise tends to present a somewhat sanitized and simplified view of nature — a virtual nature. Ultimately, this may do little to foster a deep appreciation for the true breadth of the natural world. The more remote the locations featured in such products, the more limited is their ability to engender a genuine appreciation for nature close-at-hand (Orr 1993). A focus on distant lands and species that most people will rarely see, unbalanced by intimate contact with nature, also tends to cultivate a welfare mentality toward biological diversity — a precarious situation in economic bad times (Craig 1997).

Urban dwellers, including ecologists and environmentalists, have to come to value what is on their doorstep and hence develop a desire to conserve and manage it wisely. Although the biotic communities remaining in cities may not be intact or full of rare species, they are close-at-hand and present complex management challenges. They also often retain unique local elements of biodiversity, which are increasingly threatened by the biotic homogenization under way across the globe (Hobbs & Mooney 1997).

Kellert (1993) argued that Society's obligation is not to bemoan the seeming absence of nature in the inner city or among the poor but to render its possibility more readily available. There is an urgent need to develop science curricula from the primary to the university level that draws on local examples of biodiversity to illustrate larger issues in conservation biology. This is especially critical for students in urban environments who may only have an abstract notion of tropical rainforests or coral reefs. It is important to communicate that many of the same ecological processes taking place in the Wild Kingdom also occur, with perhaps less charismatic players, in one s own backyard. As Leopold (1966) observed, The weeds in a city lot convey the same lesson as the redwoods......Perception.... cannot be purchased with either learned degrees or dollars; it grows at home as well as abroad, and he who has little may use it to as good advantage as he who has much .

Local action and activity are considerably easier to achieve than national or international action — as Handy (1994) points out, In a city you can make a difference in your spare time. At the national level making a difference is a whole career. Moreover, conservation and restoration activities in urban neighborhoods or local greenspace can act as a catalyst for a broader ecological understanding (Sauer 1998). Activities at the local level may equip future generations with the skills and values to address issues beyond their neighborhoods or hometowns (Cheskey 1993). There is also evidence to suggest added benefits of group involvement in conservation activities, such as improvements in social behavior as reflected by reductions in schoolyard violence (Kaplan & Kaplan 1989). Handy (1994) reminds us that Change comes from small initiatives which work, initiatives which, imitated, become the fashion. We cannot wait for great visions from great people, for these are in short supply . It is up to us to light our own small fires in the darkness.

These efforts do not need to start in a vacuum. Community-based conservation in rural areas can serve as the model for similar city-based efforts, and we are beginning to see encouraging signs that this is indeed happening. For example, the restoration of the North Woods of Central Park demonstrates that even degraded systems in highly urbanized areas can act as the focus for real conservation and restoration efforts which not only involve but educate and enthuse the local human community (Sauer 1998). At a larger scale, the Chicago Wilderness Project is comprised of over 60 public and private organizations allied in a common effort to protect and restore ecosystems and biotic communities in the region (Brawn & Stotz *In Press*). In addition to the important work of identifying conservation priorities and implementing management plans, this consortium has made great strides in community involvement through education and outreach. The involvement of local communities has also been targeted as a high priority in the new urban LTER programs (Parlange 1998).

It has often been argued that scientists spend too much time talking to other scientists when they should be putting more effort into communicating with the other elements of society if they want their science to be relevant and to have an impact (Dunbar 1995; Saunders *et al.* 1995; Ehrlich & Ehrlich 1996; Ehrlich 1997; Wills & Hobbs 1998). Since most scientists, most politicians, and indeed most people live in urban areas, cities would seem to be the logical place to initiate such communication. The future well-being of our natural heritage may well depend on our willingness to do so.

CONCLUSIONS

From the various perspectives we have provided here, there seems to be a clear case for a much greater emphasis in conservation biology on urban areas. The bits of nature remaining in areas where an increasing proportion of the world s population actually lives have received remarkably little conservation or scientific attention, and are hence undervalued as a potential resource for motivating local action and catalyzing broader-scale change. Although there are signs that this is changing, progress is slow and much more could be done. More ecologists and conservation biologists need to make the shift from concentrating on pristine and far-away places to looking at what lies on their doorstep. If city dwellers are to value and appreciate nature, this is more likely to happen through direct experience with the biota found in the city, rather than through idealized views of the wilderness and wildlife glimpsed on the television screen or recounted second-hand by privileged professionals who have been fortunate enough to travel more widely. With a heightened awareness and appreciation of the local biota may come a greater desire to halt its decline and replacement by the aggressive generalist species which are leading to an increasingly homogeneous environment. Only with such local, city-based support will we stand a chance of conserving the world s biotic diversity into the next increasingly urbanized century.

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Table 2.1. Number of references to city and urban in the index of a selection of recent books on conservation and conservation biology.

Book	City	Urban
Fiedler and Karieva 1998	0	0
Jacobson 1995	0	0
Moritz and Kikkawa 1994	0	1
Noss and Cooperrider 1994	0	1
Primack 1993	0	0
Reaka-Kudla *et al.* 1997	0	0
Saunders *et al.* 1995	0	2
Spellerberg 1996	0	0
Szaro and Johnston 1996	0	0
Western and Pearl 1989	0	2

CHAPTER III

HOW DOES URBANIZATION AFFECT BIRD COMMUNITIES IN RIPARIAN HABITATS? AN APPROACH AND PRELIMINARY ASSESSMENT.

ABSTRACT

Riparian areas in the western United States are important sources of natural diversity and contain some of the most diverse avifaunas in North America. Watercourses are also centres of human settlement, and this may negatively impact the riparian bird communities. Human settlement often involves the replacement of the native flora with exotic vegetation and leads to increases in the density of human commensal species. Such species often prey upon or compete with native species.

We investigated the effects of development on bird communities in lowland riparian areas along the Front Range of Colorado. At 16 sites arrayed along gradients of urbanization on 4 drainages, we conducted bird censuses from 1995 to 1997. We also investigated changes in predation rates along these gradients using experimental nests and by monitoring natural nests. Preliminary results indicate that overall species richness and the number of migrant birds increase from developed to rural sites. At highly developed sites, species richness increased with riparian width, but was still lower

compared to rural sites with relatively narrow riparian zones. Species that are characteristic of surrounding habitats were more evident in urban riparian areas than in rural areas. Daily mortality rates on experimental nests at rural sites were significantly higher than in developed areas on all 4 drainages. Daily mortality rates on experimental nests also increased with distance from recreational trails in the riparian zone. Daily mortality rates on active nests were not higher in developed versus rural areas, but were actually lower on one drainage. Overall, predation rates were substantially lower for active nests compared to experimental nests, suggesting that parental nest defense may be an important factor in determining nest success.

These preliminary results suggest that both human activities in the riparian zone and land use in the surrounding landscape matrix influence ecological processes affecting bird communities in riparian habitats. Surrounding land use may partially negate the effect of local habitat characteristics, such as riparian width. Because land-use decisions are often made at the lowest level of government and at very small scales relative to riparian systems, successful conservation of these habitats and the biota they harbour will require not only explicit statements of management objectives, but also careful integration with conservation priorities at larger scales.

INTRODUCTION

In arid and semiarid regions of the world, water is life. The natural landscape surrounding a watercourse is often a mosaic of grasslands and shrublands intersected by tendrils of riparian woodlands. Such riparian areas, which include the alluvial floodplain on either side of a stream or river and the vegetation growing there (*sensu* Ohmart 1994), provide habitat for a large number of species not found in the sparser, dryer vegetation and may act as corridors that enhance population and landscape connectivity (Naiman *et al.* 1993). Riparian zones are also centres of human settlement; throughout history, humans have been attracted to watercourses as places to live. This juxtaposition of human settlement and riparian habitats may result in conflict between the need to maintain the ecological integrity of riparian systems and the need to provide for human welfare.

This potential for conflict is particularly apparent in the western United States, where riparian zones are critical sources of natural diversity (Thomas *et al.* 1979) with unusually high value for vertebrate faunas (Johnson 1989, Terborgh 1989, Finch and Ruggiero 1993). Although riparian zones at lower elevations comprise less than 1% of the total land area in the western U.S. (Bottorff 1974, Knopf *et al.* 1988), up to 80% of the terrestrial vertebrate species in this region depend on them for at least part of their life cycles (Chaney *et al.* 1990). These riparian habitats contain some of the most diverse avifaunas in North America (Johnson *et al.* 1977, Stevens *et al.* 1977, Ohmart 1994), serve as critical habitat for migrating birds (Stevens *et al.* 1977, Knopf *et al.* 1988) and provide habitat for more species of breeding birds than any other western plant community (Stamp 1978, Knopf and Samson 1994). In northeastern Colorado, 82% of breeding bird species occur in riparian vegetation (Knopf 1985).

As human populations have grown and become increasingly concentrated in urban areas, however, the potential impacts on natural environments have increased dramatically. Urbanization involves profound alteration of natural ecosystems, producing massive changes in the flows of energy, water, and materials (Douglas 1994). In arid and semiarid regions, human demands on water are especially great, and the pressures on riparian areas and the biota that they harbour may be severe. Recognizing these pressures (and in some cases adding to them), land-use managers, residential developers, and landscape architects in many urban areas of the western United States have made riparian systems an integral part of their planning efforts (Adams and Dove 1989, Binford and Buchenau 1993). In many instances these efforts have been part of broader attempts to control or direct growth.

Various planning tools may be used to regulate development (Duerkson *et al.* 1997). At the county or municipal level in the U.S.A., for example, zoning may restrict the types of growth that can occur or set limits on residential density in a given area. Floodplains are by definition subject to flooding, especially in semiarid areas where rainfall events may be sporadic but intense, and for this reason zoning regulations often limit development in riparian habitats. In Colorado, many counties and cities are also implementing open space or greenway programs (Smith and Hellmund 1993) or are actively seeking to expand their land-holdings (e.g., City of Fort Collins 1992, Larimer County 1993, Boulder County Planning Commission 1997, City of Boulder Planning Department 1997). Non-governmental organizations have also become involved in acquiring land in growth areas for purposes other than development. Land acquisition and zoning regulations are often intended to benefit people living in the immediate vicinity - the protection of mountain views or provision of recreational opportunities, for example. Increasingly, however, a primary consideration in such endeavours is the preservation of biological diversity. Similar deliberations are carried out elsewhere in the world where urbanization is rampant, such as Australia (Adam 1995), New Zealand (Wilson, this volume), and Singapore (Briffett *et al.*, this volume).

Conservation is problematic in areas undergoing rapid growth, and decisions are often made in the absence of baseline information. Such information is generally lacking because ecologists have traditionally avoided areas of human habitation when selecting research sites (Pickett *et al.* 1992). Indeed, although some ecologists have called for a greater focus on populated areas (McDonnell and Pickett 1993, Platt *et al.* 1994), there is still some debate in conservation circles as to whether this type of research should be a priority (Wuerthner 1994, Siegel 1996; but see Keeley 1993). Whatever the relative merits of these opinions, the lack of data has resulted in a situation in which land-use planning is often founded more on land availability or its perceived conservation value (based on data collected in unpopulated areas) than on an understanding of the relationship between urban activities and the natural functioning of ecosystems. This gap in understanding is especially great in the case of riparian areas.

Here, our first objective is to generate predictions about the effects of urban and suburban development on bird communities in riparian areas. We do this by examining the salient features of developed lands with regard to birds in the context of previous studies of urban avifaunas. Next, we describe our approach to testing these predictions in lowland riparian areas in Colorado and present preliminary results of our studies. Finally, we comment on research and conservation priorities in such urban-riparian interfaces.

URBANIZATION

Habitat Alteration

To develop predictions about the effects of urbanization on riparian bird communities, we can first examine these effects in a broader context. By definition, urban and suburban development involves the replacement of relatively natural habitat with a human-dominated environment. Post-development native habitats often exist as small remnants that are contiguous with a wide variety of anthropogenic landscape elements (Keeley 1993, Nassauer 1997). Buildings, paved surfaces, and traffic may serve as urban barriers for some birds that continue to occupy such remnants, and impose a degree of isolation on native populations that is disproportionately great in relation to the actual distances involved (Soul *et al.* 1992; Foppen and Reijnen 1994). This isolation may prevent recolonization of habitat fragments in the event of local extinction, to which small populations are especially prone (Shaffer 1981). Our understanding is quite limited, however, with regard to the ways in which the multitude of fragmenting features in urban environments affect various native species (Engels and Sexton 1994). For this reason, the application of the habitat fragmentation paradigm, which has been largely derived from landscapes where extractive activities predominate, is not straight-forward in settled areas.

It is important to recognize that the impacts of settlement on natural habitats are in some respects qualitatively different from impacts brought on by the types of land-use changes that have served as the traditional focus of applied ecology. The latter (logging, agriculture, water development) often drive fundamental conversions of land cover, from forest to clear cut, from grassland to cultivated field. These conversions produce correspondingly dramatic changes in the operation of ecological processes, and this has been the traditional domain of applied ecological research. High-density urban areas represent a substantial conversion of cover types to a patchwork of alternative land uses, but this may not be the case with all forms of development (Duerkson *et al.* 1997). Instead, existing land cover may be "perforated" with urban structures, as is often the case in lower-density areas and in wooded habitats, rather than isolated by them (e.g. Norton, this volume). The effects of such perforation are far more subtle than those which accrue from the large-scale conversion of cover types.

In arid and semiarid areas, urban and (especially) suburban development are often accompanied by the planting of trees and shrubs. Along the Front Range in Colorado, xeric shortgrass prairie is converted to the rough equivalent of a wooded savanna, and open grasslands and shrublands are perforated by mesic deciduous woodlands. In towns and suburbs, the native flora is further reduced by extensive cultivated lawns.

In addition to the physical alteration of habitat, post-development environments are characterized by new suites of species. The most obvious and prolific, of course, is man. Humans and their activities may adversely affect some species, particularly during critical phases of an animal=s life cycle such as the post-natal or breeding period (Hockin *et al.* 1992). Furthermore, animals that are commensal with humans tend to reach high densities in urban areas and often compete with or predate the native fauna (see below).

Urban Avifaunas

How do these habitat changes affect birds? Clearly, some species respond to the transformation from native to non-native vegetation. In the United States, a strong correlation between reductions in native vegetation and native birds has been reported in the Northeast (DeGraaf 1987), East (Geis 1974), Midwest (Beissinger and Osborne 1982), and Southwest (Mills *et al.* 1989). Such species tend to persist, however, in areas where a large proportion of native trees and shrubs are left undisturbed, such as cemeteries (Lussenhop 1977) and golf courses (Terman 1994).

While some avian species decline in response to habitat alteration, others thrive and may reach higher densities than exist in the predevelopment landscape. Although overall bird density is often reported to be higher in urban versus less intensively-used areas, fewer species account for most of the density (Batten 1972, Emlen 1974, Geis 1974, Beissinger and Osborne 1982, DeGraaf 1987). Some of these species, such as the introduced European starling (*Sturnus vulgaris*) and house sparrow (*Passer domesticus*) in the United States, are able to displace other species by virtue of sheer numbers and aggressive behaviour (Johnston and Garrett 1994). Several workers have reported shifts from native to exotic species and from migrant species to year-round residents with increasing urbanization, both temporally and spatially (Walcott 1974, Aldrich and Coffin 1980, DeGraaf and Wentworth 1986, DeGraaf 1987, Friesen *et al.* 1995, Blair 1996). Many of the Aincreaser≡ species have had a long history of cohabitation with humans and can use artificial structures for nesting (Geis 1974, Weber 1975, DeGraaf and Wentworth 1986). Birds that nest on or near the ground may be particularly vulnerable in urban environments (Emlen 1974, Guthrie 1974, Weber 1975, Vale and Vale 1976), perhaps as a result of predation, human activity, or a lack of low vegetation. Ground-gleaners, seed-eaters, and omnivorous species that can exploit expansive lawns and bird-feeders often tend to dominate the avifauna, particularly in winter (Emlen 1974, Beissinger and Osborne 1982, Bezzel 1985, DeGraaf 1987, Mills *et al.* 1989, Brittingham 1991).

Nest Predation

Nest predation is thought to be the primary cause of reproductive failure in birds (Ricklefs 1969, Best and Stauffer 1980, Martin 1988), although evidence to support this claim in developed areas is largely circumstantial. In one of the few studies investigating this phenomenon, Wilcove (1985) found that predation rates were higher on artificial nests in suburban woodlots than in more remote areas.

One might expect nest predation rates to be greater in areas that are more developed for several reasons. Fragmented landscapes tend to be associated with elevated levels of nest predation (Andrén *et al.* 1985, Herkert 1994, Robinson *et al.* 1995), especially near habitat edges (Gates and Gysel 1978, Angelstam 1986, Donovan *et al.* 1997). The fragmented nature of most urban areas, coupled with the high degree of edge associated with the native areas that remain, suggests one reason why nest predation rates may be high there.

This scenario is exacerbated by the tendency for a number of nest predators to reach higher densities in human-dominated environments. Examples include Pied

Currawongs (*Strepera graculina*) in some Australian cities (Major *et al.* 1996), raccoons (*Procyon lotor*) and striped skunks (*Mephitis mephitis*) in the United States (Hoffman and Gottschang 1977, Haspel and Calhoon 1989, Rosatte *et al.* 1991), or dogs (*Canis familiaris*) and domestic cats (*Felis catus*) worldwide (Churcher and Lawton 1987). Increases in predator densities may be attributable to a combination of the availability of supplemental food and shelter. Moreover, Soul *et al.* (1988) noted that populations of small to medium-sized predators may reach higher densities in the absence of larger carnivores, and large carnivores tend to be absent from urban areas. The implication is clear: higher densities of nest predators will result in greater levels of nest predation (Soul *et al.* 1988, Harris and Silva-Lopez 1992, Noss 1993).

At a finer scale, one might also expect to find higher predation rates at particular locations within human-dominated environments, again attributable to locally high concentrations of potential predators. For example, people often allow their dogs to run loose in parks or along hiking trails, and omnivorous animals such as corvids or raccoons may be attracted to garbage or food scraps at these sites. In developed areas, the mere presence of certain predators may be sufficient to exclude sensitive species from otherwise suitable habitat (Engels and Sexton 1994).

Levels of nest predation in urban environments probably change over time. As the composition of the avifauna changes, species with nesting strategies that are better suited to developed areas may be selected for. Martin and Clobert (1996) documented lower rates of nest predation for human-dominated areas in Europe in comparison with those in the United States; they suggested that this difference may be a function of the former=s longer history of large-scale human disturbance.

Predictions

How might these features of urban/suburban habitat changes and avifaunas apply to bird communities in riparian zones that are embedded in developed areas? Riparian habitats in arid or semi-arid regions are usually more or less linear and are relatively narrow, so they may be particularly susceptible to detrimental influences from beyond their boundaries (Janzen 1986). These effects might be especially great in urban areas. Likewise, Backhouse (1987) has observed that long, narrow reserves may be particularly susceptible to internal disturbance resulting from human activities, such as might be associated with recreational trails. On the other hand, the wooded overstory of these riparian habitats may blend into the vegetation of the surrounding landscape more smoothly in developed (especially residential) areas than in more natural settings, facilitating the spread of some species into the riparian zone. These observations lead us to predict that:

! Avifaunas in riparian habitats associated with development are characterized by a decrease in species richness compared with less-developed areas.

! Riparian areas associated with development will contain bird species that are also characteristic of the surrounding habitats, while this will be less evident in less developed settings. Migrants will be less abundant in riparian habitats near developed areas.

! Nest predation rates will increase with increased development in the surrounding matrix.

! Nest predation rates will increase with proximity to recreational trails in the riparian area.

APPROACH

How can one test these predictions? One could consider urban and suburban areas as Atreatments≅ to be compared with less-developed Acontrols,≅ but there is so much variation among either developed or less-developed areas that true replication would be difficult. We chose instead to consider riparian habitats along gradients of urbanization and to follow a gradient-based design (Austin and Heyligers 1991, Wiens and Parker 1995). Because streams flow along topographic contours, they provide a well-defined gradient along which sampling may be conducted. We arrayed our samples along several riparian watersheds that intersected a spectrum of development, from city centres to suburbs to rural countryside.

Study Area

Our study sites are comprised of 16 parcels situated along Coal Creek, South Boulder Creek, and Boulder Creek in Boulder County, and the Cache la Poudre River in Larimer County, Colorado, U.S.A. (Fig. 1). These sites are located on the shortgrass steppe at the base of the Front Range of the Rocky Mountains and were chosen to represent a gradient from relatively high levels to low levels of development on each drainage. Elevations range from approximately 1640 m at the foothills/plains interface to approximately 1550 m in eastern Boulder and Larimer Counties. The overall study area is essentially that of the Plains Grassland life zone as described by Marr (1961, 1964). The riparian woodland overstories are dominated by plains cottonwood (*Populus deltoides*), crack willow (*Salix fragilis*), and hybrids (*Populus* x *acuminata*) of plains cottonwood and narrowleaf cottonwood (*Populus angustifolia*), while snowberry (*Symphoricarpus occidentalis*), chokecherry (*Prunus virginiana*), and sandbar willow (*Salix exigua*) are typical of the understory.

Methods

Avian Communities. We sampled the avifauna at each site three times during the breeding season in 1995, 1996, and 1997, using point transects. Each transect had a randomized starting point and census points 110 m apart (Bibby *et al.* 1992). Individual trained observers rotated visits to a given site in order to minimize observer bias, and sampling effort was distributed as evenly as possible among sites that were associated with different levels of development (Verner 1985). Bird surveys were conducted between sunrise and approximately 0830 on days with no rain and windspeeds < 32 km/h. At each point, a motionless observer recorded the species and number of all birds seen and heard during an 8-minute sampling period, including the best approximation of exact distance, to be used for estimating densities (Buckland *et al.* 1993), and an indication of whether the bird was seen or heard, or both. Birds in flight were recorded and annotated as such. At the beginning of each transect, the observer recorded pertinent site information on temperature, estimated wind speed, and estimated cloud cover.

Because avian species richness and composition have been reported to be strongly correlated with vegetation structure in riparian areas (Stauffer and Best 1980, Rice *et al.* 1984) and in urban areas (Beissinger and Osborne 1982, Mills *et al.* 1989), we estimated the percent coverage for the canopy, subcanopy, shrub, and ground layers at each census point. We also quantified tree diameters and heights as well as species composition for trees, saplings, and shrubs, and the number of dead stumps. The width of the riparian zone has been shown to have a strong influence on the composition and abundance of bird species found there (Stauffer and Best 1980); it was assessed at each census point on the basis of the extent of woody riparian vegetation using aerial photos and a Geographic Information System.

Nest Predation. To study nest predation, ideally one would locate and monitor a large number of active nests. This is difficult, however, when the objective is to compare a number of sites for a number of species. Alternatively, experimental nests provide a means of investigating patterns and causes of nest loss while standardizing factors such as nest appearance and egg size (Martin 1987, Haskell 1995), and this method has been used to describe patterns of nest predation across sites in different landscape contexts (Andr n *et al.* 1985, Wilcove 1985, Ratti and Reese 1988, Donovan *et al.* 1997). Not all variables that potentially influence predation rates on natural nests are controlled, however (e.g., parental activity at the nest). Predation rates on experimental nests should therefore be viewed as an index of predator activity and relative predation risk among sites and interpreted with caution.

We established transects of experimental nests (20 per transect in 1995 and 30 per transect in 1996 and 1997) at 12 of our study sites between late May and early July in order to examine differences in predation rates related to surrounding levels of urbanization. In 1995 and 1996, we also investigated more localized effects on nest predation related to human activity in the riparian zone. Here, we chose two sites (treatments) that had recreational trails adjacent to the stream and two control sites on the same streams that did not have trails. At each of the treatment sites we placed one transect of nests (n=20) on the trail side of the stream and one on the opposite (non-trail) side. A nest transect was also placed on a randomly chosen side of the stream at each of the control sites.

For both experiments we used commercially-available wicker canary nests modified with grass and mud in order to resemble natural nests more closely. Such modifications are thought to facilitate the recognition of these nests as prey items by predators (Martin 1987, Sieving 1992). Each transect of experimental nests had a randomized starting point. Nests were alternately placed 10-20 m on either side of an imaginary line at 30-m intervals, resulting in a between-nest distance of approximately 40 m. This arrangement was chosen in order to simulate natural nest densities in these habitats and to avoid repeated predation by a predator following a linear course, or Atraplining.≅ Nests were placed 0.5-2.5 m above ground in trees and shrubs and baited with two Japanese quail eggs (*Coturnix coturnix*) plus one egg made of modeling clay.

The latter served two purposes; first, it was closer in size to songbird eggs than were the quail eggs, thus avoiding biases that may be associated with the use of quail eggs (Roper 1992, Haskell 1995, DeGraaf and Maier 1996), and second, it allowed us to obtain tooth/beak impressions of the nest predators (M ller 1988, Nour *et al.* 1993, Major 1991). The clay egg was tethered to the nest by a thin piece of wire so that it could be recovered after a predation event (Major *et al.* 1994). Every effort was made to place nests in locations similar to those in which real bird nests are found. We checked nests every third day for 15 days, which simulates the combined egg-laying and incubation periods for most passerines (Martin 1987). At each check we noted the number of eggs remaining as well as egg and nest condition. Experimental nests were considered to be predated when one or more eggs were disturbed.

We also monitored natural bird nests at 4 sites in 1996 (n=149) and again in 1997. These data provide a basis for comparison with predation rates on experimental nests. We concentrated on finding nests of the American Robin (*Turdus migratorius*) because this species was present on all areas and was thought to exist in numbers great enough to constitute adequate sample sizes. Nests of other passerine species, however, were also monitored when found. Natural nests were checked approximately twice per week from the time we found them until they either fledged young or failed.

For examinations of nest predation where the level of development surrounding a site was of interest, we summed the number of buildings within 100 m of the watercourse. We did this using a Geographic Information System and land-use maps made available by the offices of the county tax assessors.

Data Analysis

When quantifying species richness and community composition, birds flying over an area were excluded. We also excluded nocturnal and crepuscular species, aerial insectivores (e.g., swallows and swifts), raptors, shorebirds, and waterfowl, because point counts are not an effective way to census such species (Bibby *et al.* 1992). A species was classified as a migrant if it travels >300 km to its breeding grounds and no individuals are present year-round on our study areas (Peterson 1990, Andrews and Righter 1992).

We quantified predation pressure for nests at each site using the methods of Mayfield (1961) as modified by Johnson (1979). Predation is determined using the total number of nests depredated and the total days that observed nests were exposed to predation, and is expressed as a daily mortality rate, or the probability of predation per day (Mayfield 1961). We conducted an overall test for homogeneity in daily mortality rates among sites on a given drainage using Chi-Square analyses and multiple comparisons (Sauer and Williams 1989). When the null hypothesis was rejected, we conducted tests on a pairwise basis using a sequential Bonferroni correction for multiple comparisons (Rice 1989).

RESULTS AND DISCUSSION

This study is continuing, and therefore both the analyses and results presented here should be considered as preliminary. We report and discuss the results of our initial analyses, which were conducted on data collected in 1996 unless otherwise noted.

Avian Communities.

For purposes of describing avian community composition, we focus on three sites per drainage that we have designated as high, medium, or low, reflecting the level of development in the surrounding landscape (Table 1). Overall, the number of bird species tends to increase as development decreases along a given drainage (Fig. 2), lending support to our first prediction. This trend is most striking along the Boulder Creek drainage. The high-urbanization end of the Boulder Creek gradient is our most urbanized site overall (Fig. 1, site 5), with many buildings and a heavily-used recreational trail in close proximity to the creek. This site also has the longest history of urbanization, and several other workers have reported a gradual decrease in species richness with time since development (Batten 1972, Walcott 1974, Aldrich and Coffin 1980).

South Boulder Creek and Coal Creek also showed increases in richness with decreased urbanization but there were slightly more species at the sites with intermediate levels of development than at the low-development sites, and overall differences along these gradients were not as pronounced as on Boulder Creek. It is important to remember that the designations of high-medium-low were made relative to other sites on the same drainage. On Coal Creek for example, one end of the transect at the medium site is within several hundred meters of a residential area, whereas there is no development within 6 km of the low site. The relative designations are therefore correct, but it may be that the differences are not sufficient to affect breeding birds in the riparian zone. Furthermore, development at the most urban sites on these drainages is both more recent and less extensive than on Boulder Creek. These observations underscore some of the limitations of a categorical approach to describing urbanization. We have begun to quantify the type and extent of land use in the matrix surrounding each site using digital maps made available by county planners. Such an approach will ultimately allow us to treat development as a continuous rather than a categorical variable.

Species richness in the study areas along the Poudre River increased with decreasing urbanization, but here the differences were less pronounced than on the other drainages. This may be attributable to the relatively greater width of the woody riparian zone along the Poudre (Table 1), and thus greater distances to nearby development. Several other studies have shown a strong correlation between the width of the riparian zone and bird species richness (Best and Stouffer 1980, Darveau *et al.* 1995, Hodges and Krementz 1996). This relationship appears to be influenced by landscape context, however, as evidenced by the medium and low sites on Coal Creek. These areas were among the narrowest in terms of riparian width, but compared favourably with wider, more-developed sites in terms of the number of avian species that they support during the breeding season. This result lends further support to the observation that narrow riparian habitats have conservation value for some species (Darveau *et al.* 1995, Fisher and Goldney 1997).Species richness is one measure of avian response to urbanization, but it is not the only one. It may actually mask important variation if the number of species at two sites is similar, but the composition differs considerably. In our initial examination of the composition of the bird assemblages at our study sites, we asked whether species that breed in adjacent areas also occurred in riparian habitats. On each gradient, we examined the riparian avifauna at the highly developed site for birds that are characteristic of towns and cities in general (Andrews and Righter 1992). Likewise, we examined the avifauna at rural riparian sites for species that generally breed in the surrounding grasslands. The results support our prediction that riparian areas associated with development will contain bird species that are also characteristic of the surrounding habitats, while this will be less evident in less developed settings (Fig 3a). We suggest that this is a function of the planting of trees in urban areas that once existed as shortgrass prairie. Riparian vegetation is therefore less distinct in urban settings and provides habitat for human commensals in much the same way that a park or tree-lined street might.

Migration strategy was the second lens through which we viewed compositional changes in riparian avifaunas. The percentage of migrant species tended to increase with decreasing levels of urbanization (Fig. 3b), and again, this trend is supported by our 1995 data. Thus, not only do urban areas generally have fewer species, but a smaller percentage of those species tend to be migrants. What factors might account for this observation?

Other researchers have also noted decreasing numbers of migrant species in urban areas when compared with rural sites (Walcott 1974, DeGraaf 1987, Friesen *et al.* 1995). One explanation is that resident species in urban areas are simply more tolerant of a substantial human presence (Cooke 1980, Burger and Gochfeld 1991). A second, though not mutually exclusive, possibility is a function of the flora often found in urban areas. Non-native and ornamental trees and shrubs may support fewer insects (Southwood

1961). Migrant species, which are often insectivorous, would thus be selected against when compared with omnivores and seed-eaters. A more thorough examination of the differences in ecological and life-history traits of these avian species, plus consideration of the structural and floristic attributes of riparian vegetation at these sites, is necessary to understand the patterns of habitat occupancy that we have observed.

Nest Predation

We predicted that we would find greater daily mortality rates at the urban end of our gradients, in accordance with commonly accepted dogma regarding nest predation (e.g., Soul *et al.* 1988, Harris and Silva-Lopez 1992, Noss 1993). We extended this thinking to areas near recreational trails, and reasoned that people often allow their dogs to wander near trails and that picnic areas and garbage cans associated with such sites might attract potential nest predators. Wilcove (1985) found predation rates on experimental nests to be nearly 150% higher in woodlots near suburban development as compared to more rural sites, and attributed this difference to increased densities of human commensals such as Blue Jays (*Cyanocitta cristata*), Common Grackles (*Quiscalus quiscula*), Raccoons (*Procyon lotor*), gray squirrels (*Sciurus carolinensis*), dogs (*Canis familiaris*), cats (*Felis catus*), and rats (*Rattus norvegicus*) near suburban areas.

Contrary to our predictions, we found no evidence that predation rates on experimental nests were higher at human-dominated sites. Rather, when we compared predation pressure as a function of building density, rates were significantly lower for high-development sites compared with rural sites on all 4 drainages (Fig. 4). The case was much the same regarding sites with recreational trails. Daily mortality rates increased with distance from trails on both drainages and in both years (Fig. 5a and b). Furthermore, there was no evidence that daily mortality rates for natural nests were greater at developed sites (Fig. 6). Rather, there was no difference in predation rates on Coal Creek, and the low-development site on South Boulder Creek had a higher rate than did the high-development site.

What factors might account for the discrepancy between our study and the prevailing dogma? As stated earlier, ecologists have often avoided areas of high human activity when selecting research sites, and thus biotic interactions in such areas are relatively unexplored (Pickett *et al.* 1992, McDonnell and Pickett 1993). Moreover, little is known about the ecological integrity of riparian systems that occur in an urban or suburban matrix, or about the impacts of recreational activities that often occur in these corridors on wildlife species (Adams and Dove 1989). Consequently, the prevailing dogma regarding nest predation in human-dominated areas is largely untested.

First and foremost, we stress that one must exercise caution when interpreting results based on experimental nests. Although experimental nests provide a means for gathering data on nest predation in a controlled manner, there are several important differences between these nests and active bird nests, such as the lack of nestlings, differences in scent, etc. Rather than dismissing this method as a result of its limitations, we suggest that careful comparisons of experimental nest results with data on the nest success of select species may provide insights into the mechanisms that determine predation rates and guide future efforts in this area. For example, we found daily mortality rates on experimental nests to be much higher than on active American Robin nests. This species is a vigorous defender of its eggs and young, as we were made aware each time we checked nest contents. This suggests that parental activity may play a strong role in reducing rates of nest predation, and suggests potentially fruitful areas for future study.

It is possible that human activities that occur near recreational trails influence predation rates, but not in the way that we initially predicted. Rather, it may be that the human presence in these areas actually serves to dampen predation rates for species able to nest there. Some support for this notion is derived from studies of avian breeding success in environments that are associated with various levels of human activity. Osborne and Osborne (1980) found that Blackbirds (*Turdus merula*) nesting near sidewalks or buildings at the University of Exeter not only enjoyed significantly higher breeding success, but were much less discriminating in nest site characteristics than were birds in more remote locations. Similarly, the amount of nest predation for birds breeding in two urban parks in Poland was negatively correlated with the frequency of human visits (Tomialoj and Profus 1977).

Finally, it is possible that our most rural sites are not remote enough, as even the most rural area is within 6 km of suburban development. It would be interesting to measure predation rates in riparian areas even farther from human activity. This is not only logistically difficult, but as one moves farther from developed areas in Colorado, other factors increasingly confound comparisons, such as differences in vegetational, geomorphological, and topographical features. Ultimately, there are no pristine riparian sites at low elevations to use as baselines in the western U.S. (Ohmart 1994), one reason being that conservation interest in these areas has only developed over the last two decades.

Ecology, Urban Planning, and Conservation

At this point, it is premature to offer detailed prescriptions for urban planners and natural resource managers on the basis of this study. There are some suggestive patterns in our data, however, that bear closer scrutiny. It does seem that, other things being equal, wider riparian areas support more species than narrow ones. It also appears that the nature of the surrounding landscape matrix influences species richness, so that a narrow riparian habitat in favourable surroundings may harbour more species than a wider area in a less suitable setting. Our data suggest that human activities in the riparian zone may also play a role in determining which species persist there. It may be that certain advantages are conferred on birds that are able to tolerate a human presence - not all species may be able to do so. More research in addition to further analyses of our data is needed in order to gain a better understanding of both local and extrinsic factors that affect avian conservation in riparian habitats.

By their very nature, riparian systems transcend political boundaries. A single stream or river may bisect numerous cities and towns, and flow through a number of counties or, in some cases, states. When one also considers a network of associated tributaries, it soon becomes apparent that such a dendritic system poses a host of conservation issues. For this reason, the implementation of policy based on sound ecology is challenging because authority for decisions on land use is often relegated to the lowest possible level of government. Land-use change over very large areas can develop as the result of many fine-scale decisions. Often these decisions are made "one at a time" with little or no consideration for their overall impact at larger scales. Because these choices are numerous and diffuse in time and space, it is difficult for ecologists to support them in a meaningful fashion. It is therefore critical that agencies or groups whose mission is conservation not only cooperate across political boundaries, but also be quite explicit about what it is that they are trying to conserve.

Knopf and Samson (1994) note that generalist species tend to dominate bird communities at most riparian sites in the west. On a regional scale, this would seem to be true at our study sites. It is also true, however, that these may be the only habitats where some of these species occur over smaller scales, such as the county. As human populations shift toward urban areas, connections to nature become increasingly tenuous. Because conservation action, even in remote or rural areas, may depend on the support of people in urban areas, the preservation of native bird species as well as other components of biological diversity in areas where people live takes on added importance. It may be our best hope for fostering a greater appreciation of our natural heritage.

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Table 3.1. Average width of the woody riparian zone for three sites on each drainage. High, medium, and low refer to the relative level of development surrounding each site.

Drainage	Site	Average Width (m)
South Boulder Creek	High	56
	Medium	96
	Low	48
Coal Creek	High	73
	Medium	53
	Low	51
Boulder Creek	High	76
	Medium	66
	Low	127
Poudre River	High	115
	Medium	130
	Low	120

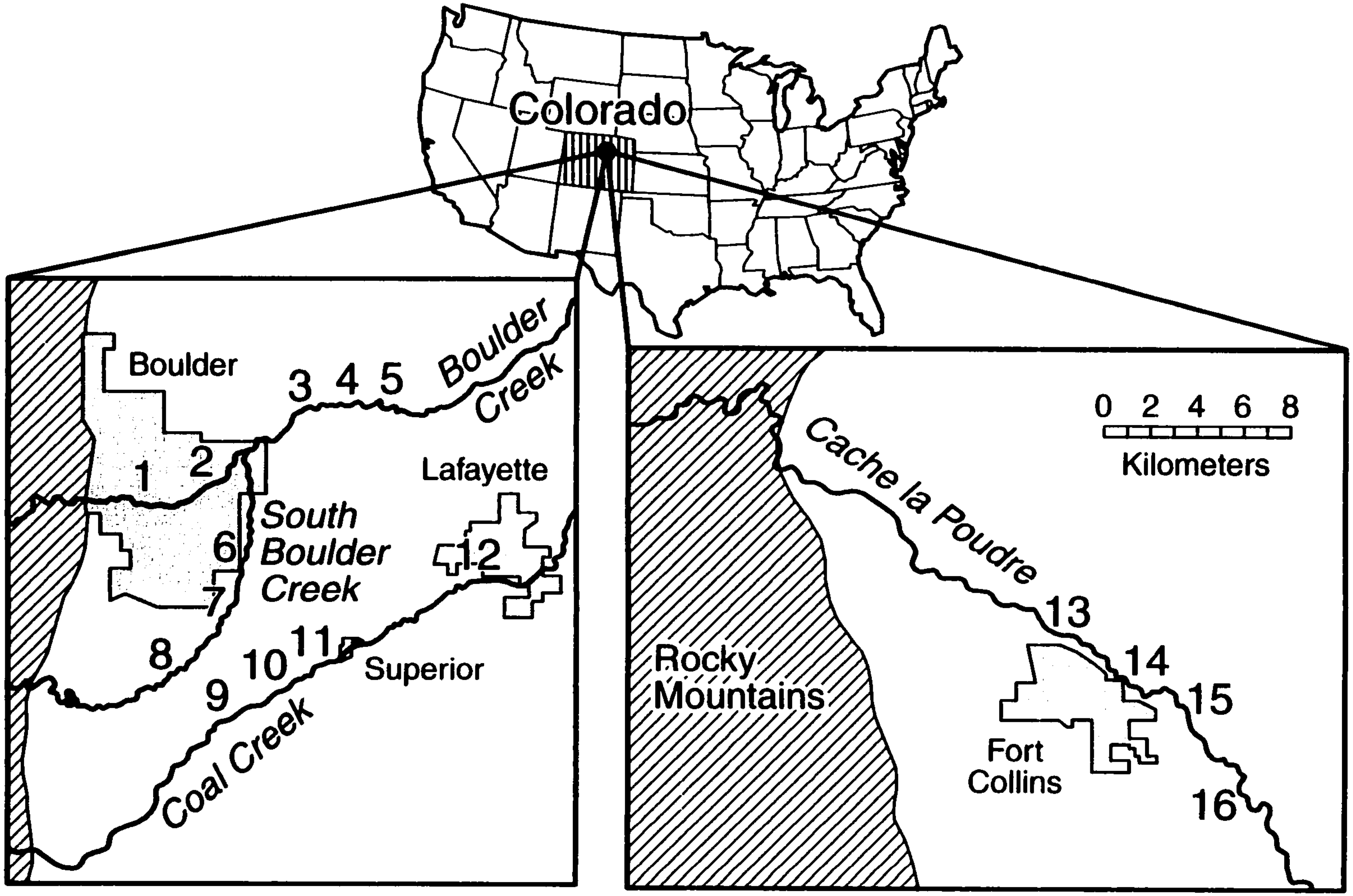

Fig. 3.1. Map of the study area. Numbers indicate study sites, cross-hatched areas indicate the Rocky Mountains, and gray areas indicate cities and towns.

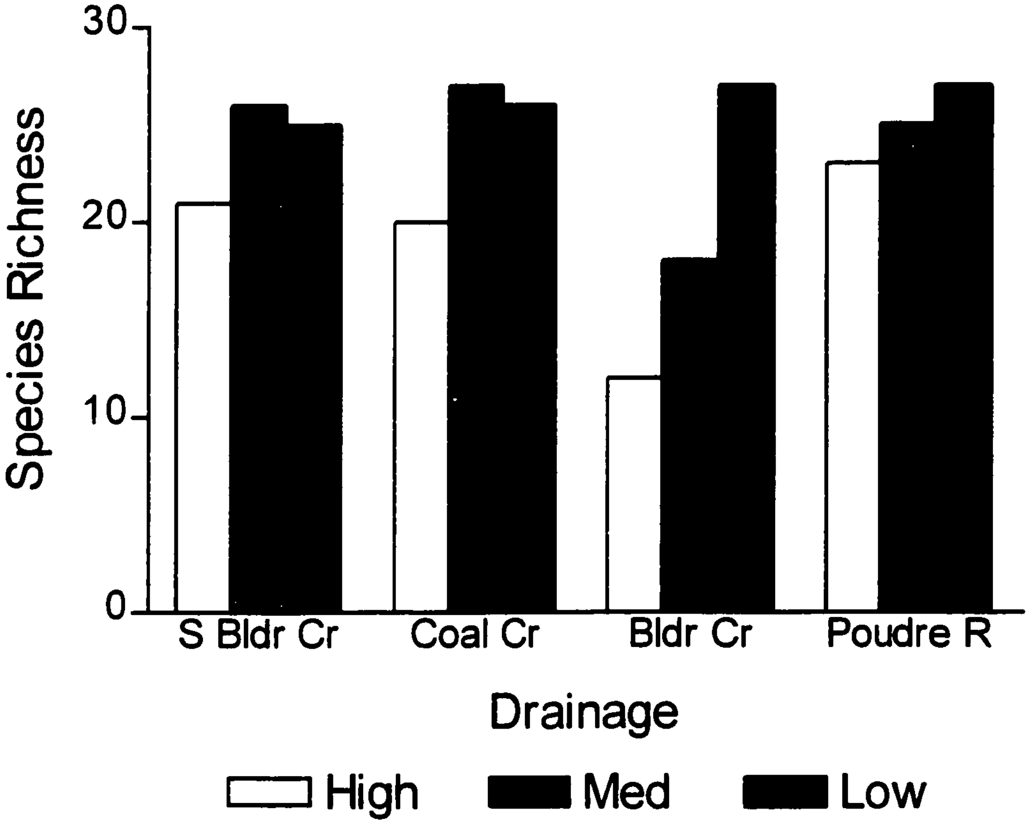

Fig. 3.2. Avian species richness in 1996 for three sites each on South Boulder Creek, Coal Creek, Boulder Creek, and the Poudre River. Only species known to breed in riparian areas have been included, while nocturnal and crepuscular species, aerial insectivores (e.g., swallows and swifts), raptors, shorebirds, and waterfowl have been excluded. High, medium, and low refer are relative designations for the level of urbanization in the landscape surrounding each site.

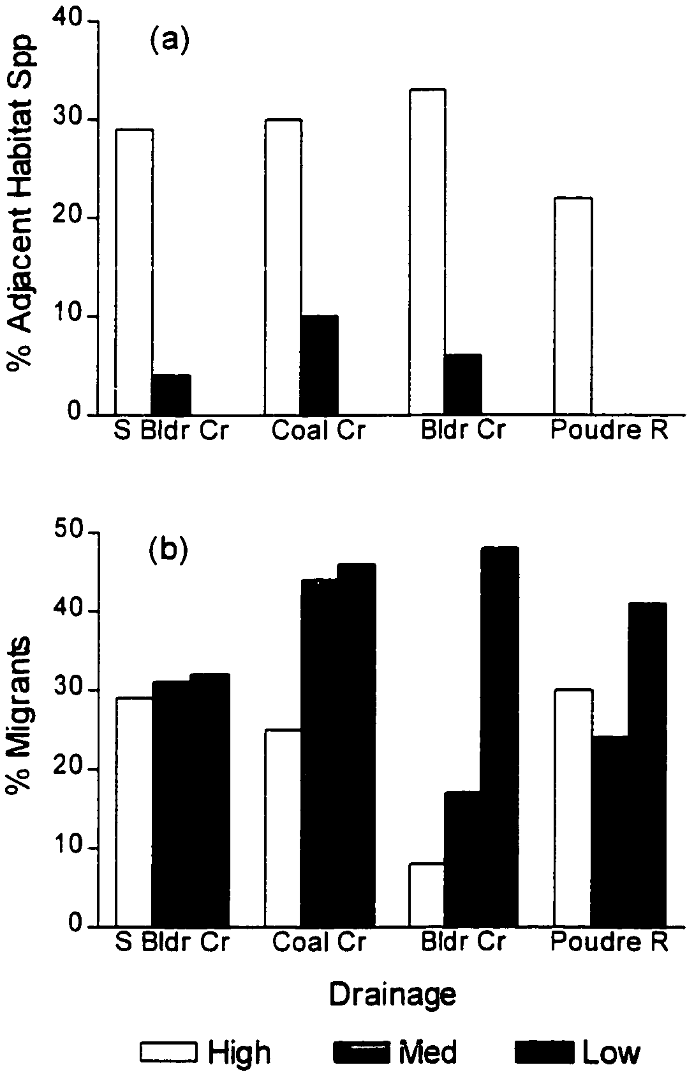

Fig. 3.3. For South Boulder Creek, Coal Creek, Boulder Creek, and the Poudre River during the 1996 avian breeding season (a) the percentage of the bird community consisting of species characteristic of urban habitats (for the high urbanization site) and grassland habitats (for the low urbanization site) as described by Andrews and Righter (1992), and (b) the percentage of the bird community at each of three sites per drainage that consists of birds that winter in the neotropics but breed in Colorado's lowland riparian areas. For (b), we have excluded nocturnal and crepuscular species, aerial insectivores (e.g., swallows and swifts), raptors, shorebirds, and waterfowl. High, medium, and low are relative designations for the level of urbanization in the landscape surrounding each site.

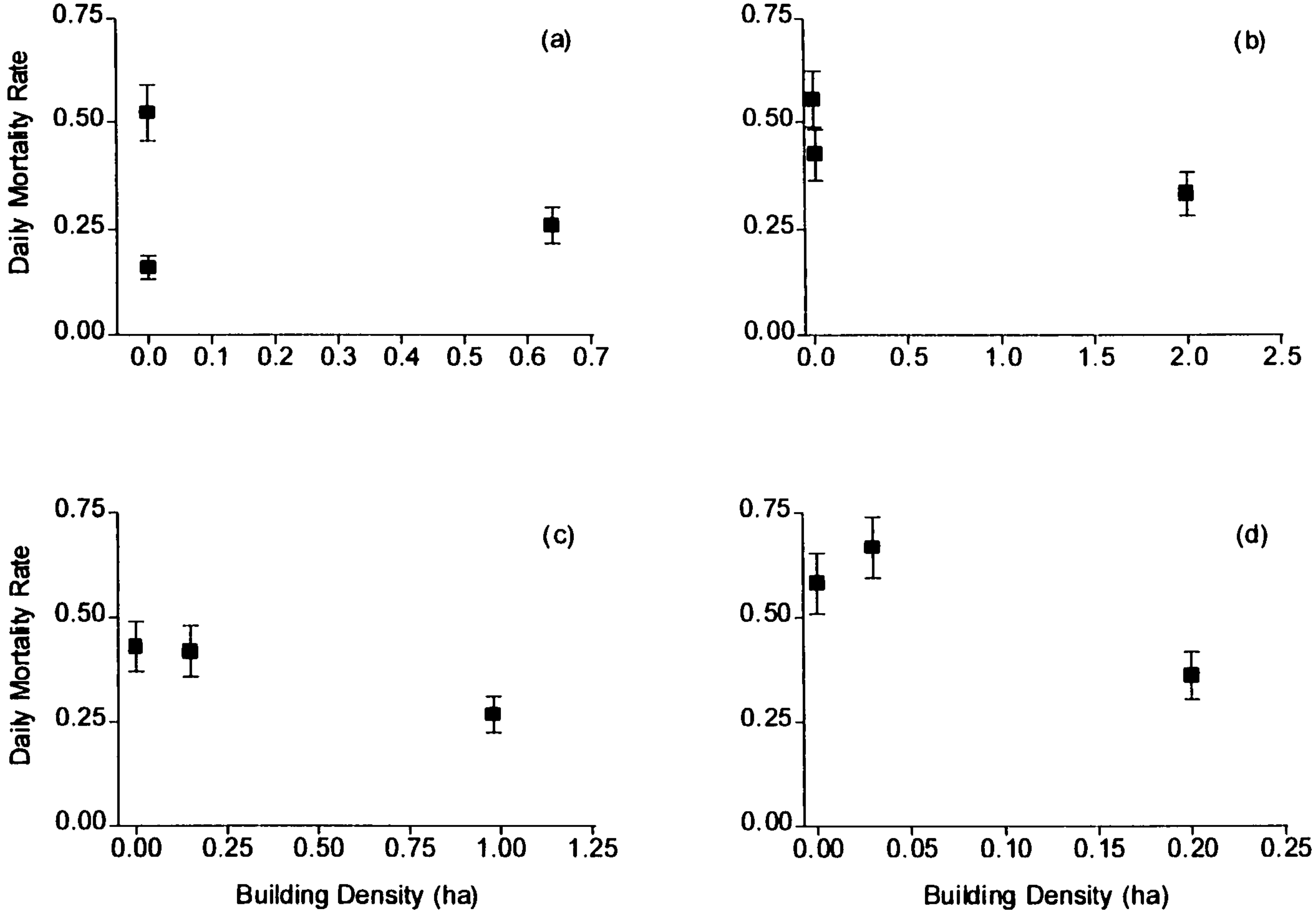

Fig. 3.4. Daily mortality rates ± 1 SE vs. building density per ha for experimental nests at each of three sites on (a) South Boulder Creek, (b) Coal Creek, (c) Boulder Creek, and (d) the Poudre River in 1996. Building density is based on the number of buildings within a 100 m radius buffer surrounding the study reach of each watercourse. We tested for overall homogeneity in rates on each drainage (a: $p<0.001$; b and c: $p<0.05$; d: $p<0.01$), and conducted pairwise tests for rates on each drainage for most- vs. least-developed sites (a and b: $p<0.001$; c: $p<0.03$; d: $p<0.02$).

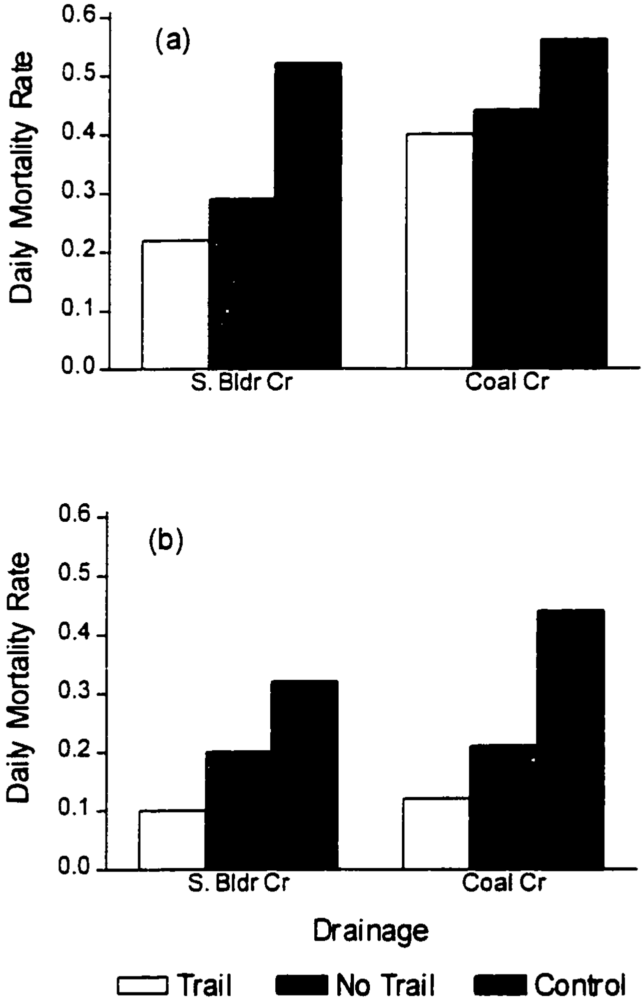

Fig. 3.5. Daily mortality rates on experimental nests at each of two sites on South Boulder Creek and on Coal Creek in 1996 (a) and 1995 (b) as a function of distance from recreational trails. "Trail" refers to nests on the trail side of a stream, "No Trail" refers to nests on the opposite side of the stream, and "Control" refers to nests at a site on the same stream that is not associated with a trail in the riparian zone.

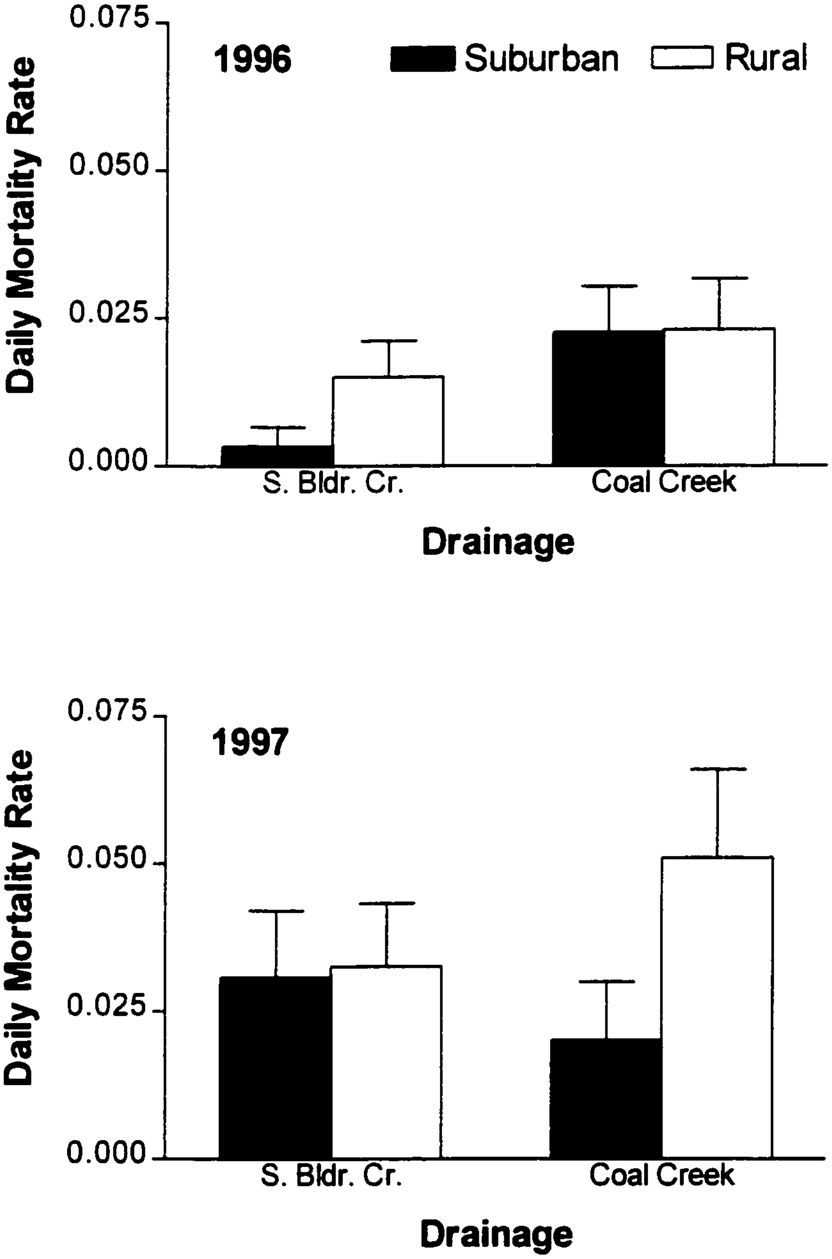

Fig 3.6. Daily mortality rates ± 1 SE vs. building density per ha for American Robin *(Turdus migratorius)* nests at each of two sites on Coal Creek and South Boulder Creek in 1996.

CHAPTER IV

HUMAN SETTLEMENT AND AVIAN COMMUNITIES IN LOWLAND RIPARIAN AREAS

ABSTRACT

Riparian habitats in western North America have been characterized as centers of avian diversity, important to both migrating and breeding birds. Human settlement also tends to occur near riparian areas. We studied the relationship between avian communities in lowland riparian areas and the intensity of human settlement in the surrounding landscape. From 1995-1997, we censused birds at 16 study sites on four drainages near the Front Range of Colorado. Sites were chosen to represent a gradient of development on each drainage. At each census point, we measured a number of features of the vegetation. For each site, we measured the width of the woody riparian zone, the number of bridges, intensity of recreational trail use, and building densities within 100, 500, and 1500 m of the watercourse.

We then used multiple regression to determine the relationship between environmental variables and three measures of the avian community: species richness, relative abundance (mean number of individual birds detected per point per site), and point diversity (mean number of species detected at each point). The relationships among

environmental variables, breeding bird species, and study sites were investigated using Canonical Correspondence Analysis. We used multiple linear regression to examine the relationships between individual bird species and environmental variables.

Native tree and shrub species decreased with increasing urbanization. Tree height tended to increase whereas canopy cover, ground cover, and shrub cover tended to decrease with increasing development. More-developed sites were associated with substantial recreational trail use and tended to have more bridges than less-developed sites.

The best model for species richness included postive terms for building density and riparian width. The best model for relative abundance included a positive term for height of herbaceous vegetation and a negative term for shrub cover. Point diversity had a strong correlation with species richness, and the best model for point diversity included positive terms for building density and herbaceous height. At the sites associated with the highest level of development on each drainage, a substantial portion of the riparian avifauna consisted of birds typical of cities. At rural sites, however, there was little overlap between the riparian avifauna and that of the surrounding grasslands. The CCA axes explained most of the variation in the species data, with an overall separation between migrant and resident species. Resident species reached their greatest abundances at more-developed sites whereas migrants tended to be associated more with rural sites and also with increasing shrub cover.

INTRODUCTION

The expansion of lands dominated by human activities is driving declines and extinctions of native species worldwide. Human settlement is arguably the most profound type of land-use change, both in terms of the intensity of land surface alteration and the extent of associated ecological impacts. This phenomenon, however, has received scant attention from ecologists (Pickett *et al.* 1992, McDonnell and Pickett 1993, Botkin and Beveridge 1997), undermining the scientific basis for decisions in settled areas, particularly those regarding conservation.

People have always tended to settle near creeks and rivers. One of the guidelines proposed by the Ecological Society of America s Committee on Landuse and intended to assist decision-makers in conservation efforts is to preserve rare landscape elements [that] provide critical habitats or ecological processes (Dale *et al.*, In Press). Any reasonable interpretation of this guideline would lead to consideration of riparian areas under this rubric. The ecological importance of riparian areas is disproportionately large relative to their spatial extent and increases as surface water becomes more scarce. Riparian habitats play a key role in numerous ecological processes (e.g., floods, seedling establishment, water filtration, nutrient cycling) and are commonly regarded as centers of biological diversity (Malanson 1993, Naiman *et al.* 1993, Naiman and Decamps 1997), especially in arid environments.

In the western United States, riparian areas account for less than 1% of the total land area, and yet up to 80% of vertebrate species depend on these habitats during part or all of their life cycles (Chaney *et al.* 1990). Riparian areas in this region provide critical resources for migrating and breeding birds (Stevens *et al.* 1977, Knopf and Samson 1994, Skagen *et al.* 1998) and feature some of the most diverse avian assemblages in North America (Johnson *et al.* 1977, Ohmart 1994). In Colorado, lowland riparian areas harbor more species of birds than any other habitat (Bottorff 1974). In the state s northeastern short-grass prairie, for example, Knopf (1985) reported that 82% of breeding bird species occurred in riparian vegetation.

Although birds are perhaps the best-studied taxon in human-dominated areas, our understanding of the effects of human settlement on bird communities is in its infancy (Marzluff *et al.* 1998). General trends that have been reported include a decrease in the number of avian species but an increase in the number of individual birds with increasing settlement intensity (Batten 1972, Emlen 1974, Geis 1974, Aldrich and Coffin 1980, Beissinger and Osborne 1982, Bezzel 1985, DeGraaf and Wentworth 1986, Blair 1996). Increases in density are often accounted for by a few exotic species such as the European Starling (Sturnus vulgaris), Rock Dove (Columbia livia), and House Sparrow (Passer domesticus) (Geis 1974, Aldrich and Coffin 1980, Beissinger and Osborne 1982, Bezzel 1985, DeGraaf and Wentworth 1986).

For many species, changes in the structure and composition of vegetation as human settlement progresses are often cited as determinants of habitat suitability (Beissinger and Osborne 1982, Green *et al.* 1989, Jokimaki and Suhonen 1993, Rolando *et al.* 1997, Germaine *et al.* 1998). Bird communities, however, are affected not only by direct alteration of habitats, but also by activities occurring on surrounding lands. In Texas, Engels and Sexton (1994) reported declines in the Golden-cheeked Warbler

(Dendroica chrysoparia) in habitats that were relatively undeveloped but near urban areas. Similarly, bird diversity in forest patches in southwestern Ontario declined with increasing residential development in the surrounding area (Friesen *et al.* 1995). These findings have particular relevance for riparian bird communities because although building codes often prohibit development in the floodplain itself, human settlement nearly always occurs in close proximity to watercourses. Smith and Schaefer (1992) found higher avian species richness in rural areas versus urban areas in riparian habitats in Florida during the breeding season. Similarly, Rottenborn (1999) reported decreased bird species richness and densities as development increased on lands adjacent to riparian areas in California.

We studied avian assemblages in lowland riparian areas across a gradient of human settlement near the Front Range of Colorado. Colorado is typical of states in the Rocky Mountain region with a growth rate that is three times the national average and manifested in urban and suburban sprawl. These phenomena are particularly acute in counties along Colorado s Front Range, where approximately 80% of the state s population lives. There, annual population increases exceeding 4-6% are not uncommon (U.S. Census Bureau 1998). We wished to describe bird communities in lowland riparian areas and to examine the relationship between these assemblages, fine-scale habitat features, and the intensity of human settlement in the surrounding landscape. Our objectives were to: (1) describe and compare lowland riparian bird communities at sites associated with varying levels of development on adjacent lands; and (2) to investigate the degree to which variation in the structure and composition of bird communities can be explained by characteristics of the surrounding landscape and local habitat features.

METHODS

Study Sites

We selected 16 study sites on four drainages: Coal Creek, South Boulder Creek, and Boulder Creek in Boulder County and the Cache la Poudre River in neighboring Larimer County, Colorado, U.S.A (Fig. 1; Appendix I). The overall study area is located on the western edge of the Plains Grassland zone as described by Marr (1961, 1964). Elevations range from approximately 1550 m in eastern Boulder and Larimer counties to 1640 m in western portions of the study area near the Front Range of the Rocky Mountains. These sites were initially chosen to represent a gradient of human settlement on each drainage as well as a gradient across drainages (Austin and Heyligers 1991, Wiens and Parker 1995), based on familiarity with the areas and visual assessments. Sites in Boulder County were all under the jurisdiction of either Boulder County Parks and Open Space or City of Boulder Open Space Department, and sites in Larimer County were managed by the Fort Collins Department of Natural Resources.

While it is impossible to select study areas that are true replicates in such landscapes, sites were selected to be as similar as possible with regard to riparian habitat structure. All sites were wooded and relatively narrow, averaging 60 — 110 m in the width of the woody riparian zone, with a shrub understory. Dominant tree species included plains cottonwood (*Populus deltoides*), crack willow (*Salix fragilis*), and hybrids (*Populus* x *acuminata*) of plains cottonwood and narrowleaf cottonwood (*Populus angustifolia*). The understorys were dominated by snowberry (*Symphoricarpus occidentalis*), chokecherry (*Prunus virginiana*), wild rose (*Rosa woodsii*), lead plant (*Amorpha fruticosa*), and sandbar willow (*Salix exigua*).

Portions of the study sites at Superior, Vista View, the Mine, Eldorado Springs were grazed by cattle during the course of the study. Other sites with relatively low levels of development in the surrounding area or with recent development were grazed to varying extents in the past, but are now fenced from grazing.

Landscape and Local Habitat Measures

Habitat characteristics believed to be important for riparian bird communities were measured at several scales (Table 1 and Table 2). At the broadest scale, we quantified the intensity of human settlement by deriving building densities (Marzluff *et al.* 1998, Theobald *In Press*) from digital parcel maps. Parcel maps delineate property boundaries and provide standardized information on whether or not a property is developed, the number and type of buildings located there, and the type of zoning. Parcel data are produced by county tax assessors offices and are being made increasingly available in GIS form by county and city planning departments. For describing land use in developed areas, these data are among the most detailed available.

In 1996 and 1997, the locations of all avian census points were determined to within 3 m using a GPS. These data were digitized and combined with the parcel data. We then identified polygons centered on each census point containing all buildings within 1500 m that were closer to that point than to any other point. These data were then used to determine the density of buildings within 1500 m, 500 m, and 100 m of each point on a transect and, as a measure of the variability of settlement intensity at a site, the standard deviation of building density along each transect. For each site, we also derived an inverse weighted density score using the formula $WDENS = \sum(1/D)/1000$ where D is the distance from each building to the nearest census point.

Riparian vegetation at our study sites tended to form continuous bands more often than discrete patches. In such cases, the width of the woody riparian zone is a surrogate for patch size and has been shown to have a strong influence on the composition and abundance of bird species found in streamside woodlands (Stauffer and Best 1980). We measured the width of woody riparian vegetation using 1:24,000 digital aerial photos and a GIS at each census point along an axis that was perpendicular to the stream. We also counted the number of bridges within each stream reach or within 200 m of the ends of each reach using these same photos. Bridges have been used as a measure of habitat fragmentation for riparian areas and been shown to account for substantial variation in measures of bird community structure (Rottenborn 1999).

At a finer scale, numerous measures of avian community structure have correlated strongly with vegetation structure and floristics in riparian habitats (Stauffer and Best 1980, Rice *et al.* 1984) and in urban areas (Beissinger and Osborne 1982, Mills *et al.* 1989). We therefore quantified local vegetational features using a modified point-center-quarter method (Friedman *et al.* 1996). At each census point, we identified the 10 closest trees. The distance to the farthest tree served as the radius of a circle used in estimates of tree density and other habitat features. This method provided an efficient means for gathering data over a large number of points and, for our purposes, offered two advantages over the traditional point-center-quarter method (Cottam and Curtis 1956): (1) sample size for estimating tree density was fixed, which was especially important where trees were sparse; and (2) time was saved in densely wooded areas.

At each point, we noted the species and measured the dbh and height above ground of each of the 10 trees. Total basal area for each point was later derived from dbh measurements. Indices of total cover for the canopy (trees > 4 m in ht.), subcanopy (trees 2-4 m in ht.), shrub (0.5-2 m), and herbaceous layers were derived by multiplying estimates of a particular layer s coverage within the circle by the density of that layer within the area covered. These data were visually estimated using discrete categories: >75%, 50-75%, 25-50%, 5-25%, and <5%. At each point, we also noted the presence of individual shrub species and recorded the number and species composition of saplings as well as the number of snags.

Avian surveys

We surveyed the avifauna at each site three times during the breeding season using point transects (Bibby *et al.* 1992). Each transect was located in the woody riparian zone and ran parallel to a watercourse with a randomized starting point and 11 census points spaced at 110-m intervals. This spacing arrangement was based on pilot data collected in the summer of 1994 in which the average truncation distance for point counts was approximately 50 m (Miller and Craig, unpublished data). The results of this pilot study were also in general agreement with point counts conducted in riparian habitat in Arizona, where the average detection distance was 37 m (Szaro and Jakle 1985).

Individual trained observers rotated visits to each site throughout the breeding season in order to minimize observer bias. On each day that censuses were conducted, sampling effort was distributed as evenly as possible among sites that had different levels of development (Verner 1985). Bird surveys were conducted between sunrise and approximately 0830 on days with no rain and windspeeds < 32 km/h. At the beginning of each transect, observers noted the temperature and estimated wind speed and cloud cover. At each point, a motionless observer recorded the species and number of all birds seen and heard within 50 m during an 8-minute sampling period, as well as the approximate distance from the census point. Birds in flight were recorded and annotated as such.

Observers all had experience conducting point counts and were familiar with the avifauna of this region. Surveys were conducted each year by 3-4 observers and of these, two individuals participated in surveys during each of the three years. Prior to each field season, all observers underwent a two-week training period for purposes of sharpening identification skills and to aid in distance estimation, with periodic recalibration throughout the field season. Before the first field season, distances to obvious landmarks were measured at each census point to facilitate measurements when surveying.

In 1997, we also counted people using recreational trails during each of our avian surveys and also for a two-hour period in the early evening (i.e., between 01700 h and 2000 h). These counts were averaged to give us a measure of human activity at each site.

Data analysis

Only species that were seen or heard and that occurred on >1 census for each site were included in community analyses. Species flying through or over the census plots were not included because we could not be sure if they were using riparian habitat, given the narrow width of our study areas. We also excluded nocturnal and crepuscular species, aerial insectivores, raptors, shorebirds, and waterfowl because point counts are not an effective method for counting such species (Bibby *et al.* 1992).

Because of small sample sizes, we were not able to derive distance-based density estimates for most species (Buckland *et al.* 1993). We therefore used the maximum count of each species recorded at a site during each year as a measure of relative abundance. We used maximum rather than average counts because some species were either not present or were not singing during some visits, depending on migratory patterns or breeding cycles. Averaging in zero values would therefore result in misleading estimates of relative abundance. We tried to minimize differences in detectability among species, which can bias estimates of relative abundance, by choosing structurally similar study sites and by limiting maximum detection distances to 50 m.

For each site, we derived the following community measures: (1) species richness (species known to breed in lowland riparian habitats in Colorado), (2) relative abundance (average number of individuals/point), and (3) point diversity (average number of species per point recorded at each site); the latter is expected to vary independently of species richness if horizontal habitat heterogeneity is pronounced (Willson and Comet 1996).

We screened habitat variables initially for collinearity using Spearman rank correlations with ∀=0.01. We first examined correlations among variables associated with building density. From this group, we selected variables that were not significantly correlated and measured the degree of association between them and the variables for trail use, number of bridges, and riparian width — again, selecting only those variables with non-significant correlations. Similarly, we selected uncorrelated variables from the group associated with vegetation structure and composition.

For variables selected in the initial screening procedure as well as the community measures, we assessed normality and homogeneity of variance using stem-and-leaf plots, normal quantile plots, and residual scatterplots. BDEN 1500 and BDEN 100 were log-transformed to stabilize variances and normalize data. We used multiple linear regression to examine the relationship between measures of avian community structure and all possible subsets of independent variables. Regression models were compared and evaluated on the basis of their adjusted R^2, ability to meet assumptions, and influential cases. We assessed the influence of individual observations on the fitted models by examining leverage plots and Cook=s distance (Weisberg 1985, Tabachnick and Fidell 1996).

To investigate the degree to which riparian habitats are distinct from the landscapes surrounding them, we quantified the proportion of the avifauna at the most- and least-urbanized sites on each drainage that are associated with habitats in the surrounding landscape matrix. For the more developed site, this would consist of birds typically associated with urban areas and for the least-developed site, this would consist of species associated with grassland habitats. For each of these groups, we relied on the descriptions of Andrews and Righter (1992).

We used Canonical Correlation Analysis in an exploratory fashion to graphically depict the relationships among study sites, environmental variables, and individual bird species. Canonical ordination represents a class of techniques for relating data on species composition to their environment (ter Braak 1992). Canonical Correspondence Analysis (CCA, ter Braak 1986, ter Braak and Prentice 1988) is a robust direct gradient analysis technique that allows one to examine the part of variation in species composition that can be explained by a particular set of environmental variables (i.e., constrained ordination). Linear combinations of environmental variables are selected to create synthetic axes (gradients) that produce maximum separation of the species distributions (ter Braak and Prentice 1988). CCA results in an ordination diagram in which environmental variables are depicted by arrows, and species and sites are marked by points. Species points approximate their weighted average in relation to the environmental variables, and each site point lies at the centroid of the species points that occur at that site (ter Braak 1986, ter Braak and Prentice 1988).

We used a manual forward-selection procedure to screen variables for entry into the CCA model. At the first step, variables are shown in order of extra fit, or the eigenvalue of the CCA if the corresponding variable were the only one in the model. Here, we included the variable with the highest extra fit in the model. At the second step, the remaining variables are again listed in descending order of extra fit — in this case, the difference between the variation explained with only the variable selected in the first step in the model and the variation accounted for with the corresponding variable added to the one selected in the first step. At each step, we tested the statistical significance of the variable with the greatest extra fit using a Monte Carlo simulation test with 199 iterations and the threshold for entry into the model set at ∀=0.05.

To examine the relationship between habitat characteristics and the abundance of individual bird species, we used interactive model building techniques and multiple linear regression. We selected several migrant and resident species that had sufficient data to permit statistical analyses. Criteria for evaluating models were the same as those described above.

RESULTS

Over the three-year period, observers recorded 15,473 detections representing 95 species (Appendix II). Of these, 50 species met criteria for inclusion in analyses, including 42 species known to breed in riparian areas. The most abundant species were the American Robin (*n*=518), Common Grackle (*n*=577), and European Starling (*n*=837). These species were also among the most widespread, occurring at all 16 sites. Other species recorded at 14 or more sites in order of decreasing abundance included the House Wren (*n*=403), Red-winged Blackbird (*n*=346), Yellow Warbler (*n*=311), American Goldfinch (*n*=235), Song Sparrow (*n*=231), Black-billed Magpie (*n*=231), Bullock s Oriole (*n*=172), Mourning Dove (*n*= 164), Brown-headed Cowbird (*n*=142), Northern

Flicker (*n*=173), and Downy Woodpecker (*n*=76). Four species of non-native birds were recorded: European Starling, House Sparrow, Blue Jay, and Rock Dove.

Of the variables associated with building density, we retained BDENS 1500 and BDENS 100 for use in subsequent analyses (Table 3). BDENS 1500 had a high degree of association with BRIDGE and TRAIL, and these two variables were excluded from further consideration. Based on significant associations with other variables, we also excluded GRND, DBH, SDTREE, NTREE, and SCAN from further analyses (Table 4).

For breeding species richness, the best model included the terms BDEN 1500 and WIDTH (adj. R^2=0.652). Building density, which accounted for nearly 60% of the variation, had an inverse relationship with richness, and riparian width had a slightly positive association. The most robust model for relative abundance included the variables SHRUB and HERB (adj. R^2=0.442); both variables had a positive relationship with abundance. The best model for point diversity also two terms: BDEN 1500 and HERB (adj. R^2=0.564). Building density was negatively associated with point diversity and height of herbaceous vegetation was positively related to diversity. Species richness and point diversity did not vary independently, but instead were highly correlated (r=0.817). Diagnostics revealed that the study sites at 30th St. and especially at CU on Boulder Creek both exerted a strong influence on the regressions in all cases.

On all drainages, a greater proportion of species associated with the surrounding areas were observed at more highly-developed riparian sites than at rural sites. The percentage of urban birds found in riparian habitats near development were >3 times the proportion of grassland birds observed at sites in rural areas.

Variables for building density, trail use, canopy cover, shrub cover, and herbaceous height were chosen in the forward selection process. The first two axes of the CCA explained 33.6 and 14.8% of the variation in the species data. The first axis was strongly correlated with urbanization, as measured by building density (*r*=0.936). The second axis had a strong inverse correlation with the height of herbaceous vegetation (*r*=-0.905) and tends to separate sites that are either currently grazed or feature narrow riparian zones in a highly developed matrix (Fig. 2). Based on these environmental variables and the species data, the steepness of the gradients of urbanization varied among drainages. Resident species tended to increase with increasing urbanization, but most residents reached their greatest abundances at sites with intermediate levels of development (Fig. 3). Migrant species also tended to reach their greatest abundances at sites surrounded by intermediate levels of development, but these birds were absent at the sites at the urban end of the gradient. Several migrant species also tended to increase at sites with increasing shrub cover.

DISCUSSION

Urban-rural gradient

In the western United States., people have tended to modify their environments to reflect the places that they came from (Limerick 1987), usually regions with wetter climates. One of the most obvious examples of this phenomena is the planting of trees, shrubs, and bluegrass lawns. In semi-arid regions, trees are often scarce and the process of urbanization is therefore not so much one of removing vegetative structure, as is typical in forested regions (Sharpe et al. 1986), but instead results in the addition of structure. In our study area, human settlement on the mixed-grass prairie tends to create wooded savannas.

We found that the proportion of native trees and shrubs decreased with increasing development, a phenomenon that has also been reported elsewhere (Beissinger and Osborne 1982, Mills *et al.* 1989, Germaine *et al.* 1998). Ornamental vegetation may be favored over native vegetation as a result of the familiarity factor alluded to above, or perhaps for aesthetic reasons. In our study areas, tree height tended to increase with development while canopy cover, ground cover, and shrub cover each tended to decrease with increased development. The latter may be at least in part related to a preference for lower shrub densities in areas of high human use as a deterrent to crime.

A number of non-vegetative habitat features in riparian areas were also associated with increasing development in the surrounding landscape, making it difficult to tease apart the individual influences of these variables. Recreational trails, for example, were located more often in riparian zones near highly-developed areas and trails proximate to development were associated with much higher human use compared to trails in rural areas. It is thus difficult to determine unequivocally the effect of high trail use in areas with little or no development (but see Miller and Hobbs, In Review). Bridges also tend to increase with development, possibly resulting in greater fragmentation of riparian habitats (Rottenborn 1999).

In general, patterns of land use are more variable at fine scales in developed vs. undeveloped areas. This is largely the result of smaller parcel sizes in towns and cities than in areas dominated by, for example, agriculture. Thus, a riparian area in an agricultural matrix may be surrounded by only one type of land use, but in urban areas the environment is much more heterogeneous, with changes in land use potentially occurring every few hundred meters. Habitat conditions in semi-natural native vegetation, like riparian zones, may also change abruptly and over short distances.

Bird community

Our findings for bird community characteristics generally parallel those of other workers in other developed areas. Species richness of breeding birds in riparian habitats decreased with increasing development. Exotic species and human commensals tended to dominate bird assemblages at our most urban sites whereas migrant species tended to avoid these areas (Walcott 1974, Beissinger and Osborne 1982, DeGraaf 1987, Friesen *et al.* 1995, Mills *et al.* 1989, Blair 1996). In contrast to other studies, however, avian abundance did not increase with increasing urbanization (Marzluff *et al.* 1998). Instead, we found fewer individuals in riparian areas surrounded by developed areas when compared with our rural sites.

There may be fewer individuals in lowland riparian areas in an urban context because the riparian habitat is much less distinct from its surroundings. As we have shown, typical urban bird species in Colorado are found more frequently in riparian habitats that are surrounded by development than grassland birds are found in riparian areas that are surrounded by prairie. The reason is simple: whereas there are profound structural differences in riparian habitats vs. mixed-grass prairie, this is not the case in areas of intense human settlement. People have planted trees and shrubs in great numbers and the boundaries of the woody riparian zone are diffuse. Although irrigated farms may also be associated with riparian-like vegetation in the uplands, the vegetation still tends to occur in well-defined narrow strips (along irrigation canals, for example). Riparian zones tend to have higher production, greater accumulation of biomass, and more structural diversity than the uplands in arid or semi-arid environments (Malanson 1993). In suburbs and cities, riparian habitats probably do not compare as favorably to their surroundings. There may be, for example, greater foraging opportunities in the human environment, consisting of human refuse, bird feeders, and the like (also see Miller and Hobbs, In Review).

Our work confirms the observation that several bird species that are typically associated with the built environment in other parts of the U.S. seem to avoid highly-developed areas in Colorado. Examples include the Northern Mockingbird (Versaw 1998) and the Warbling Vireo (Barrett). Brewer s Blackbird, a species that was once common in Colorado parks and suburbs (Melcher 1998) was found only at the rural end of the gradient formed by our study sites. Andrews and Righter (1992) proposed that the decline of Brewer s Blackbirds in developed areas may be the result of competition with the Common Grackle, a species that has greatly increased in Colorado in recent decades (Andrews and Righter 1992).

As mentioned previously, the ordination diagram shows clearly that migrant species appear to favor the rural end of the gradient. Similar observations have been made by other workers in other regions. Even the Yellow Warbler, which was included in the urban avifauna by Andrews and Righter (1992) and did occur at our highly-developed sites, reached greater abundances at the extreme of the rural end of our gradient. It has been suggested that this phenomenon may reflect diminished food resources in urban areas. The vast majority of migrants are insectivorous during the breeding season and exotic trees and shrubs (i.e., the vegetation typical of human-dominated environments) may support fewer native insects (Beissinger and Osborne 1981). There is only meagre evidence to support this notion (Southwood 1961) and it is logistically difficult to test. The species that do predominate in developed areas tend to be either omnivorous or seed-eaters, further suggesting that dietary constraints for insectivorous species may be an important determinant of habitat use in urban areas. The ultimate resolution of this question will require a study design different than the one that we employed.

Conservation

Human settlement has had a profound impact on lowland riparian areas in Colorado and its effects extend far beyond urban and suburban areas. A regional perspective is useful in evaluating the degree to which these habitats have changed in the last 150 years. Early explorers and settlers reported that trees were quite scattered or nonexistent along rivers and streams of the Great Plains (e.g., Fremont 1988, Mattes 1969), although tree density may have been somewhat greater near the Rocky Mountain front (Michael Scott, USGS Midcontinent Ecological Science Center, , personal communication). With settlement, water impoundments and diversions tended to increase low flows and to moderate peak flows. This ultimately led to narrowed channels (Nadler and Schumm 1981, Eschner *et al.* 1983) bordered by continuous bands of trees.

Newly-vegetated corridors across the Great Plains allowed bird species of eastern North American forests to cross this former isolating barrier (Mengel 1970). This phenomenon is reflected in recent arrivals, such as the Blue Jay, as well as in hybridization between eastern and western species such as the Lazuli and Indigo Buntings or the Baltimore and Bullock s Orioles. When exotic species and increased densities of human commensal species are added to the mix, it soon becomes apparent that neither the habitat nor the avifauna can be considered natural.

This is not to say that lowland riparian habitats in Colorado are without avian conservation value. Although Knopf and Samson (1994) pointed out that many bird species in riparian habitats on the Great Plains are habitat generalists with wide distributions, several of these species exhibit different habitat preferences in Colorado than they do in other parts of North America, as described above. Moreover, the value of these habitats to over-wintering and migrating species should not be underestimated (Knopf and Samson 1994). In some ways, the conservation value of these habitats in some ways is heightened by their proximity to human populations. Familiarization and appreciation for local biological diversity on the part of people who live in urban or suburban areas may foster sympathy and support for conservation issues in more distant places. Ultimately, a clear statement of conservation objectives coupled with integration of management strategies across various levels of government is needed if we are to maintain and enhance the native diversity that remains.

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Table 4.1. Habitat variables that were recorded for each census point, for each site, and for the landscape surrounding each site for lowland riparian areas near Colorado's Front Range.

Variables	Code	Description
Landscape		
Building density	BDENS (1600, 500, 100)	Density of buildings within 1500 m, 500 m, and 100 m.
Weighted building density	WDENS (1600, 500, 100)	Density of buildings wherein units are weighted by their distance from the nearest point on a given transect (see text).
Std. dev. of building density	SDENS (1600, 500, 100)	Standard deviation of building density, measured using Thiessen polygons centered on each census point at a site and used to represent heterogeneity in building densities along a transect.
Site		
Trail use	TRAIL	Number of people per h using recreational trails at a site.
Bridges	BRIDGE	Number of bridges crossing a watercourse within the length of a point transect or within 200 m of either end of the transect.
Point		
Riparian width	WIDTH	The width of the woody riparian zone (m).
Tree density	TDENS	Density of trees (ha).
Std. dev. tree density	SDTREE	Standard deviation of tree densities at each point, represents horizontal heterogeity of tree distributions.
Tree height	HT	Average tree height (m).
Tree dbh	DBH	Average diameter (cm) at 1.5 m above ground
Basal area	BASAL	Average basal area (m^2/ha)
Native trees	NTREE	Percentage of trees native to Colorado.
Tree canopy*	CAN	Total coverage of tree canopy (trees > 8 m in height).
Subcanopy*	SUBCAN	Total coverage of the subcanopy (trees 3-8 m in height).
Ground*	GRND	Total ground coverage of herbaceous vegetation.
Herbaceous	HERB	Average height of the herbaceous vegetation (cm).
Shrubs*	SHRUB	Total coverage of shrubs (0.5-3 m in height).
Native shrubs	NSHR	Percentage of shrubs native to Colorado.
Saplings	SAPL	Number of saplings (dbh<15 cm)
Snags	SNAG	Number of standing dead trees.

*These variables are each the product of two separate measures: (1) the proportion of the vegetation plot that is covered, and (2) the density of vegetation within the proportion covered. Each measure was visually estimated using discrete categories: >75%, 50-75%, 25-50%, 5-25%, and <5% (categories were subsequently scored 1-5, respectively). Thus, a score of 25 would describe a vegetation plot that had very little coverage of variable of interest and within that small area, very low density.

Table 4.2. Summary statistics on landscape and site characteristics for 16 lowland riparian areas near the Front Range of Colorado.

Variable	Units	Mean	1 SE	Minimum	Maximum
Building density 1600	no./ha	1.5	0.4	0.0	6.6
Building density 500	no./ha	0.9	0.3	0.0	3.3
Building density 100	no./ha	0.2	0.1	0.0	1.5
Weighted bldg dens 1600	no./ha	2270.8	655.0	1.6	9563.6
Weighted bldg dens 500	no./ha	652.5	216.2	0.0	2428.1
Weighted bldg dens 100	no./ha	142.7	55.5	0.0	861.7
Std. dev. bldg. dens 1600	no./ha	193.3	30.7	0.1	385.8
Std. dev. bldg. dens 500	no./ha	121.8	36.6	0.0	432.8
Std. dev. bldg. dens 100	no./ha	101.8	64.9	0.0	1034.8
Bridges	no.	1.4	0.3	0.0	4.0
Mean trail use	no./h	21.9	9.9	0.0	141.2
Mean riparian width	m	84.9	27.8	48.7	129.7
Mean tree density	no./ha	282.8	30.1	80.0	476.0
Std. dev. tree density	no./ha	247.0	29.9	79.0	437.0
Mean tree height	m	11.4	0.6	6.5	14.78
Mean d.b.h.	cm	29.9	2.8	16.0	67.8
Mean basal area	0-25	44.6	4.0	12.9	77.5
Mean abundance native trees	%	56.7	6.8	13.0	98.0
Mean canopy cover	0-25	6.3	0.6	4.2	14.5
Mean subcanopy cover	0-25	5.8	0.6	3.5	10.8
Mean sapling density	no./ha	4.4	0.7	1.5	9.8
Mean snag density	no./ha	0.3	0.0	0.1	0.7
Mean ground cover	0-25	1.9	0.2	1.0	3.8
Mean herbaceous height	cm	33.6	2.0	16.2	47.0
Mean shrub cover	0-25	8.3	0.7	3.0	12.4
Mean abundance native shrubs	%	81.5	3.7	60.0	99.0

Table 4.3. For 16 lowland riparian sites near Colorado s Front Range, Spearman s rank correlations for building density, buildling density weighted by the distance of each building from a census point, and the standard deviation of building density along a point transect. Each measure was calculated for buildings within 1500 m, 1000 m, and 500 m of a site. See Table 1 for variable codes.

	Bdens 1500	Bdens 500	Bdens 100	Wdens 1500	Wdens 500	Wdens 100	Sdens 1500	Sdens 500	Sdens 100
Bdens 1500	1.00								
Bdens 500	**0.86	1.00							
Bdens 100	0.58	**0.83	1.00						
Wdens 1500	**0.99	**0.79	0.51	1.00					
Wdens 500	**0.87	**0.84	0.60	**0.90	1.00				
Wdens 100	0.58	**0.83	**0.93	0.51	0.58	1.00			
Sdens 1500	**0.95	**0.90	0.56	**0.92	**0.87	0.60	1.00		
Sdens 500	**0.75	**0.94	*0.68	*0.66	0.62	**0.80	**0.79	1.00	
Sdens 100	*0.66	**0.82	**0.85	0.59	*0.68	**0.90	*0.62	**0.78	1.00

* = $p<0.01$, ** = $p<0.001$

Table 4.4. For 16 lowland riparian sites near Colorado's Front Range, Spearman's rank correlations for each measure were calculated for buildings within 1500 m, 500 m, and 100 m of a site. See Table 1 for variable codes.

	BDEN 1500	BDEN 100	BRIDGE	TRAIL	SDTREE	WIDTH	TDENS	HT	DBH	BASAL	NTREE	CAN	SCAN
BDEN 1500	1.00												
BDEN 100	0.57	1.00											
BRIDGE	*0.65	0.20	1.00										
TRAIL	**0.88	0.48	0.59	1.00									
SDTREE	0.13	0.42	0.01	-0.03	1.00								
WIDTH	0.27	0.42	0.19	0.03	0.46	1.00							
TDENS	0.51	0.48	0.48	0.38	**0.79	0.46	1.00						
HT	*0.63	0.22	0.29	0.36	-0.08	0.24	0.19	1.00					
DBH	0.46	0.28	0.27	0.27	0.02	0.53	0.19	**0.78	1.00				
BASAL	0.43	0.11	0.22	0.37	-0.13	0.32	0.08	0.58	**0.86	1.00			
NTREE	-0.62	-0.17	-0.35	-0.30	0.03	-0.38	-0.15	**-0.85	*-0.73	-0.58	1.00		
CAN	-0.23	0.05	-0.22	-0.08	0.30	-0.25	0.06	-0.55	*-0.64	-0.59	0.35	1.00	
SCAN	0.48	0.47	0.16	0.26	0.08	0.11	0.22	*0.69	0.45	0.15	-0.45	-0.36	1.00
GRND	0.60	0.59	0.45	0.64	0.34	0.47	*0.63	0.16	0.29	0.24	-0.07	-0.27	-0.36
HERB	-0.04	-0.20	-0.08	-0.28	0.15	0.60	-0.06	0.15	0.33	0.20	-0.42	0.06	-0.05
SHRB	0.51	0.50	0.28	0.28	0.55	*0.68	0.62	0.51	0.58	0.35	-0.47	-0.21	0.55
NSHRB	*-0.64	-0.62	-0.20	-0.44	-0.37	*-0.68	-0.45	-0.36	-0.43	-0.36	0.48	-0.60	-0.28
SAPL	0.48	0.05	0.30	*0.66	-0.38	-0.37	-0.08	0.14	-0.01	0.35	-0.15	-0.03	0.00
SNAG	0.20	0.25	0.35	0.07	0.06	-0.15	0.28	-0.14	-0.43	-0.49	0.12	0.21	0.24

* = $p<0.01$, ** = $p<0.001$

Table 4.4 (continued).

	GRND	HERB	SHRB	NSHRB	SAPL	SNAG
BDEN 1500						
BDEN 100						
BRIDGE						
TRAIL						
SDTREE						
WIDTH						
TDENS						
HT						
DBH						
BASAL						
NTREE						
CAN						
SCAN						
GRND	1.00					
HERB	-0.11	1.00				
SHRB	0.62	0.43	1.00			
NSHRB	-0.61	-0.21	-0.55	1.00		
SAPL	0.14	-0.23	-0.11	-0.01	1.00	
SNAG	0.13	-0.16	-0.03	-0.12	0.03	1.00

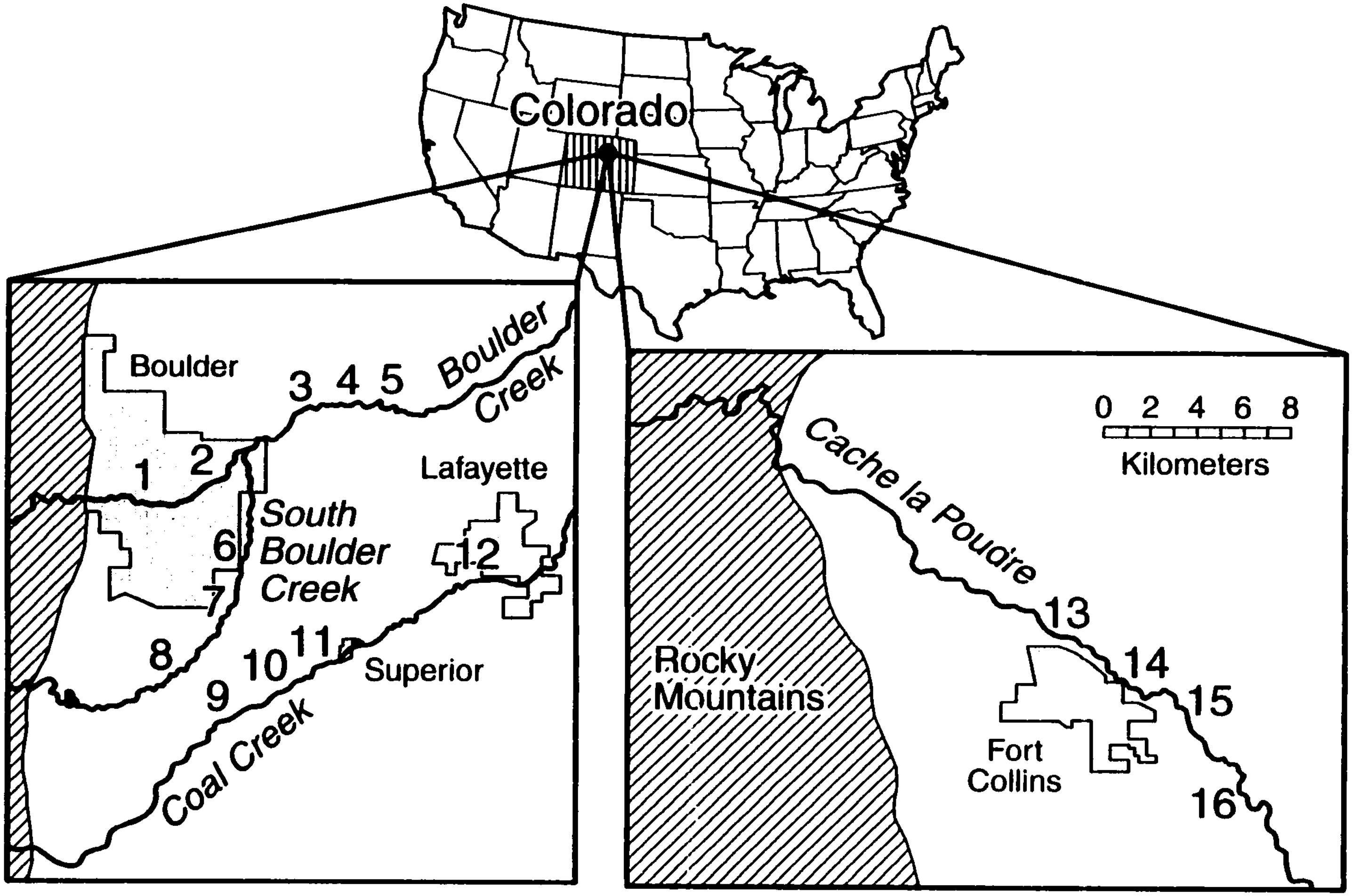

Fig. 4.1 Location of study sites used to examine the relationship between avian communities in lowland riparian areas and human settlement in Larimer and Boulder counties, Colorado, U.S.A. Numbers indicate study sites: (1) CU, (2) 30th St., (3) Walden, (4) Kaufman, (5) Ertl, (6) Bobolink, (7) Eldorado, (8) South Vale, (9) Vista View, (10) Mine, (11) Superior, (12) Lafayette, (13) Shields, (14) Lemay, (15) 7 Ponds, (16) Gateway, Cross-hatched areas indicate the Rocky Mountains, and gray areas indicate cities and towns. See Appendix I for detailed descriptions of study site locations.

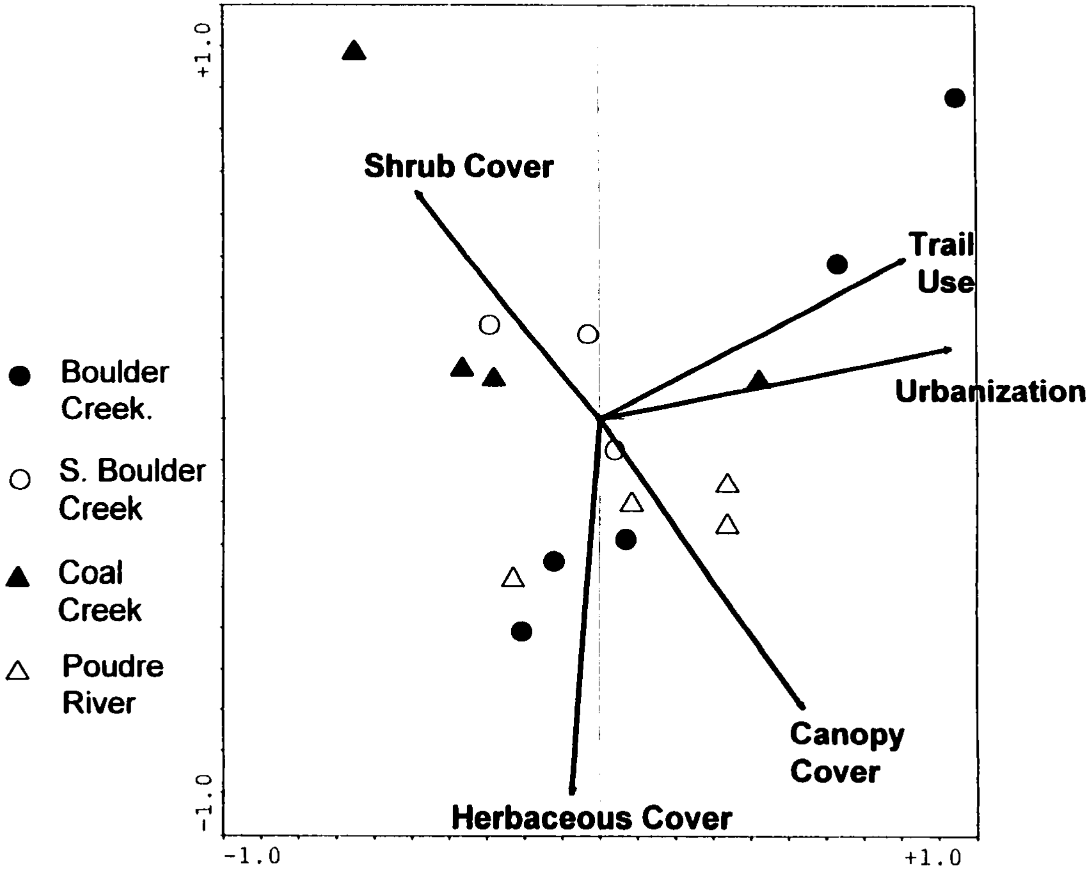

Fig. 4.2. Plots of CCA space defined by the first two axes of the ordination of environmental variables and breeding bird abundance. Study sites are shown by drainage and are derived from linear combinations of environmental measures. The lengths of the arrows indicate the relative importance of each environmental variable in the model and the direction of each arrow indicates how well the environmental variable is correlated with each axis.

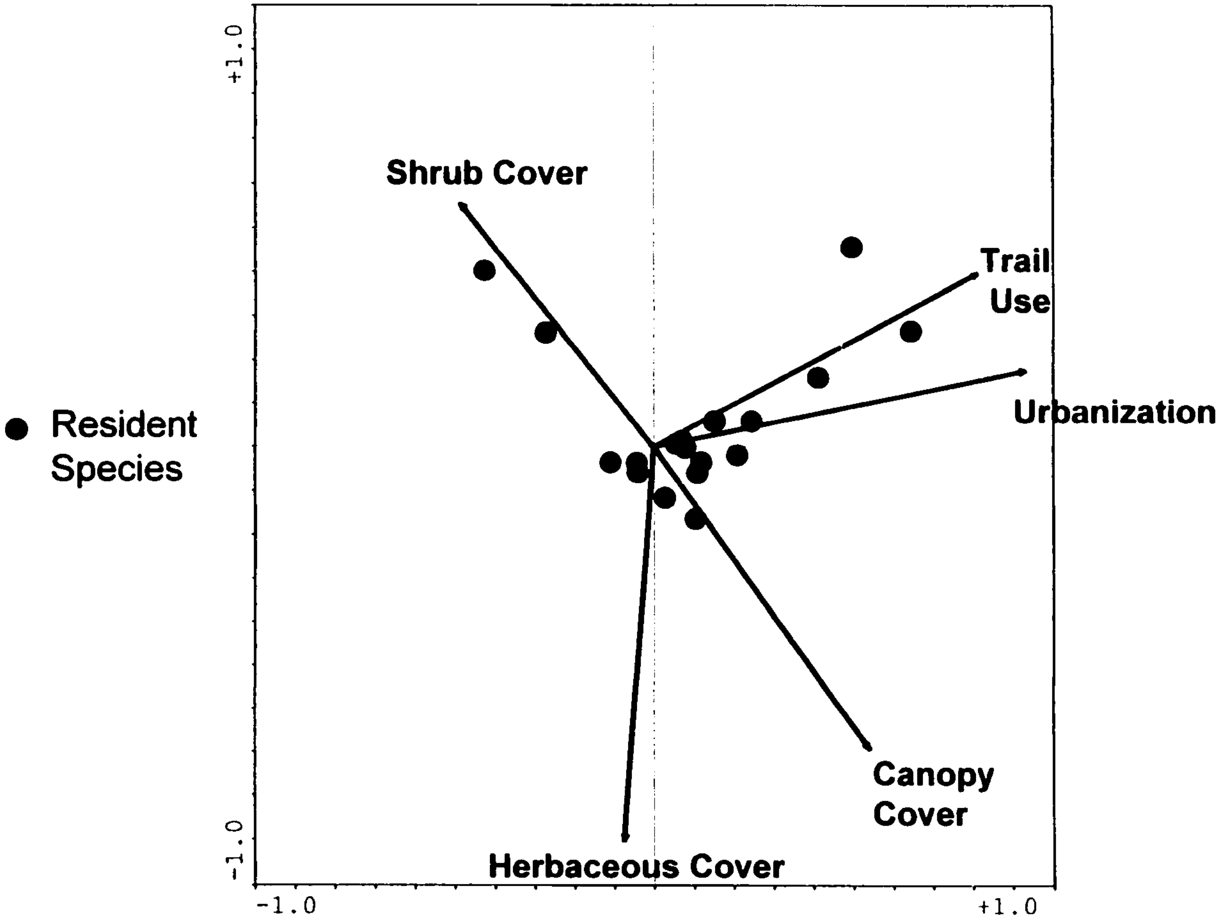

Fig. 4.3. Plots of CCA space defined by the first two axes of the ordination of environmental variables and breeding bird abundance for 16 riparian sites in Colorado. Only resident species are depicted here. The lengths of the arrows indicate the relative importance of each environmental variable in the model and the direction of each arrow indicates how well the environmental variable is correlated with each axis. The location of each species relative to site locations and arrows indicates the sites and environmental conditions associated with that species occurrence.

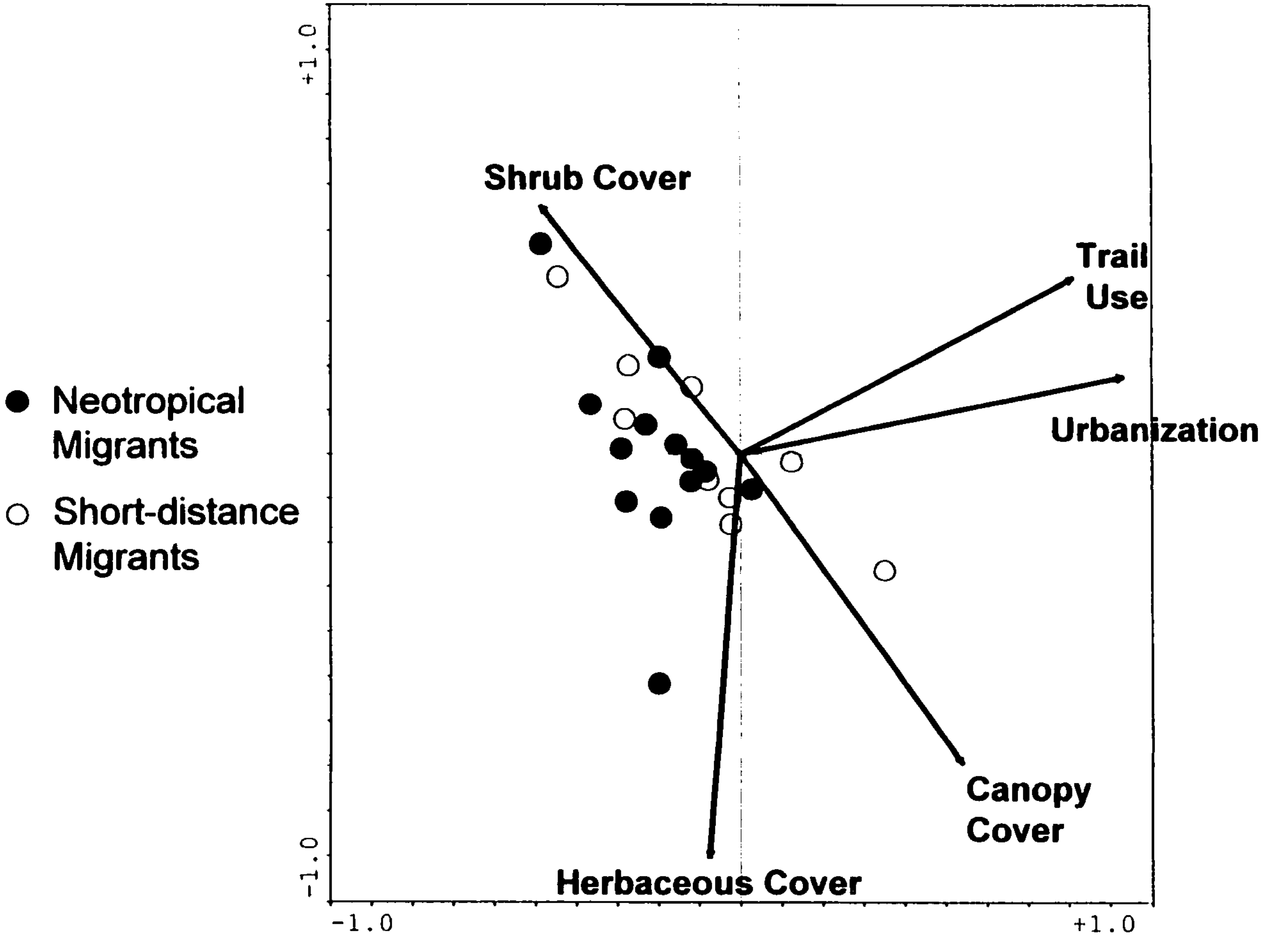

Fig. 4.4. Plots of CCA space defined by the first two axes of the ordination of environmental variables and breeding bird abundance for 16 riparian sites in Colorado. Only migrant species are depicted here. The lengths of the arrows indicate the relative importance of each environmental variable in the model and the direction of each arrow indicates how well the environmental variable is correlated with each axis. The location of each species relative to site locations and arrows indicates the sites and environmental conditions associated with that species occurrence.

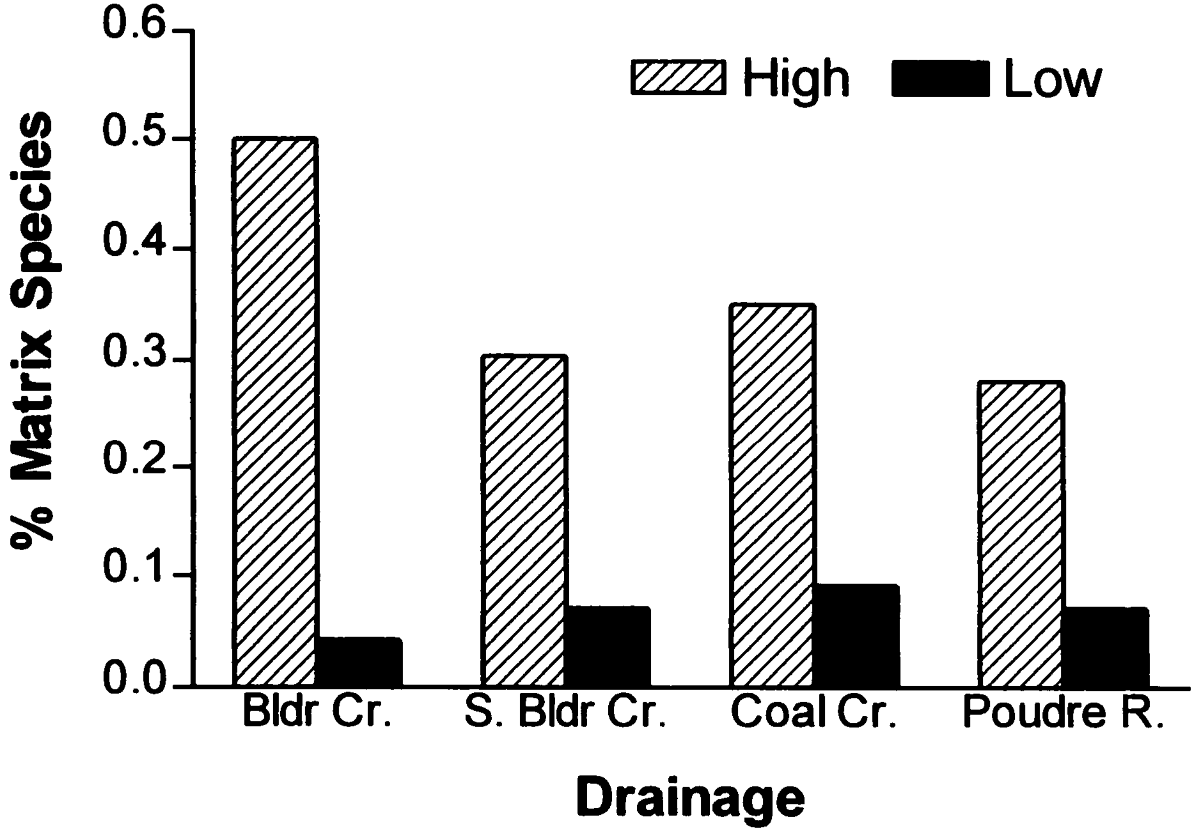

Fig. 4.5. For Boulder Creek, South Boulder Creek, Coal Creek, and the Cache la Poudre River: the percentage of the riparian bird community consisting of species characteristic of the surrounding matrix at the site associated with the highest level of urbanization vs. the site with the lowest level of urbanization (i.e., urban habitats for the high urbanization site and grassland habitats for the low urbanization site), based on data collected during the breeding season, 1995-1997. Species habitat affiliations as described by Andrews and Righter (1992).

CHAPTER V

THE EFFECT OF HUMAN SETTLEMENT ON NEST PREDATION IN LOWLAND RIPARIAN WOODLANDS

ABSTRACT

In the western United States, lowland riparian habitats harbor more species of breeding birds than any other plant community. Human settlement also tends to occur near watercourses and this may lead to increased rates of nest predation. We investigated the association between rates of nest predation in lowland riparian habitats and the level of development in the surrounding landscape between late May and late June in 1995 and 1996. We selected three study sites on each of four drainages on the mixed-grass prairie of Colorado near the Front Range. At each site, we placed a transect of artificial nests (*n*= 20 nests/transect in 1995, *n*=30 nests/transect in 1996). Each nest was baited with 2 Japanese Quail eggs and one clay egg. We also monitored American Robin nests at two sites on each of two drainages in 1996 (*n*=78) and 1997 (*n*=76).

Overall, 93% of artificial nests were depredated. There was a significant negative relationship between daily mortality rates on artificial nests and building density in 1995 but not in 1996. Predation rates on artificial nests were higher in 1996 compared to 1995. Predation rates at the most-developed site were significantly lower than the predation rate

at the least-developed site on two of the four drainages in 1995 and on all four of the drainages in 1996. Based on impressions in the clay eggs, corvids exerted the most predation pressure, followed by House Wrens, mice, and fox squirrels. Predation pressure exerted by corvids correlated with the relative abundance of corvids based on point counts, but this was not true for House Wrens. Predation rates on American Robin nests were signifantly lower at a suburban site relative to a rural site on one of the two drainages in 1996 and on the other drainage in 1997. Robins tended to nest higher near recreational trails and higher nests were depredated more often.

INTRODUCTION

Riparian areas are centers of biodiversity, especially in semi-arid regions. In the western United States, lowland riparian habitats harbor more species of breeding birds than any other plant community and contain some of the most diverse avifaunas in North America (Johnson *et al.* 1977, Knopf and Samson 1994, Ohmart 1994, Skagen et al. 1998). On the short-grass prairie of northeastern Colorado, for example, 82% of the breeding bird species occur in riparian vegetation (Knopf 1985).

For millenia, human settlement has also tended to occur near watercourses, especially in semi-arid regions. One consequence of the juxtaposition of human settlement and concentrations of breeding birds may be an increase in nest predation - the primary cause of nest failure in passerines (Ricklefs 1969, Skutch 1985, Martin 1992). Nesting success may be reduced in settled areas because some nest predators tend to increase in abundance with increasing development (Wilcove 1985). This is true for introduced animals, including domestic dogs and cats (Churcher and Lawton 1987), as well as native species such as raccoons (*Procyon lotor*) and striped skunks (*Mephitis mephitis*) (Hoffman and Gottschang 1977, Haspel and Calhoon 1989, Rosatte *et al.* 1991). Higher predator densities are attributable to the greater availability of supplemental food and shelter in settled areas, but the absence of larger carnivores in urban environments may also contribute to elevated numbers of small and medium-sized nest predators (Soulé *et al.* 1988).

If the nests of some bird species are preyed upon more frequently than others, or if some species are not able to compensate for losses through renesting, nest predation could influence community structure. Evidence suggests that ultimately predation may influence habitat selection and the evolution of life-history traits (Martin 1995). Although it is often assumed that rates of nest loss rise with increasing development (e.g., Soulé *et al.* 1988, Harris and Silva-Lopez 1992, Noss 1993, Marzluff *et al.* 1998), there have been few studies examining this phenomenon.

There are several ways to study the influence of human settlement on nest predation, but none of them is perfect. Ideally, one could locate and monitor a large number of natural nests. This is logistically difficult, however, when the goal is to compare numerous sites for a number of species and it also presents difficulties regarding standardization among sites — differences in density, for example. Artificial nests provide a means of studying patterns of nest loss while controlling for factors such as nest appearance and location, and this technique has been used to describe patterns and causes of nest loss across sites in different landscape contexts (Andrén *et al.* 1985, Wilcove

1985, Donovan *et al.* 1997). Because some variables that may influence nest predation rates, such as parental activity at the nest, are excluded in artificial-nest treatments, predation rates on artificial nests can be regarded as an index of predator activity and relative predation risk among sites, not a measure of true predation rates (Paton 1994, Sieving and Willson 1998).

Riparian areas are biologically critical habitats in the western U.S., where human population growth is especially rapid. We examined the relationship between the intensity of nest predation in lowland riparian areas and the level of human settlement in the surrounding landscape near the Front Range of Colorado. Because of the difficulties associated with studying nest predation, a combination of methods may be warranted (Major 1991). We used artificial and natural nests to test the prediction that predation risk increases with increasing development. We conducted point counts and used clay eggs and automatic cameras to describe predator assemblages along the gradient of urbanization.

METHODS

Study sites

To assess predation risk and identify nest predators in lowland riparian areas, we selected three study sites on each of four drainages: Coal Creek, South Boulder Creek, and Boulder Creek in Boulder County and the Cache la Poudre River in Larimer County, Colorado, U.S.A. These sites were chosen to represent gradients from high to low levels of human settlement on each drainage (Austin and Heyligers 1991, Wiens and Parker

1995; Fig. 1). Sites in Boulder County were under the jurisdiction of either Boulder County Parks and Open Space or City of Boulder Open Space Department, and sites in Larimer County were managed by the Fort Collins Department of Natural Resources. All riparian areas were located in the mixed-grass prairie with elevations ranging from approximately 1640 m near the foothills/plains interface to approximately 1550 m in eastern Boulder and Larimer counties.

While it is impossible to select habitats that are true replicates in such landscapes, we selected sites to be as similar as possible with regard to riparian habitat structure. All sites were wooded with a shrub understory and were relatively narrow, averaging 60 — 110 m in the width of the woody riparian zone. Dominant tree species included plains cottonwood (*Populus deltoides*), crack willow (*Salix fragilis*), and hybrids (*Populus* x *acuminata*) of plains cottonwood and narrowleaf cottonwood (*Populus angustifolia*). The understorys were dominated by snowberry (*Symphoricarpus occidentalis*), chokecherry (*Prunus virginiana*), wild rose (*Rosa woodsii*), lead plant (*Amorpha fruticosa*), and sandbar willow (*Salix exigua*).

Artificial nests

Between the first week of June and the first week of July in 1995 and 1996, we placed a transect of experimental nests parallel to the watercourse in the woody riparian zone at each site. We used 20 nests per transect in 1995, but raised this number to 30 in 1996 in order to increase our ability to detect differerences in predation rates between sites.

Nests were placed alternately 10-15 m on either side of the transect at 30-m intervals at heights ranging from 0-2 m in shrubs and trees, resulting in an effective between-nest distance of approximately 40 m. This arrangement was chosen in order to simulate natural nest densities in these habitats and to avoid repeated predation by a predator following a linear course, or Atraplining.≅ Nests were placed in locations similar to those in which natural bird nests are found. We did not mark nests in the field because some predators appear able to cue into identifiers such as tags, colored ribbon, or or wooden stakes (Picozzi 1975). Instead, we relied on written descriptions of nest locations that incorporated naturally-occuring landmarks.

Nests were commercially-available canary wicker baskets (10.5 cm in diameter x 5.5 cm deep) that were modified with grass and mud to provide the appropriate search image to predators (Martin 1987, Sieving 1992). Each nest was baited with two Japanese Quail (*Coturnix coturnix*) eggs. 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, we added to each nest in 1996 a third egg made of modeling clay (Plastaline Modeling Clay; Van Aken International, Rancho Cucamonga, CA 91729) that approximated the dimensions of a typical songbird egg (20 x 15 mm, see Harrison 1978). These clay models also enabled us to obtain tooth or bill impressions of nest predators (M ller 1988, Nour *et al.* 1993, Major 1991) and were tethered to each nest with heavy-duty thread to prevent their removal.

We checked nests every third day for 15 days, which simulates the combined egg-laying and incubation periods for most passerines (Martin 1987). At each check we noted the number of eggs remaining as well as egg and nest condition. Experimental nests were considered to be depredated when one or more eggs were disturbed.

Transects of artificial nests (30 nests/transect) containing quail and clay eggs were also placed at the same sites on Coal Creek and South Boulder Creek, but not Boulder Creek or the Cache la Poudre River, in 1997. These data were not incorporated in the primary analyses because only some sites were sampled. We do not report these data in detail here but instead use this third year of sampling to confirm or challenge patterns seen in the first two years.

Natural Nests

To provide a basis for comparison with predation rates on experimental nests, we also monitored natural bird nests at four sites in 1996 and 1997. On both South Boulder Creek and Coal Creek, we chose a developed site (Bobolink and Louisville) and a rural site (South Vale and Vista View; Fig. 1). We concentrated on finding nests of the American Robin (*Turdus migratorius*) because this species was present at sites across the gradient of human settlement in numbers great enough to constitute adequate sample sizes. Moreover, this species was reported to have experienced 100% nest loss at the Bobolink site in 1994 (Carl Bock, personal communication). Nests of other passerine species were also monitored when found, but were not included in our statistical analyses. Natural nests were checked every 3-4 d until they either fledged young or failed.

Once a nest was no longer active, we quantified several nest-site characteristics that may influence nest survival. We measured nest height because nests at different heights may be susceptible to different predators (refs). If the distributions of predator species differ among habitats, survival could then vary by height. Also, both suburban sites included recreational trails in the riparian zone and these trails received substantial human use. Because recreational trails may influence nesting success (Miller *et al.* 1998, Miller and Hobbs *In Review*), we measured the shortest linear distance from the base of the nest tree or shrub to the trail at each of these two sites. Finally, numerous studies have reported a positive relationship between nest survival and nest concealment (Best and Stauffer 1980, Martin and Roper 1988, Norment 1993). For nests in 1997, we used an index of concealment that was based on the average proportion of a 25-cm circle centered on each side of the nest (including top and bottom) that is concealed by vegetation.

Nest predator identification and surveys

We compared marks on clay eggs that were retrieved from artificial nests with a reference set created using museum specimens. For each potential nest predator that is known to occur in lowland riparian habitats, we made tooth or bill impressions on clay eggs using skulls from the collections of the Department of Biology, Colorado State University, and the Denver Museum of Natural History.

In June and July of 1997, we set out 15 remote-controlled cameras in riparian forests on Boulder Creek and South Boulder Creek to photograph nest predation events. These camera nests provided a second means of identifying predators associated with impressions left on clay eggs. We used Olympus AF-10 all-electronic cameras with remote microswitches that were attached to artificial nests, similar to the set-up described by Danielson *et al.* (1996). When an egg was disturbed, the switch tripped a shutter-release mechanism and flash. Because we did not use cameras at all sites and some set-ups were moved more often than others, no statistical comparisons were made for the number of individuals or species photographed.

Impressions on clay eggs resulting from predation or conspecific nest destruction were assigned to 1 of 6 categories on the basis of comparison with the museum collection and eggs from camera nests. Some categories included more than one species if their respective tooth or bill marks could not be reliably differentiated. These categories were House Wrens (*Troglodytes aedon*), Corvids and Grackles (including the Blue Jay, *Cyanocitta cristata*; Black-billed Magpie, *Pica pica*; and Common Grackle, *Quisculus quiscula*), mice, squirrels (most likely the fox squirrel, *Scuirus niger*), and other mammals (raccoon, *Procyon lotor*; red fox, *Vulpes vulpes*). House Wrens do not consume egg contents but their propensity for conspecific and interspecific egg destruction is well-documented (Belles-Isles and Picman 1986, Quinn and Holroyd 1989, Pribil and Picman 1991) and the outcome in terms of reproductive success is the same for nesting birds. We therefore included House Wrens as one of our predator categories.

To determine how well avian abundance reflects predation pressure on clay eggs, we surveyed avian nest predators using point transects (Bibby *et al.* 1992) and 8-min point counts at each site in each year. Transects were located in the woody riparian zone and ran parallel to the watercourse. We visited each site three times between the last week of May and mid-July in each year. Between sunrise and 0900, a single trained observer recorded all birds seen and heard within 50 m of each census point. This truncation distance was based on pilot data collected in the summer of 1994 (Miller and Craig, unpublished data). To minimize biases, 3-4 observers rotated visits to study sites throughout the breeding season each year and sampling effort was distributed as evenly as possible among sites associated with different levels of development on each day that censuses were conducted (Verner 1985).

Urban — rural gradient

Initially, we categorized sites on each drainage qualitatively, based on a visual assessment of the level of development in the surrounding area (high, medium, and low). To quantify the intensity of human settlement, we later derived building densities for areas within 500 m of each study site from digital parcel maps. Acquired from the respective county tax assessors, parcel maps delineate property boundaries and provide information on whether a given property is developed or undeveloped, the number of buildings there, and the type of land use for which it is zoned. To derive building densities, we assumed that buildings were located at the center of their respective parcels. For each site, we also derived an inverse weighted density score using the formula 3 (1/

D_i)/1000 where D_i is the distance from each building to the nearest point on the artificial nest transect.

Data analysis

The intensity of predation at each site was quantified using the methods of Mayfield (1961) as modified by Johnson (1979). For each site, we calculated a daily mortality rate as the total number of predated nests divided by the total number of days that the nests were exposed to predation. The daily mortality rate is thus the probability of predation per day (Mayfield 1961).

To examine predation risk solely as a function of building density (i.e., without regard to drainage), we treated building density as a continuous variable and used linear regression to examine its relationship with nest predation rates. Building densities were log-transformed and predation rates received standard arcsine square root transformations to meet assumptions, and data for different years were analyzed separately. We then conducted an overall test for homogeneity in daily mortality rates among sites on each drainage using Chi-Square analyses and multiple comparisons (Sauer and Williams 1989). For unplanned pairwise comparisons, we applied a sequential Bonferroni adjustment to ∀ to control for Type I error (Rice 1989). Designations of high, medium, and low were based on building densities within 500 m of each site. Similar analyses were conducted on the 1997 data for South Boulder Creek and for Coal Creek.

Chi-Square analyses were also used to test for homogeneity in daily mortality rates between suburban and rural sites for American Robin nests (Sauer and Williams

1989). We used logistic regression to determine the relationship between nest survival and nest site characteristics such as nest height, distance to trail, and nest concealment. To determine if human disturbance was related to increases in nest height, we ranked nests by their distance from trails and by their heights at the two suburban sites.

We used linear regression to determine the extent to which the abundance of avian predator species reflects predation pressure. For individual predator species, we also examined the relationship between certain habitat features and the level of predation attributed to each species or group of species. Earlier work suggested that trails and human activity may affect different predator species in different ways and that mice in particular may show an aversion to trails (Miller and Hobbs, In Review). We tested for differences in predation pressure by mice at sites with recreational trails versus those sites without trails using a Wilcoxon rank-sum test. We also ranked sites by their associated level of trail use and ranked predation pressure by mice, corvids, House Wrens, and fox squirrels to investigate the relationship between trail use and predation pressure by different species.

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.

Results

Artificial nests

Over all study sites and years, we recovered of 577 of 600 nests, approximately 93% of which showed signs of predation. Twenty-three nests were never found, despite extensive searches of the general locations. It is possible that some predators, such as squirrels or raccoons, could have stolen some nests. Alternatively, wind dislodged some nests and some could have been lost if close to rising water, during an evening thunderstorm for example. Finally, it is possible that our written directions were not adequate to relocate nests in some instances.

When treating building density as a continuous variable, the regressions for building density vs. daily mortality rate tended to have a negative slope, significantly different than 0 for 1995 (p=0.0.081) but not 1996 (p=0.304; Fig. 2). The intercepts of the two lines were significantly different (p<0.001) but the slopes were not (p>0.999). We detected heterogeneity among predation rates on Boulder Creek, Coal Creek, South Boulder Creek, and the Poudre River in 1995 (p=0.002, p<0.001, p< 0.01, and p=0.069) and in 1996 (p=0.034, p<0.030, p<0.001, and p=0.002; Fig. 3). In 1995, predation rates were significantly higher at least- vs. most-developed sites on Boulder Creek (p=0.041) and Coal Creek (p<0.001), but no differences were detected on South Boulder Creek (p=0.767) or the Cache la Poudre River (p=0.351). In 1996, predation rates were significantly higher at least- vs. most-developed sites on all drainages (Boulder Creek: p=0.027, Coal Creek: p=0.008, South Boulder Creek: p<0.001, and Cache la Poudre River: p=0.017).

In 1997, we again detected heterogeneity in predation rates on South Boulder Creek ($p<0.001$) and on Coal Creek ($p=0.01$; Fig. 4). On each drainage, however, low-development sites were associated with significantly lower predation rates than were high-development sites ($p<0.001$ and $p<0.024$, respectively).

Natural nests

We located and monitored 78 American Robin nests in 1996 and 76 nests in 1997. Of these, 34% were depredated. In 1996, daily mortality rates were greater at the rural site than the suburban site on Coal Creek ($O^2 =$, df = 1, $p = 0.086$) but not on South Boulder Creek ($O^2 =$, df = 1, $p = 0.281$; Fig. 5). In 1997, however, the predation rate was greatest at the rural site on South Boulder Creek ($O^2 =$, df = 1, $p = 0.091$) but did not differ among sites on Coal Creek ($O^2 =$, df = 1, $p > 0.90$).

Nest height was the best predictor of nest success ($O^2 = 4.317$, $p = 0.038$) with depredated nests tending to be lower in the vegetation (t-test, $p = 0.037$; Fig. 6); terms for study site and for nest concealment (1997 only) did not improve the model. There was no evidence that the probability of predation was related to distance from recreational trails ($n = 74$, $O^2 = 0.517$, $p = 0.472$), but a Spearman s rank correlation test did show that robins tend to nest higher near trails ($p = 0.0643$, $r = -0.218$).

Nest Predator Identification and Habitat Use

Cameras at artificial nests yielded 79 photos that captured nest predators and we were able to identify the species in 75 of them. Black-billed Magpies (*Pica pica*) and fox squirrels (*Scuirus niger*) accounted for >50% of the photos while Blue jays (*Cyanocitta cristata*) and House Wrens (*Troglodytes aedon*) each appeared in nearly 20% of the images. Other photographs included Common Grackles (*Quisculus quiscula*) and raccoons, and these species accounted for <10% of the photos. We identified impressions resulting from nest predation or egg destruction on 303 clay eggs from the 339 nests that we recovered in 1996. For the remaining 36 nests, the clay eggs were either missing, no impressions were found, or there was uncertainty as to whether impressions resulted from predation.

The total number of impressions exceeded the total number of eggs preyed upon because some eggs had marks belonging to more than one category. Of the 303 eggs that showed signs of predation, 70.0% had impressions of corvids or grackles. Mice left marks on 15.8% of the clay eggs and trapping data from some of the same sites as well as other nearby riparian areas (Armstrong *et al.* 1996), indicate that the deer mouse (*Peromyscus maniculatus*) was probably responsible. Fox squirrels and other mammals predated 11.6% and 4.6% of the eggs, respectively, while peck marks from House Wrens were found on 10.2% of clay eggs.

Rank-sum tests revealed a positive association between predation pressure by larger birds and the abundance of corvids and also corvids plus Common Grackles (r=0.610, p=0.035 and r=0.499, p=0.935). No relationship between nests (i.e., eggs) destroyed by House Wrens and House Wren abundance was evident (r=0.402; p=0.311).

Mice depredated fewer eggs at trail sites vs. non-trail sites in 1996 (O^2=4.910, df=1, p=0.033). There was a significant and negative association between predation pressure by mice and trail use (r=-0.703, p=0.011) and a positive association between squirrel predation and trail use (r=0.350, p=0.037). There was no association between corvids or House Wrens and trail use (p=0.823 and p=0.112, respectively).

Discussion

Nest predation is generally thought to increase with increasing levels of development (Wilcove 1985). In lowland riparian areas in Colorado, we observed differences in predation rates both for artificial nests and for natural nests across a gradient of human setttlement, but the overall trend in 1995 and 1996 was for predation rates on artificial nests to decrease, not increase, with increasing levels of development in the surrounding landscape. The risk of predation was significantly higher for rural sites versus more-developed sites on two of four drainages in 1995 on all four drainages in 1996. Predation rates on American Robin nests were an order of magnitude lower than those on artificial nests, but tended toward increased nest losses at suburban as opposed to rural sites. What factors might account for the differences between our results and the prevailing wisdom?

Because ecologists have tended to avoid areas dominated by human activity when selecting research sites, relatively little is known about the ecological processes that occur there (Pickett *et al.* 1992, McDonnell and Pickett 1993). Consequently, prevailing notions regarding nest predation in densely-settled areas are largely untested. Lowland riparian habitats in an urban or suburban context are unique in a number of respects compared to their rural counterparts, especially in semi-arid regions.

As annual precipitation declines, riparian areas tend to become increasingly distinct from the surrounding landscape. On the plains of eastern Colorado, for example, there tends to be a high structural contrast between the wooded riparian zone and the prairie uplands. This distinction becomes increasingly fuzzy as one moves toward the urbanized end of the gradient of human settlement. Because people have planted trees and shrubs throughout urban and suburban environments, the boundaries of the riparian zone become less clear. Much has been made of the attraction of nest predators to high-contrast habitat boundaries — the so-called edge effect (Paton 1994, Yahner *et al.* 1989). Moreover, our study sites were fairly narrow and consisted solely of edge habitat as defined by most assessments of edge-effect distances for nest loss (Paton 1994). If predators are attracted to sharply-defined edges, it follows that nest losses could decrease as edges become less distinct.

The use of recreational trails at our study sites increased with increasing levels of human settlement nearby. The impacts of recreational activities on native diversity are still rudimentary (Knight and Gutzwiller 1995) and this is especially true for urban environments (Adams and Dove 1989). Human activity may prevent some birds from nesting nearby (Miller *et al.* 1998), but may confer an advantage to species that are able to nest there because some predators may be displaced by people. Our data on American Robin nests suggest that even species that that nest in proximity to high levels of human activity may compensate by, for example, increasing nest height. The results of our work also indicate that although predation pressure by birds did not appear to be related to levels of human activity, mice seemed to avoid nests at sites that had trails and particularly high trail usage. Although mice are nocturnal in their foraging habits, diurnal human activity may still exert an influence on their behavior. Canine scent, for example, may be enough to cause avoidance in some instances (Forman 1995). Because trail usage was positively correlated with development intensity, there may be other factors associated with settlement that contributed to the patterns that we observed. Nonetheless, a parallel study on trail effects supports the contention that at least some predators appear to avoid trails (Miller and Hobbs, In Review).

Many nest predators are omnivorous, including corvids, raccoons, mice, and squirrels. As development increases, so do foraging opportunities for such species. Human refuse, for example, increases with human population density and allows these species to attain higher densities in suburbs and cities. Simply put, predation pressure on bird nests may be higher in rural areas simply because food resources for predators are more limiting there.

Again, we stress that results of artificial nest experiments should be interpreted with caution. Although experimental nests provide an efficient means for gathering data on nest predation in a semi-controlled manner, there are several important differences between these nests and active bird nests. Rather than dismissing this method as a result of its limitations, we suggest that when used in combination with other approaches, artificial nests may provide insights into the mechanisms that determine predation rates and determine the structure and composition of bird communities (Sieving and Willson

1998). The difference between rates of nest loss for American Robin versus artificial nests, for example, suggests several possible factors that could influence predation risk. The most obvious is parental nest defense. American Robins vigorously defend their nests and this could certainly account for discrepancies between natural and artificial nests. Body size may also be a factor; at approximately 80 g, American Robins are 3-4 times larger than most songbird species (Dunning 1992). Although larger nest predators, such as fox squirrels (750 g) and raccoons (6000 g.; Fitzgerald *et al.* 1994), are likely to be formidable adversaries, it is difficult to imagine a 20-g mouse successfully depredating a nest with adult Robins nearby.

Predation rates on artificial nests reflected nest predator abundance, at least for corvids. Sieving and Willson (1998) reported that the same was true for mammalian predators in their study. In our study, however, this was not the case for House Wrens. This may be related to the fact that nest losses due to House Wrens are not linked to foraging behavior. It is reasonable to suggest that for foraging nest predators, rates of nest loss would be proportional to predator population densities, but in the case of House Wrens, it is more likely to be a function of the proximity of their nests to artificial nests. If this is the case, we would not expect rates of nest loss to be as tightly coupled with House Wren abundance.

The fact that we observed stronger patterns of nest predation within drainages than we did across all sites (i.e., disregarding drainage) suggests that there may be differences among streams that were not captured in our analyses. Still, our results underscore some of the salient features of lowland riparian areas and argue against generalizations about nest predation based on studies conducted in other habitats or in other regions. Conservation in human-dominated areas presents numerous unique opportunities (Miller and Hobbs, In Review), but more information about the ways that people affect native diversity is urgently needed to form the basis for management and policy.

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Table 5.1. Characteristics of nest site location for American Robins at four lowland riparian sites near Colorado s Front Range in 1996 (n=78) and 1997(n=76).

Year	Variable	Units	Mean	1 S.E.	Minimum	Maximum
1996	Height	m	4.36	0.35	0.50	11.00
	Concealment	%	-	-	-	-
	Distance from trail*	m	25.08	4.01	0.30	130.00
1996	Height	m	4.63	0.43	0.75	15.50
	Concealment	%	50.11	2.06	15.00	81.00
	Distance from Trail*	m	25.09	4.61	0.00	150.00

*Only two sites are included for this variable (1996: n=41; 1997: n=33).

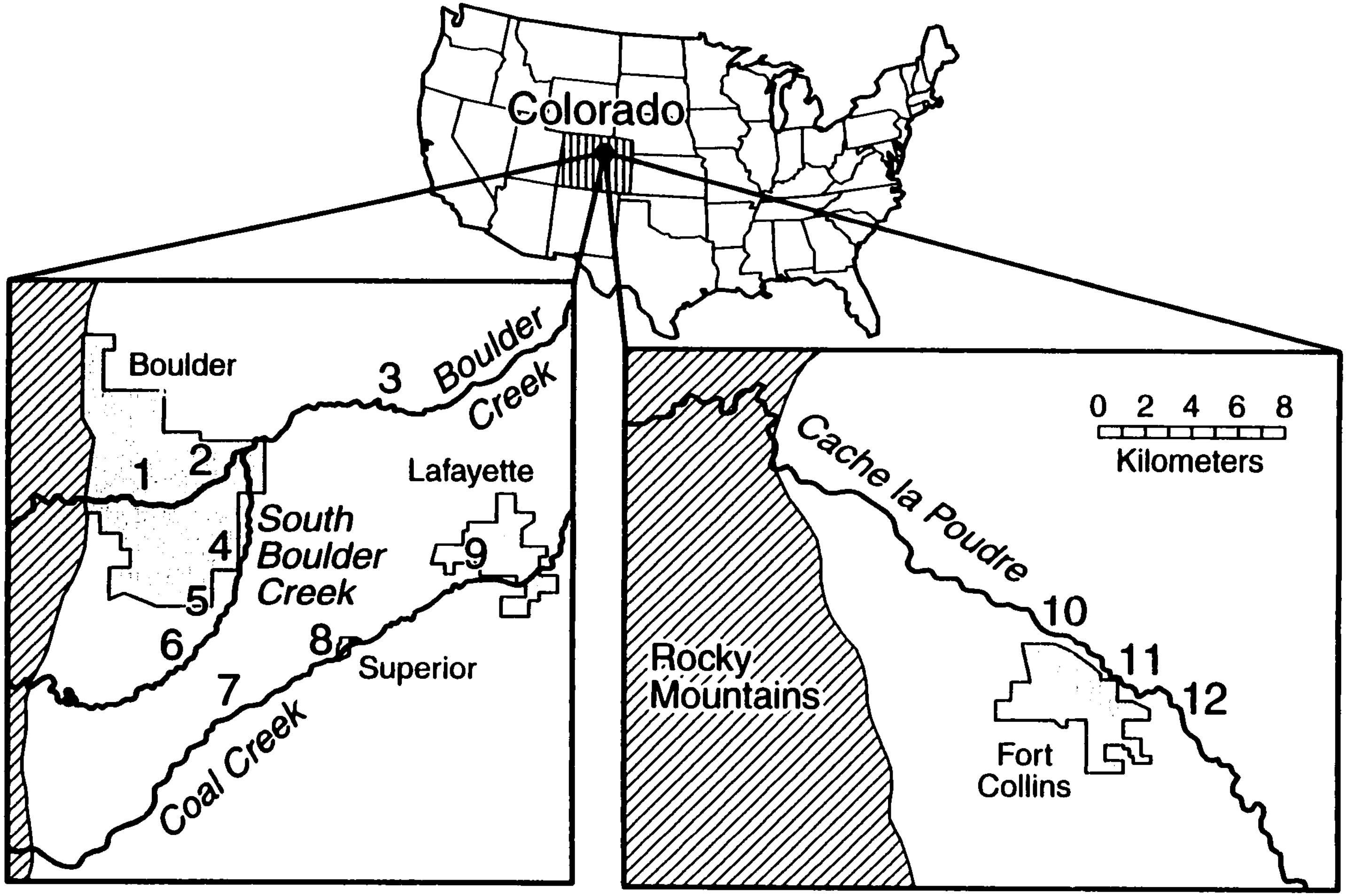

Fig. 5.1. Location of study sites used to examine the relationship between nest predation and predator assemblages in lowland riparian areas and human settlement in Larimer and Boulder counties, Colorado, U.S.A.. Numbers indicate study sites: CU (1), 30th St. (2), Ertl (3), Bobolink (4), Eldorado (5), South Vale (6), Vista View (7), Superior (8), Lafayette (9), Shields (10), Lemay (11), 7 Ponds (12). Cross-hatched areas indicate the Rocky Mountains and gray areas indicate cities and towns. See Appendix I for detailed descriptions of study site locations.

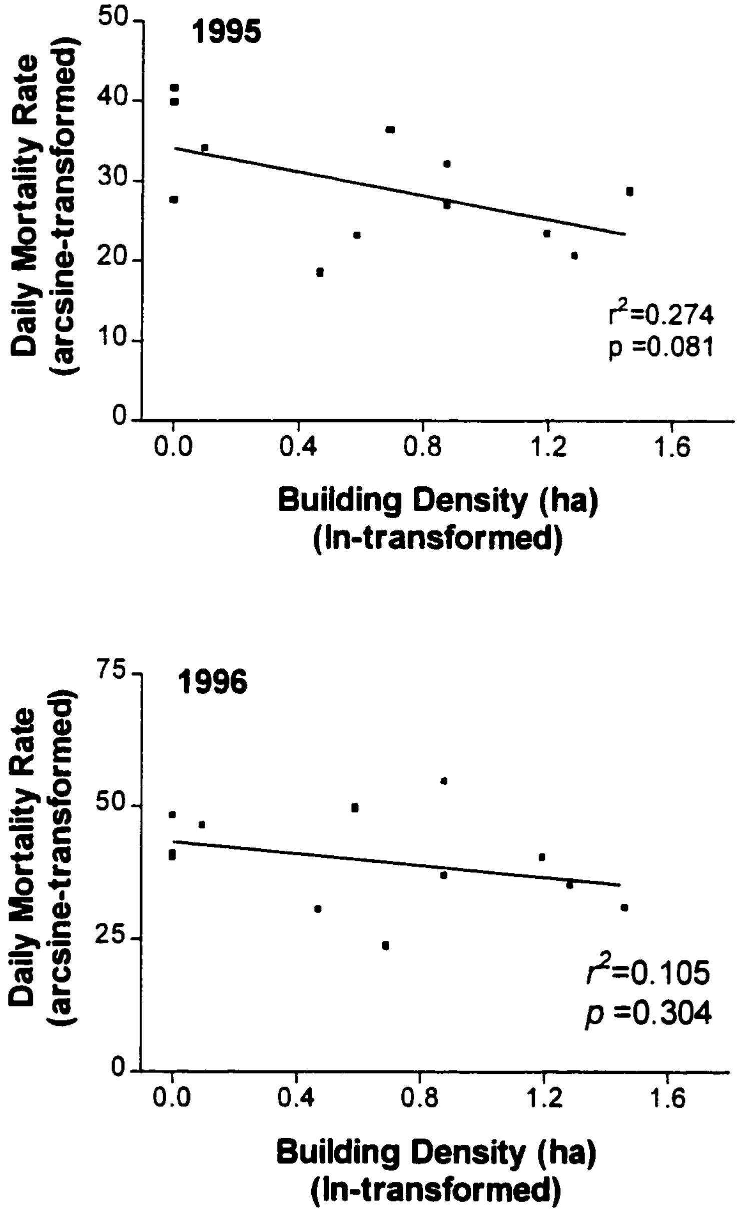

Fig. 5.2. Regression lines for rates of predation on artificial nests vs. building density at 12 lowland riparian sites in 1995 (r^2=0.216, p=0.128) and 1996 (r^2=0.109, p=0.295). Daily mortality rates and building density were transformed using standard arcsine square-root and log transformations, respectively.

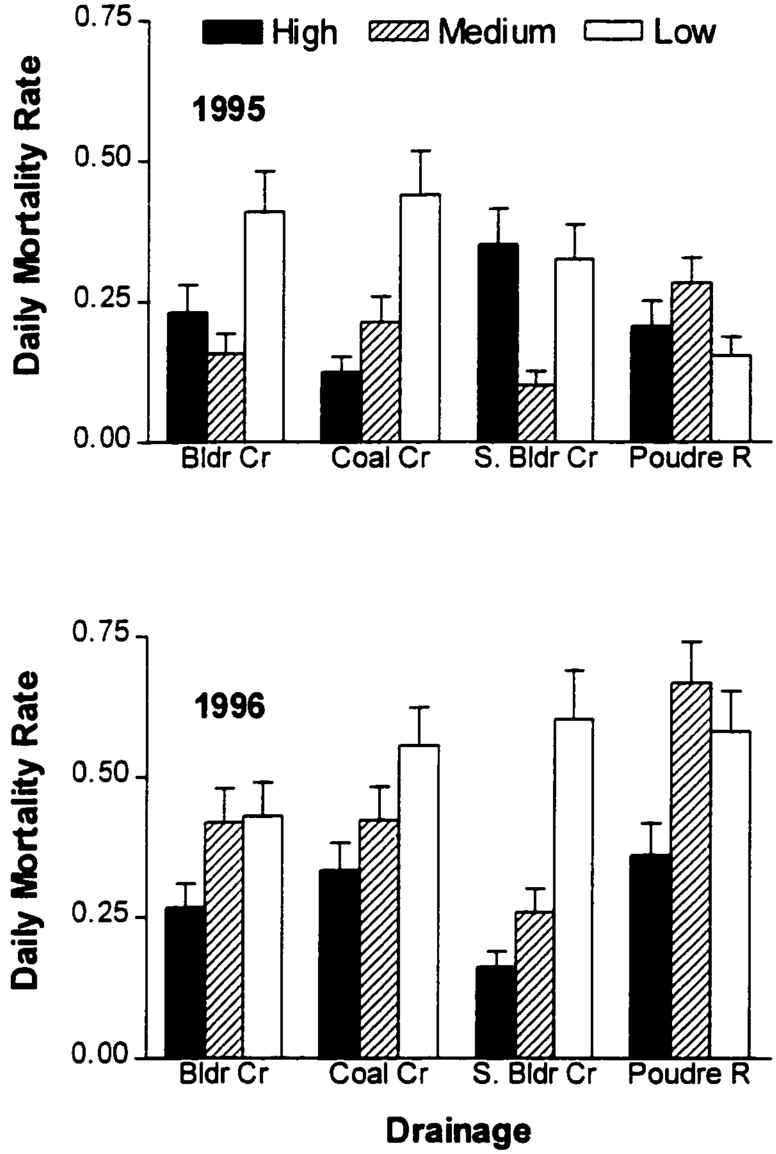

Fig. 5.3. Daily mortality rates ± 1 SE for artificial nests at each of three sites on South Boulder Creek, Coal Creek, and Boulder Creek in Boulder County and the Cache la Poudre River in Larimer County, Colorado, in 1995 (*n* = 20 nests/site) and 1996 (*n* = 30 nests/site). High, medium, and low refer to the relative intensity of human settlement on each drainage as measured by building density within 500 m of the study sites.

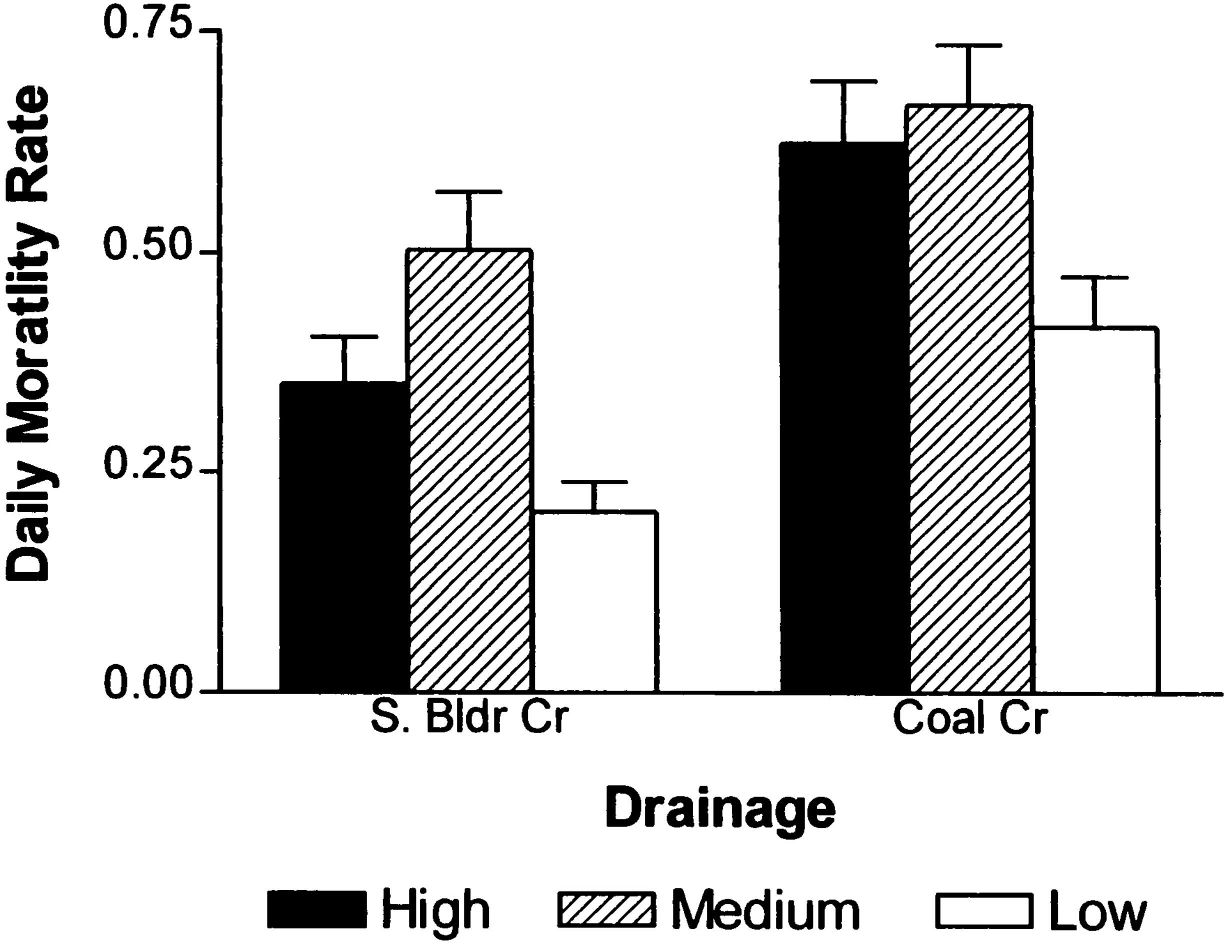

Fig. 5.4. Daily mortality rates ± 1 SE for artificial nests at three sites on South Boulder Creek and three sites on Coal Creek in 1997. High, medium, and low refer to the relative intensity of human settlement on each drainage as measured by building density within 500 m of the study sites.

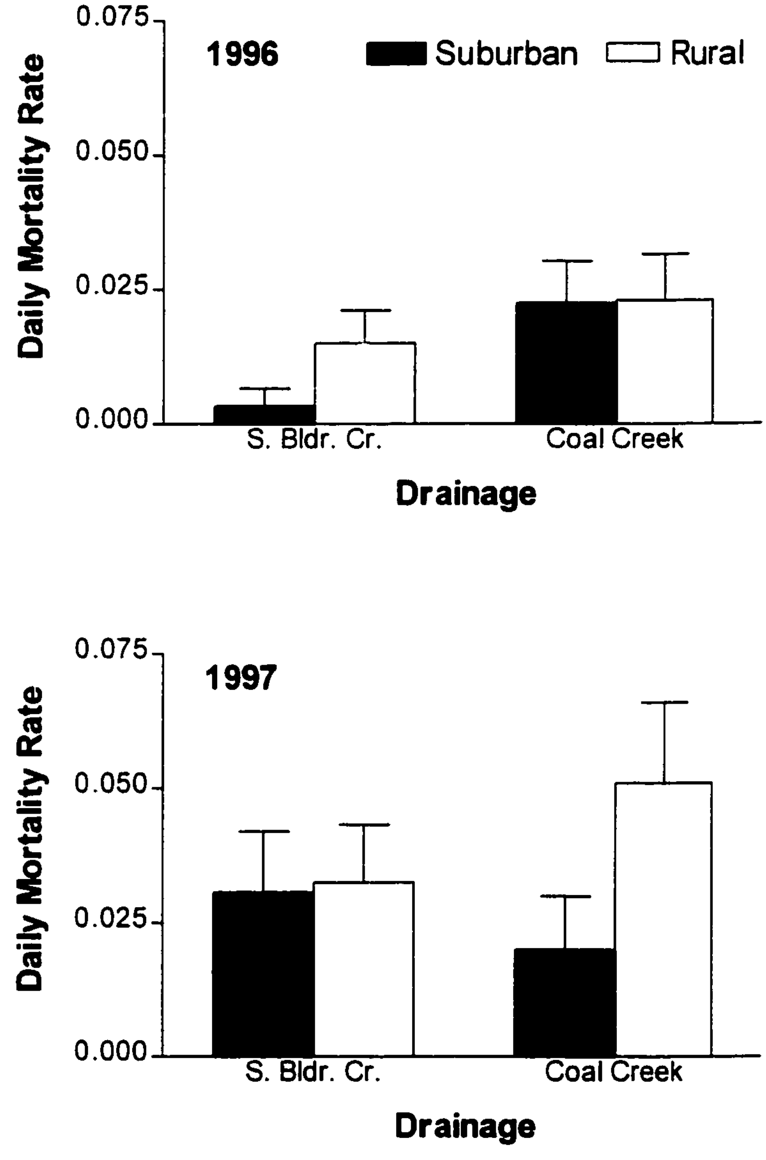

Fig. 5.5. Daily mortality rates ± 1 SE for American Robin *(Turdus migratorius)* nests at suburban vs. rural sites in 1996 and 1997 in Boulder County, Colorado (Bobolink vs. South Vale on South Boulder Creek and Lafayette vs. Vista View on Coal Creek; see Fig. 1 for locations).

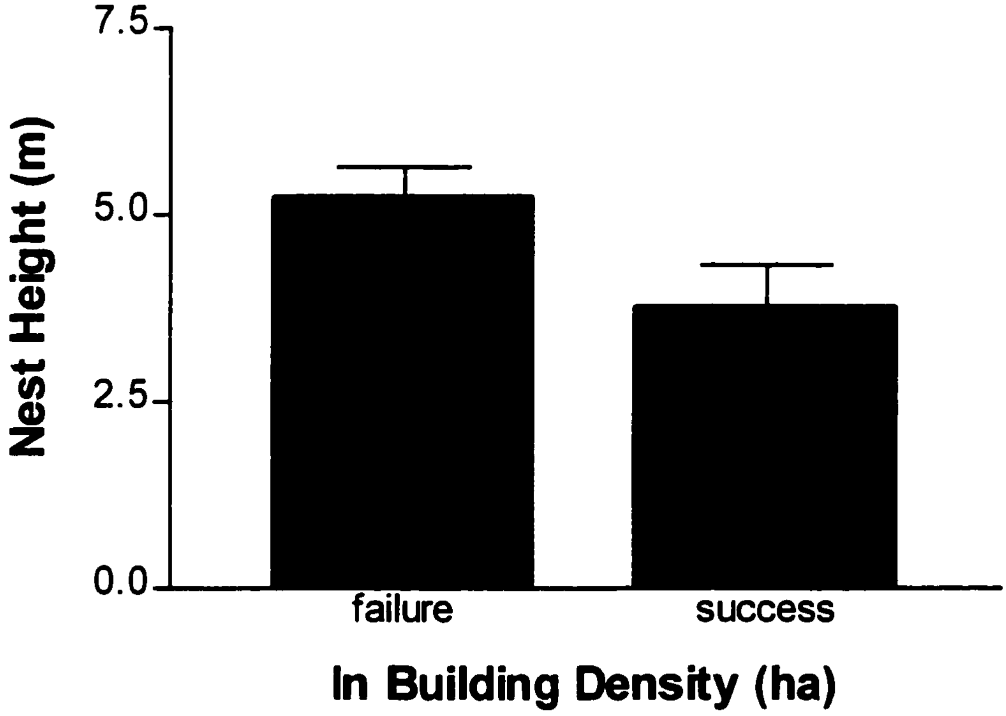

Fig. 5.6. Mean nest height ± 1 SE for successful vs. failed American Robin *(Turdus migratorius)* nests.

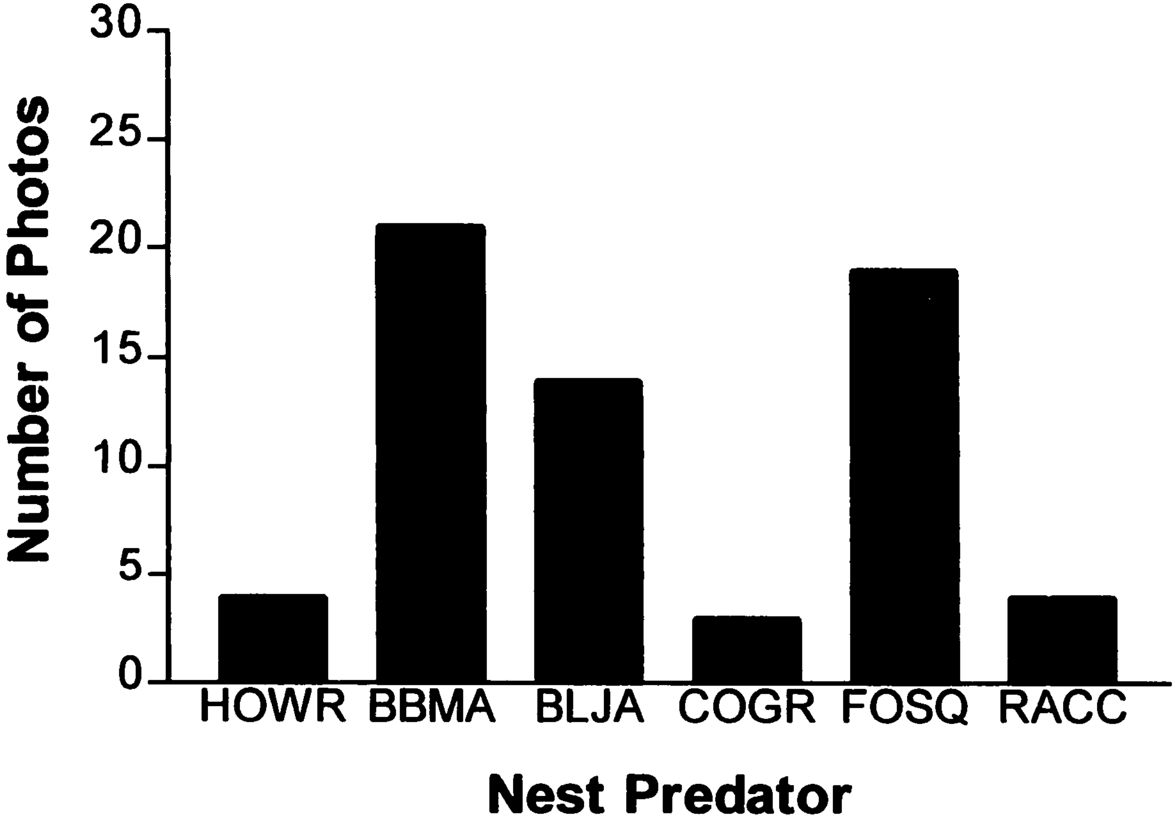

Fig. 5.7. Number of photographs of various individual predator species taken at artificial nests in lowland riparian areas in Colorado: HOWR (House Wren), BBMA (Black-billed Magpie), BLJA (Blue Jay), COGR (Common Grackle), FOSQ (fox squirrel), RACC (raccoon).

CHAPTER VI

RECREATIONAL TRAILS, HUMAN ACTIVITY, AND NEST PREDATION IN LOWLAND RIPARIAN AREAS

ABSTRACT

Attention to human-dominated environments is important when developing comprehensive conservation strategies. 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 on the agents of predation at four lowland riparian sites along the Front Range of Colorado. At one site on each of two streams, we placed a transect of experimental nests near a recreational trail and another transect on the opposite side of the stream. We also placed a 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, but in 1996 a clay egg was also included to assist us in identifying nest predators.

Overall, predation rates were high (94%). There were significant differences in vulnerability to predation on the different transect types, with a tendency for increasing

predation rates with distance from trails, and there was also a significant year effect. In1996, 83% of the clay eggs that were recovered showed signs of predation and some eggs registered more than one predator. 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 preyed on 12% of the eggs. Birds attacked significantly more nests near trails than away from trails, whereas mammals appeared to avoid trails. These data suggest that recreational trails in these riparian areas influence both predation rates and also individual predator species. It may be important, therefore, to consider such effects when deciding where to locate trails and in developing overall conservation strategies in human-dominated areas.

INTRODUCTION

Conservation of biotic resources in areas where people live and work has emerged as an essential part of comprehensive strategies for preserving biological diversity (Franklin 1993, Craig *et al.* 1999). In landscapes dominated by human settlement, remnants of semi-natural vegetation are often set aside as parks or greenways. These areas may represent the only locally available habitat for some native species. Such parcels of open space also tend to be the focus of increasingly popular recreational activities such as hiking, biking, jogging, exercising pets, and wildlife viewing (Smith and Hellmund 1993, Flather and Cordell 1995).

Although conservation is often a stated or implied goal of greenway management plans (Adams and Dove 1989, Schiller and Horn 1997), the compatibility of this goal with human recreational uses remains poorly understood (Harris and Hector 1994). Outdoor recreation has been shown to harm most native species that have been studied (Boyle and Samson 1985), but data are few and our understanding of such effects is still 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). People have a deep-rooted affinity for watercourses, and lands bordering creeks and rivers are often among the last available for conservation in settled landscapes because 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 activities is relatively unexplored.

Lowland riparian areas in semi-arid regions contrast sharply with the adjacent uplands and increased rates of nest parasitism and predation have been reported near high-contrast edges in other habitats (Brittingham and Temple 1983, Angelstam 1986, Andrϑn and Angelstam 1988, Paton 1994, but see Yahner *et al.* 1989). One might therefore expect birds breeding near the edge of riparian woodlands to experience increased rates of nest loss, especially in landscapes dominated by human activity. Nest predation is the primary cause of nest mortality for landbirds (Ricklefs 1969, Skutch 1985, Martin 1992) and is thought to influence both habitat selection and community structure (Sieving and Wilson 1998).

Given their linear nature, these habitats are also extremely sensitive to disturbance from within (Backhouse 1987). 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 recreational trails may also affect habitat use by breeding birds and by nest predators (Knight and Gutzwiller 1995). If habitat use by predators is influenced by the presence of trails, then predation pressure may vary as a function of proximity to trails.

We studied the effects of recreational trails on rates of nest predation and on predator assemblages in lowland riparian areas along the Front Range of Colorado. Specifically, we investigated the relationship between predation rates and proximity to recreational trails, and also examined changes in the identity of nest predators with increasing distance from trails. We predicted higher predation rates near trails because evidence suggests that nest predators are attracted to narrow corridors in wooded habitats (Hickman 1990, Recher and Serventy 1991, Miller *et al.* 1998).

STUDY SITES AND METHODS

We worked in 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* x *acuminata*) of plains cottonwood and narrowleaf cottonwood (*Populus angustifolia*). Typical understory species included snowberry (*Symphoricarpos occidentalis*), chokecherry (*Prunus virginiana*), and sandbar willow (*Salix exigua*). These riparian woodlands had an average width of approximately 60 m.

To examine the effect of proximity to recreational trails on nest losses, we selected two study sites on each of two streams: South Boulder Creek (SBC) and Coal Creek (CC). On each stream, the treatment site had a paved 2.5 m-wide recreational trail in the riparian zone and was paired with a control site that was not associated with a trail (Fig. 1). Treatment sites were chosen to be as similar to one another as possible, as were control sites. Both treatment sites had suburban development within a few hundred meters on one side of the stream and mixed-grass prairie adjacent to riparian woodlands on the other side; mixed-grass prairie predominated on both sides of the riparian zone at control sites. There were some signs of human use at both sites on the streamside opposite the trail, primarily consisting of unimproved footpaths or social trails, but activity there was minimal relative to that on the paved trails.

SBC sites were separated by 3 km and CC sites were 12 km apart. At each treatment site, one transect of experimental nests (*n*=20) was placed on the trail side of the stream (hereafter, Trail) and a second transect of nests was placed on the opposite side (hereafter, Opposite). A third transect of nests was placed on a randomly chosen side of the stream at each control site (hereafter, Control). The starting point for each transect was determined randomly. In order to avoid repeated predation by a predator travelling along a linear course, or Atraplining,≡ 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.

Between the first week of June and the first week of July in 1995 and 1996, experimental nests were placed 0.5 - 2 m above-ground 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 91729). The clay egg was tethered to the nest with heavy-duty thread, enabling us to obtain tooth or bill impressions of nest predators (M ller 1988, Nour *et al.* 1993, Major 1991). 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 x 15 mm, see Harrison 1978).

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 the condition of the nest 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 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.* 1994), 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). Nest-check routes were varied to prevent the creation of well-worn paths that might provide cues to predators regarding nest locations.

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, Control) as the main effect. For post-hoc comparisons of DMRs between sites on a stream, we used Chi-Square analyses (Sauer and Williams 1989) and applied a sequential Bonferroni adjustment to $\forall$ to control for Type I error (Rice 1989).

To test whether particular species accounted for differences in the probability of predation among the three transect types, we identified nest predators in 1996 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 nests in lowland riparian areas in 1996 and 1997 where the predator was photographed using automatic cameras (J. Miller, unpublished data). Associations between predators and transect types were assessed using Likelihood Ratio tests. We used a significance level of 0.1 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 individiual test statistics to allow the reader to use an alternative significance level if desired.

RESULTS

Of the 240 nests used in this study, 226 were scored as 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 there was a consistent trend for predation rates to increase with distance from trails (Fig. 2). In 1995 on SBC, predation rates on the Trail transect were significantly lower than rates on the Opposite ($O^2 = 3.88$, df = 1, $P < 0.05$) and Control ($O^2 = 11.55$, df = 1, $P < 0.0001$) transects. The predation rate on the Control transect was higher than rates on the Trail ($O^2 = 14.47$, df = 1, $P < 0.0001$) and Opposite ($O^2 = 6.99$, df = 1, $P < 0.01$) transects for CC in 1995 and for SBC in 1996 ($O^2 = 15.27$, df = 1, $P < 0.0001$).

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 vs. 1995 on SBC for the Trail ($O^2 = 5.71$, df = 1, $P < 0.02$) and Control transects ($O^2 = 6.85$, df = 1, $P < 0.01$) and on CC for the Trail ($O^2 = 9.72$, df = 1, $P < 0.002$) and Opposite ($O^2 = 7.92$, df = 1, $P < 0.005$) transects.

Impressions on clay eggs resulting from predation were assigned to 1 of 7 categories, some of which included more than one species if their respective tooth or bill marks could not be reliably differentiated (Fig. 3). The total number of impressions exceeded the total number of eggs preyed upon because some eggs had marks belonging to more than one category. These categories included House Wrens (*Troglodytes aedon*), Corvids and Grackles (Blue Jay, *Cyanocitta cristata*; Black-billed Magpie, *Pica pica*; Common Grackle, *Quisculus quiscula*), Mice, Squirrels (Fox Squirrel, *Scuirus niger*), Other Mammals (raccoon, *Procyon lotor*; red fox, *Vulpes vulpes*), and Missing (nests that were knocked down or stolen, or had clay eggs removed). House Wrens were responsible for impressions on 11% of the 96 eggs that were destroyed. House Wrens are known to destroy eggs in the nests of other birds, but they are not nest predators in that they do not consume the egg contents (Belles-Isles and Picman 1986, Quinn and Holroyd 1989, Pribil and Picman 1991). Of the 96 clay eggs that showed signs of predation, 69%

had impressions of Corvids or Grackles. We suspect that Common Grackles played a relatively minor role in this group based on the photographic evidence (21 photos of Black-billed Magpies and 14 of Blue Jays vs. 3 photos of Common Grackles). Twenty-five percent of the destroyed eggs showed signs of predation by Mice, while House Wrens and Squirrels each accounted for 11.5%. Based on trapping data from some of the study sites and other nearby riparian areas (Armstrong *et al.* 1996), we surmise that the most likely predator in the Mice category was the deer mouse (*Peromyscus maniculatus*).

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, whereas 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).

DISCUSSION

Overall predation was quite high at these riparian sites, with more than 94% of the nests being affected. Contrary to our prediction, however, the risk of predation increased with distance from trails. These results were consistent with those of Boag *et al.* (1984), who found that predation on artificial nests was lower near trails in coniferous forests and that most nest losses were attributable to rodents. Conversely, Miller *et al.* (1998) reported greater predation pressure on natural nests near trails in forested and grassland habitats. Miller and his colleagues suggested that elevated rates of nest loss were attributable to greater numbers of avian nest predators near trail edges, as has been reported for other narrow corridors in woodland habitats (Hickman 1990, Recher and Serventy 1991, but see Rich *et al.* 1994). To further confuse matters, Gale *et al.* (1997) found similar predation rates for natural nests regardless of their distance from edges created by narrow roads in deciduous forests. 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.

Human activity on trails could affect nesting success by displacing nest predators, although the intensity of such activity is rarely reported. 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 (Tomialoj and Profus 1977), and similar results were reported for breeding birds in London s parks (Tomialoj 1979). In the present study, both trails received substantial human visitation. Based on 2-h counts (n=3) conducted on separate mornings during the 1997 avian breeding season, trail use averaged 22.2 people/h on the trail at SBC and 16.6 people/h on the trail at CC (J. Miller, unpublished data). The SBC trail is, in fact, the most heavily-used in the entire City of Boulder Open Space system (C. Miller, 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 counts conducted as part of a larger investigation of riparian bird communities showed that Black-billed Magpies were more numerous at both treatment sites in 1995 and at the treatment site on SBC in 1996 when compared with the control sites. Blue Jays were more numerous at the SBC treatment site in both years with no difference between treatment and control sites on CC (J. Miller, unpublished data).

Mice and 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. At least for mice, edge-induced changes in microclimate near trails may have accounted for this avoidance but there is some doubt as to whether narrow corridors are associated with such effects (Paton 1994). Rather, we suspect that two factors, either singly or in combination, accounted for the pattern that we observed. First, people on trails may indirectly affect mammalian predators because they are often accompanied by domestic dogs and canine scent could cause other mammals to avoid these areas (Forman 1995). Second, larger mammalian carnivores such as coyotes (*Canis latrans*) are known to follow linear features (Bider 1968, Harris and Gallagher

1989) and use trails at night (Forman 1995; D. Armstrong, personal communication); we found coyote scat on or near trails on numerous occasions. These larger predators may be suppressing numbers of smaller mammals such as those that we have identified as nest predators.

We saw an increase in predation rates in the second year and increased nest predation over time has been reported in multi-year studies by other workers (Willebrand and Marcstrom 1988, Cresswell 1997, Marini 1997, Hannon and Cotterill 1998). Although the addition of clay eggs to experimental nests in 1996 could have caused this increase because clay eggs were more conspicuous than quail eggs, studies that have specifically examined predation rates on different-colored eggs do not support this contention (Janzen 1978, Slagsvold 1980, Yahner and Delong 1992). Nest predators may have habituated to experimental nests, but there are numerous multi-year studies that have not found significant differences in predation rates over time (e.g., Storaas 1988, Burger *et al.* 1994, Bayne *et al.* 1997, Danielson *et al.* 1997). We suggest that the increases we observed are equally likely to reflect population fluctuations 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.

Experimental nests are not perfect surrogates for natural nests. We recognize the biases associated with experimental nests as well as the advantages they confer, such as the ability to control for nest appearance and location (Major and Kendall 1996). These nests clearly lack certain cues that natural nests provide to predators, such as the scent of live birds or parental activity. Rather than dismiss the use of experimental 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, we found predation rates on experimental nests to be an order of magnitude higher than rates on active American Robin nests (Miller and Hobbs, unpublished data). American Robins are vigorous defenders of their nests, suggesting that a comparative study between species that vary in their intensity of nest defense might prove fruitful.

Differences between experimental and natural nests should not be a cause for complacency about trail effects in riparian areas, however. Outdoor recreational activity is predicted to increase nationally (Flather and Cordell 1995), with a concommitant increase in the construction and use of recreational trails. 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). Our results may have important implications for efforts to protect the Preble s meadow jumping mouse (*Zapus hudsonius*), a species with strong affinities for lowland riparian habitats in this region. Furthermore, our data support the contention that in some cases a reproductive advantage is 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. 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, with some species exhibiting greater sensitivity than others (van der Zande *et al.* 1984, van der Zande and Vos 1984, Miller *et al.* 1998).

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. Until we understand the ways that different predators respond to trails and other artifacts, we will be limited in our ability to generalize from the findings of predation studies in human-dominated areas or make sense of apparently contradictory results. Although it is often assumed that recreational activities do not adversely affect wildlife, there is increasing evidence to the contrary. We therefore suggest that the compatibility of multiple uses should receive greater scrutiny, especially in habitats that are at once rare and important to biological diversity.

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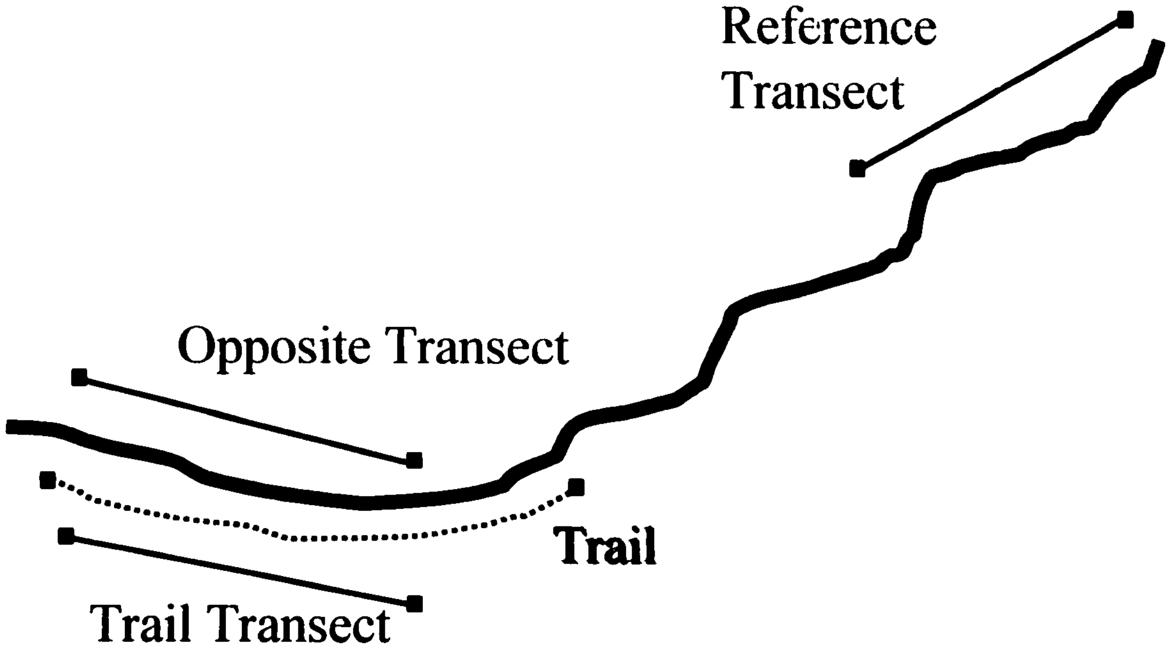

Fig. 6.1. Characterization of the study design indicating the placement of the three experimental-nest transects relative to the recreational trail and the stream.

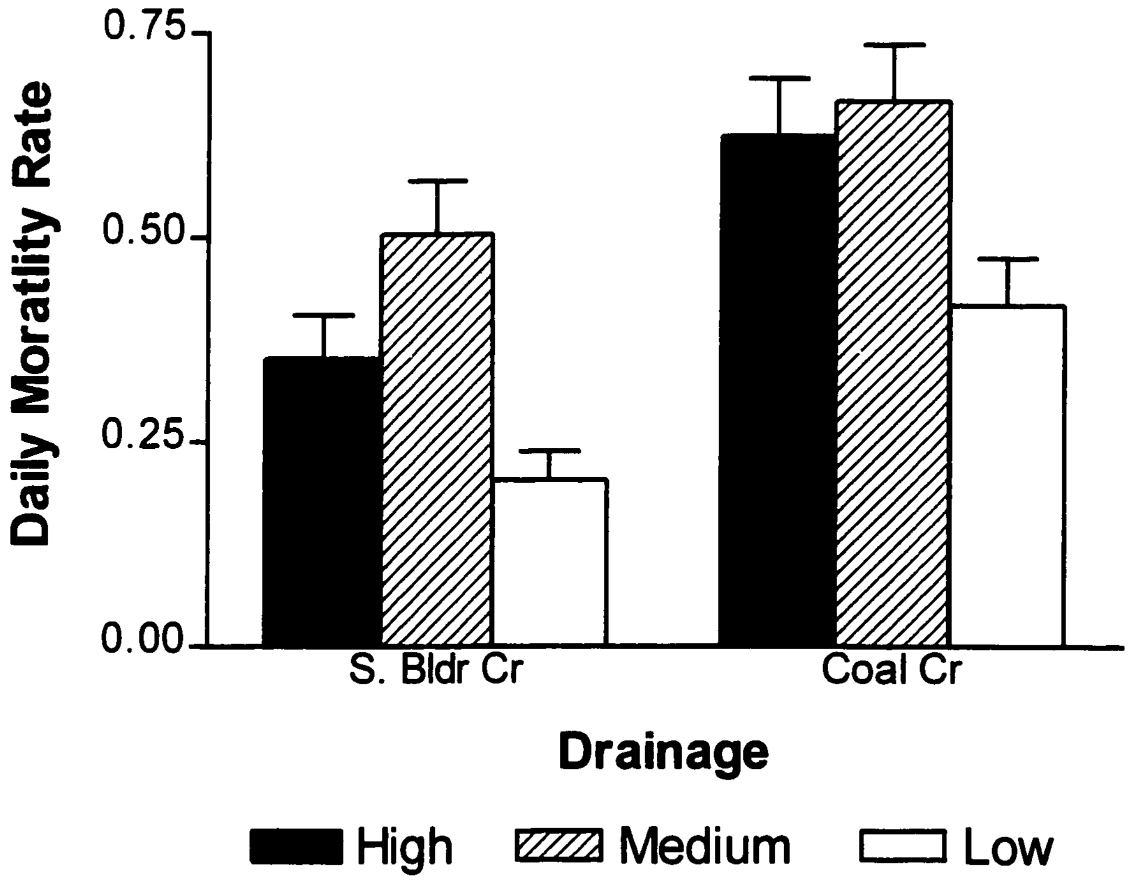

Figure 6.2. Daily mortality rates (+ 1 SE) on South Boulder Creek and Coal Creek, Boulder County, Colorado, for experimental nest transects near recreational trails, on the opposite side of the stream from trails, and at control sites without trails.

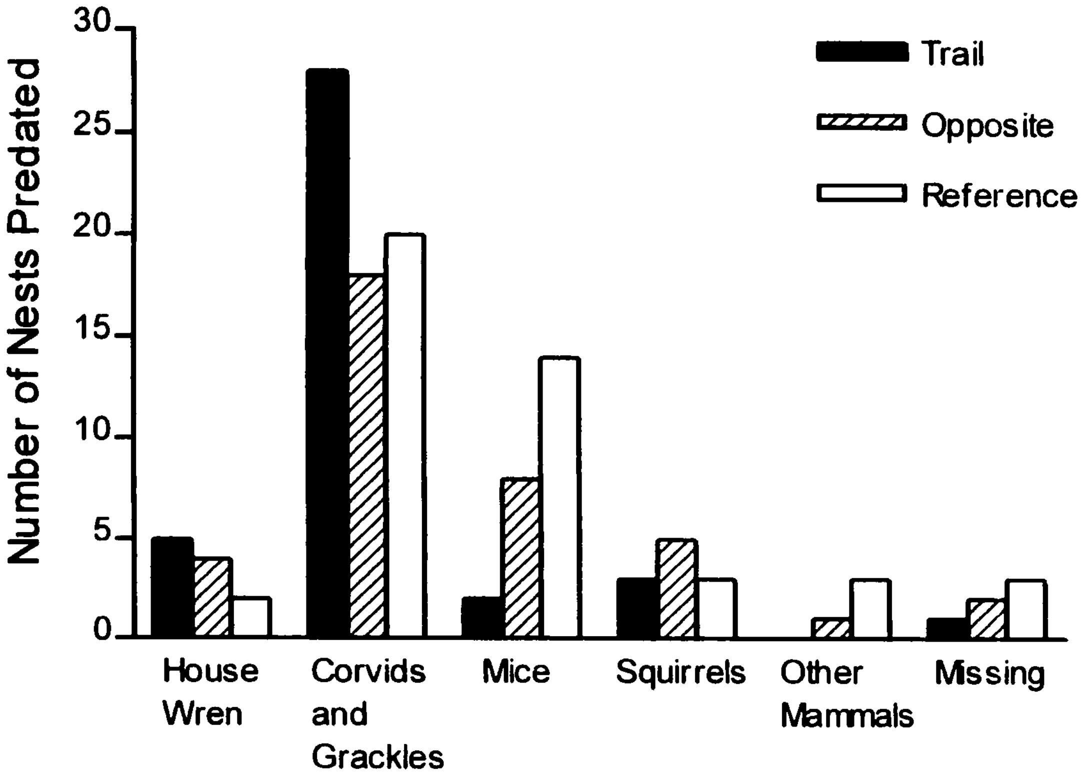

Fig. 6.3. Frequency distribution of experimental nests preyed upon in two lowland riparian areas, based on tooth and bill impressions on clay eggs. Transects of nests were placed near trails, on the opposite side of the stream from trails, and at control sites without trails. Tooth or bill impressions were assigned to 1 of 7 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).

CHAPTER VII

URBANIZATION, AVIAN COMMUNITIES, AND LANDSCAPE ECOLOGY

ABSTRACT

Human settlement is a prevalent source of land-use change worldwide, but our understanding of the effects of settlement on avian communities is limited. Here, our goal is to contribute to the dialogue on ways to further this understanding. First, we discuss the advantages of a gradient approach to studying the effects of development on birds, especially the ability to identify important thresholds in the response of birds to settlement. We suggest that the low-density end of the urbanization gradient should receive greater attention by researchers.

Studies at relatively fine scales are useful for investigating the influence on birds of proximate factors, such as vegetation structure and composition, in human-dominated areas. Such studies, however, must be coupled with investigations at broader scales in order to gain a more complete understanding of the ways that human settlement affects bird communities. We suggest that ecologists use metrics that are amenable to a gradient approach when describing the intensity of settlement at landscape scales. Such metrics are continuous as opposed to categorical, and might include human population density, road density, and building density. We also propose a research protocol for studying the

effects of settlement on birds at regional scales. This involves the distribution of study sites among land-cover types and across the gradient of settlement intensity, followed by the progressive aggregation of data gathered at local scales. These data serve as the basis for interpolation to areas not sampled using traditional statistical tools and geostatistical methods. The predicted patterns then serve as hypotheses for further testing.

There are numerous challenges to developing effective conservation strategies for birds in human-dominated areas. The greatest hurdle may be the diffuse nature of land-use decisions. Meeting such challenges requires a multi-scale approach, not only with regard to data collection and analysis, but also for integrating policy across levels of government. Scientists must assure that the products of their research are relevant, easily understood, and readily accessible to decision makers. Finally, conservation must be focused on landscape mosaics, not habitat patches, and areas where people live and work should be recognized as important components of such landscapes.

INTRODUCTION

Development associated with human settlement has emerged as a prevailing source of land-use change throughout the world (Berry 1990, United Nations Centre for Human Settlements 1996, Cohen 1997). In the U.S.A. alone, nearly 6 million ha of forest and rangeland were converted to housing and assorted infrastructure between 1982 and 1992 (NRCS 1995). Such development is not evenly distributed geographically, nor is it limited to urban areas. Extensive landscape transformation in the Rocky Mountain region, for example, is the result of a population growth rate that is three times the national average. Colorado is a bellwether of change for this region, with 6 of the 10 fastest-growing counties in the nation (including the top 3) - all exceeding 6% population increases per year between 1990 and 1998 (U.S. Census Bureau 1998). Although much of this growth is manifest in typical urban and suburban sprawl, the conversion of agricultural and forested land to low-density residential development is occurring at unprecedented rates (Knight *et al.* 1995, Riebsame *et al.* 1996).

Urbanization clearly harms some native bird species (Marzluff, this volume). Our understanding of the mechanisms underlying such effects remains rudimentary, largely because many ecologists have avoided human-dominated systems as locations for study. In the relatively few studies that have focused on settled areas, researchers have usually concentrated on urban or suburban environments while areas of lower residential density have generally been ignored. Furthermore, most studies have been conducted at relatively fine scales (but also see Blair 1996, Nilon *et al.* 1995, Clergeau *et al.* 1998). For these reasons, the scientific basis for avian conservation in developed areas remains weak, particularly in areas of lower settlement densities and at landscape and regional scales.

Our goal is to contribute to the dialogue on the direction of future research on bird communities in human-dominated areas. We begin by examining gradients of human settlement with special attention to portions of such gradients that have thus far received scant attention by avian ecologists. Next, we consider issues of spatial scale and stress the importance a multi-scale approach to examining the effects of development on birds.

Finally, we discuss a number of important challenges in designing and implementing effective policies for the conservation of avian diversity in areas of human settlement.

GRADIENT OF HUMAN SETTLEMENT

Ecologists have often treated urban as a separate type of land cover, akin to agriculture or grassland. This is similar to the way that settlement is portrayed on roadmaps, where only towns or cities above some minimum population threshold are depicted, or in land-use databases such as USGS LandUse/LandCover (Anderson *et al.* 1976), where the only distinction is between urban and non-urban areas. The true extent of development, however, may be vastly underestimated by such conceptualizations (Fig. 1). In fact, urban is an endpoint on a gradient of human settlement — a gradient that extends from sparsely populated rural areas to large cities (Table 1). As one travels outward from densely-populated urban areas to suburban development, there is a noticeable increase in parcel size (and thus a decrease in human density), the amount of greenspace, and the density of trees and shrubs. Suburban areas, in turn, often give way to exurban residential development that is characterized by still larger parcel sizes and greater amounts of vegetation. Ultimately, one encounters rural areas dominated by agricultural activites which, in some cases, border wildlands. Settlement is not a matter of either-or but one of degree.

The gradient paradigm has long been used in ecology as the basis for examining environmental variation that is ordered in space (Whittaker 1967) and has been applied to the study of bird communities at a variety of spatial scales (Terborgh 1971, Cody 1975, Wiens and Rotenberry 1981). The underlying assumption is that the structure and function of ecological systems varies in space, and understanding this variation can enhance our knowledge of system-level processes. McDonnell and Pickett (1990) have characterized urbanization as a complex environmental gradient and suggested that the gradient paradigm is therefore a powerful organizing tool for ecological research in human-dominated environments.

An important advantage of the gradient approach, as opposed to binary comparisons (e.g., urban vs. rural or suburban vs. wildland), lies in its ability to identify thresholds or breakpoints where human impacts cause marked changes in biotic responses (Wiens 1989). Such thresholds might be found, for example, in measures of human density or in terms of distances from human-dominated areas. Thresholds are important is simply because they offer a clear basis for policy — deterimining buffer distances and zoning regulations, for instance.

We recently reviewed 41 peer-reviewed studies of avian communities in areas of human settlement that were published between 1970 and 1999. Of these investigations, 12 utilized a gradient-type research design, although in most cases the gradients were restricted in the levels of development that were sampled. Only 5 studies covered the spectrum from urban or suburban to rural. In fact, the lower-density portion of the gradient has not received much attention generally; only 4 of the 41 studies included sites at the exurban or rural levels.

In Colorado, exurban development expanded at a pace of 8.3% annually between 1960 and 1990 - nearly three times the rate of population growth (Theobald *In Press*).

This type of low-density development is expected to continue in Colorado and elsewhere, fueled by the growth of recreation-, service-, and information-based industries; dissatisfaction stemming from various problems associated with urban living; aesthetic considerations; and recreational opportunities. Locations near federal lands such as National Parks and Forests, places often viewed as conservation areas, appear to be particularly attractive (Nelson 1992, Howe *et al.* 1997).

Although individual buildings are by definition more widely spaced in lower-density forms of development, this does not necessarily mean that the effects of settlement are restricted to a small portion of the landscape. As rural areas are converted to exurban residential development, road density is likely to increase. Existing roads will experience greater traffic because widely dispersed development means more vehicles per household and more trips per day per vehicle (Romme 1997). Roads are associated with an effect zone — an area of ecological impact on either side of the road itself — that extends outward from tens to hundreds of meters (Forman and Alexander 1998). Both grassland and forest birds have been found to avoid roads (Ferris 1979, van der Zande *et al.* 1980). Research in the Netherlands showed that the effect-distances (the distance from a road at which population decreases were detected) varied with traffic density and habitat; 60% of the bird species present occurred at lower densities near roads, and songbird declines were coincident with thresholds in traffic noise (Reijnen *et al.* 1995, Reijnen *et al.* 1996). Moreover, evidence suggests that mammalian predators travel along low-traffic roads (Bennett 1991, Forman 1995) and increased rates of nest predation have been found near low-traffic road edges (Small and Hunter 1988). Roads may also alter avian community composition by attracting edge species, particularly in forested habitats (Hanowski and Niemi 1995).

One can imagine that buildings are also attended by an effect zone, although this phenomenon has not received as much attention from ecologists. A building-effect zone with reference to birds might be a function of human activity, noise, or free-ranging pets (Fig. 2). Although the effect of any one building on the surrounding matrix is probably small, the cumulative effect of many buildings may be substantial (Theobald *et al.* 1997). Building effects might cause avoidance in some species, while species that are tolerant of a human presence may benefit. Blackbirds (*Turdus merula*) nesting near buildings and busy sidewalks on a college campus, for example, were found to experience greater nesting success than birds nesting farther away (Osborne and Osborne 1980).

Ultimately, it is important to determine the effect zone or footprint of various building types or clusters of buildings. We believe that research leading to this sort of determination should be afforded a high priority by ecologists interested in the effects of development on native diversity. We also urge that greater consideration be given to the full spectrum of development when studying the effects of human settlement on avian communities.

MATTERS OF SPATIAL SCALE

Local scales

Traditionally, ecologists have focused on within-habitat diversity when conducting research on bird communities and have ascribed differences in avian diversity to variation in habitat features such as foliage-height diversity or horizontal habitat heterogeneity (MacArthur and MacArthur 1961, Karr and Roth 1971, Willson 1974). In an effort to reduce spatial variation and thereby allow fair comparisons, samples have usually been collected over small plots or quadrats, usually < 0.5 km^2, located in a single habitat type.

Study designs based on within-habitat diversity have also been common in research on urban birds. Several workers have examined relationships between avian community composition and attributes of urban woodlots (Tilghman 1987) or parks (Gavareski 1976, Cicero 1989) including vegetation, patch area, or the presence of human artifacts such as recreational trails. Similarly, DeGraaf and Wentworth (1986) described suburban bird assemblages in Amherst, Massachussetts, and attributed differences in avian community structure to various aspects of the built environment, particularly those relating to vegetation. At a finer scale, Major *et al.* (1996) found that nest predation increased with nest height and tree density in residential backyards located in Australian urban areas.

As another example of research that focuses on fine scales, we examined nest predation in lowland riparian areas adjacent to suburban development along the Front Range of Colorado as a function of distance from recreational trails (Miller *et al. In Press*). On each of two streams, transects of experimental nests were placed near the trail and on the opposite side of the stream at a treatment site. A third transect was placed at a control site where there was no trail. As in the studies mentioned above, sites were chosen to be as similar as possible in order to focus on the effects of trails and human activity and to minimize potential biases. We found that mamalian nest predators tended to avoid trails, whereas avian predators tended to prey more on nests near trails (Miller and Hobbs, unpublished data), similar to the effects of buildings and human activity reported by Osborne and Osborne (1980).

Studies at fine or local scales have advanced our understanding of proximate factors that affect bird distributions in areas of human settlement. Vegetation structure and floristics, for example, have been frequently cited as important determinants of habitat suitability for some species (Beissinger and Osborne 1982, Green *et al.* 1989, Jokimaki and Suhonen 1993, Rolando *et al.* 1997, Germaine *et al.* 1998). An exclusive focus on fine-scale attributes of human-dominated areas, however, reflects the belief that local features are synonymous with habitat. It is possible (indeed likely) that in many cases additional factors emerging at broader scales may also influence avian community structure.

Landscape Context

Landscape context may influence ecological processes such as those that determine local avian diversity because birds are highly mobile organisms and likely respond to habitat features across a range of spatial scales (Hostetler, this volume). Hildϑn (1965) suggested that habitat selection by migratory birds could best be viewed as a hierarchical decision process that starts at regional and landscape scales and proceeds to fine-scale habitat characteristics. If this is true, then we might expect similar habitats to support different bird assemblages in some cases, depending on the structure and composition of the surrounding landscape matrix. Pearson (1993) found that variation in the abundance and diversity of wintering birds could be explained solely by landscape variables. Moreover, although several workers have reported a positive relationship between the width of a riparian area and avian diversity (Stauffer and Best 1980, Darveau *et al.* 1995, Hodges and Krementz 1996), this relationship does not always hold when wider riparian areas are surrounded by urban or suburban development (Miller et al. *In Press*).

There are many mechanisms mediating the effects of landscape context on avian communities in a given habitat type. Birds nesting in forest fragments may be subjected to different nest predators and experience different rates of nest predation depending on the nature of the areas surrounding these patches (Andrén 1992). Szaro and Jakle (1985) found that birds associated with riparian habitats comprised nearly a third of avian assemblages found in desert scrub but that this percentage decreased with distance from the riparian zone. Clearly, conclusions drawn on the sole basis of local habitat features without consideration of landscape context may be misleading.

As the geographical extent of an investigation is expanded, one might classify the matrix in a categorical fashion. For example, in our assessment of the influence of urbanization in the surrounding landscape on riparian bird assemblages in Colorado, we initially categorized development as high-medium-low based on familiarity with the sites and a visual assessment (Miller *et al. In Press*). A quantitative description of the surrounding landscape, however, allows a more rigorous analysis of the influence of landscape features on avian communities. Moreover, the detection of critical thresholds in the response of birds to these features depends on such descriptions, as mentioned above.

Ecologists have typically measured landscape structure using indices describing cover-type, patch size, adjacency, nearest-neighbor, amount of edge, etc. (McGarigal and Marks 1993, Gustafson 1998). This tradition reflects the focus of ecologists on landscapes where the primary anthropogenic impacts involve the conversion of land-cover types such as forest and woodland to clearcuts and cropland, commonly thought of as habitat fragmentation (Harris 1988, Saunders *et al.* 1993, Schwartz 1997). Indeed, contemporary thinking about anthropogenic impacts on landscapes is dominated by the fragmentation paradigm, by the idea that the integrity of many ecosystems is diminished by human activities that isolate habitat patches in an ecologically compromised matrix. Although fragmentation may apply well to landscapes in which the primary effects of development involve conversion of land-cover types, it is not especially faithful to effects caused by settlement, particularly settlement at low density.

In their study of the Golden-cheeked Warbler (*Dendroica chrysoparia*), Engels and Sexton (1994) noted that it is difficult to delineate patches in urban and suburban areas in a meaningful way because the effects on birds of the defining features of built environments, such as streets and buildings, are poorly understood. Engels and Sexton (1994 : 287) observed that the woodlands in the vicinity of Austin, Texas are more frequently speckled by urban structures than isolated by them into discrete islands. Generalizing this idea, we suggest that in many instances the effects of human settlement may be better represented as "perforations" of landscapes rather than agents of fragmentation (Fig. 3).

If we focus on gradients of human settlement rather than attempting to characterize landscapes as habitat patches embedded in a uniform and human-dominated matrix, how might we quantify such gradients? There are several metrics that indicate the intensity of settlement, are easy to define, and are readily quantifiable. These include population density, building density, and road density. In our work with riparian bird communities in Colorado, we are using parcel maps to describe the level of development in the surrounding landscapes. These maps were acquired from county tax assessor s offices. In addition to allowing us to measure building densitites and quantify the spatial pattern of settlement, they provide information on the age of development as well as the zoning restrictions for a given parcel.

It is also important to note that most research on human settlement has been conducted in forested regions (Marzluff, this volume). In this context, it is not surprising that ecologists have asserted that urbanization is synonymous with the simplication of habitat structure and leads to overall reductions in avian diversity (Geis 1974, Aldrich and Coffin 1980, Beissinger and Osborne 1982, DeGraaf and Wentworth 1986). Development, however, can result in a more complex habitat structure compared to the presettlement landscape. Human settlement in treeless arid and semi-arid regions of North America is often accompanied by the planting of trees, shrubs, and expansive lawns as people try to recreate the familiar landscapes from which they came (Limerick 1987). As a result, habitat structure becomes more complex and the diversity of birds associated with the built environment in these areas is, in some cases, greater than that of the predevelopment landscape (Guthrie 1974, Vale and Vale 1976, Sodhi 1992). The same may be said of development in areas formerly dedicated to intensive agriculture, as monocultures are replaced with more diverse habitats. Again, context matters.

Regional Perspectives

A regional perspective is also important, both in assessing the effects of settlement and in managing human population growth. Marzluff (this volume), for example, noted that growth control in Portland, Oregon, has simply transferred development pressure to outlying communities. Just as landscapes are perforated by individual buildings and small residential clusters, regions are perforated by cities, towns, and larger suburban enclaves surrounded by exurban development and linked by transportation networks. The cumulative effects of settlement at this scale are virtually unknown. Most studies of the impacts of urbanization on bird communities have been conducted in a single town or city or, in some cases, a portion of the surrounding countryside, with only a handful encompassing larger areas (Fig. 4).

One way of expanding our perspective in a research context is simply to expand the geographical extent of a study and include a greater number of replicate sites. We investigated the effects of development on lowland riparian bird communities using 5 drainages in two Colorado counties and multiple sites representing a gradient of settlement on each drainage; building densities ranged from 0 to 640 units/km^2 (Miller *et al. In Press*). Although this approach is useful when examining impacts on birds associated with a particular habitat type across a range of landscape contexts, an understanding of the cumulative effects of development over an entire region is unlikely to emerge.

Because we will never be able to measure processes and states for more than a tiny fraction of a region, we need sampling designs that allow us to extrapolate to unmeasured areas. We therefore propose a multi-scale research protocol for assessing the impacts of human settlement on avian communities at regional scales (Fig. 5). Traditional census techiques (point or line transects, circular plots) in combination with fine-scale habitat measurements (vegetation structure and floristics) are the foundation of this method. Sets of local surveys are distributed across the spectrum of land-cover types in a region using a stratified random design and a geographic information system (GIS). For our purposes, land-cover types are defined by of measures of human settlement (road density, building density, etc.) superimposed on habitat types (forest, grassland, etc.) so as to represent the full gradient of settlement occurring in the region, including undeveloped areas. The sampling design is hierarchically nested so that surveys conducted at fine scales may be progressively aggregated at broader scales.

A spatial model is then developed that can be used to correlate coarse-scale data derived from satellite imagery or aerial photography and measures of settlement intensity with fine-scale data on bird communities and habitat structure. To examine spatial dependencies among variables, one might use traditional statistical methods such as stepwise regression in combination with geostatistical tools such as trend-surface analysis

(Gittens 1968). It then becomes possible to interpolate for areas not sampled (Robertson 1987), essentially generating hypotheses that could be tested with another set of surveys.

This research protocol can be used for a variety of purposes. Theobald and Hobbs (1998) developed and tested models of land-use change that predict the spatial distribution of residential development in response to demographic and economic drivers. One might use such models in combination with our multi-scale protocol to identify areas that are particularly vulnerable to the effects of settlement.

We believe that our proposed design could prove useful in addressing basic as well as applied research questions. For example, beta diversity is generally thought to increase with an increasing number of habitat types. How is this relationship altered by the effect of human settlement? In this vein, one of us (JMF) is conducting a study in the Colorado Front Range of the Rocky Mountains. The overall study area encompasses two counties and is dominated by ponderosa pine (*Pinus ponderosa*), Douglas fir (*Pseudotsuga menziesii*), lodgepole pine (*Pinus contorta*), aspen (*Populus tremuloides*), and alpine meadows. The research focuses on several small towns that lie along a north-south axis. The basic premise is that if areas of human settlement tend to be more similar to one another in terms of habitat structure than they are to the pre-development landscape (Schneider 1996), it follows that their associated avian assemblages would exhibit greater similarity to one another than to those found in surrounding areas. There is evidence to support this assertion in larger developments at lower elevations in other regions (Aldrich and Coffin 1980, Beissinger and Osborne 1982, DeGraaf and Wentworth 1986), but we are unaware of any studies of this type focusing on smaller settlements or exurban areas in western coniferous forests. Given the pace of development in the Rocky Mountains (Reibsame *et al.* 1996, Theobald *et al.* 1996, Theobald *In Press*), the outcome of this research have important implications for avian conservation in this region.

POLICY

Historically, ecologists and conservation biologists have exerted their greatest impact on environmental protection by influencing decisions at the national level. The Clean Air Act, the Clean Water Act and the Endangered Species Act are all examples of policies that extend "top-down" from the federal government to influence local actions. However, most decisions affecting bird communities in urban and suburban areas are made at the base of the government hierarchy by county governments, municipalities, and landowners (Beatley 1994).

This creates several challenges for implementing conservation policy. The first challenge is created by the diffuse nature of land-use decisions. Many seemingly small decisions — choices made at many different times and locations — accumumulate to cause large-scale impacts. The fact that these choices are diffuse in time and space means that it is difficult for experts to inform them. It follows that many of these local decisions are made without the benefit of scientific input regarding their ecological impacts. Second, the fact that many local jurisdictions, including individual landowners, are responsible for land-use decisions implies that conservation policy at the regional scale must include input from many decision makers. Achieving consensus or even agreement among these many jurisdictions may be impossible, and when consensus is reached it may be forged from compromises that fail to deal with fundamental conservation issues. Finally, the large degree of discretion granted to landowners by the U.S. Constitution (Smith 1993, Cullingworth 1997) means that conservation policy developed by government may have very little impact on what happens on the landscape. Unless we are content with merely cleaning up the infrastructure, it will be imperative to find ways to compensate private landowners for not developing their land.

Rising to these challenges will require the development of strategies for conserving and managing avian communities at multiple scales and the integration of actions by state, county, and municipal governments with those of landowners. This is a daunting task, but there are encouraging examples to guide our efforts (DeGrove 1992, Lee 1993, Beatley 1994, Duerksen *et al.* 1997). These multi-scale strategies must achieve reasonable compromises between maintaining local and regional diversity of species and habitats. For example, if regional conservation plans emphasize a species that is abundant locally, local protection my fail to enhance local diversity even though it contributes regionally. Regional development of conservation areas and reserves must take advantage of unique opportunities afforded by variation among avian communities in local areas.

Achieving conservation objectives in the face of rapid human settlement requires a new set of responses by scientists. We must assure that data and analyses are both readily understood and easily accessible to decision makers and to the citizens who wish to influence decisions in established review processes. We must be willing to work locally to contribute to the solution of regional problems. Finally, we must communicate to land managers and conservationists the message that areas of human activity, particularly areas of low-density development, must be considered as important components of landscape mosaics in management plans rather than being written off in terms of conservation value because they have a human presence. Such areas are, in fact, part of the solution, not just part of the problem.

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Table 1. Levels of development based on lot size per building (sensu Theobald *In Press*).

Level of Development	Lot Size (ha)
urban	< 1
suburban	1 - 4
exurban	4 - 32
rural	> 32

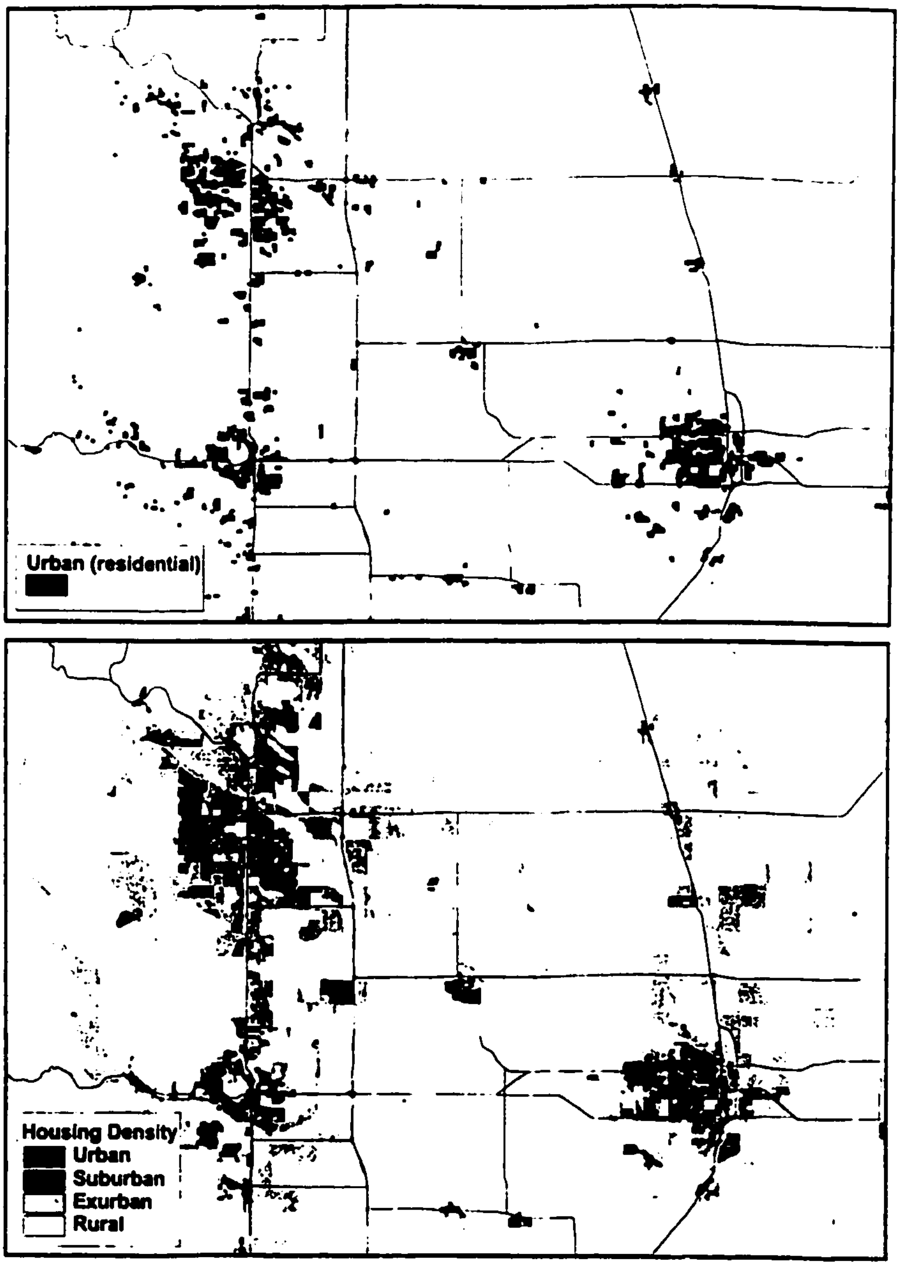

Fig. 7.1. Human settlement along the northern Front Range of Colorado (both panels: Fort Collins-top, Loveland-bottom, and Greeley-right). (A) Areas classified as residential urban land cover from the USGS 1:250,000 LU/LC map series. (B) The full gradient of housing densities from urban to rural using U.S. Census Bureau block-level data.

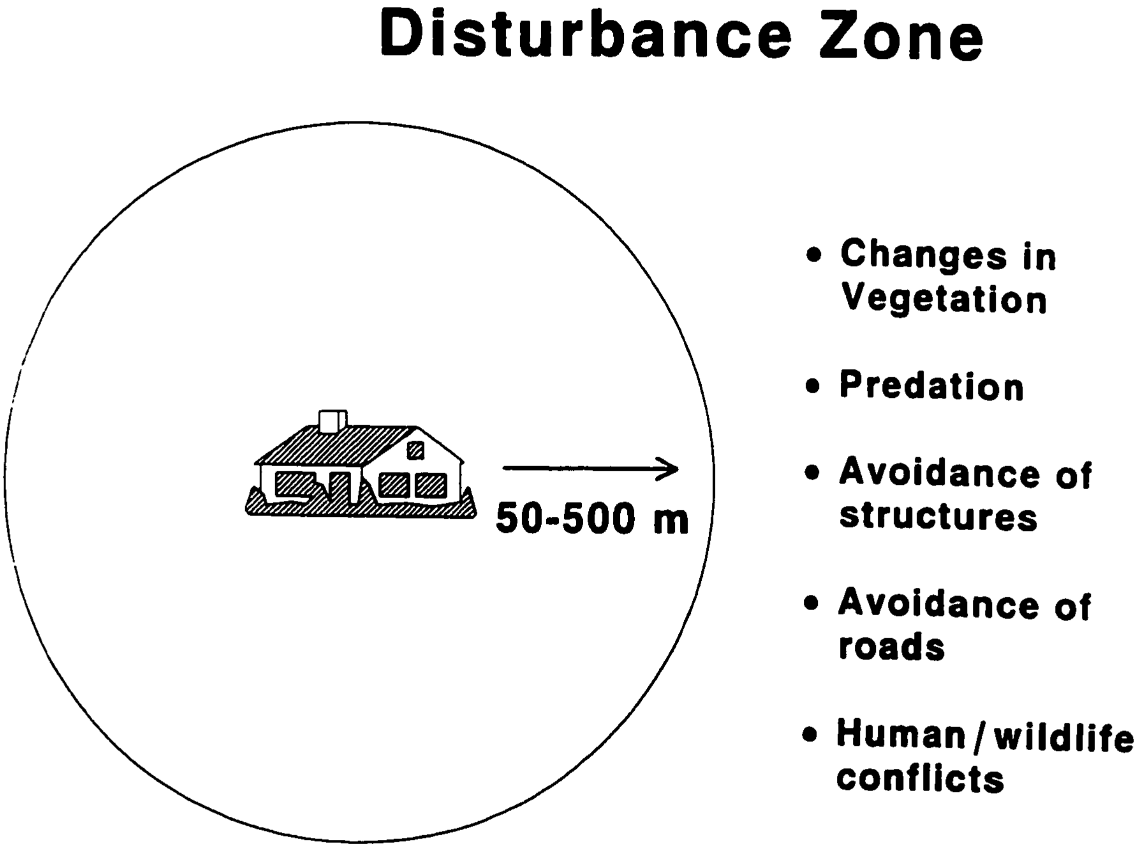

Fig. 7.2. Hypothetical effect zone ("footprint") of a single residence and possible mechanisms that reduce habitat quality for birds.

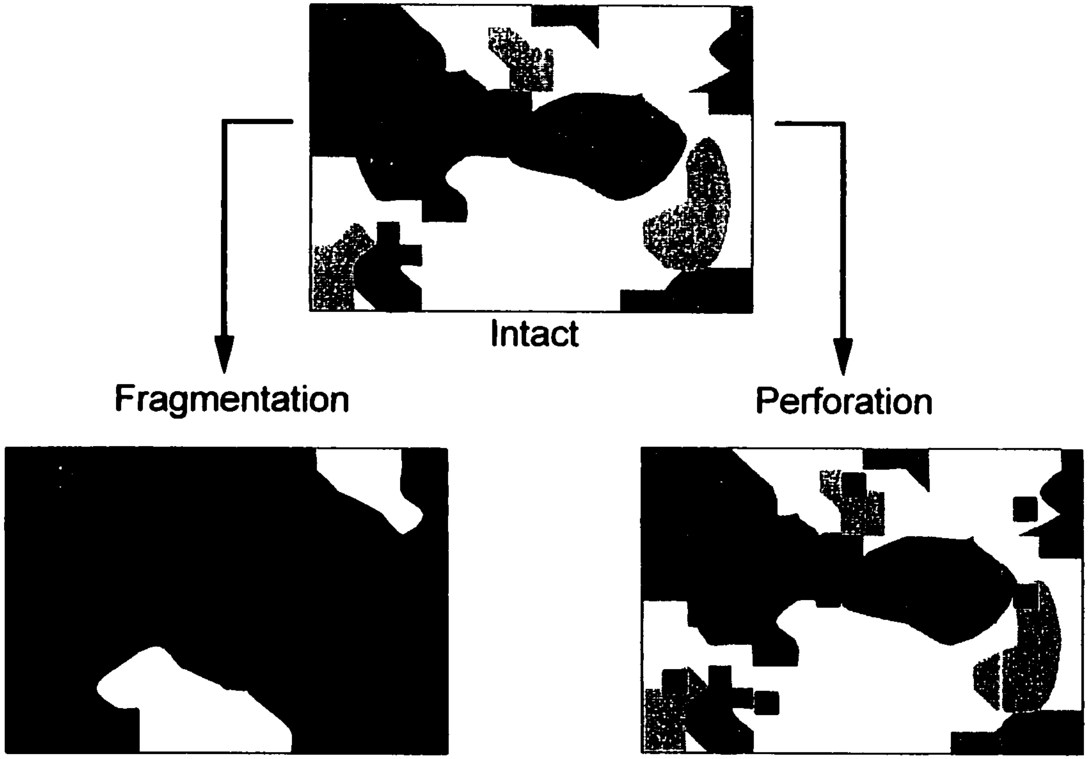

Fig. 7.3. Contrasting landscape patterns associated with habitat fragmentation and habitat perforation. Black areas in the lower panels represent habitat removal; fragmentation results in the conversion of land-cover types (by timber harvest or agriculture, for example) and discrete patches surrounded by a highly-altered matrix, whereas habitat perforation results in a landscape speckled with disturbance points (such as individual houses or clustered developments).

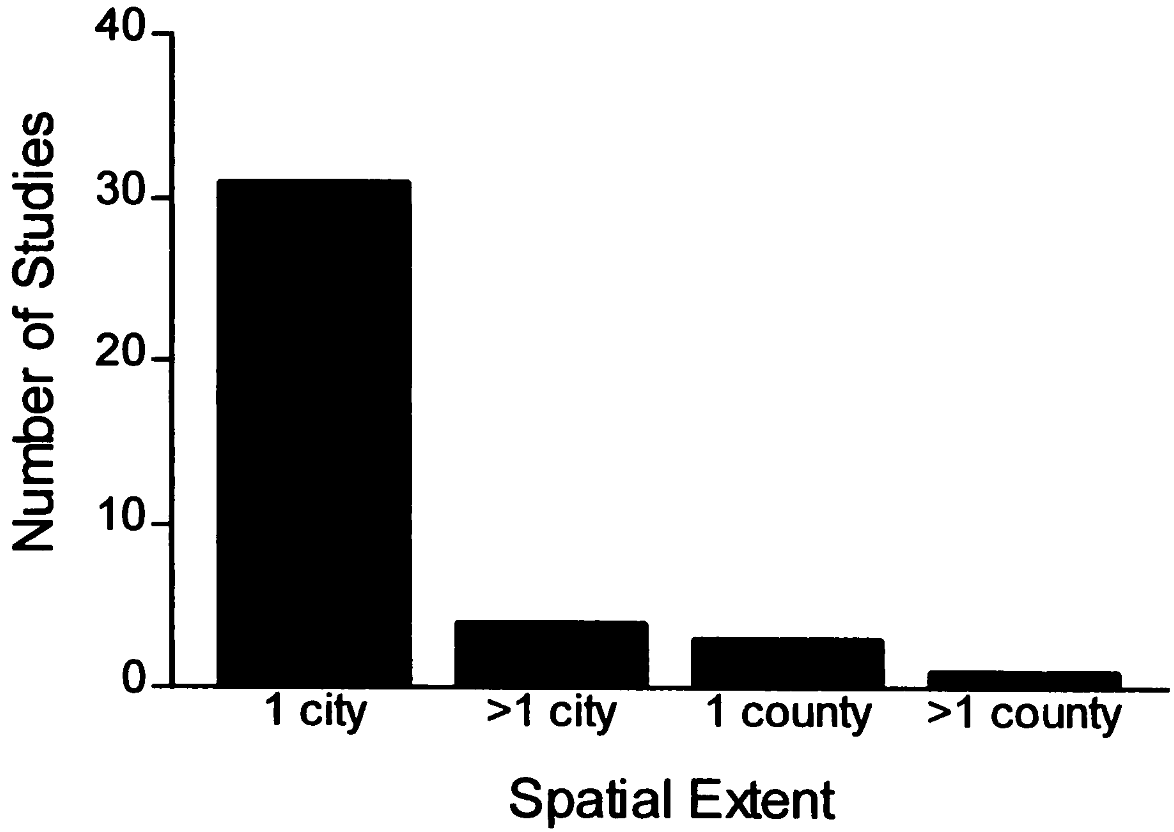

Fig. 7.4. Geographical extent of peer-reviewed avian community studies in areas of human settlement published between 1970 and 1999, based on a literature search of the Biosis database.

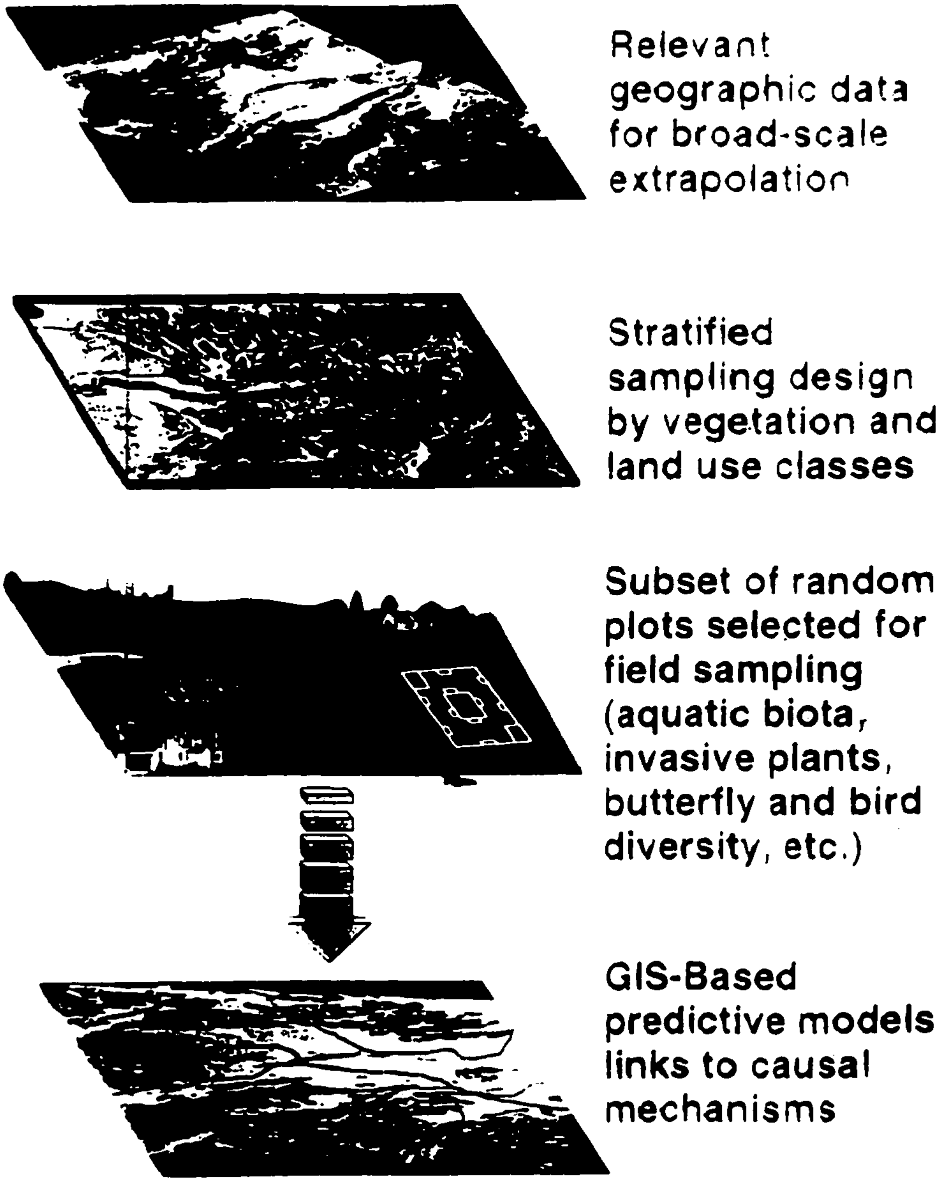

Figure 7.5. Stages of a generalized multi-scale research design. The top panel represents broad-scale data, derived from satellite images or aerial photographs. Study sites are then selected using a stratified random sampling design based on vegetation and land-use classes. A subset of these sites are selected for field sampling and data collected at these sites are then used to develop predictive models regarding species occurrence at sites that were not sampled initially.

CHAPTER VIII

THE EFFECT OF HUMAN SETTLEMENT ON BIRD COMMUNITIES IN LOWLAND RIPARIAN AREAS: SYNTHESIS

Human settlement has had a strong influence on lowland riparian areas along the Front Range of Colorado. Other workers have demonstrated that riparian habitats have been changed by impoundments and diversions at regional scales. At a finer resolution, my data show that these riparian woodlands have also been affected by settlement at the scale of the landscape, as exemplified by the increase in non-native trees and shrubs as well as other changes in habitat structure with increasing development (Chapter 4). Although it is difficult to know with certainty, all the evidence suggest that these habitats have changed considerably from those that existed prior to the recent spread of settlement.

Bird communities associated with these riparian woodlands have also been transformed by settlement. Habitat characteristics that have correlated strongly with features of riparian bird communities in other regions, such as the width of the riparian zone, were overshadowed by development in this study (Chapter 4). Several of the species that dominate these sites were either not present prior to the westward expansion of the U.S. or were present in much lower numbers.

Some species appear to be able to compensate for an increased human presence, as my data suggest for the American Robin (Chapters 4 and 5). Although it is reasonable to expect human commensal species to reach their greatest abundance at sites with higher levels of development, the same can be said for some native species such as the House Finch (Chapter 4). Species that used sites at the developed end of the urban gradient tended to be resident year-round, and either omnivorous or seed-eaters. Species at the rural end of the gradient tended to be migrants and insectivorous.

Numerous studies have shown that urban avifaunas are dominated by a few species that are quite abundant. At the riparian sites in this study, both abundance and richness decreased with development (Chapter 4). My co-authors and I suggested that riparian habitats near development may provide fewer foraging opportunities when compared to the surrounding landscape, especially for omnivorous species. These same sites also tended to be associated with a great deal of human activity in the riparian zone. Such factors may account for decreased abundance at more urban sites.

Although many species were only found at sites that were relatively undeveloped, this does not mean that productivity for these birds is necessarily high. Depredation of artificial nests was quite high at all sites and in all years, but nests in rural areas were generally at greater risk (Chapter 4). The fact that nest success was high across sites for the American Robin not only demonstrates that at least some species may be able to compensate for greater predation risk, but also highlights several differences between artificial and natural nests. More data are needed on the nesting success of other species to assess the value of these for breeding birds.

Just as human activity in the riparian zone may depress bird abundance, it may also moderate predation risk (Chapter 5). Some predators, particularly mice, appear to avoid recreational trails whereas other predators, such as corvids, do not. Thus, nest success in these habitats depends on (1) the degree to which species tolerate human activity, (2) the degree to which individual predator species forage in these areas, and (3) the vulnerability of individual bird species to predation by various nest predators. Data collected on artificial nests in 1997 also indicate that there is annual variability in predation rates, and that although the overall trend is for predation to increase with development, this relationship does not always hold. This observation suggests that caution be exercised when interpreting the results of predation studies that are limited to one year or to one season. Annual variability in nest predator populations, avian abundance, and/or the availability of alternate prey may all affect predation intensity on bird nests.

The land uses occurring in the areas surrounding the riparian woodlands that I studied influenced the bird communities. Clearly, we must consider the nature of the landscape matrix in which riparian habitats are imbedded, in addition to local habitat features, when describing patterns of habitat use by birds (Chapter 7). Overall, the gradient of human settlement as defined by these sites was an effective tool for examining the relationship between birds, study sites, and habitat characteristics. The relationship between predation risk and building density, however, suggests that other factors that may vary among drainages were also influential, although the exact nature of these influences was not captured by our analyses.

The bird communities that I have described include many habitat generalists with wide geographic distributions. For many of these species, the center of their range is in other regions; indeed, a number of them are at the edges of their distributions. Given the modification of these habitats since settlement, current levels of development, and future projections of human population growth, it might be tempting to focus conservation efforts elsewhere. In Colorado, however, many of these species (particularly native birds) are found primarily or exclusively in lowland riparian areas. Moreover, some of the species that attain greater densities in other regions appear to exhibit different habitat preferences in Colorado. It is also important to remember that other studies suggest that these habitats have value for migrating and over-wintering species. There are still many questions that must be answered before comprehensive evaluation of the conservation value of these riparian woodlands can be made.

An important consideration regarding conservation efforts in lowland riparian areas, especially those that are near human settlement, may extend beyond the realm of science, however. Colorado, like many other parts of the world, is faced with not only an expanding population but one with increasingly tenuous connections to the natural world (Chapter 2). The educational value of riparian habitats is substantial. People have a natural affinity for these areas. Even riparian woodlands that are relatively close to suburban development, especially if the riparian zone is somewhat buffered by adjoining grasslands, are associated with a substantial amount of avian diversity. Development will proceed, but if some riparian areas are allowed to remain relatively isolated from human activity, we can also begin to address numerous ecological questions about the adverse impacts of recreational activity on native species. To the extent that people appreciate the native diversity that occurs in areas where they live and work, they will be more likely to support conservation measures elsewhere.

APPENDIX I

Study site locations by drainage. Numbers provided parenthetically after each site refer to locations on Figure 4.1.

Boulder Creek

_CU_ (1): 13 census points, with 11 on the north side of Boulder Creek beginning approximately 150 m southeast of the intersection of Arapaho and 13th Streets in the City of Boulder, behind Boulder High School, and terminating approximately 200 m west of the Folsom St. underpass on the Boulder Creek Trail. The remaining 2 points were located in a large riparian woodlot on the south side of Boulder Creek between the creek and the CU campus and between points 3 and 5 on the north.

_30th St._ (2): 15 census points, with 8 points beginning approximately 100 m east of 30th St. in the City of Boulder and terminating approximately 75 m west of the Arapaho Rd. underpass, 2 points located between Arapaho and 47th Streets, and the final 5 points beginning approximately 150 m east of 47th St. and continuing east along the creek.

Walden (3): Total of 15 census points with the first 10 points beginning approximately 100 m west of 75th St., east of the City of Boulder, and extending to the western boundary of the Sewage Disposal property, and the remaining 5 points on private land.

Kaufman (4): Total of 15 census points with the first 6 points beginning approximately 125 m west of 75th St., east of the City of Boulder, and terminating approximately 75 m west of the Wiser property, with the remaining 9 census points beginning approximately 35 m east of the Wiser/Kaufman property line and terminating approximately 500 m west of the Wiser/Ertl property line.

Ertl (5): 15 census points, beginning approximately 60 m west of the East-Boulder White Rocks Trail on Valmont Rd., east of the City of Boulder, and terminating approximately 50 m east of the Wiser property.

South Boulder Creek

Bobolink (6): 14 census points, beginning 60 m south of the Bobolink Trail parking lot at Baseline Road in the City of Boulder, and terminating approximately 100 m north of the water pipe near South Boulder Road.

South Vale (7): 15 census points, beginning approximately 300 m south of I-36 and terminating near the southern boundary of Open Space property (just north of Marshall Road).

Eldorado (8): 13 census points, beginning approximately 300 m south of the Open Space Operations Center on South Broadway St. in the City of Boulder and terminating at the northern boundary of the private property adjacent to the Mesa Trail where it crosses South Boulder Creek.

Coal Creek

Vista View (9): 13 census points, with 7 between Highways 93 and 128, just south of the City of Boulder, and the remaining 6 beginning just north of Highway 128 at the pumping station and continuing northeast, terminating at the gravel mine.

Gravel Mine (10): 12 census points, beginning at the western edge of the gravel mine east of Highway 128 south of the City of Boulder and terminating at the southwestern edge of the Town of Superior inholding.

Superior (11): 13 census points, beginning at the eastern edge of the Town of Superior inholding and terminating approximately 200 m west of the Town of Superior border.

Lafayette (12): 12 census points, beginning approximately 150 m north of intersection of the Rock Creek-Coal Creek Trail and Empire Rd. on the southern boundary of the City of Lafayette and terminating approximately 1.5 km to the east on this trail (due to construction).

Poudre River

Shields (13): 15 census points, beginning approximately 125 m east of Shields St. in Ft. Collins and terminating approximately 400 m west of College Avenue.

Lemay (14): 15 census points, beginning approximately 75 m east of Lemay St. in Ft. Collins and terminating at the western edge of the long treeless stretch, opposite and approximately 200 m west of the Riverbend Ponds Open Space.

7 Ponds (15): 15 census points, beginning approximately 65 m north of the Prospect Rd. underpass in Ft. Collins and terminating opposite and approximately 40 m west of Riverbend Ponds.

Harmony Gateway (16): 12 points, with 3 beginning at the eastern terminus of Horsetooth Rd. in Ft. Collins and the southern boundary of the Western Mobile property adjacent to the former site of the Strauss cabin and terminating at the drainage ditch south of the Strauss cabin, and the remaining 9 beginning south of the drainage ditch and terminating approximately 100 m north of Harmony Rd.

APPENDIX II

Common and scientific names and codes of bird species that are known to breed in lowland riparian areas in Boulder and Larimer Counties, Colorado (Andrews and Righter 1992, Kingery 1998). Species detected during point counts (from late-May to mid-July, 1995-1997) at the following sites are marked with an "X - South Boulder Creek (SBC): Bobolink (BO), Eldorado (EL), and South Vale (SV); Coal Creek (CC): Lafayette (LA), Superior (SU), Mine (MI), and Vista View (VV); Boulder Creek (BC) - CU, 30th St. (30), Walden (WA), Kaufman (KA), and Ertl (ER); Cache la Poudre River (PR): Shields (SH), Lemay (LE), 7 Ponds (7P), and Gateway (GW). See Figure 4.1 and Appendix I for the locations of these sites. This list includes nocturnal and crepuscular species, aerial insectivores (e.g., swallows and swifts), raptors, shorebirds, or waterfowl that were detected while conducting point counts. It should be noted, however, that point counts are an unreliable method for censusing such species (Bibby *et al.* 1992) and it is possible that they may also occur at sites other than the ones indicated, even though our point counts did not detect them. Species that are not thought to breed in lowland riparian areas in Boulder and Larimer Counties but that were detected on point counts are indicated with an asterisk.

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Kingery, H. (editor). 1998. Colorado Breeding Bird Atlas. Colorado Bird Atlas Partnership and Colorado Division of Wildlife, Denver.

Species	Species Code	SBC BO	EL	SV	CC LO	SU	MI	VV	BC CU	30	WA	KA	ER	PR SH	LE	7P	GW
American White Pelican ***Pelecanus erythrorhynchos***	AWPE	X															
Double-crested Cormorant ***Phalacrocorax auritus***	DCCO											X	X			X	X
Great Blue Heron ***Ardea herodias***	GBHE				X						X	X	X		X	X	X
Great Egret ***Casmerodius albus***	GREG																
Black-crowned Night Heron ***Nycticorax nycticorax***	BCNH				X								X			X	
Wood Duck ***Aix sponsa***	WODU									X		X	X		X		
Blue-winged Teal ***Anas discors***	BWTE																
Mallard ***Anas platyrhynchos***	MALL	X	X	X				X	X		X	X	X	X	X	X	X
Common Merganser ***Mergus merganser***	COME														X	X	X
Gadwall ***Anas strepera***	GADW		X	X													X
Canada Goose ***Branta canadensis***	CAGO		X										X			X	
Sharp-shinned Hawk ***Accipiter striatus***	SSHA																
Red-tailed Hawk ***Buteo jamaicensis***	RTHA		X										X				
Swainson's Hawk ***Buteo swainsoni***	SWHA											X					

Species	Species Code	SBC BO	EL	SV	CC LO	SU	MI	VV	BC CU	30	WA	KA	ER	PR SH	LE	7P	GW
Prairie Falcon ***Falco mexicanus***	PRFA																
American Kestrel ***Falco sparverius***	MAKE	X	X	X	X	X	X		X	X		X	X	X	X	X	X
Wild Turkey ***Meleagris gallopavo***	WITU																
Northern Bobwhite ***Colinus virginianus***	NOBO																
Killdeer ***Charadrius vociferus***	KILL		x	x	X	x	X			X		X	x	X	X	X	X
American Avocet ***Recurvirostra americana***	AMAV																
Sora ***Porzana carolina***	SORA															X	
Spotted Sandpiper ***Actitis macularia***	SPSA		X	X			x						X	X	X	X	X
Common Snipe ***Gallinago gallinago***	COSN	X	X	X			X	X				X			X		
Mourning Dove ***Zenaida macroura***	MODO	X	X	X	X	X	X	X			X	X	X	X	X	X	X
Rock Dove ***Columbia livia***	RODO		X						X	X		X		X	X		
Eastern Screech-Owl ***Otus asio***	ESOW	x					x										
Great Horned Owl ***Bubo virginianus***	GHOW			X			x	X				x	X				
Common Nighthawk ***Chordeiles minor***	CONI		x														

Species	Species Code	SBC BO	EL	SV	CC LO	SU	MI	VV	BC CU	30	WA	KA	ER	PR SH	LE	7P	GW
Broad-tailed Hummingbird ***Selasphorus platycercus***	BTHU	X	X	X					X				X	X			
Belted Kingfisher ***Ceryle alcyon***	BEKI			X	X	X	X				X	X	X	X	X	X	X
Northern Flicker ***Colaptes auratus***	NOFL	X	X	X	X	X	X		X	X	X	X	X	X	X	X	X
Downy Woodpecker ***Picoides pubescens***	DOWO	X	X	X	X	X	X		X	X	X	X	X	X	X	X	X
Hairy Woodpecker ***Picoides villosus***	HAWO												X				
Western Wood-Pewee ***Contopus sordidulus***	WWPE	X	X	X	X	X	X	X	X		X	X	X	X		X	
Dusky Flycatcher* ***Empidonax oberholseri***	DUFL						X	X							X		
Cordilleran Flycatcher ***Empidonax occidentalis***	COFL										X						
Say's Phoebe ***Sayornis saya***	SAPH						X	X									
Eastern Kingbird ***Tyrannus tyrannus***	EAKI			X	X	X	X	X			X	X	X	X		X	X
Western Kingbird ***Tyrannus verticalus***	WEKI			X		X	X	X			X	X	X				
Loggerhead Shrike ***Lanius ludovicianus***	LOSH																
Warbling Vireo ***Vireo gilvus***	WAVI	X	X		X	X	X	X	X	X		X	X	X	X	X	X

Species	Species Code	SBC BO	EL	SV	CC LO	SU	MI	VV	BC CU	30	WA	KA	ER	PR SH	LE	7P	GW
Red-eyed Vireo ***Vireo olivaceus***	REVI		X	X	X		X										
Plumbeus Vireo ***Vireo plumbeus***	PLVI																
American Crow ***Corvus brachythynchos***	AMCR	X	X		X				X	X	X			X	X		
Common Raven ***Corvus coraxr***	CORA		X				X										
Blue Jay ***Cyanocitta cristata***	BLJA	X	X	X	X		X	X	X	X	X	X		X	X	X	X
Black-billed Magpie ***Pica pica***	BBMA	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Tree Swallow ***Tachycineta bicolor***	TRSW																
Violet-green Swallow ***Tachycineta thalassina***	VGSW								X								
Bank Swallow ***Riparia riparia***	BNSW	X	X	X	X	X	X	X			X	X	X	X	X	X	
Cliff Swallow ***Hirundo pyrrhonota***	CLSW	X	X	X	X	X	X	X		X	X		X	X		X	X
Barn Swallow ***Hirundo rustica***	BASW	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Northern Rough-winged Swallow ***Stelgidopteryx serripennis***	RWSW	X	X	X	X	X		X			X	X	X			X	X
Red-breasted Nuthatch* ***Sitta canadensis***	RBNU					X	X								X		X

Species	Species Code	SBC BO	EL	SV	CC LO	SU	MI	VV	BC CU	30	WA	KA	ER	PR SH	LE	7P	GW
White-breasted Nuthatch ***Sitta carolinensis***	WBNU													X			
Black-capped Chickadee ***Parus atricapillus***	BCCH	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
House Wren ***Troglodytes aedon***	HOWR	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Veery ***Catharus fuscescens***	VEER																
Swainson's Thrush* ***Catharsus ustulatus***	SWTH				X						X				X	X	
Hermit Thrush* ***Catharus guttatus***	HETH																
American Robin ***Turdus migratorius***	AMRO	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Gray Catbird ***Dumetella carolinensis***	GRCA		X				X	X		X						X	X
Northern Mockingbird ***Mimus polyglottos***	NOMO						X	X									
Brown Thrasher ***Toxostoma rufum***	BRTH						X	X							X		
Cedar Waxwing ***Bombycilla cedrorum***	CEWX							X						X			
European Starling ***Sturnus vulgaris***	EUST	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Orange-crowned Warbler* ***Vermivora celata***	OCWA															X	

Species	Species Code	SBC BO	EL	SV	CC LO	SU	MI	VV	BC CU	30	WA	KA	ER	PR SH	LE	7P	GW
Yellow-rumped Warbler* ***Dendroica coronata***	YRWA		X												X		
Chestnut-sided Warbler ***Dendroica pensylvanica***	CSWA															X	
Ovenbird* ***Seirus aurocapillus***	OVEN															X	
Northern Waterthrush* ***Seiurus noveboracensis***	NOWA															X	
Yellow Warbler ***Dendroica petechia***	YEWA	X	X	X	X	X	X	X		X	X	X	X	X	X	X	X
Common Yellowthroat geothlypis trichas	COYE	X	X	X			X	X		X	X	X	X	X	X	X	X
Yellow-breasted Chat ***Icteria virens***	YBCH					X	X	X			X	X					
American Redstart ***Setophaga ruticilla***	AMRE					X							X				
Lark Sparrow ***Chondestes grammacus***	LASP																
Song Sparrow ***Melospiza melodia***	SOSP		X	X	X	X	X	X		X	X	X	X	X	X	X	X
Spotted Towhee ***Pipilo maculatus***	SPTO		X	X	X	X	X	X									
Green-tailed Towhee* ***Pipilo chlorus***	GTTO					X		X									
Chipping Sparrow* ***Spizella passerina***	CHSP					X	X								X	X	

Species	Species Code	SBC BO	EL	SV	CC LO	SU	MI	VV	BC CU	30	WA	KA	ER	PR SH	LE	7P	GW
Vesper Sparrow* ***Pooecetes gramineus***	VESP		X				X	X									
Clay-colored Sparrow* ***Spizella pallida***	CCSP					X	X										
Brewer's Sparrow* ***Spizella breweri***	BRSP						X										
Grasshopper Sparrow* ***Ammodramus savannarum***	GRSP							X									
White-crowned Sparrow* ***Zonotrichia leucophrys***	WCSP						X	X									
Lincoln's Sparrow* ***Melospiza lincolnnii***	LISP		X	X				X								X	
Blue Grosbeak ***Guiraca caerulea***	BLGR			X		X	X	X				X	X	X	X	X	X
Lazuli Bunting ***Passerina amoena***	LZBU		X			X	X	X				X	X		X	X	X
Indigo Bunting ***Passerina cyanea***	INBU		X		X	X	X					X			X		
Black-headed Grosbeak ***Pheucticus melanocephalus***	BHGR					X		X									X
Rose-breasted Grosbeak* ***Pheuticus ludovicianus***	RBGR					X	X										
Bobolink* ***Dolichonyx oryzivorus***	BOBO											X					
Red-winged Blackbird ***Agelaius phoeniceus***	RWBL	X	X	X	X		X	X		X	X	X	X	X	X	X	
Brewer's Blackbird ***Euphagus cyanocephalus***	BRBL	X	X	X	X	X	X	X		X		X	X	X	X	X	

Appendix II (continued).

Species	Species Code	SBC BO	EL	SV	CC LO	SU	MI	VV	BC CU	30	WA	KA	ER	PR SH	LE	7P	GW
Yellow-headed Blackbird* ***Xanthocephalus xanthocephalus***	YHBL															X	
Western Meadowlark* ***Sturnella neglecta***	WEME	X	X	X	X	X	X	X			X	X	X	X	X	X	X
Bullock's Oriole ***Icterus bullockii***	BUOR	X	X	X		X	X	X		X	X	X	X	X	X	X	X
Orchard Oriole ***Icterus spurius***	OROR											X	X				
Brown-headed Cowbird ***Molothrus ater***	BHCO	X	X	X	X	X	X	X			X	X	X	X	X	X	X
Common Grackle ***Quiscalus quiscula***	COGR	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Lesser Goldfinch ***Carduelis psaltria***	LEGO		X	X		X	X	X		X		X	X				
American Goldfinch ***Carduelis tristis***	AMGO	X	X	X	X	X	X	X		X	X	X	X	X	X	X	X
House Finch ***Carpodacus mexicanus***	HOFI	X	X	X	X	X	X		X	X	X		X	X	X	X	
Red Crossbill* ***Loxia curvirostra***	RECR																
Pine Siskin ***Carduelis pinus***	PISI						X										
House Sparrow ***Passer domesticus***	HOSP	X	X		X	X			X	X	X			X	X	X	