INTRODUCTION: HABITAT FRAGMENTATION AND WESTERN BIRDS

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Habitat fragmentation and loss due to human activities has been identified as the most important factor contributing to the decline and loss of species worldwide (Noss and Cooperrider 1994). Although the response of species to habitat loss generally is clear, the effects of habitat fragmentation are much more complex (Fahrig 1997, Bunnell 1999). Over the last two decades, our understanding of the effects of habitat fragmentation on bird populations has increased tremendously. Early studies viewed habitat fragments as islands and interpreted patterns of species richness in the context of island biogeography theory (Forman et al. 1976, Galli et al. 1976). It soon became apparent, however, that in contrast to oceanic islands, the habitat or matrix surrounding fragments profoundly influenced the ecological conditions within those fragments. In particular, rates of nest predation and cowbird parasitism of ground-nesting and cup-nesting birds were found to be extremely high close to forest edges (Ambuel and Temple 1983) and in small forest fragments (Wilcove 1985, Robinson 1992). Further study revealed that patterns of nest predation, and especially nest parasitism, were influenced by forest cover in the surrounding landscape (Andrén and Angelstam 1988; Andrén 1992, 1994, 1995; Robinson et al. 1995, Donovan et al. 1997). Taken together, these results suggested that declines and losses of birds from small forest fragments were related to elevated rates of nest predation and parasitism. These observations led to the development of a top-down hierarchical model that included regional, landscape-level, and local effects to explain variation in nesting success across the landscape and subsequent changes in abundance and distribution of the affected species (Thompson et al. this volume). Because much of the empirical support for this model derives from studies conducted in the eastern United States (i.e., east of the Rocky Mountains), this model embodies what can be viewed as the "eastern paradigm."

As better understanding of the human-imposed dynamics and the natural ecological processes that govern western landscapes has accrued in recent years, applicability of the eastern paradigm to landscapes of the western United States has become more tenuous. First, the nature of the matrix in most western ecosystems differs dramatically from the East. Habitat fragments studied in the eastern United States frequently are embedded in agricultural or urban landscapes, but most studies of habitat fragmentation in the West have focused on forest fragments created by timber harvest. Logging operations result in fragments of mature or oldgrowth forest that are embedded in a matrix of young, regenerating forest. Landscapes composed of young forest, in contrast to agricultural and exurban landscapes, may not harbor high densities of predators and brood parasites, and consequently birds inhabiting fragments may not suffer the high rates of nest predation and parasitism observed in the East. While the extent of urban and agricultural development is increasing in the West, it is substantially less than in the East (Fig. 1). As a result, fragments of natural vegetation generally are embedded in a matrix of agricultural and urban land in the East, but urban and agricultural lands generally are isolated in a matrix of unconverted habitat in the West (Fig. 2). Clearly there are some regions in the western United States that exhibit patterns similar to the East. For instance, 71% of California's Central Valley and 63% of Oregon's Willamette Valley have been converted to agricultural or urban uses, which is similar to the high levels of conversion in many eastern and Midwestern regions (T. L. George, unpubl. data).

A second suite of fundamental differences between eastern and western landscapes results in a higher degree of natural heterogeneity in the West. Greater aridity, the greater spatial extent and temporal frequency of fires, and greater topographic diversity made western landscapes inherently more patchy than eastern landscapes long before European settlement (Hejl et al. this volume, Kotliar et al. this volume). Having contended with the natural heterogeneity of western landscapes for thousands of generations, avian populations inhabiting this region may be less affected by fragmentation processes and consequences than avian populations of the relatively more homogeneous landscapes of the pre-European-settlement eastern United States. If nothing else, these differing selective milieus make it difficult to predict the responses to disturbance (whether natural or anthropogenic) by species inhabiting western landscapes.

The primary objective of this volume was to



FIGURE 1. Proportion of land converted to agriculture or man-made structures in the conterminous United States in 66 physiographic regions. Proportions were calculated from the U.S. Geological Survey Land Use and Land Cover (LULC) database compiled between 1975–1985 (Mitchell et al. 1977). The LULC database included 45 categories (Anderson et al. 1975); we combined all agricultural and developed land into an "altered" category (see Appendix) and calculated the proportion of altered and unaltered land within each region. The physiographic regions are those used by Robbins et al. (1986) for analyses of the Breeding Bird Survey data.

examine the effects of habitat fragmentation on western bird populations, particularly in the context of predictions derived from eastern paradigms. We defined the western United States as the area from the Rocky Mountains west to the Pacific Coast in the conterminous United States. The following chapters are grouped into three sections covering theory and continental-scale comparisons, effects of fragmentation in specific western ecosystems, and studies of focal species.

Thompson et al. begin by describing and summarizing evidence for the eastern paradigms and provide a multi-scale working hypothesis for the effects of habitat fragmentation on birds. Franklin et al. provide a definition of habitat fragmentation, paying particular attention to the distinction between habitat fragmentation and habitat heterogeneity, and Sisk and Battin review the concept of habitat edge as it applies to western landscapes. The ubiquitous role of fire in shaping western landscapes and their associated avifaunas is addressed by Kotliar et al.

Studies that span the continent offer a unique opportunity to compare the response of birds and their nest predators and parasites to fragmentation in the East and the West. Morrison and Hahn summarize studies of the response of Brown-headed Cowbirds (Molothrus ater) to fragmentation in the East and the West. Cavitt and Martin examine differences in rates of nest predation and parasitism between fragmented and unfragmented areas in the East and the West using data on the outcome of tens of thousands of nests in the BBIRD database (Martin et al. 1997). Employing data from the Cornell Laboratory of Ornithology's "Birds in Forested Landscapes" project, Hames et al. compare the responses of tanagers, thrushes, and Brownheaded Cowbirds to forest fragmentation across the United States.

Six chapters focus on individual western ecosystems selected to reflect both the relative importance of specific vegetation communities and the constraint of where fragmentation-related re-





FIGURE 2. Examples of the distribution of altered and unaltered habitat in the midwestern and the western United States. Land cover data were obtained from U.S. Geological Survey Land Use and Land Cover (LULC) database compiled between 1975–1985 (Mitchell et al. 1977).

search has been conducted in the West. Three chapters focus on coniferous forests. George and Brand summarize studies in redwood (Sequoia sempervirens) forests, Manuwal and Manuwal summarize research in the wet coniferous forests of the Pacific Northwest, and Heil et al. examine forests of the northern Rocky Mountains. Knick and Rotenberry describe avian responses to fragmentation in the Intermountain shrubsteppe, Bolger summarizes a wealth of studies that have been conducted in the highly urbanized coastal sage scrub and chaparral regions of southern California, and Tewksbury et al. analyze riparian bird communities across seven riparian systems in five western states. Notably lacking are summaries of the effects of fragmentation on birds in the southern Rocky Mountains and the desert Southwest. There were too few studies on the effects of habitat fragmentation on birds in these regions to warrant reviews. A recent publication by Knight (2000) provides an overview of the effects of habitat fragmentation in the southern Rocky Mountains.

Finally, as a reflection of the relatively great attention paid to loss and fragmentation of oldgrowth forests in the western United States, two chapters are devoted to multi-scale assessments of focal species in the context of loss and fragmentation of their old-growth forest habitats. Franklin and Gutiérrez synthesize information across subspecies of Spotted Owls (*Strix occidentalis*), and Raphael et al. examine Marbled Murrelets (*Brachyramphus marmoratus*). Both of these species have had a significant impact on management of western forests.

Although the picture is far from complete, the contents of this monograph illustrate the state of our knowledge regarding fragmentation effects on western bird populations at the beginning of the 21st century. We hope this volume will serve as a landmark contribution to the ecological and conservation literature by presenting a solid synthesis and foundation to buttress future research, and by conveying important policy implications for public land management in the western United States.

Anderson ^a land use category	Altered
Urban or built-up land	1
Residential	1
Commercial and services	1
Industrial	1
Transportation, communication, utilities	1
Industrial and commercial complexes	1
Mixed urban or built-up land	1
Other urban or built-up land	1
Agricultural land	1
Cropland and pasture	1
Orchards, groves, vineyards, nurseries, and ornamental horticultural	1
Confined feeding operations	1
Other agricultural land	1
Rangeland	0
Herbaceous rangeland	0
Shrub and brush rangeland	0
Mixed rangeland	0
Forest land	0
Deciduous forest land	0
Evergreen forest land	0
Mixed forest land	0
Water	0
Streams and canals	0
Lakes	0
Reservoirs	0
Bays and estuaries	0
Wetland	0
Forested wetland	0
Nonforested wetland	0
Barren land	0
Dry salt flats	0
Beaches	0
Sandy areas not beaches	0
Bare exposed rock	0
Strip mines, quarries, gravel pits	0
Transitional areas	0
Tundra	0
Shrub and brush tundra	0
Herbaceous tundra	0
Bare ground	0
Wet tundra	0
Mixed tundra	0
Perennial snow or ice	0
Perennial snowfields	0
Glaciers	0

APPENDIX. Land Use Categories in USGS Database Designated as Altered (1) or Unaltered (0) for Figures 1 and 2 $\,$

^a From Anderson et al. (1922).