AN ABSTRACT OF THE THESIS OF

Oriane Williams Taft for the degree of Doctor of Philosophy in Wildlife Science presented on June 4, 2004.
Title: Influence of Wetland Landscape Structure on Shorebirds Wintering in an Agricultural Valley

Abstract approved: Redacted for Privacy

Susan M. Haig

Understanding how wetland birds use habitat is pivotal to developing successful and beneficial conservation strategies. Although it has been an ardent topic in forest research for some time, how species interact with the spatial patterning of habitat across a landscape (i.e., landscape structure) has been more or less neglected in wetland research. There is every reason to believe that landscape structure might influence wetland birds, especially since most species are highly mobile and so many wetland landscapes are inherently heterogeneous. Moreover, as a result of the agricultural development of riverine valleys, many former wetland landscapes have undergone profound changes in landscape structure. To ultimately determine how such landscapes should be restored, researchers need to integrate information generated from three basic questions: what was the historical nature of the landscape?, what is the present-day distribution of habitat and resources?, and most importantly, how do wetland species currently interact with local (within wetlands) and landscape (within a region) habitat distribution?

This dissertation examines these questions for the Willamette Valley ("Valley") of northwestern Oregon, USA. The Valley is an excellent model landscape

for such a study as wetland loss from agriculture and urban development has been severe, waterbirds use the many unprotected agricultural wetlands distributed across the region, and many agencies and coalitions are interested in restoring the Valley using an integrated landscape approach. To understand how conservation efforts should proceed at both a local and landscape scale, I assessed the: 1) historical (circa 1840) nature and waterbird use of Valley wetlands, 2) typical distribution of wetland habitat and invertebrate resources today, and 3) current influences of wetland landscape structure and local conditions on winter wetland habitat use by a highly mobile but relatively understudied group of waterbirds – shorebirds (*Charadriiformes*). I began by compiling a profile of the historic Valley from historical land cover data and primary accounts (e.g., from naturalists, settlers, fur trappers). The distribution of 'shorebird habitat' (wet, $\leq$50% vegetation cover) during two winters of vastly differing rainfall (1999-2000: wet winter, 2000-2001: dry winter) was then mapped using a combination of remotely sensed imagery and data acquired in the field. I estimated invertebrate resources of Valley wetlands by sampling the benthos of sites potentially attractive to shorebirds. Finally, I monitored wetland use (frequency of occurrence, abundances) by two focal shorebird species (Dunlin *Calidris alpina*, Killdeer *Charadrius vociferus*) over the same two winters (wet and dry) and examined how use of regions and individual wetland sites were related to wetland landscape structure (amount of shorebird habitat within regions) and landscape context (amount of shorebird habitat surrounding sites), respectively. I also used locally measured features (availability of shorebird habitat and invertebrate abundance within wetlands) to assess evidence for hierarchical habitat use (influence

of shorebird habitat within and surrounding sites) and to determine if landscape context mediated the influence of local food abundance on bird use. I analyzed data using multiple linear regression and information theoretic (AIC$_c$) approaches to model selection.

Historical research revealed that Valley wetlands were of three valuable types to nonbreeding waterbirds (i.e., emergent wetlands, riverine wetlands, and wetland prairie) and the numbers and diversity of waterbirds using these wetlands was generally much greater than they are today. The most extensive wetland habitat type was wetland prairie, which functioned as valuable fall/winter habitat for waterbirds, but only while native Kalapuyans managed the region with fire. Current land cover data from the winters of 1999-2001 indicate that while prime shorebird habitat (wet, unvegetated) on agricultural land can be abundant and widely distributed in wet years, it is typically scarce and more aggregated during dry winters. Compared to resource levels in winter at other important wintering regions in North America, invertebrates of Valley wetlands were of moderate abundance for most sites sampled. Finally, model selection results indicated that landscape structure was an important positive determinant of Dunlin abundances within regions and within wetlands, but only during the dry winter. Dunlin abundances at sites were also positively associated with local conditions (amount of available wet habitat, percent of soil exposed, invertebrate food abundance) during the dry winter. Killdeer use of sites was unrelated to landscape structure and local conditions during both winters.

Overall, results from this dissertation indicate that wetland landscapes like the Valley hold great potential for restoration and that landscape planners should consider

the spatially-explicit nature of wetland sites (where they are located in relation to others) when prioritizing sites to conserve. Within individual wetlands prioritized for conservation, managers should then promote certain local conditions (shallowly flooded and exposed substrates, productive invertebrate communities) that benefit foraging shorebirds and other waterbirds. Contributing to the field of landscape ecology, this study is among the first to examine the relationship between landscape pattern and ecological processes in wetland systems, specifically for wetland birds in winter. It illustrates the potential influence of landscape structure in any wetland region, and thus the importance of considering the spatial distribution of habitat for the successful conservation of wetlands and waterbirds.

Influence of Wetland Landscape Structure on Shorebirds
Wintering in an Agricultural Valley

by
Oriane Williams Taft

A DISSERTATION

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Doctor of Philosophy

Presented June 4, 2004
Commencement June 2005

Doctor of Philosophy dissertation of Oriane Williams Taft presented on June 4, 2004.

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I understand that my dissertation will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my dissertation to any reader upon request.

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Oriane Williams Taft, Author

ACKNOWLEDGEMENTS

I owe much gratitude to my graduate advisor, Susan Haig, for all her support,

guidance, professional advice, friendship and incredible patience as she saw me

through all phases of this project. I thank my committee members, Robsen

Bonnichsen, Gay Bradshaw, John Hayes, Nathan Schumaker, and David Williams for

their expertise, support and encouragement. Gay has been pivotal in encouraging me

to think creatively, and has treated me to many enlightening discussions; John has

provided me with invaluable advice on tenable research hypotheses and study design

and encouraged me to stay up-to-date by participating in many graduate seminars over

the years; and Nathan has provided much enthusiastic advice from the mind of a

modeler, always guiding me to synthesize and see the big picture.

I am forever indebted to my field assistants, Jennifer Dhundale, Matt

Henschen, Wendy Jensen, Heidi Packard, and Michael Taft for their immense and

CONTRIBUTION OF AUTHORS

This project was performed in the laboratory of Dr. Susan Haig, who provided

financial support, original thought, aid with study design, assistance in manuscript

organization and writing, and wet lab and office space throughout the study. Chris

Kiilsgaard contributed to the research presented in chapter 2 by helping with the

collection of ground reference data, and processing and classifying RADARSAT

imagery to develop final land cover maps of the Willamette Valley during the winter

of 1999-2000.

TABLE OF CONTENTS

TABLE OF CONTENTS (Continued)

TABLE OF CONTENTS (Continued)

TABLE OF CONTENTS (Continued)

TABLE OF CONTENTS (Continued)

LIST OF FIGURES

LIST OF TABLES

This dissertation is dedicated to my family - Michael and Fiona -

for their patience, support and sacrifice towards the completion of my degree.

1. Influence of Wetland Landscape Structure on Shorebirds Wintering in an Agricultural Valley

1.1. General Introduction

Understanding how wildlife species use habitat is the cornerstone to developing predictive wildlife-habitat models and successful strategies for habitat conservation (Verner et al. 1986, Manly et al. 1993). Although habitat has been most simply described as an area with the combination of resources and environmental conditions promoting occupancy and allowing individuals to survive and/or reproduce (Krebs 1985, Morrison et al. 1992), habitat for most species varies at a number of spatial and temporal scales (Wiens 1985, Hansson et al. 1995). While the former component of this definition tends to focus on habitat components at small scales within a particular species' perceived environment (e.g., nest sites, foraging locations), the latter considers distribution of resources at much larger scales (e.g., across a species' regional winter range). How the spatio-temporal nature of habitat influences the distribution of wildlife species has been generally overshadowed by traditional research on the local characteristics influencing species' use of habitat (e.g., characteristics within individual forest stands, within individual wetlands, or surrounding nests; MacArthur and MacArthur 1961, Cody 1985). This is most likely because management plans have typically focused on relatively small parcels of land (e.g., refuges) rather than on integrated landscapes (Saunders et al. 1991). Clearly, to develop predictive models and conservation plans for entire regions will require expanding the scales at which we conduct research.

For many systems, questions addressed by landscape ecologists have greatly advanced research approaches to studying wildlife-habitat associations. Landscape ecology addresses how the spatial and temporal patterning of habitats influences ecological processes (Forman and Godron 1986, Turner 1989). A basic tenet of the field is that all natural ecosystems are spatially and temporally heterogeneous, that all species live in such environments, and that this heterogeneity has important ecological implications for the organisms inhabiting them (Pickett and White 1985, Forman and Godron 1986, Turner 1989, Hansson et al. 1995). *Landscape* can be interpreted as an area of land that encompasses this heterogeneity (Turner 1989), a dynamic mosaic of patches of differing habitat suitability (e.g., Wiens 1985, Forman and Godron 1986, Wiens et al. 1993), or a land area intermediate in size between a typical individual's home range and the regional distribution of the species (Noss 1991, Dunning et al. 1992). It is the amount and spatial patterning of patches, a feature termed *landscape structure* (Turner 1989) that not only distinguishes different landscapes apart (Dunning et al. 1992, Gustafson 1998), but likely influences ecological processes such as resource use (Wiens 1989). Recognition of the potential importance of landscape structure has led to a recent surge of habitat studies undertaken at landscape scales (100s of meters to 100s of kilometers; e.g. Farmer and Wiens 1998, Howell et al. 2000, Austen et al. 2001, Roshier et al. 2001, Luck and Daily 2003).

Recent interest in the consequences of landscape structure has been driven by concerns over the detrimental effects of habitat loss and fragmentation, particularly in forested ecosystems (Lubchenco et al. 1991, Noss and Csuti 1994). However, wetland

landscapes have been similarly, if not more, affected by habitat degradation (Mitsch et al. 1994). Worldwide, wetlands have suffered a long history of degradation and fragmentation from agricultural and urban development because most wetlands occur in association with fertile and topographically flat coastal or inland floodplains, (Howe 1987, Saunders et al. 1991). Consequences of this loss (as much as 50% for many countries; Dahl 1990, Mitsch 1994) have been similar across landscapes: entire wetlands have been lost or compromised in size and quality, thus changing formerly expansive wetland regions into mosaics of small and isolated wetlands in a matrix of urban or agricultural land (Gibbs 1993, Semlitsch and Bodie 1998). Despite these vast and discouraging changes, species' responses to landscape structure have only recently gained the attention of wetland ecologists (e.g., Haig et al. 1998, Naugle et al. 1999, Calmé and Desrochers 2000, Fairbairn and Dinsmore 2001, Riffell et al. 2003).

Among wetland-dependant species, shorebirds (Order *Charadriiformes*) are a likely group to respond to the spatial pattern of wetlands in a landscape. Most shorebirds are wetland obligates, relying for their survival on invertebrate food resources that flourish and are accessible under a restricted set of aquatic conditions. Thus, shorebirds likely perceive wetlands as true patches in a relatively inhospitable matrix (*sensu* MacArthur and Wilson 1967). Moreover, shorebirds are extremely mobile, and able to opportunistically find available habitat both locally (in meters; e.g., Conners et al. 1981, Warnock and Takekawa 1996) and regionally (in kilometers; Warnock and Takekawa 1995, Warnock et al. 1995, Roshier et al. 2002, Sanzenbacher and Haig 2002a). In winter when local food resources are relatively scarce, shorebirds

likely supplement energy intake by visiting multiple wetlands in a landscape (*sensu* Dunning et al. 1992). These traits increase the likelihood that wetland landscape structure is of importance to the distribution of shorebird species in many regions.

The Willamette Valley of northwestern Oregon ("Valley") provides an excellent model landscape, and the wintering population of shorebirds that reside here a useful model group, with which to address the influence of wetland landscape structure on wetland dependent species. As a result of agricultural and urban development over the last 200 years, the Valley has undergone a long history of alteration to the spatial distribution of wetlands (up to 70% loss/conversion of native wetlands; chapter 2: Taft and Haig 2003). Today, Valley wetlands primarily occur on federal and state refuges and private agricultural lands, and collectively support as many as 40,000 or more shorebirds throughout the winter. Spatial patterning of wetlands across a landscape most likely influences mobile species during periods when local resources are scarce or easily depleted, a situation shorebirds likely experience in the Valley during the winter. Moreover, various government agencies and non-profit coalitions have committed to protect, enhance and restore wetland habitat in the future, but they are in need of information to help design spatially strategic and effective conservation plans.

Research presented in this dissertation was designed to aid conservation design in the Valley while also breaking new ground in wetland landscape ecology by exploring how wintering shorebirds interact with the spatial and temporal distribution of wetland habitat at large (over kilometers) and hierarchical scales, and whether the

spatial nature of habitat mediates influences of other local characteristics (i.e., food abundance within wetlands) on habitat use. My overall objectives were to: 1) gain perspective on historical wetlands and waterbird use in the Valley, 2) quantify present-day spatial distribution of wetland habitat under differing winter conditions (e.g., dry, wet), 3) assess typical invertebrate resources in wetlands occurring on agricultural land, and 4) understand how landscape structure influences shorebird use of wetland patches, including potentially mediating the influence of wetland invertebrate abundance.

1.2. Dissertation Organization

This dissertation consists of five chapters written with my coauthors for peer-reviewed journals. Chapters 2 and 3 have been published, and chapters 4-6 are to be submitted in 2004 for publication.

Chapter 2 provides a profile of native wetlands and their use by nonbreeding waterbirds (e.g., waterfowl, wading birds, and shorebirds) within the Willamette Valley circa 1840. We developed this profile by synthesizing information from historical primary accounts (e.g., from explorers, travelers, settlers, farmers 1820-1880) with contemporary knowledge of these wetland systems. Chapter 2 was a necessary foundation for this dissertation as knowledge of the extent, spatial distribution, condition, and use of historic habitat provides invaluable insight regarding the relative importance of restoring wetlands in a region, where spatially

restoration efforts should focus, and manipulations needed to emulate historic functions of wetland habitat.

Using the Willamette Valley as an example, Chapter 3 documents the use and value of radar remote sensing (RADARSAT) to map the distribution of wetland habitat used by shorebirds in an agricultural landscape. In regions where cloud cover is persistent, such as occurs for much of the duration of winter months in Oregon, optical sensors (e.g., Landsat Thematic Mapper) are unreliable for collecting necessary data to develop land cover maps. Moreover, existing land cover maps for the Valley were insufficient to quantify wetland landscape structure for components of this dissertation pertaining to wetland spatial ecology (chapters 4 and 6). We therefore acquired imagery on three dates coinciding with the early, mid, and late winter periods of 1999-2000 (an average year for rainfall) and simultaneously collected ground reference data to classify radar signatures and evaluate map accuracy of four habitat classes (class 1: wet, $\leq$50% vegetation cover; class 2: wet, >50% vegetation cover; class 3: dry, $\leq$50% vegetation cover, class 4: dry, >50% vegetation cover). We considered class 1 of greatest value to most wintering shorebirds.

In the agricultural setting of the Willamette Valley, Chapter 4 examines the influence of wetland landscape structure and context on intensity of site use (frequency of occurrence and bird abundances) by two shorebird species (Dunlin *Calidris alpina* and Killdeer *Charadrius vociferus*). Research presented in this chapter is based on the hypothesis that during winter when invertebrate food can be locally limited within wetlands and mobile birds are thus compelled to supplement

energy intake by using multiple sites, the spatial pattern of wetlands across a landscape should influence site use. We compared relationships among three seasons (early, mid, late) within the wet winter of 1999-2000 and between years [wet winter (1999-2000) vs. dry winter (2000-2001)] as each of these time periods differed in rainfall and subsequent distribution of habitat. We took a dual-level approach to studying this question by analyzing shorebird use within a sample of 100 km^2 regions differing in landscape structure [area (ha) of shorebird habitat (wet, unvegetated) in region] and intensity of use of individual sites differing in landscape context (wetland area within a species-defined radius). At the site level, we additionally assessed the influence of two local characteristics (percent of exposed soil and area of wet habitat) to evaluate multi-scale use of habitat.

Chapter 5 assesses variation in abundance (density individuals/m^2, biomass mg/m^2) and general community composition of benthic invertebrates at a sample of wetlands potentially used by shorebirds on agricultural land in the Willamette Valley during the same two winters (1999-2000, 2000-2001) differing in rainfall. Chapter 5 focuses on quantifying food abundance in agricultural wetlands to evaluate the relative importance of wetland landscapes like the Valley to wintering shorebirds. Such research also provides a first step towards evaluating the potential carrying capacity of a region through restoration and enhancement of wetland food resources.

Chapter 6 combines aspects of chapters 4 (influence of landscape structure) and 5 (local invertebrate abundance at sites) by evaluating whether the landscape contexts of sites (amount of wetland habitat surrounding sites) mediates the influence

of local food abundance on wetland use by Dunlin and Killdeer over a wet (1999-2000) and dry winter (2000-2001). Like chapter 4, chapter 6 is based on the premise that during winter when local invertebrate resources may be limited and mobile wetland birds are compelled to use multiple sites, wetland spatial distribution is likely influential. However, for chapter 6, we focused on the degree to which the discovery (and subsequent revisiting) of wetland sites with high food abundance might be influenced by their particular location in the landscape (their landscape context). Thus to understand the combined influence of food abundance and landscape context, we monitored bird use (frequency of occurrence and abundance) at a sample of wetlands differing in invertebrate density and biomass, the amount (ha) of adjacent shorebird habitat within a 2-km radius, and distance to nearest wetland neighbor.

Chapters 4 and 6 highlight a number of implications for the conservation (i.e., protection, enhancement and restoration) of wetland landscapes like the Valley, and provide specific recommendations for spatial planning and wetland enhancement to maximally benefit shorebirds and other waterbirds.

HISTORICAL WETLANDS IN OREGON'S WILLAMETTE VALLEY: IMPLICATIONS FOR RESTORATION OF WINTER WATERBIRD HABITAT

Oriane Williams Taft and Susan M. Haig

2. Historical Wetlands in Oregon's Willamette Valley: Implications for Restoration of Winter Waterbird Habitat

2.1. Abstract

Before agricultural expansion in the 19th century, river valleys of North America supported expanses of wetland habitat. In restoring these landscapes, it is important to understand their historical condition and biological function. Synthesizing historical primary accounts (from explorers, travelers, settlers, and farmers) with contemporary knowledge of these wetland systems, we developed a profile of the wetlands and their use by nonbreeding waterbirds (e.g., waterfowl, wading birds, and shorebirds) within the Willamette Valley, Oregon, ca. 1840. We found evidence for three types of wetlands used by non-breeding waterbirds in fall, winter, and spring: emergent wetlands, riverine wetlands, and wetland prairie. The most extensive wetland type was wetland prairie, which functioned as fall/winter habitat for waterbirds, but only while native Kalapuyans managed the region with fire. Since the mid-1800s, four species, in particular, have decreased their use of the Willamette Valley: Trumpeter Swan (*Cygnus buccinator*), Snow Goose (*Chen caerulescens*), Sandhill Crane (*Grus canadensis*), and Long-billed Curlew (*Numenius americanus*). Information suggests that ca. 1840, waterbirds and their habitats were more abundant in the Willamette Valley than today. Restoration of the Willamette Valley landscape is warranted, and today's agricultural wetlands – former wetland prairie – hold highest restoration potential.

2.2. Introduction

Conversion of river valleys into agricultural landscapes accounts for the earliest and most profound loss of North American wetlands (Dahl 1990, Vileisis 1997, Mitsch and Gosselink 2000). The most vulnerable river valleys were characterized by open wet prairies and wide river floodplains. These features made them fertile farmland and facilitated their conversion into agricultural land by Euro-American settlers in the 1800s (Robbins 1997, Vileisis 1997, Nelson et al. 1998). Moreover, the extensive and spatially-uniform nature of agricultural settlement resulted in loss of these wetlands on a landscape scale (Maizel et al. 1998).

In the last few decades, there has been an increased recognition of wetland loss (>50% for many countries), the valuable functions of wetland ecosystems (e.g., flood control, water quality, wildlife habitat), the decline of numerous migratory waterbirds (Orders Anseriformes, Charadriiformes, Ciconiiformes, Gruiformes) and other wetland-dependant species, and the importance of conservation and restoration efforts at large spatial scales (Smith et al. 1989, National Research Council 1992, USFWS and CWS 1994, Mitsch and Gosselink 2000, Brown et al. 2001). As a result, many agencies are beginning to acknowledge the need to design and implement region-wide wetland restoration and wildlife conservation plans for agricultural river valleys in North America.

Successful restoration efforts rely on knowledge of the ecological condition of landscapes prior to European settlement (National Research Council 1992, Sisk 1998). For waterbird conservation, knowledge of the extent, spatial distribution, condition,

and use of historic habitat provides insight regarding the relative importance of restoring wetlands in a region, effective spatial locations for restoration, and manipulations needed to emulate historic functions of wetland habitat. Although we can deduce the location of historic wetland sites from hydric soils data, inferring their biological characteristics and the diversity and abundance of waterbirds that used them requires historical research.

For many pioneers in the 1840s, the Willamette Valley of Oregon was viewed as a paradise (Gibson 1985, Boag 1992, Robbins 1997). The Willamette Valley ("Valley") would undergo a substantial transition in land use since then, impacting native wetlands and other habitats (Gibson 1985, Robbins 1997). Today, remaining wetlands are primarily dispersed among small urban remnant wetlands, a few duck hunting clubs, four state and federal wildlife refuges, and hundreds of scattered agricultural wetlands. Unlike refuge wetlands, however, agricultural wetlands receive no formal protection. Collectively, these wetlands annually support at least 200,000 waterfowl and 40,000 or more shorebirds in winter and an unknown number of migrants in spring and fall (Johnson 1993, Gilligan et al. 1994, Nehls 1994, Sanzenbacher and Haig 2002 a,b, Robert Trost *pers. comm.*).

With large estimates for Valley-wide wetland losses and conversions (Hulse et al. 1998, Daggett et al. 1998, Christy et al. 2000) and continued yearly loss of habitat (Bernert et al. 1999), local and federal agencies and coalitions recognize the need to protect and restore Valley wetlands (Good and Sawyer 1998, Drut and Buchanan 2000, Morlan 2000, Oregon Wetlands Joint Venture 2001, Willamette Restoration

Initiative 2001). However, the historical importance of these habitats to waterbirds and the impact of land-use change on waterbird populations have not been considered fully. We investigated the historical Willamette Valley at the time of early Euro-American settlement (ca. 1840). Our objectives were to deduce 1) the nature of historical wetland habitat suitable for waterbirds, 2) the spatial extent of these wetlands, and 3) their historical use during the non-breeding season (fall, winter, spring) by waterbirds. In addition, we present the history of changes to Valley wetlands and waterbird use.

2.3. Study Area

The historical landscape of the Willamette Valley is a 9100 km^2 area of lowland plains within the Willamette Basin of western Oregon, varying in width from about 20 to 60 km, and covering a north-south length from Portland to Eugene of roughly 290 km (Benner and Sedell 1997, Hulse et al. 1998). The prominent hydrologic feature of the Valley is the northerly-flowing Willamette River and its 13 major tributaries, which drain 29,000 km^2 (Gregory et al. 1998). The climate of this region is cool Mediterranean, with an average annual rainfall of 100-125 cm, 75% of it falling between October and March (Jackson and Kimerling 1993). Average temperatures range from 1° C in January to 30°C in July (Oetter et al. 2000). The Valley includes two distinct topographic sub-ecoregions: 1) *Willamette River and Tributaries Gallery Forest* - the river, tributaries and associated bottomland forests within the floodplain and 2) *Prairie Terrace* - a flat fluvial terrace upslope of the bottomland floodplain

(Clark et al. 1991, Pater et al. 1997). Today, lands in these regions grow a variety of crops, including grass seed, vegetable crops, fruit orchards, nursery and greenhouse stock, peppermint, and Christmas trees; grass seed fields are most prevalent (Hulse et al. 1998, Oetter el al. 2000). Currently, 70% of Oregon's population lives in the Valley (Hulse et al. 1998).

2.4. Methods

Although waterbirds as a group are associated with a wide variety of aquatic habitats, we looked for information on shallow-wetland species only, namely shorebirds (order Charadriiformes), dabbling ducks, geese, and swans (order Anseriformes), wading birds (order Ciconiiformes) and cranes (order Gruiformes). We did not consider certain cryptic species (e.g., American bittern *Botaurus lentiginosus* Rackett, rail spp.) that may have been common, but too inconspicuous to provide historical information. Within each of these groups, we searched for information on 21 species that presently winter and/or migrate through the Valley, plus four species that were formerly common but presently uncommon or even rare: Trumpeter Swan (*Cygnus buccinator* Ord), Snow Goose (*Chen caerulescens* Linnaeus), Sandhill Crane (*Grus canadensis* Linnaeus), and Long-billed Curlew (*Numenius americanus* Bechstein) (Gabrielson and Jewett 1940, Gilligan et al. 1994, Nehls 1994, Marshall et al. 2001).

Waterbirds generally feed in wetlands with features that maximize the abundance and accessibility of their foods, such as seeds (primarily dabbling ducks),

new shoots of wetland plants (geese), tubers and rhizomes (geese, swans), and aquatic invertebrates (shorebirds and waterfowl) (Fredrickson and Reid 1986, Helmers 1991). These features include saturated or shallowly flooded (<25 cm) substrates (e.g., for dabbling ducks and shorebirds) that are relatively open with soft sediments (e.g., unvegetated mudflats for shorebirds) or covered with new, short grass or wetland plant shoots (e.g., for grazing waterfowl) (Colwell and Oring 1988, Ehrlich et al. 1988, Hands et al. 1991, Baldassarre and Bolen 1994). Consequently, to understand the nature of Valley wetlands for waterbirds, we sought historical information on degree of saturation/flooding and vegetative structure of Valley habitats.

We searched the literature beginning with Lewis and Clark's 1805-06 expedition to the Columbia River (when the Willamette River was first described; Perrine 1924), but we focused on the period 1820-1880, the years of Euro-American exploration and settlement of the Willamette Valley (Robbins 1997). Primary sources included fur trapper's journals, explorer/naturalist's logs, missionary writings, early settler-farmer diaries, promotionist's reports, and government documents. Secondary sources included habitat maps, geomorphology studies, anthropological research, and prior work on the historical Willamette River and its floodplain.

2.5. Results and Discussion

2.5.1. Historical Wetlands

Christy et al. (2000) reconstructed a map of historical (ca. 1850) Willamette Valley land cover using data from General Land Office (GLO) surveys (e.g., Nelson et al.

1998) and other sources (e.g., Soil Survey Geographic (SSURGO) database (USDA 2000)). We combined classes described by Christy et al. (2000) into wetland categories important to waterbirds following Cowardin et al. (1979) terminology. These were *emergent wetland* (i.e., permanent, semi-permanent, or seasonally flooded emergent marsh and aquatic bed according to Cowardin et al. (1979)), *riverine wetland* (i.e., emergent, scrub-shrub, forested and open water wetlands and sloughs associated with the river floodplain), and *wetland prairie* (i.e., emergent seasonal wet grassland, which generally occurs on poorly drained flat to gently sloping lowland soils (Wilson 1998)). Wetland prairie was most extensive at 121,488 ha (Christy et al. 2000; Figure 2.1). In wetland prairie, poor drainage and low evaporation allow winter precipitation to accumulate, resulting in shallow, standing water (Finley 1995, Wilson 1998). Coverage for riverine wetlands was not calculated, but the estimate of 117,917 ha by Christy et al. (2000) for total "riparian and wetland forest" plus "open water" (rivers, sloughs, beaver ponds, lakes) illustrates the potential of this habitat. Emergent wetlands (3,599 ha) comprised a small fraction of total wetland habitat.

2.5.1.1. Emergent Wetlands. The largest examples of this wetland type were located in the Tualatin Basin (Wapato Lake) and near present-day Salem (Lake Labish; Figure 2.1; Henderson et al. 1916, Scott 1923, Christy et al. 2000). Between the 1830s and 1890s, observers mentioned in passing habitats that were likely emergent wetlands (Hines 1850, Nash 1882, Henry 1897, Scott 1923, Ellison 1932). Other emergent wetlands were associated with the river or tributary streams and maintained by river
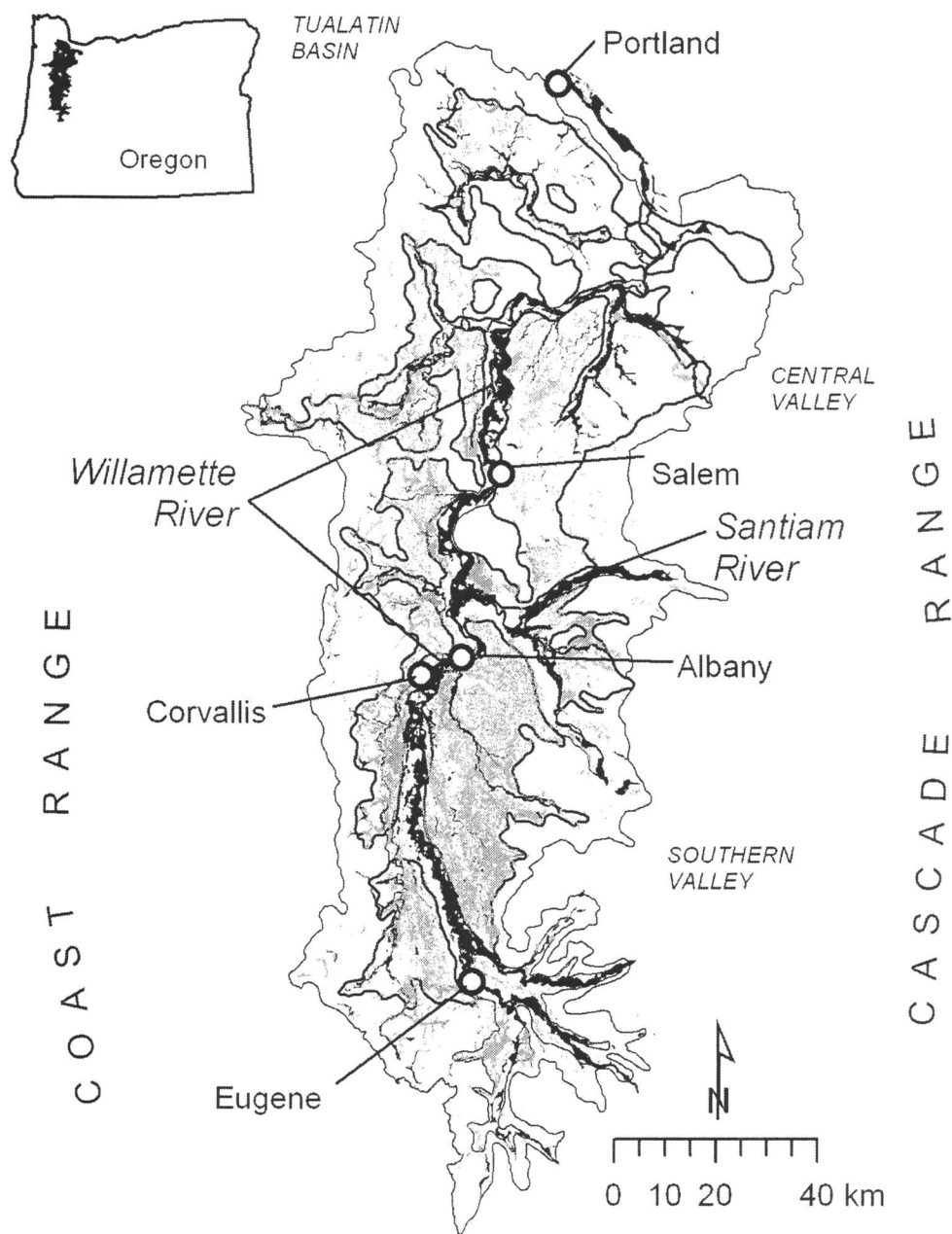
Figure 2.1. Historical (ca. 1850) wetland habitats of the Willamette Valley,
Oregon, with wetland prairie shown in gray and riparian/wetland forest (locations of
probable riverine wetlands) shown in black (modified from Christy et al. 2000).
Emergent wetlands were too scarce to display at this scale. Although not considered
part of the Willamette Valley lowlands, the *Valley Foothills* sub-ecoregion is
displayed surrounding the *Prairie Terrace* and the *Willamette River and Tributaries
Gallery Forest* sub-ecoregions of the Valley lowland proper (Clark et al. 1991, Pater et
al. 1997).

overflow and a higher water table (Sedell and Froggatt 1984, Holland 1994, Gregory et al. 1998).

2.5.1.2. Riverine Wetlands. Historically, the winter volume of the Willamette River dispersed across its 1.5- to 3.5-km-wide floodplain (Benner and Sedell 1997, Miller 1999). This active floodplain was broadest in the southern Valley where the alluvium was more gently-sloping (Sedell and Froggatt 1984). As a result, riverine wetlands were historically more numerous in the southern Valley. There were numerous floodplain tributaries draining the upland terrace and foothills (Benner and Sedell 1997). Dynamic river processes (high water events, gravel movement, large wood recruitment, sediment erosion and deposition) maintained extensive off-channel habitats - side channels, alcoves, sloughs, shallow lakes and linear ponds (Sedell and Froggatt 1984, Benner and Sedell 1997, Landers et al. 2002). Prior to trapping in the early 1800s, beaver (*Castor canadensis* Kuhl) also contributed to this complexity by ponding water (Sedell and Froggatt 1984, Benner and Sedell 1997, Robbins 1997). Snags and wood jams created slackwater pools and trapped organic debris. Floods were relatively frequent and played an important role in connecting the active river channel to the floodplain (Benner and Sedell 1997, Miller 1999). Flooding would also increase area of temporary flooded lowlands (Perrine 1924).

These processes resulted in an extensive surface area of shallow riverine shoreline with slow-moving or stagnant waters (Benner and Sedell 1997, Hulse et al. 1998). Such habitat would be of value to foraging and resting waterbirds, especially

waterfowl and large wading birds (family Ardeidae). Side channels created islands within the floodplain (Gregory et al. 1998, Landers et al. 2002), which along with floodwater scouring, provided open (unvegetated) roosting habitat for waterbirds, especially shorebirds. Finally, the floodplain supported a dense riparian forest (Sedell and Froggatt 1984, Gregory et al. 1998, Hulse et al. 1998) whose organic material provided nutrients and substrates necessary to sustain river invertebrates (Sedell and Froggatt 1984).

Between 1811 and 1852, observers referred to the floodplain surrounding the river as "swampy" with "low ravines or sloughs overflowed with water" in late-fall and winter (Lee 1916, Kendall 1935, Franchere 1954, Palmer 1983). Moreover, many remarked on the regularity with which the river level would rise temporarily with winter rains to overflow into surrounding bottomlands (Hines 1850, Mills 1882, Henry 1897, Wilkes 1911, Howison 1913, Gary 1923, Ellison 1932, Wyeth 1969, Farnham 1977, Palmer 1983, Clyman 1984). Riverine wetlands persisted through spring migration as river overflow from spring snowmelt (Hines 1850, Victor 1872, Mills 1882, Lee 1916, Gary 1923, Parker 1967).

2.5.1.3. Wetland Prairie. Historical accounts from the 1800s and more recent analyses indicate that open prairie was the dominant feature of the Valley before settlement (Minto 1908, Douglas 1959, Habeck 1961, Johannessen et al. 1971, Farnham 1977, Clyman 1984). Given the distribution of hydric soils across the prairie terrace (Parsons et al. 1970, Daggett et al. 1998), roughly half of the Valley prairie

was wetland (Hulse et al. 1998, Figure 2.1). Wet prairie lands were most extensive and continuous south of the Santiam River (between Albany and Eugene), averaging 32 km in width. North of this, wetland prairie was more common west of the Willamette River but patchily distributed east of the river (Bowen 1978, Holland 1994, Figure 2.1). Common wet prairie plant species included Tufted Hair-grass (*Deschampsia cespitosa* Linnaeus) and Camas (*Camassia quamish* Pursh).

The combination of aboriginal fire and ponding from winter rainfall likely shaped the Valley wetland prairie into valuable habitat for many waterbirds. In summer and autumn, the indigenous Kalapuya set fire to prairie vegetation to promote maintenance of food plants, facilitate crop harvesting, and aid in hunting (Zenk 1976, Boyd 1986; see Whitlock and Knox (2002) for a contrary view on the role of aboriginal fire in shaping Valley vegetation). Because fires took place annually, fuel buildup was low and burns were of low intensity (Boyd 1986). Burning was spatially extensive (e.g., Hines 1850, Wilkes 1911, Lee 1916, Scott 1923, Douglas 1959, McLeod 1961, Farnham 1977, Clyman 1984), as also indicated by the pre-contact size of the Kalapuya population (ca. 13,000 people; Boyd 1986) and their dispersed distribution (Poesch 1961). Moreover, the most prominent plant component of the Kalapuya diet was camas bulbs (Zenk 1976, Boyd 1986) that were abundant via reduction of competing woody plants through fire (Wilson 1998).

After fire, birds could access the substrate for food and increase their vigilance for predators. Defoliation from fire was evident from historical accounts in the early 1800s. Many commented on the difficulty in finding fodder for horses (Hines 1850,

Wilkes 1911, Lee 1916, Scott 1923, Douglas 1959, McLeod 1961, Farnham 1977, Clyman 1984) and others observed that vegetation of burned prairies was only 7 cm high in November (Clyman 1984) and 15 cm tall by February (Ball 1833). Moreover, the horizontal structure of prairies was relatively open historically, as mature plants were segregated spatially, with unvegetated spaces between them (Wilson 1998).

Exposed prairie soils would not be attractive to most waterbirds unless saturated or flooded. Evidence for ponding of wetland prairies in the Valley comes from a number of historical accounts. In 1834, trapper John Work reported on prairie lands that were currently or previously inundated from winter rains, mostly in the south Valley (Scott 1923). Prior to the 1880s, many commented on the prairie in winter and spring as "wet and muddy," "covered with water," "too wet for the plow," "percolating quicksands," and in general poorly-drained (Victor 1872, Murphy 1879, Nash 1882, Shafer 1909, Wilkes 1911, Henderson et al. 1916, Hancock 1927, McLeod 1961, Parker 1967, Palmer 1983, Clyman 1984). Consequently, early settlement occurred on the upland prairie-woodland edges of the Valley (Kendall 1935, Bowen 1978, Boag 1992, Bunting 1993). Prevalence of standing winter water was further supported by the springtime presence of mosquitos (Gary 1923, Douglas 1959) and outbreaks of malaria among the Kalapuya (Boyd 1975).

Wetland prairies potentially held valuable food resources for waterbirds. Among common native wet prairie plants identified for the Valley (Wilson 1998), spikerushes *(Eleocharis* spp.), sedges (*Carex* spp.), wild barley (*Hordeum* spp.), and buttercup *(Ranunculus* spp.) have been found in waterfowl diets (Martin and Uhler

1939). For grazing species like geese and American Wigeon (*Anas americana* Gmelin), new forbs and shoots from grasses would have presented browse. Invertebrates important to shorebirds and dabbling ducks (e.g., oligochaetes, diptera larvae, and other aquatic insects) are widespread in their distribution among wetland prairies (Coupland 1979, Pennak 1989).

Contemporary research indicates that the combined effects of burning and flooding can increase the abundance and accessibility of food in wetlands (Lynch 1941, de Szalay and Resh 1997), as well as use by waterbirds (Schlichtemeier 1967, Vogl 1973, Kantrud 1986, Stone 1994). Fire has been used commonly as a waterbird management technique in some marshes and ricefields in North America (Ward 1968, Rutkosky 1978, Kantrud 1986, Weller 1987, Fredrickson and Laubhan 1994, Brouder and Hill 1995, Gabrey et al. 1999). Burning fertilizes and may increase protein content of regenerating plants (Singh and Joshi 1979, Smith et al. 1984, Weller 1987). For invertebrates, fire and standing water at mild temperatures (at least 4^0 C) accelerate decomposition of organic debris by microbes (Kantrud 1986, Brouder and Hill 1995). Finally, fire and flooding aids waterbird access to food (Brouder and Hill 1995).

The Kalapuya subsisted primarily on a diverse assemblage of wild plants and, secondarily, on wild game (Boyd 1986, Boag 1992), including waterfowl harvested during migration and in winter (Jacobs 1945, Zenk 1976). In addition to burning for immediate effects (e.g., to harvest tarweed and collect grasshoppers), they burned for long-term goals (e.g., to promote the continued growth of camas; Boyd 1986), which

allows for the possibility that one long-term goal was to maintain habitat for waterbirds. That the Kalapuya may have used fire to manage for winter waterbirds is also supported by early settler John Minto (1908).

2.5.2. Use By Waterbirds

The most valuable accounts of waterbird use of wetlands are from fur trappers of the 1820-30s because they traversed the Valley in winter as well as fall. Accounts generated from early zoological expeditions (e.g., Newberry 1857, Peale 1858) were less thorough, as they only catalogued birds in fall during migration. Resources were most often recorded in terms of their economic importance (Bunting 1993, Robbins 1997). Thus, birds that were large, gregarious, and hunted more easily made their way into journal entries, while the small, inconspicuous, and non-hunted likely escaped observation. Travels for scientific inventory and other purposes were carried out in fall, spring, and summer, whereas winter travel was avoided.

Most accounts only described a species' presence during a season. Fewer described relative abundances and associated habitats. Among wetland types, there are generally more accounts of waterbirds using wetland prairie. Given that the prairie terrace and rivers were similarly traversed by Euro-Americans (Boag 1992, Robbins 1997), one could interpret this to indicate that waterbirds primarily used wetland prairies for feeding and roosting. We found few accounts of birds using what we thought to be emergent wetlands, perhaps because of their low relative abundance or because of settler's general avoidance of marshes (Robbins 1997).

2.5.2.1. Waterfowl. Waterfowl were the most widely noticed group. Many species of swans, geese, and dabbling ducks were considered abundant during migration and winter (Howison 1913, Clyman 1984; Table 2.1). Of hunted waterfowl, the Kalapuya recognized one swan, three geese, and three duck species (Jacobs 1945, Zenk 1976). Among Euro-Americans, most swans were thought to be Tundra Swans (see Table 2.1 for scientific names), although it is possible that some were Trumpeter Swans. Although common but relatively rare compared to other waterbirds during migration (Newberry 1857, Johnson 1880), there is no direct information on the occurrence of trumpeter swans in winter. Snow Geese were widespread and abundant during migration and winter (Hartlaub 1852, Douglas 1959). In fall, Peale (1858) commented on the large numbers of Snow Geese roosting with White-fronted Geese and cranes on wetland prairie. Kalapuya recognized Snow Geese as distinct from other waterfowl, and they were among waterfowl species hunted regularly (Zenk 1976). Among dabbling ducks, Northern Shoveler and Gadwall seemed to be less abundant than other species.

Early accounts indicate that waterfowl were associated with all three wetland types. On emergent wetlands, Peale (1858), Minto (1908), and Clyman (1984) observed abundant waterfowl during fall. In winter, Prill (1895) observed several species of geese on the "marshes of the valley." Of greater emphasis was the degree to which riverine wetlands were frequented by geese (Wilkes 1911, Farnham 1977) and dabbling ducks (Johnson 1880, Wilkes 1911, Farnham 1977) during migration, and by all waterfowl, including swans, in winter (Prill 1895, Minto 1908, Parker 1967,

TABLE 2.1. Presence and abundance of 25 waterbird species in the Willamette Valley during migration (primarily fall) and winter from 1820 to 1900. Literature searched include accounts from the Willamette Valley to and including the confluence with the Columbia River. Status categories include *abundant* (terms used in accounts include 'abundant,' 'numerous,' 'millions'); *common* - present, but usually indicated in low numbers (terms used in accounts include 'common,' occasional,' 'present'); *rare* - few records (terms used include 'rare'); and *unknown* - no records found for species.

GROUP Species Common Name	Order *Scientific Name*[a]	Status Migration	Winter	Sources
WADING BIRDS	Ciconiiformes	common	common	Bancroft 1886
Great Blue Heron	*Ardea herodias* Linnaeus	common	common	Newberry 1857, Anthony 1886, Prill 1895, Pope 1895-96, Clyman 1984
Great Egret	*Ardea alba* Linnaeus	common	common	Johnson 1880, Pope 1895-96
Black-crowned Night Heron	*Nycticorax nycticorax* Linnaeus	common	unknown	Peale 1858
CRANES	Gruiformes			
Sandhill Crane	*Grus canadensis* Linnaeus	abundant	abundant	Hartlaub 1852, Newberry 1857, Peale 1858, Johnson 1880, Nash 1882, Anthony 1886, Bancroft 1886, Pope 1895-96, Minto 1908, Clyman 1984

TABLE 2.1. (Continued).

GROUP Species Common Name	Order *Scientific Name*[a]	Status		Sources
		Migration	Winter	
SWANS	Anseriformes	abundant	abundant	Allen 1848, Bancroft 1886, Law 1887, Minto 1908, Howison 1913, Parker 1967, Farnham 1977, Clyman 1984
Trumpeter Swan	*Cygnus buccinator* Richardson	common	unknown	Newberry 1857, Murphy 1879, Johnson 1880, Pope 1895-96, Douglas 1959
Tundra Swan	*Cygnus columbianus* Ord	abundant	abundant	Murphy 1879, Johnson 1880, Anthony 1886, Pope 1895-96, Douglas 1959, plus general sources
GEESE	Anseriformes	abundant	abundant	Nash 1882, Bancroft 1886, Prill 1895, Minto 1908, Douglas 1959, Parker 1967, Farnham 1977, Clyman 1984

TABLE 2.1. (Continued)

GROUP Species Common Name	Order *Scientific Name*[a]	Status		Sources
		Migration	Winter	
Canada Goose	*Branta canadensis* Linnaeus	abundant	abundant	Peale 1858, Murphy 1879, Johnson 1880, Fagan 1885, Anthony 1886, Law 1887, Pope 1895-96, Pope 1896, Douglas 1959
Greater White-fronted Goose	*Anser albifrons* Scopoli	abundant	abundant	Newberry 1857, Peale 1858, Murphy 1879, Johnson 1880, Pope 1895-96, Douglas 1959
Snow Goose	*Chen caerulescens* Linnaeus	abundant	abundant	Hartlaub 1852, Peale 1858, Murphy 1879, Johnson 1880, Nash 1882, Fagan 1885, Law 1887, Elliot 1898, Douglas 1959

TABLE 2.1. (Continued)

GROUP Species Common Name	Order *Scientific Name*[a]	Status		Sources
		Migration	Winter	
DABBLING DUCKS	Anseriformes	abundant	abundant	Allen 1848, Murphy 1879, Fagan 1885, Bancroft 1886, Minto 1908, Howison 1913, Parker 1967, Farnham 1977, Clyman 1984
Mallard	*Anas platyrhynchos* Linnaeus	abundant	abundant	Newberry 1857, Johnson 1880, Nash 1882, Anthony 1886, Bancroft 1886, Law 1887, Pope 1895-96, plus general sources
Gadwall	*Anas strepera* Linnaeus	abundant	common	Johnson 1880, Nash 1882, Anthony 1886, Law 1887, Pope 1895-96, plus general sources
Northern Pintail	*Anas acuta* Linnaeus	abundant	abundant	Newberry 1857, Johnson 1880, Nash 1882, Anthony 1886, Law 1887, Pope 1895-96, plus general sources

TABLE 2.1. (Continued)

GROUP Species Common Name	Order Scientific Name[a]	Status		Sources
		Migration	Winter	
American Wigeon	*Anas americana* Gmelin	abundant	common	Newberry 1857, Peale 1858, Johnson 1880, Law 1887, Pope 1895-96, plus general sources
Northern Shoveler	*Anas clypeata* Linnaeus	abundant	common	Johnson 1880, Law 1887, plus general sources
American Green-winged Teal	*Anas crecca* Linnaeus	abundant	abundant	Peale 1858, Johnson 1880, Nash 1882, Anthony 1886, Bancroft 1886, Law 1887, Prill 1895, Pope 1895-96, plus general sources
SHOREBIRDS	Charadriiformes	common	common	Murphy 1879
Black-bellied Plover	*Pluvialis squatarola* Linnaeus	rare	unknown	Johnson 1880, Law 1887, Minto 1908
Killdeer	*Charadrius vociferous* Linnaeus	abundant	abundant	Newberry 1857, Peale 1858, Johnson 1880, Anthony 1886, Bancroft 1886, Law 1887, Pope 1895-96, Pope 1896, Clyman 1984

TABLE 2.1. (Continued)

GROUP Species Common Name	Order Scientific Name[a]	Status		Sources
		Migration	Winter	
Greater Yellowlegs	*Tringa melanoleuca* Gmelin	common?	common?	Pope 1895-96[b]
Long-billed Curlew	*Numenius americanus* Bechstein	common	common	Peale 1858, Minto 1908
Dunlin	*Calidris alpina* Linnaeus	common	unknown	Johnson 1880
Western Sandpiper	*Calidris mauri* Cabanis	unknown	unknown	none found
Least Sandpiper	*Calidris minutilla* Vieillot	unknown	unknown	none found
Dowitcher spp.	*Limnodromus*	common	unknown	Johnson 1880
Common Snipe	*Gallinago gallinago* Linnaeus	common	common	Newberry 1857, Johnson 1880, Nash 1882, Fagan 1885, Anthony 1886, Law 1887, Pope 1896, Minto 1908, Clyman 1984
Red-necked Phalarope	*Phalaropus lobatus* Linnaeus	common	unknown	Peale 1858, Johnson 1880

[a] From American Ornithologists' Union (1998).

[b] Considered "common?" because Pope 1895-96 only lists Greater Yellowlegs as present in Oregon without specifying season or location of occurrence. Pope was a resident of the Willamette Valley.

Clyman 1984). We found additional observations of geese and dabbling ducks using riverine wetlands, but the particular non-breeding seasons were not specified (Murphy 1879, Nash 1882, Pope 1896). Nash (1882) observed geese roosting on sand and gravel bars of the river during fall. Lastly, wetland prairies were used extensively by foraging and roosting waterfowl. Throughout the early 1800s, swans and geese were commonly noticed feeding and roosting on the "moist prairies" in migration (Peale 1858, Douglas 1959, Clyman 1984) with dabbling ducks joining them on "overflown lowlands" and "grasses of the damp lands" in winter (Allen 1848, Hartlaub 1852, Minto 1908, Howison 1913, Douglas 1959, Clyman 1984).

2.5.2.2. Wading Birds and Cranes. Among wading birds, herons and egrets were considered common in migration and winter (Table 2.1). Newberry (1857) and Clyman (1984) commented that Great Blue Heron were abundant in the 1840-1850s. The Kalapuya recognized this species as distinct from other wading birds (Zenk 1976). We found no information on the association of wading birds with wetland habitat types. During the non-breeding season, wading birds are not gregarious, typically foraging alone or in small groups (Ehrlich et al. 1988). This trait may explain why early observers did not notice these species more often.

Sandhill Cranes were among the waterbird species recognized by the Kalapuya (Zenk 1976), but there is no indication they were hunted. Most accounts of the 1800s speak to the regularity with which cranes were seen during autumn (Table 2.1), but two accounts assert that they were also common in the Valley in winter (Hartlaub

1852, Minto 1908). Most spoke of the Sandhill Crane's affinity to wet prairie (Hartlaub 1852, Clyman 1984), but Minto (1908) noted that cranes wintered in great numbers on all three wetland types. Peale (1858) wrote that migrant cranes prefer "moist open grounds, and roost generally on small sand-bars in the rivers."

2.5.2.3. Shorebirds. There are not as many early (pre-1860) references to shorebirds as there are to waterfowl (Table 2.1). Accounts are mostly of the larger-bodied shorebirds, perhaps because only large species were hunted (Anonymous 1913). Killdeer, Common Snipe, and Long-billed Curlew were the most commonly noted species (Table 2.1). The only early record found for Dunlin was from Johnson (1880), and he commented that they were seen only occasionally during migration. As popular usage of terms was loose, some accounts of snipe may have been of Long-billed Dowitchers or other shorebirds. Indeed, an early common name for Long-billed Dowitcher was "Red-breasted Snipe" (Newberry 1857) and "Jack Snipe" (Takekawa and Warnock 2000). The Kalapuya recognized at least three shorebird species, one of which was presumed to be Common Snipe (Zenk 1976).

Some shorebird species were observed on small "ponds with vegetation" or "wet boggy localities," which we suppose were emergent wetlands (Pope 1896, Minto 1908, Clyman 1984). Peale (1858) collected a Red-necked Phalarope on the Willamette River, and Minto (1908) included shorebirds among the waterbirds observed in winter on riverine sloughs. On wetland prairie, Peale (1858) observed

shorebirds during migration, and Minto (1908) and Clyman (1984) observed them in winter.

Long-billed Curlew were observed on small "ponds with vegetation" (Minto 1908), which we presume were emergent wetlands. Minto (1908) included curlew among waterbirds observed in winter on riverine sloughs. On wetland prairie, Peale (1858) remarked that curlew were "quite common on the prairies of Oregon" during fall, and Minto (1908) found them among the waterbirds that "wintered on the grasses and roots of the damp lands of the valleys." Among shorebirds described by the Kalapuya, one was characterized as "a bird somewhat resembling the crane, but smaller, little, long-legged" (Zenk 1976). We speculate this was the Long-billed Curlew.

2.5.3. Land-Use Changes

2.5.3.1. Chronology and Consequences. Suppression of annual prairie burning was potentially the most overlooked of land-use changes to impact habitat, especially wetland prairie. Malaria left only 600 Kalapuya in the Valley by 1841, and by the mid-1840s, immigrant settlers forced an end to widespread burning (Boyd 1986). Consequently, by 1850, the nature of wetland prairie had changed dramatically. Although the first homesteaders settled on upland dry prairie habitats that were naturally well-drained, by 1871, expansion of railroads on both sides of the river led to an extension of farming activities into the wetland prairie (Woodward et al. 1998). Wheat farming on the wetland prairie gradually diminished wet habitat. With

recognition that these lands were too wet for farming, surface ditching became a major activity between 1860 and 1880 (Bunting 1993, Robbins 1997). By 1880, wheat production had increased from 7 to 176 million liters per year (Boag 1992, Robbins 1997). Surface ditching continued until the early 1900s, at which time, the state of Oregon advocated installation of tile drains as a superior means of draining wet prairie (Williams 1914, Oregon State Planning Board 1938). Thus, by the time burning came into practice again with grass seed farming in the 1940s (Svart 1970), much of the wetland prairie had been drained. Between the 1940s and 1970s, the Valley experienced another intensive effort to drain any remaining problematic areas (USDA Soil Conservation Service 1977).

Wheat farming also resulted in a number of changes to riverine wetlands once the Willamette River became a conduit for agricultural commerce (Sedell and Froggatt 1984, Benner and Sedell 1997). Changes to channel morphology to improve navigation altered natural processes that maintained riverine wetlands (Benner and Sedell 1997, Landers et al. 2002). Steamboats appeared on the river in 1850 (Woodward et al. 1998). Efforts to simplify the river system began in the 1870s when the U.S. Army Corps of Engineers used cut-off dams and dredge spoils to isolate secondary channels and off-channel habitats from the mainstem (Sedell and Froggatt 1984, Benner and Sedell 1997). In-channel large wood was removed and revetments were constructed to constrain the main channel. With bottomland riparian forests felled and loss of secondary channels, off-channel habitats (e.g., sloughs, oxbows, swales, small depressions) adjacent to the river were more easily converted to

farmland (Benner and Sedell 1997). These modifications continued to the 1940s
(Robbins 1997). Along the 25-km stretch between Harrisburg and the McKenzie
River confluence, the Willamette provided 250 km of shoreline in 1854; by 1946, only
82 km of shoreline remained (Sedell and Froggatt 1984). Between 1940 and 1980,
dam construction to restrict flooding events (Hulse et al. 1998) further added to loss of
riverine wetlands (Benner and Sedell 1997).

Loss of Valley wetlands undoubtedly impacted use by many waterbirds.
Described by settler Minto (1908:131):

> "The ditching to drain roadbeds, and drains for field crops and
> cultivated fruits...have all tended to absorb the life-giving surface
> moisture...and the general effect is that the Willamette Valley has
> ceased to be the home of the crane, curlew, gray plover, and
> even the snipe, as well as the...wild duck."

Hunting for sport and the plume market also decreased numbers of many waterbirds,
especially larger shorebirds and wading birds (Finley 1909, Anonymous 1913, Storm
1941). Among species currently occurring in the Valley, Trumpeter Swan, Snow
Goose, Sandhill Crane, and Long-billed Curlew are rare (Gilligan et al. 1994, Nehls
1994, Marshall et al. 2001). Trumpeter Swan, Snow Goose, and Long-billed Curlew
were considered scarce in the Valley as early as 1902 (Woodcock 1902). Gabrielson
and Jewett (1940) considered all four species as rare by 1940.

2.5.3.2. Estimates of Loss/Conversions of Wetlands Used by Waterbirds. Although
estimates of wetland habitat loss and conversion are varied, they provide a general
sense of the extent to which waterbird habitat has been compromised. Hulse et al.

(1998) estimated 57% loss of emergent wetland habitat, 72% loss of bottomland forest, and 99% loss of native wetland prairie. For all wetland types combined (but not including most conversions to agricultural wetlands as extant habitat), Gabriel (1993) estimated a 41% loss/conversion of wetland habitat. Using the Daggett et al. (1998) estimate of 80,848 ha of extant non-agricultural wetlands and the Christy et al. (2000) estimate for historical wetlands, we hypothesize a 67% total loss/conversion of wetland habitat.

2.5.3.3. Restoration Implications. Western settlement and agricultural enterprise of the mid-1800s changed wetland landscapes elsewhere in the Pacific Flyway. Estuarine wetlands along the coasts of Washington (Puget Sound, Grays Harbor, Willapa Bay), Oregon (Columbia River and 21 smaller estuaries), and Northern California (Humboldt Bay) were diked and drained for farmland or urban development (Bortleson et al. 1980, Shapiro and Associates, Inc. 1980, Thomas 1983, Boulé and Bierly 1987). Wetland losses vary from 50 to 95% among these locales (Boulé and Bierly 1987). Further south, reclamation for agriculture, flood control, and development reduced wetland habitat by 75% (Klamath Basin, San Francisco Bay) to 94% (California's Central Valley; Akins 1970, Dennis and Marcus 1984). Thus, given the mobility of migratory waterbirds, negative trends in Valley bird use are likely in response to changes in local habitat availability and to loss of waterbird habitat throughout the flyway. Widespread loss of habitat and populations argues for local restoration of habitat wherever possible.

Understanding historical Valley wetlands and how they functioned for waterbirds provides insight on how to approach local restoration. Numerous agencies are currently involved in Valley wetland inventory, protection, mitigation, and regulation (i.e., Oregon Division of State Lands, U.S. Army Corps of Engineers, U.S. Environmental Protection Agency), as well as wetland creation and restoration (i.e., Oregon Department of Fish and Wildlife, USDA-Natural Resources Conservation Service, U.S. Fish and Wildlife Service). Moreover, two coalitions (Willamette Restoration Initiative, Pacific Northwest Ecosystem Research Consortium) have formed to find sustainable ways to stem further loss and restore habitats in the Valley, including wetlands (Hulse et al. 1998, Willamette Restoration Initiative 2001). However, these agencies and coalitions have focused on emergent wetlands or wetlands associated with the river floodplain. Although much of the former wetland prairie holds the greatest potential for restoration, it has not been factored into overall restoration plans.

Most of the former wetland prairie is now "agricultural wetland," palustrine emergent farmed wetlands that are seasonally flooded (Cowardin et al. 1979). These are cultivated lands where winter ponding temporarily persists, supporting hydrophytes if farming were discontinued (Daggett et al. 1998). Inventories estimate that agricultural wetlands account for at least half of the non-forested wetlands that remain (Daggett et al. 1998, Bernert et al. 1999). To some degree, plowed and newly-planted fields emulate historical fall-burned prairies, and where rainfall is allowed to collect on the field's surface, they somewhat mimic historical winter wetland prairies.

These habitats are used extensively by waterbirds (Budeau 1992, Sanzenbacher and Haig 2002 a,b) but receive little regulatory protection (Morlan and Peters 1999). It is important to identify these wetlands during the rainy season, map their winter distribution (chapter 3: Taft et al. 2004), and work with farmers to examine sustainable ways to enhance their function.

Finally, our findings speak to the potential importance of historic wetland prairie to waterbirds in other landscapes of North America. The east-west spread of agricultural cultivation from 1760 to the present explains why wet prairies are among North America's most endangered ecosystems (Samson and Knopf 1994, Noss et al. 1995, Prince 1997, Maizel et al. 1998). However, outside of the Prairie Pothole Region (i.e., the Dakotas, Minnesota, Saskatchewan, Manitoba), the historic value of wet prairie as migratory and wintering habitat for waterbirds has not been recognized. While many have recognized the value of historic palustrine wetlands in general (e.g., Smith et al. 1989), the value of the specific palustrine wetland type of wet prairie is rarely highlighted. Wet prairies of the river valleys of the Upper Mississippi states between the Missouri and Ohio Rivers (e.g., Illinois, Indiana, Ohio), the eastern Great Plains, and the Central Valley of California likely provided valuable migratory and wintering habitats for many waterbirds. These regions were characterized by river floodplains and vast wetland prairies and meadows on poorly-drained flat lowlands (Prince 1997, Vileisis 1997). Aboriginal groups of these areas similarly used fire as a management tool (Barrett 1980, Boyd 1986, Kantrud et al. 1989, Askins 1997, Nelson et al. 1998), and burning accompanied by surface ponding potentially rendered them

valuable foraging habitat for nonbreeding waterbirds. Like the Willamette Valley, early agricultural settlement resulted in the drainage of their prairies (Winsor 1987, Prince 1997, Nelson et al. 1998) and improved navigation and flood control disconnected rivers from their floodplains (Gregory et al. 1998). Recognition of the historic significance of these former wetland prairie landscapes should bring new resonance to the wetland restoration of agricultural landscapes for waterbirds.

2.6. Acknowledgements

USE OF RADAR REMOTE SENSING (RADARSAT) TO MAP
WINTER WETLAND HABITAT FOR SHOREBIRDS
IN AN AGRICULTURAL LANDSCAPE

Oriane Williams Taft, Susan M. Haig and Chris Kiilsgaard

3. Use of Radar Remote Sensing (RADARSAT) to Map Winter Wetland Habitat for Shorebirds in an Agricultural Landscape

3.1. Abstract

Many of today's agricultural landscapes once held vast amounts of wetland habitat for waterbirds and other wildlife. Successful restoration of these landscapes relies on access to accurate maps of the wetlands that remain. We used C-band (5.6 cm wavelength), HH-polarized radar remote sensing (RADARSAT) at a 38° incidence angle (8 m resolution) to map the distribution of winter shorebird (Charadriiformes) habitat on agricultural lands in the Willamette Valley of western Oregon. We acquired imagery on three dates (10 December 1999, 27 January 2000 and 15 March 2000) and simultaneously collected ground reference data to classify radar signatures and evaluate map accuracy of four habitat classes: 1) wet with ≤50% vegetation (considered optimal shorebird habitat), 2) wet with >50% vegetation, 3) dry with ≤50% vegetation, and 4) dry with >50% vegetation. Overall accuracy varied from 45-60% among the three images, but accuracy of focal class 1 was greater, ranging from 72-80%. Class 4 coverage was stable and dominated maps (40% of mapped study area) for all three dates while coverage of class 3 slightly decreased throughout the study period. Among wet classes, class 1 was most abundant (30% coverage) in December and January, decreasing in March to approximately 15%. Conversely, class 2 increased dramatically from January to March, likely due to transition from class 1 as vegetation grew. This approach was successful in detecting optimal habitat for shorebirds on agricultural lands. For modest classification schemes, radar remote

sensing is a valuable option for wetland mapping in areas where cloud cover is persistent.

3.2. Introduction

Wetlands have received worldwide recognition in the last few decades, especially in light of their alarming loss and significant value to society. Western settlement and agricultural conversion are responsible for the vast majority of the estimated 53% loss of wetlands in the lower 48 U.S. states (Dahl 1990, Mitsch and Gosselink 2000). In the Pacific West, statewide losses are estimated at 31% for Washington, 38% for Oregon, and 91% for California (Dahl 1990) and local losses for estuaries and river basins range from 50% to 95% (Akins 1970, Dennis and Marcus 1984, Boulé and Bierly 1987). Wetland loss has been no less severe for one wetland region in the Pacific Northwest - the Willamette Valley of western Oregon (chapter 2: Taft and Haig 2003). Through modification of river channel morphology and drainage of mesic prairies, the majority of native winter riverine wetlands and wetland prairies that once provided habitat to countless wintering and migrating waterbirds (e.g., waterfowl, wading birds, shorebirds, cranes) have been lost to agriculture. Today, remaining wetlands in the Willamette Valley ("Valley") are primarily dispersed among small urban remnant wetlands, a few duck hunting reserves, four larger state and federally-protected wildlife refuges, and hundreds of scattered unprotected agricultural wetlands ("palustrine emergent-farmed wetlands," Cowardin et al. 1979). The latter represent the legacy of a once vast wetland prairie. With estimates for total

native wetland loss/conversion as high as 67% (chapter 2: Taft and Haig 2003) and continued yearly loss of habitat (Bernert and others 1999), a number of local and federal agencies and coalitions now recognize the urgent need to identify, protect, and restore extant Valley wetlands on a region-wide scale (e.g., Good and Sawyer 1998, Drut and Buchanan 2000, Morlan 2000).

Developing strategic wetland restoration plans on a landscape scale requires a series of maps depicting the spatial and temporal distribution of wetland habitats. While the U.S. Fish and Wildlife Service has completed National Wetlands Inventory (NWI) coverage for the Willamette Valley (USFWS 1991), these maps only portray Valley wetlands that typically occur during the spring growing season, not during the rainy winter months when wetlands are most prevalent. Other comprehensive Valley mapping efforts were also based on imagery acquired in fall or spring (e.g., Kiilsgaard 1999, Oetter and others 2000). Consequently, the principal type of wetland habitat in the Valley – ephemeral agricultural wetlands – has been entirely overlooked. Because these wetlands hold great potential for restoration, it is essential to understand their spatial distribution and temporal dynamics.

Wetland mapping has undergone considerable advancement in the last two decades as researchers have realized the application potential of various satellite remote sensing techniques. While many sensoring platforms have been used to inventory wetlands for monitoring and regulatory purposes (see Lee and Lunetta 1995), wetland biologists have only recently recognized the value of satellite remote sensing in wetland wildlife conservation. The most prominent application of remote

sensing for wetland wildlife conservation has been to map specific habitats important to wetland species on a regional scale (e.g., Wickware and others 1980, Jacobson 1991, Kempka and others 1992, Gratto-Trevor 1996). With auxiliary data on the spatial distribution of individuals and their preferences for different habitats, imagery depicting habitat types can also be used to predict regional distribution or density of a species (e.g., Avery and Haines-Young 1990, Goss-Custard and Yates 1992, Aspinall and Veitch 1993, Morrison 1997, Scott and others 2002). Specialized projects to map particular wetland habitat types are becoming more common as the spatial, temporal or informational resolution of already existing wetland maps often do not match the needs of wetland wildlife biologists.

Most satellite remote sensors are optical {e.g., Landsat Multispectral Scanner (MSS) and Thematic Mapper (TM), Systeme Pour l'Observation de la Terre (SPOT)}, reliant on collecting reflected energy from the Earth's surface at wavelengths in the visible portion of the electromagnetic spectrum (Avery and Berlin 1992, Lee and Lunetta 1995). While these have been used to identify and monitor a variety of wetland types, they exhibit a number of limitations including spectral confusion of wetland and non-wetland categories (Jensen and others 1987, Henderson and others 1999, Bourgeau and others 2001) and most notably an inability to map land surface during periods of cloud cover (Ramsey 1999). Unlike optical sensors, radar sensors (e.g., satellites ERS-1/2, JERS-1, and RADARSAT) do not rely on cloud-free conditions (Metternicht 1999). These actively transmit energy at microwave frequencies (radar) to produce a black and white image from the energy returning to

the sensor after interacting with the Earth's surface. Radar sensors can penetrate clouds, rain, and haze commonly encountered during a rainy season. Moreover, radar is particularly effective at detecting boundaries between water and land, flooding, surface roughness, and moisture content of vegetation and soil, depending on parameter settings (Kasischke and others 1997, Elachi 1988, Metternicht 1999, Ramsey 1999). Wetlands used by waterbirds tend to be shallow with open water unobscured by vegetation, and any vegetation present is typically different from that found within other land cover types (Mitsch and Gosselink 2000). Such features structurally contrast them with the surrounding landscape, making them particularly favorable for radar mapping (Ramsey 1999). In areas with high incidence of rainfall, radar technologies may be useful in mapping standing shallow sheetwater or saturated soil with differing vegetation coverage, conditions common on agricultural wetlands of the Valley.

We recognized the need for a series of maps depicting the typical extent and dynamics of Valley wetlands in order to aid future restoration efforts. In addition, we had a need for such maps to complete a related project addressing determinants of habitat use by the 40,000 or more Valley wintering shorebirds (Order Charadriiformes; Johnson 1993, Nehls 1994, Gilligan and others 1994, Sanzenbacher and Haig 2002 a,b; chapter 4: Taft and Haig *in review* a). Finally, winter cloud cover in the Willamette Valley can be persistent. Thus, using remotely sensed radar (RADARSAT) data, we set out to map winter wetland habitat in the Valley, specifically focusing on agricultural wetland sites frequented by shorebirds. Our

specific objectives were to: 1) evaluate the utility and accuracy of using C-band HH polarized radar remote sensing to develop maps of ephemeral wetland habitat (primarily agricultural) important to shorebirds, and 2) produce three winter cover maps (beginning, middle, and end of winter) identifying wet (either impounded water or shallow sheetwater/saturated soil), unvegetated ($\leq$50% cover) wetland areas used by shorebirds and other waterbirds. In addition, this paper provides examples of potential uses of our maps, and suggests possible approaches for improving radar performance for this particular application.

3.3. Study Area

Within the Willamette Basin of western Oregon, the Valley encompasses 9100 km^2 area of lowland plains (including the "Prairie Terraces" and "Willamette River and Tributaries Gallery Forest" subecoregions, but excluding the "Valley Foothills"; Clark and others 1991, Pater and others 1997) varying in width from about 20 to 60 km and covering a north-south length from Portland to Eugene of roughly 290 km (Figure 3.1; Benner and Sedell 1997, Hulse and others 1998). The prominent hydrologic feature of the Valley is the northerly-flowing Willamette River and its 13 major tributaries that together drain the Willamette Basin, a 29,000 km^2 watershed between the Cascade and Coast ranges of Oregon (Oetter and others 2000). The climate of this region is considered cool Mediterranean (Jackson and Kimerling 1993), with an average annual rainfall of 100-125 cm, and average temperatures ranging from 1° C in January to 30° C in July (Oetter and others 2000).
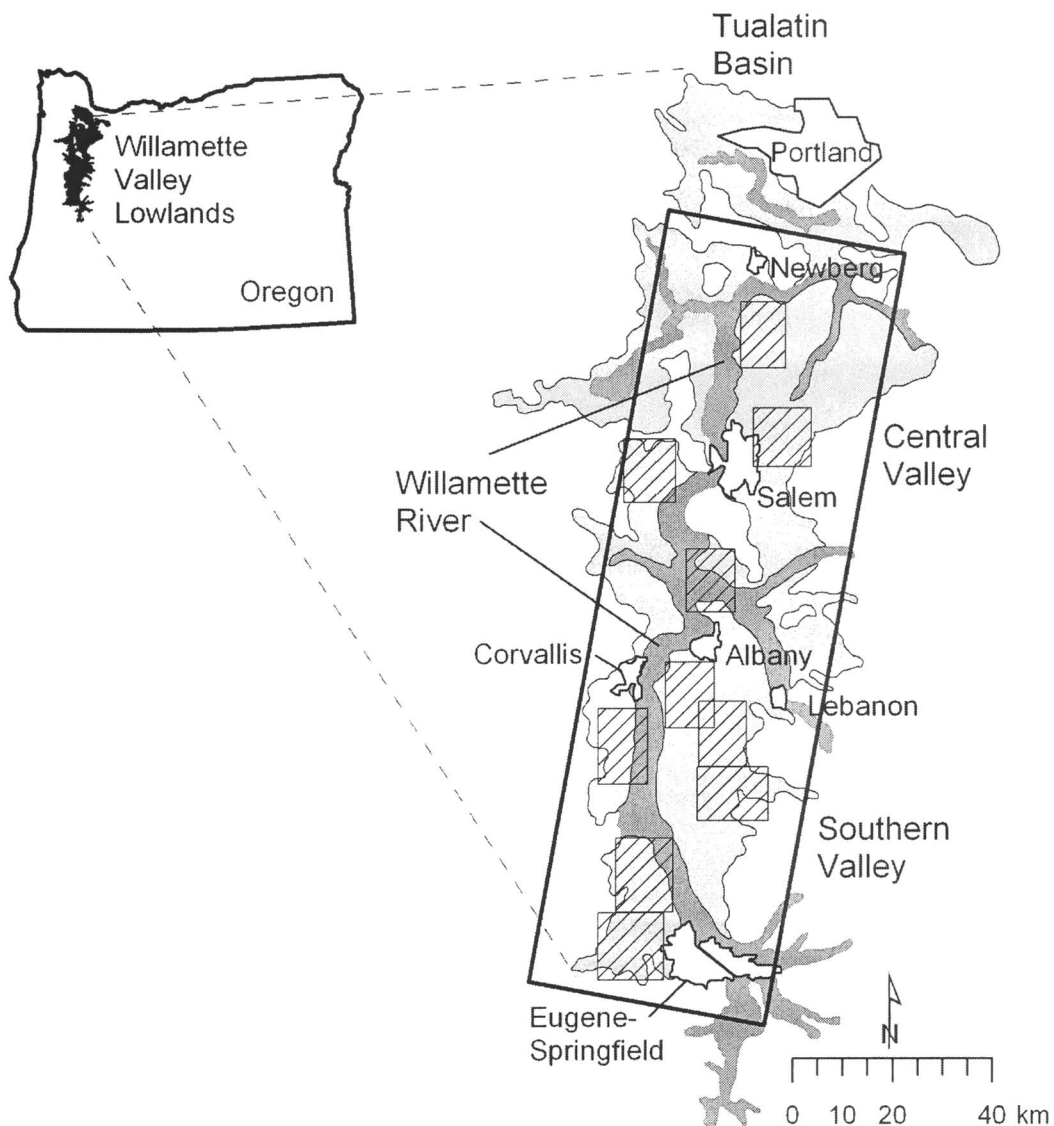
Figure 3.1. The Willamette Valley of western Oregon, including the area covered by radar imagery (large rectangle) and 10 areas of focus for ground reference data collection (small dashed rectangles). The two lowland subecoregions are highlighted in light gray (Prairie Terraces) and dark gray (Willamette River and Tributaries Gallery Forest).

Our map study area included the central and southern regions of the Valley but excluded the Tualatin basin (Figure 3.1). General landforms in the Valley include alluvial terraces and floodplains interrupted by basalt outcrops and gently sloping hills of both volcanic and sedimentary origin (Oetter and others 2000). The majority of the Valley is dominated by agriculture, primarily grass seed fields on the alluvial terraces. Other common lowland crops include vegetable crops, fruit orchards, nursery and greenhouse stock, and peppermint (Hulse and others 1998, Oetter and others 2000). Grass seed crops and peppermint are planted in the fall on plowed, leveled barren fields. While annual ryegrass is replanted every year, perennial ryegrass is generally replanted on a three-year cycle. Vegetable crops are annually plowed in fall and left fallow through the winter. By spring (March), annual grass fields are fully covered with vegetation, while perennial grass fields still provide exposed soil between plants. These agricultural fields potentially hold water in winter where hydric soils predominate (Figure 3.2). Common wintering shorebirds in the Valley include Dunlin (*Calidris alpina*), Killdeer (*Charadrius vociferus*), Common Snipe (*Gallinago gallinago*), Long-billed Dowitcher (*Limnodromus scolopaceus*), Black-bellied Plover (*Pluvialis squatarola*), Greater Yellowlegs (*Tringa melanoleuca*), and Least Sandpiper (*Calidris minutilla*).
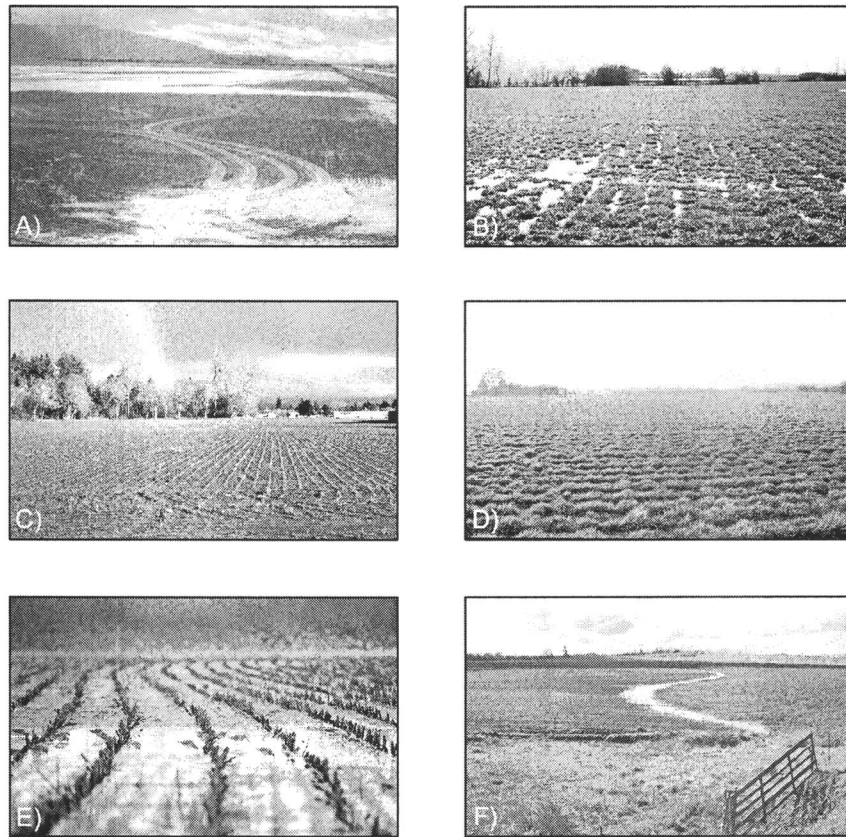
Figure 3.2. Photographs exemplifying typical habitat in the four classes mapped with radar (RADARSAT) remote sensing in the Willamette Valley of Oregon during winter 1999-2000: A) class 1, optimal shorebird habitat: wet, ≤50% vegetation; B) class 2: wet, >50% vegetation; C) class 3: dry, ≤50% vegetation; and D) class: dry, >50% vegetation. Additional photos of class 1 are shown in E) flooded allow corn field with foraging Long-billed Dowitchers (*Limnodromus scolopaceus*) and F) linear agricultural wetland/remnant slough in newly planted grass field; many of these were not mapped if less than about three 8-m pixels (25 m) wide.

3.4. Methods

3.4.1. Classification Scheme

During the winter of 1998-1999, we conducted a preliminary study on the agricultural habitat associations of Dunlin and Killdeer, the two most abundant wintering shorebirds in the Valley. Roughly 90% of fields used by Dunlin were flooded with shallow (<5 cm deep) water and/or had saturated soil. About 70% were covered with less than 50% vegetation. In contrast, Killdeer were more of a wetland generalist; only 50% of used fields held standing water/saturated soil and 55% had less than 50% vegetative cover. Thus, in mapping shorebird habitat on agricultural lands, we focused on identifying flooded fields with exposed soil (less than 50% cover; Figure 3.2E); these conditions are preferred by Dunlin and ecological allies (species in the family Scolopacidae). We designed a classification scheme of four classes based on presence of water and vegetation (Figure 3.2): 1) wet (either impounded water or shallowly flooded) with ≤50% vegetation, 2) wet with >50% vegetation, 3) dry (without visible standing water) with ≤50% vegetation, 4) dry with >50% vegetation. We considered habitat to increase in suitability for shorebirds from the highest class number to the lowest, with class 1 regarded as optimal.

3.4.2. Imagery and Preprocessing

We acquired imagery on three selected days when the Canadian RADARSAT satellite passed over the Valley study area: 10 December 1999, 27 January 2000, and 15 March 2000. Scene acquisition dates were 48 days apart, or on every other 24-day orbit pass.

With these dates we aimed to capture the extent of shorebird wetland habitat at three different time periods: at the onset of early winter rainfall (early December), at the peak of the mid-winter rainy season (January), and during waning rain activity in late winter/early spring (March).

The RADARSAT satellite carries a C-band (5.6 cm wavelength) synthetic aperture radar (SAR) with HH (horizontally transmitted/horizontally received) wavelength polarization (Corbley 1995). All scenes were taken in fine 1 far (F1F) beam mode (8-meter pixel resolution; 38.78° incidence angle) on descending orbits at 14:18 hours. There is a trade-off between pixel resolution and features one can detect with particular incidence angles. Soil moisture and water under grass canopies are best detected at steep incidence angles (<30°) to nadir (Elachi 1988, Ramsey 1995, Biftu and Gan 1999), but RADARSAT imagery at these angles are only available at resolutions of 25 m or greater. Images at 8 m resolution are acquired at larger angles. We chose F1F imagery because we were most interested in detecting standing water in open habitat and because we needed the finest resolution possible to detect small patches of standing water. Scenes at F1F are approximately 50 x 50 km, thus it took three scenes to cover our focal study area (central and southern Valley) on each acquisition date. These images were aligned and acquired north-south so that each final map, once mosaicked, would continuously cover an area roughly 50 x 150 km (4500 km^2), encompassing Valley lowlands in the two subecoregions of interest (Prairie Terraces and Willamette River and Tributaries Gallery Forest; Pater and others 1997) from Eugene to Newberg, Oregon (Figure 3.1). We used Pater and

others (1997) to mask the Valley Foothills subecoregion from radar imagery acquired in the 50 x 150 km swath. Thus, the size of the study area portrayed by final maps was 4209 km^2.

Before rectifying scenes, we used Sigma and Lee filters to reduce speckle noise (Rio and others 2000). Among nine scenes, we were able to reduce coefficients of variation for noise from 0.387-0.399 at raw imagery to 0.213-0.223 at the second pass. We then rectified all December scenes to a 1996 Landsat Thematic Mapper reference image of the Valley. Among the three December scenes, we selected between 18 and 34 ground control points (GCPs) to calculate third-order polynomial transformations used to geo-register input images to the reference scene. Among the three scenes, registration was achieved with an error of 22-28 meters, approximately the size of a Landsat TM pixel (30 m). Scenes for January (using 41-52 GCPs) and March (38-45 GCPs) were geo-registered to the rectified December scenes, also using third-order polynomial transformations. Registration errors were lower among these six scenes, ranging from 4.8-16.7 meters. We used a cubic convolution resampling procedure to assign new coordinate grids to scenes. After geo-registration, the three scenes for each date were mosaicked into composite images used in the classification effort.

3.4.3. Ground Reference Data Collection

For classification and verification, we collected ground reference data from roadsides and aerial flights within 1-2 days of each image acquisition date. Topography of the

Valley alluvial terraces is strikingly flat ($<1^0$ slope), with maximum elevation fluctuations on the order of only meters over a horizontal distance of 10-100 km (Hulse and others 1998). As a result, within individual agricultural fields, surface water tends to accumulate into numerous discrete small (on the order of decameters) shallow ponds (less than 25 cm deep) or as diffuse and widespread "sheetwater" (shallow 1-cm deep water spread across a flat surface; Figure 3.2). Such spatial patterning logistically precluded determining the exact coordinate locations of the boundaries of all individual water bodies. Instead, we considered reference "sites" as entire agricultural fields if they were homogeneous in wetness and cover, or as wet areas within otherwise dry fields (e.g., a large pond, a remnant slough). We could not feasibly quantify soil moisture, water depth, surface roughness, or percent cover of vegetation. Thus, we categorized sites into habitat classes by qualitatively noting the presence and prominence of surface water and visually estimating percent cover of vegetation as $\leq$ or $>$ 50%. We did not separately distinguish habitat with saturated soil (showing a glossy sheen but without standing water) from habitat with sheetwater because they almost always co-occur on a fine spatial scale (meters) within fields.

We selected ground reference sites opportunistically by traversing roads and taking aerial photos in areas with high incidence of hydric soils (Daggett and others 1998). For both modes of data collection, we focused on finding wet, unvegetated sites (class 1, optimal shorebird habitat). Sites in all other classes were interspersed within these areas. We documented a total of 689 reference sites for the December image, 731 for January, and 592 for March. Sites were fairly well interspersed among

classes, but wet classes were better represented. We selected sites in the north and south Valley interspersed among 10 focal areas (Figure 3.1), but due to the concentrated nature of hydric soils, sites within these areas were locally clustered. For January and March referencing, we revisited a large proportion of sites we had visited in December to assess temporal changes.

For roadside-collected data, we located reference sites by estimating the distance and direction to the focal site of interest from a GPS- or landmark-located roadside position (e.g., crossroad). During January and March, we used a laptop computer displaying the December raw imagery and a road layer overlay to concurrently mark locations of sites while in the field. We digitized sites by looking for pixels of uniform radar returns in the close vicinity of estimated locations, and then assigning the site's positional coordinate to a central pixel for each cluster. To aid analyses and temporal comparisons, one or more photos were taken of each roadside site during each of the three dates.

For data collected aerially (in a Cessna 182RG), we took oblique photos of the landscape at approximately 450 m elevation and used visible roads and landmarks to find the coordinate location of focal sites. Because vegetative cover was often difficult to estimate by air, we used aerial photos only to find sites with very little (<10%) vegetation (class 1). Wet fields were obvious because sheetwater/saturated soil appeared glossy and dark from the air.

3.4.4. Image Analysis and Final Maps

We used both supervised and unsupervised classification techniques to associate spectral signature with habitat classes. Using our field data, we were able to distinguish a specific signature to supervise the classification of class 1 habitat only; we used unsupervised training to produce signatures for the remaining classes. For supervised classification of habitat in class 1, we delineated polygons around pixel clusters of homogeneous spectral returns within class 1 reference sites, and calculated mean, standard deviation, minimum and maximum digital values for all pixels within each polygon. We then used a maximum likelihood classification algorithm to delineate class 1 habitat within mosaicked scenes. To classify habitat in classes 2-4, we separated returns remaining in the class 1-masked scene into 50 distinct spectral clusters. We chose the number 50 to accommodate the variability of signatures we expected from the myriad of permutations of wet and dry soils with varying amount of vegetation. Using roughly half of our ground reference dataset (415 sites from December, 448 sites from January, and 308 sites from March) as training sites (randomly chosen), we then visually determined which of the three categories each of the 50 return clusters represented and recoded the 50 clusters into three remaining habitat classes. Finally, we overlaid each of the final classified mosaicked images with urban, forest, and permanent open water (reservoirs, rivers, etc.) land cover using an ancillary map developed from 1996 Landsat TM imagery (Kiilsgaard 1999).

3.4.5. Accuracy Assessment

We assessed accuracy of final maps using the remaining ground reference sites not used for training; this resulted in 274 verification sites for December, 283 for January, and 284 for March. For each site, we compared its predicted class from final maps to the site's true class and constructed an error matrix of these comparisons for each date. The error assessment characterized the accuracy of each map, with commission error or "user's accuracy" (proportion of sites assigned to a class that are correctly assigned) and omission error or "producer's accuracy" (the proportion of sites of a certain class that are correctly assigned) included. For each map, we calculated overall accuracy as the number of correctly classified sites divided by the total number of testing sites.

3.5. Results

3.5.1. Spatial and Temporal Patterns

Among all three maps, the majority of the 4209 km^2 study area was categorized as class 4 (Figure 3.3), with roughly 40% coverage (Figure 3.4). For the December and January maps, class 1 was the next most abundant class predicted (~30% of study area) and class 2 was least prevalent at around 10% coverage. Moreover, optimal shorebird habitat (class 1) was generally dispersed throughout the entire study area. However, concentrations in the southern Valley occurred between Albany and Lebanon and southward, and west of the Willamette River between Corvallis and

Figure 3.3. Final cover maps of Willamette Valley wetlands for three dates in winter 1999-2000.

Legend:
- Wet, Unvegetated
- Wet, Vegetated
- Dry, Unvegetated
- Dry, Vegetated
- Forest
- Open Water
- Urban

0 5 10   20 km

December 10, 1999   January 28, 2000   March 15, 2000

Figure 3.3

■ December 10, 1999

□ January 28, 2000

▨ March 15, 2000
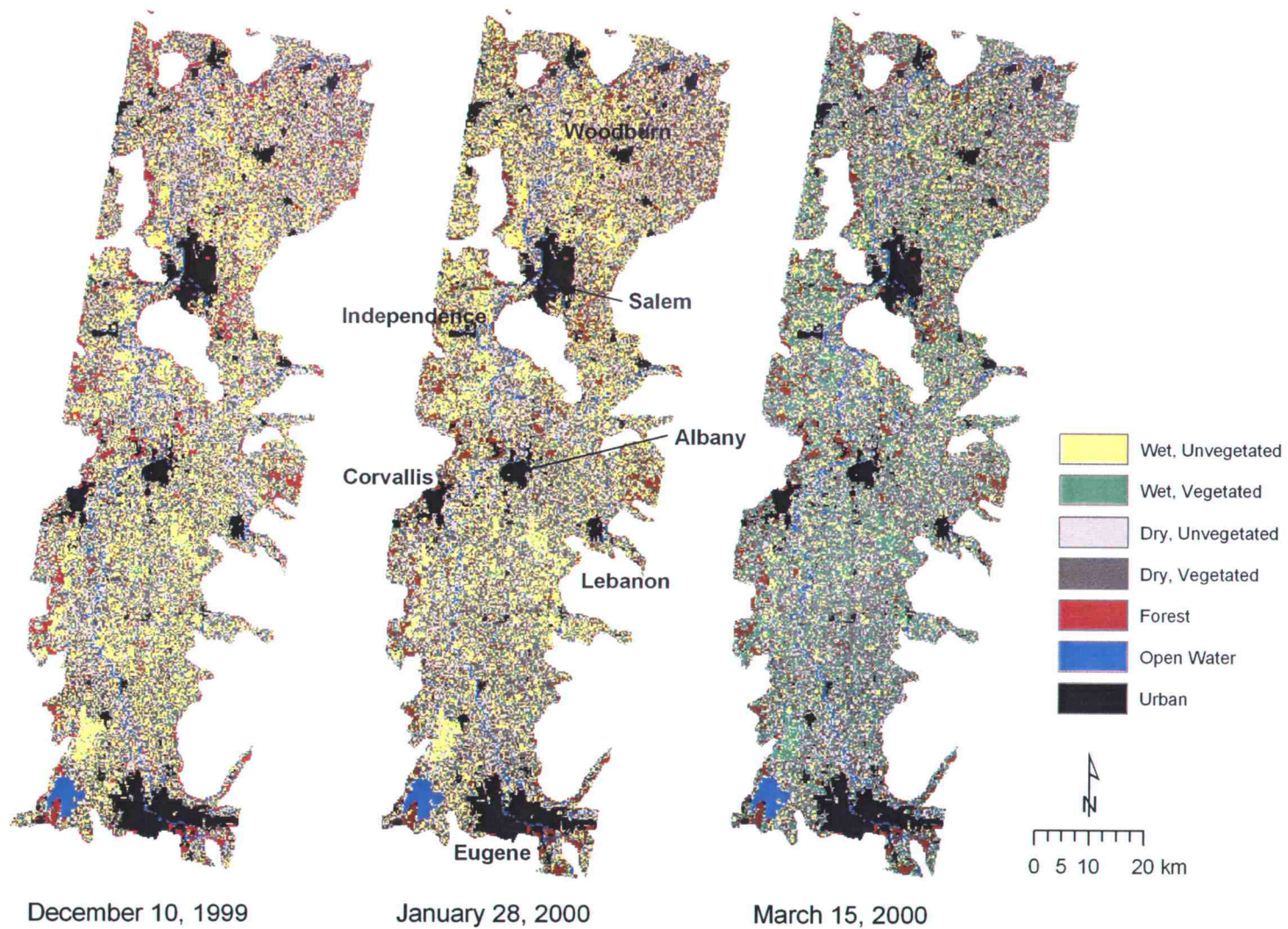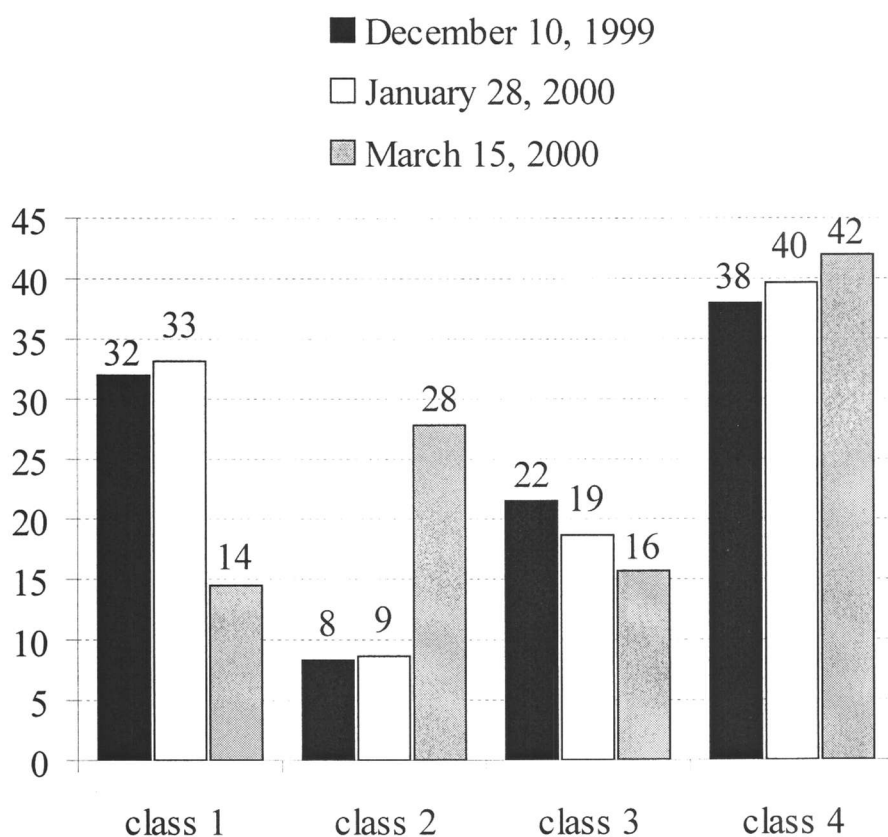
Figure 3.4. Temporal changes in percent cover (of entire Willamette Valley map study area) of four land cover classes across the three image dates during the winter of 1999-2000. Class 1 optimal shorebird habitat = wet, ≤50% vegetation; class 2 = wet, >50% vegetation; Class 3 = dry, ≤50% vegetation; Class 4 = dry, >50% vegetation.

Eugene (Figure 3.3). There were also coalesced patches of class 1 habitat around Independence. In the central Valley, class 1 habitat was most prevalent west and northeast of Salem and west of Woodburn.

Overall, winter 1999-2000 was an average season in rainfall, but precipitation varied across months. Monthly precipitation totals for Corvallis, Oregon were as follows: November (23 cm; 6 cm departure from 1961-1990 average), December (15 cm; -5 cm departure), January (20 cm; 3 cm departure), February (16 cm; 3 cm departure), and March (9 cm; -2 cm departure; Oregon Climate Service 1999-2000). Covering roughly 30% of the study area, optimal shorebird habitat (class 1) was more prevalent in December and January (slightly more in January) than in March (Figure 3.4). Although optimal habitat decreased in March, class 2 habitat increased, retaining the same proportion (40%) of wet habitat (classes 1 and 2 combined) across dates despite monthly variation in rainfall. Likewise, slight declines in coverage of class 3 were mirrored by small increases in class 4 across dates. Estimates for total coverage of wet classes should be viewed with caution, however, as class 2 accuracies were fairly low (see below). The declines of classes 1 and 3 and corresponding increases in classes 2 and 4 may be partially explained by the steady growth of agricultural vegetation. Between January and March, many sites transitioned from class 1 to 2, or from class 3 to 4.

3.5.2. Radar Signatures and Map Accuracy

Among flooded habitat, radar returns for open water found on refuge impoundments, riceponds, and shallow reservoirs (weak return, black image tones) were similar to returns from shallow sheetwater/saturated soil on unvegetated fields (weak return, dark gray image tones). We considered both signatures to display "wet" habitat. Vegetated sites with either a wet or dry substrate under grass canopies gave a brighter return (strong return, lighter gray tones) than unvegetated habitat. Radar returns from dry, unvegetated sites were darker relative to vegetated sites, but brighter (lighter in tone) relative to wet sites.

The error matrix for each map indicates an overall accuracy of 60% for December, 59% for January, and 45% for March (Table 3.1). By pooling cover types into only two classes for wetness - wet and dry – the overall map accuracy increased to 78% for December, 78% for January, and 75% for March. Pooling cover types into two classes for vegetation – ≤50% vegetation, >50% vegetation – overall map accuracies were 72% for December, 69% for January, and 57% for March. For all classification schemes, map accuracy diminished between January and March.

Among the four classes, class 1 (wet, ≤50% vegetation) was most accurately mapped, with user's accuracy for all three maps between 72-80% (Table 3.1). Producer's accuracy was also fairly high in December (83% accuracy) and January (76%). The low producer's accuracy (47%) in March was primarily due to class 1 sites being confused for class 2 (57/175 sites) and class 4 (25/175 sites).

Table 3.1. Error matrix for final land cover maps of the Willamette Valley, Oregon[a]

Map Prediction	Map	Reference				Total	User's Accuracy (%)
		Class 1	Class 2	Class 3	Class 4		
Class 1 -	10 Dec	**135**	33	8	11	187	72
Wet, ≤50%	27 Jan	**130**	33	4	14	181	72
vegetation	15 Mar	**82**	14	3	4	103	80
Class 2 -	10 Dec	6	**9**	1	2	18	50
Wet, >50%	27 Jan	11	**10**	0	1	22	45
vegetation	15 Mar	57	**22**	6	4	89	25
Class 3 -	10 Dec	9	3	**11**	7	30	37
Dry, ≤50%	27 Jan	10	2	**12**	0	24	50
vegetation	15 Mar	11	4	**9**	6	30	30
Class 4 -	10 Dec	13	13	3	**10**	39	26
Dry, >50%	27 Jan	21	11	8	**16**	56	29
vegetation	15 Mar	25	15	7	**15**	62	24
Total	10 Dec	163	58	23	30	**274**	
	27 Jan	172	56	24	31	**283**	
	15 Mar	175	55	25	29	**284**	
Producer's	10 Dec	83	16	48	33		**60**
Accuracy (%)	27 Jan	76	18	50	52		**59**
	15 Mar	47	40	36	52		**45**

[a] Numbers on the diagonal (bold) are reference sites correctly classified whereas those off diagonal signify reference sites (columns) incorrectly predicted into each class (rows). Row totals signify total number of sites predicted in each class whereas column totals signify true total sites of each class used in the analysis.

Classes 2-4 did not map as accurately as class 1. For all three maps, sites of class 2 (wet, >50% vegetation) were highly misclassified, commonly confused for class 1 or class 4 (Table 3.1). Class 3 (dry, ≤50% vegetation) was regularly misidentified as class 1 in December, and as class 4 in January and March. In general, class 4 (dry, >50% vegetation) was moderately confused with each of the other three classes, but especially class 1. The lower user's than producer's accuracy for most classes (Table 3.1) indicates that commission errors tended to be more prevalent than omission errors.

3.6. Discussion

Radar remote sensing proved an effective and valuable tool for mapping habitat important to shorebirds on agricultural lands in winter. Final maps revealed far more shorebird/wetland habitat than was previously thought to exist in the Valley during winter, pointing to the importance of including agricultural habitat in regional restoration and conservation plans. Our error assessments support the notion that single-parameter radar imagery is useful for modest wetland classification schemes (Lee and Lunetta 1995). Moreover, success depends on the number of classes that one hopes to accurately depict. Among classes, we were most interested in mapping the distribution of optimal shorebird habitat, or land in class 1 (wet, ≤50% vegetation). While overall map accuracy was fairly low (45-60%) for each date, the user's accuracy of class 1 was appreciably higher (72-80%). The accuracy of wet habitat was further supported by visually assessing the spatial correspondence of hydric soils

(Daggett and others 1998) with the distribution of classes 1 and 2. Considering class 1 as optimal shorebird habitat interspersed in a matrix of sub-optimal habitat (classes 2-4), accuracy of class 1 habitat was the most meaningful measure for map accuracy.

Some of the map error likely stems from interactions between ground features (land/water boundaries, surface roughness, moisture content) and radar parameter configurations (incidence angle, wavelength, and polarization). These interactions are highly complex and the subject of much research (Lee and Lunetta 1995, Metternicht 1999, Ramsey 1999). First, a given surface will increase in specular reflectance (appear smoother) with larger incidence angles (Avery and Berlin 1992, Sokol and others 2000). Thus, our relatively large incidence angle may have been the source of some error in the confusion of vegetated (class 2 and 4) land cover for wet, unvegetated (class 1) cover, especially habitat with close to 50% vegetation (i.e. 40-60%). Second, detecting water under a grass canopy requires a radar beam emitted at a steep incidence angle (<30 degrees) or with a long wavelength (Ormsby and others 1985, Ramsey 1995, Wang and others 1995). RADARSAT's shallow incidence angle combined with the short wavelength suggests lessened penetration through grass canopies and thus less of a return from flooded vegetated ground (Ramsey 1995, 1999). This may account for confusion among vegetated wet (class 2) and dry (class 4) sites. A third source of error may have been RADARSAT's polarization. Sensors with HH polarization are known to be less sensitive to changes in vegetation moisture content than are cross-polarized sensors (HV or VH; Avery and Berlin 1992). This

may provide an additional explanation for confusion between classes 1 and 2, as moisture in the vegetation of class 2 sites may not have been detected.

Other errors may have been caused simply by similarities among signatures. For example, grass crops of high biomass and homogeneous in horizontal cover and vertical height (e.g., rice, annual ryegrass) tend to act like a smooth surface (similar to calm standing water), decreasing radar returns (Durden and others 1995, Dobson and others 1996). Many of the annual ryegrass sites in class 4 (dry, vegetated) may have been confused for class 1 (wet, unvegetated) for this reason. Moreover, confusion of class 1 sites for class 2 in March may be explained by the fact that many class 1 sites had grown to nearly 50% cover by the third date of imagery.

Had we not chosen to use imagery with the finest resolution from one sensor (RADARSAT), different parameter settings or the use of setting combinations from multiple sensors may have improved mapping performance for non-focal habitats (classes 2-4). While some settings are pre-determined by the RADARSAT sensor (i.e., wavelength and wavelength polarization), others are adaptable to user needs (i.e., incidence angle and associated resolution). Choice of a smaller incidence angle may have lessened confusion between vegetated and unvegetated classes, and/or enabled penetration through grass canopies to distinguish vegetated areas with understory flooding. Similarly, a steeper incidence angle could have been used had detecting differences in soil moisture been our main objective (Dobson and others 1995). Additionally, because backscatter returns vary with all three radar parameters, use of multi-incidence angle, multi-wavelength, or multi-polarization imagery (e.g., Wang

and others 1995, Dobson and others 1996, Bourgeau-Chavez and others 2001) may have provided greater breadth of information for image interpretation (Hess and Melack 1994, Metternicht 1999). For example, by cross-referencing RADARSAT data at multiple incidence angles (e.g., steep 25 m resolution and shallow 8 m resolution), one may be able to produce a map depicting small bodies of standing water while also portraying more information about soil moisture. Multi-wavelength and multi-polarization imagery would require use of two different radar sensors.

Compared to other radar studies, our SAR data performed well in mapping Valley wetlands. Radar satellite sensors have been used to detect coastal wetlands (e.g., Henderson and others 1998, Dwivedi and others 1999), tidal flooding (e.g., Ramsey 1995), freshwater wetlands (e.g., Kasischke and Bourgeau-Chavez 1997), forested wetlands (e.g., Hess and Melack 1994, Bourgeau-Chavez and others 2001), forested and unforested peat bogs and marshes (e.g., Baghdadi and others 2001), and soil moisture (e.g., Dobson and others 1995, Biftu and Gan 1999). However, much of this work has focused on the relationships between radar backscatter returns and particular wetland properties (e.g., flooding, soil moisture), rather than on documenting accuracy of maps created using these relationships. Of the few studies that have documented accuracy, success has been variable. For example, Baghdadi and others (2001) defined six cover types (forested and nonforested peat bog, marsh, open water, clearing and forest) from variable radar signatures using ERS-1 C-band SAR at different polarizations. For one season, they reported a high overall accuracy of 86% for cross-polarized data and 76% for HH polarization. In contrast, Henderson

and others (1998b) examined variation in classification accuracy among ERS and RADARSAT images acquired with various incidence angles and polarizations. They classified coastal wetlands into four classes: estuarine emergent, palustrine emergent, palustrine scrub shrub, and palustrine forested wetland. Accuracy was extremely poor for both sensors and all settings, with 17% as the highest accuracy achieved for any one class. In comparison to these, our results are encouraging. High accuracies found by Baghdadi and others (2001) are partly a function of extreme structural differences among the classes they set out to classify, while high error rates found by Henderson and others (1998b) stem from complex, easily-confused wetland classes (i.e., all of their classes have some kind of flooding and vegetative cover). In contrast to these two studies, our classification scheme was modest, with classes distinct enough to yield sufficient accuracy with the parameter settings we chose.

Among wetland mapping projects that depict waterbird habitat, most have been able to use optical remote sensors (e.g., Avery and Haines-Young 1990, Jacobsen 1991, Gratto-Trevor 1996, Morrison 1997). For single pass imagery, optical sensors (particularly Landsat TM) generally still outperform radar sensors in classification accuracy (e.g., Jensen and others 1993, Gratto-Trevor 1996, Morrison 1997, Henderson and others 1998, Fuller and others 1998, Lunetta and Balogh 1999). Moreover, augmenting radar data with optical imagery will result in the greatest accuracies for wetland maps (Place 1985, Ramsey and others 1998, Pietroniro and others 2000, Töyrä and others 2001). However, for studies where cloud cover can be prevalent, using an optical sensor is seldom an option. Radar imagery enables

mapping important waterbird habitat when it otherwise would not be possible, particularly in regions with persistent cloud cover such as Oregon's Willamette Valley in winter.

Our Valley wetland maps hold promise for a number of local applications. First, the spatial distribution of extensive drainage tiling on hydric soil farmlands in the Valley is poorly documented. Hydric soils maps are not always indicative of where ponding will occur. Using our maps, restorationists can now evaluate which general areas of the Valley would be most optimal for restoration efforts. Additionally, information on the location and dynamics of class 1 habitat at local spatial scales may be useful to resource agencies or watershed councils involved in local restoration in the Valley. Finally, these maps enable examining important questions in landscape ecology that are relevant to restoration and management (e.g., Turner 1989, Scott and others 2002), namely investigating the influence of the spatial and temporal patterning of habitat on distribution, abundance and movements of wetland species in the Valley. With spatially continuous data, one can ask these questions at multiple spatial scales pertinent to the species of interest.

Although class 1 habitat invariably includes many wetlands already identified by the National Wetlands Inventory, much of it depicts agricultural wetlands that were unidentified prior to this study. Thus, by illustrating the great extent of winter wetlands on agricultural land, these maps represent a significant addition to other available wetland maps for the Valley. They also provide a much different picture of the distribution and abundance of potential waterbird habitat in the Valley. In general,

radar remote sensing has the potential to identify both intermittent and permanent flooding not necessarily extractable from National Wetlands Inventory maps with NWI categories. There are a few practical aspects that should be considered in using these maps, however. First, farming practices (affecting patterns of vegetative cover) and rainfall patterns vary annually. Thus within the subset of lands with hydric soils in the Valley, the extent and distribution of shorebird habitat will vary from year to year. Moreover, although waterfowl use agricultural wetlands (Taft and Haig *unpublished data*) and impounded wetlands, the maps fail to accurately map emergent ponds and shallow riparian areas also used by waterfowl and other wetland-dependent species (e.g., amphibians). This is primarily because our focus was on referencing and verifying shorebird habitat in particular. Therefore, final maps can be regarded as depicting the majority of habitat important to shorebirds, but only some of the habitat important to other wetland-dependent species. Lastly, radar was unable to detect linear wetlands (e.g., remnant sloughs, shallow streams) less than three pixels wide (~25 meters), habitat that is frequented by both waterfowl and shorebirds (Figure 3.2F). Consequently, these maps should be regarded as 'snapshot' views of a certain kind of wetland habitat (i.e., agricultural habitat important to wintering shorebirds) in a given year of average rainfall.

3.7. Summary

The specific radar parameters we used (C-band, HH polarization, 38° incidence angle) and our approach (single sensor, single settings for each parameter) performed

well for a modest goal of mapping shorebird habitat at a relatively fine resolution on agricultural lands in winter. When cloud cover restricts use of Landsat TM data, radar imagery may be worth acquiring for projects with similar objectives to ours, especially as availability of imagery increases commercially and financially. Moreover, we may find increased value for radar in mapping wetland habitat for wildlife as future research refines our knowledge of radar-ground feature interactions and as the accuracies of maps created with radar data are further evaluated.

3.8. Acknowledgements

4. Importance of Wetland Landscape Structure to Shorebirds Wintering in an Agricultural Valley

4.1. Abstract

Only recently has the influence of landscape structure on habitat use been a research focus in wetland systems and for wetland birds. During nonbreeding periods when food can be locally limited, spatial pattern of wetlands across a landscape may be of great importance in determining wetland use. We studied the influence of landscape structure on use of wetlands by wintering Dunlin (*Calidris alpina*) and Killdeer (*Charadrius vociferus*) in the agricultural Willamette Valley of Oregon, USA, within and among two winters (1999-2000, 2000-2001) of differing rainfall and subsequent distribution of habitat. We took a dual-level approach by studying shorebird use within a sample of 100 km² regions differing in landscape structure [area (ha) of shorebird habitat (wet, unvegetated) in region] and intensity of use of individual sites differing in landscape context (wetland area within a species-defined radius). At the site level, we additionally assessed the influence of two local characteristics: percent of exposed soil and area of wet habitat. We analyzed data using linear regression and information-theoretic methods to model selection. During the dry winter (2000-2001), Dunlin were attracted to regions with more wetland habitat and their use of sites increased with greater area of shorebird habitat both within the site and in the surrounding landscape. However, they appeared to discriminate habitat at only a local scale during the relatively wet winter (1999-2000). Killdeer distributions were unrelated to regional habitat availability and site use was unrelated to habitat

distributions at both landscape and local scales. Our findings contribute to a growing recognition of the importance of landscape structure to wetland birds and highlight a number of implications for the conservation of wetland landscapes.

4.2. Introduction

Researchers have only begun to address the influence of landscape structure on the process of vertebrate habitat use in wetland ecosystems (e.g., Naugle et al. 1997, 1999, 2000; Haig et al. 1998, Calmé and Desrochers 2000, Fairbairn and Dinsmore 2001, Riffell et al. 2003), even though most wetland landscapes are inherently heterogeneous (Skagen and Knopf 1994, Robinson and Warnock 1997, Roshier et al. 2001). Among the limited research that has addressed the influence of landscape structure on habitat use by wetland birds, there is a noticeable paucity of work conducted during nonbreeding periods when food resources at temperate latitudes can be scarce and patchily dispersed over great distances (e.g., Evans 1976, Myers 1983) and energetic costs of flight, thermoregulation, and survival are high (e.g., Kersten and Piersma 1987, Castro and Myers 1989). As nonbreeding periods comprise the majority of the annual cycle for most wetland birds, the potential influence of landscape structure has far-reaching implications for conservation.

Shorebirds (Order Charadriiformes) are a likely group to be influenced by wetland landscape structure, particularly during winter. As many shorebird species are wetland obligates, shorebirds likely perceive wetlands as patches in a relatively inhospitable matrix (*sensu* MacArthur and Wilson 1967). During nonbreeding seasons

when invertebrate resources can be scarce, dynamic, and easily depleted within wetland patches (Baker and Baker 1973, Goss-Custard et al. 1977, Szekely and Bamberger 1992), shorebirds likely supplement their energy intake by using multiple wetlands within a landscape (*sensu* Dunning et al. 1992). Finally, shorebirds are extremely mobile, able to opportunistically find available habitat both locally (in meters; e.g., Conners et al. 1981, Warnock and Takekawa 1996) and regionally (in kilometers; Warnock and Takekawa 1995, Warnock et al. 1995, Roshier et al. 2002, Sanzenbacher and Haig 2002a), increasing the likelihood that species respond to habitat availability at large and multiple spatial scales.

For wintering waterbirds compelled to forage among multiple patches in a landscape, it should be energetically favorable to concentrate in areas with proportionately high wetland densities (Evans 1976, Pyke 1983, Farmer and Parent 1997). Thus, while birds may favor certain local wetland habitat conditions, landscape context (i.e., spatial structure of surrounding habitat) may also influence bird distributions (Evans 1976, Kozakiewicz 1995) and the influence of both of these would suggest habitat use at more than one spatial scale. Moreover, wetland location may be an integral component of optimal and effective spatial designs for wetland restoration at a landscape scale (*sensu* Wu and Hobbs 2002).

The Willamette Valley ("Valley") of western Oregon, USA, has experienced extensive conversion to agriculture and associated alteration in wetland landscape structure (Sanzenbacher and Haig 2002a, b; chapter 2: Taft and Haig 2003). Once a landscape whose vast wetlands seriously impeded settlement and transportation by

early settlers (Robbins 1997; chapter 2: Taft and Haig 2003), drainage activities and agricultural development have transformed today's winter Valley into a fragmented mosaic of small and dispersed wetlands in a matrix of urban and relatively dry agricultural land. Today, the Valley serves as wintering residence to some 40,000 or more shorebirds who find accessible foraging habitat primarily on agricultural lands where poorly-drained soils facilitate ponding and farming practices provide exposed soil. Due to the variable spatial distribution of hydric soils and farming activities, the spatial configuration of this habitat varies greatly across the Valley landscape.

In an effort to contribute to conservation planning for the Valley and similar landscapes, we investigated associations between the distributions of shorebirds and their habitat within and among two winters of vastly different rainfall and subsequent distribution of wetlands. We studied the two most abundant wintering species representative of the diversity of Valley shorebirds: Dunlin (*Calidris alpina*) and Killdeer (*Charadrius vociferus*). These two species differ in movement patterns (Sanzenbacher and Haig 2002a, b) and thus scale of spatial perception (With 1994). Whereas Dunlin favor moist or flooded substrates, Killdeer are considered habitat generalists (Warnock and Gill 1996, Jackson and Jackson 2000).

We took a dual-level corroborative approach to evaluating the influence of spatial pattern of habitat on bird use. We hypothesized that if birds were disproportionately attracted to regions with higher abundance of wetlands (use at regional level), sites in these regions would be used more intensely (visited more often by more individuals) than those located in regions with little wetland habitat (use at

site level). Our first objective was therefore two-fold: 1) assess if regional abundances

of Dunlin and Killdeer increased disproportionate to the regional availability of

habitat, and 2) examine if site use intensity was related to availability of habitat

surrounding sites (landscape context). We were also interested in understanding the

extent to which shorebirds use habitat hierarchically at more than one spatial scale

(e.g., Kotliar and Wiens 1990). Thus, our second objective was to determine if site

use intensity was related both to wetland landscape context and to local availability of

habitat at the site itself.

4.3. Study Area

The Willamette Valley encompasses 9,100 km^2 of lowland plains (Clark et al. 1991,

Benner and Sedell 1997) varying in width east-west from about 20 to 60 km and

covering a north-south length of roughly 290 km (Figure 4.1; Hulse et al. 2002). The

prominent hydrologic feature of the Valley is the Willamette River and its 13 major

tributaries that drain the Willamette Basin, a 29,000 km^2 watershed between the

Cascade and Coast ranges (Benner and Sedell 1997). General landforms historically

supporting wetlands include floodplains and alluvial terraces associated with the river

(chapter 2: Taft and Haig 2003). Today, remaining Valley wetlands are dispersed

among small urban remnant wetlands, a few private duck hunting reserves, four larger

state and federally-protected wildlife refuges, and hundreds of scattered privately-

owned agricultural wetlands ('palustrine emergent-farmed wetlands' of

Figure 4.1. The Willamette Valley lowlands of western Oregon, including locations of the nine (in 1999-2000) and ten (in 2000-2001) 100 km^2 sample regions. Area in gray depicts the Willamette River floodplain, area in white depicts Valley alluvial terraces, and areas in black are urban. Boundaries of regions Beta, Butte Creek and Labish Lake differed slightly among years, thus thatched boxes represent regions studied both years (6 regions), with stippled boxes additional regions studied in 1999-2000 (3 regions), and open boxes regions studied in 2000-2001 (4 regions). Three sample regions encompassed the three national wildlife refuges (NWR) with managed impoundments: Baskett Slough (encompassing Baskett Slough NWR), Ankeny (Ankeny NWR), and Finley (Finley NWR).
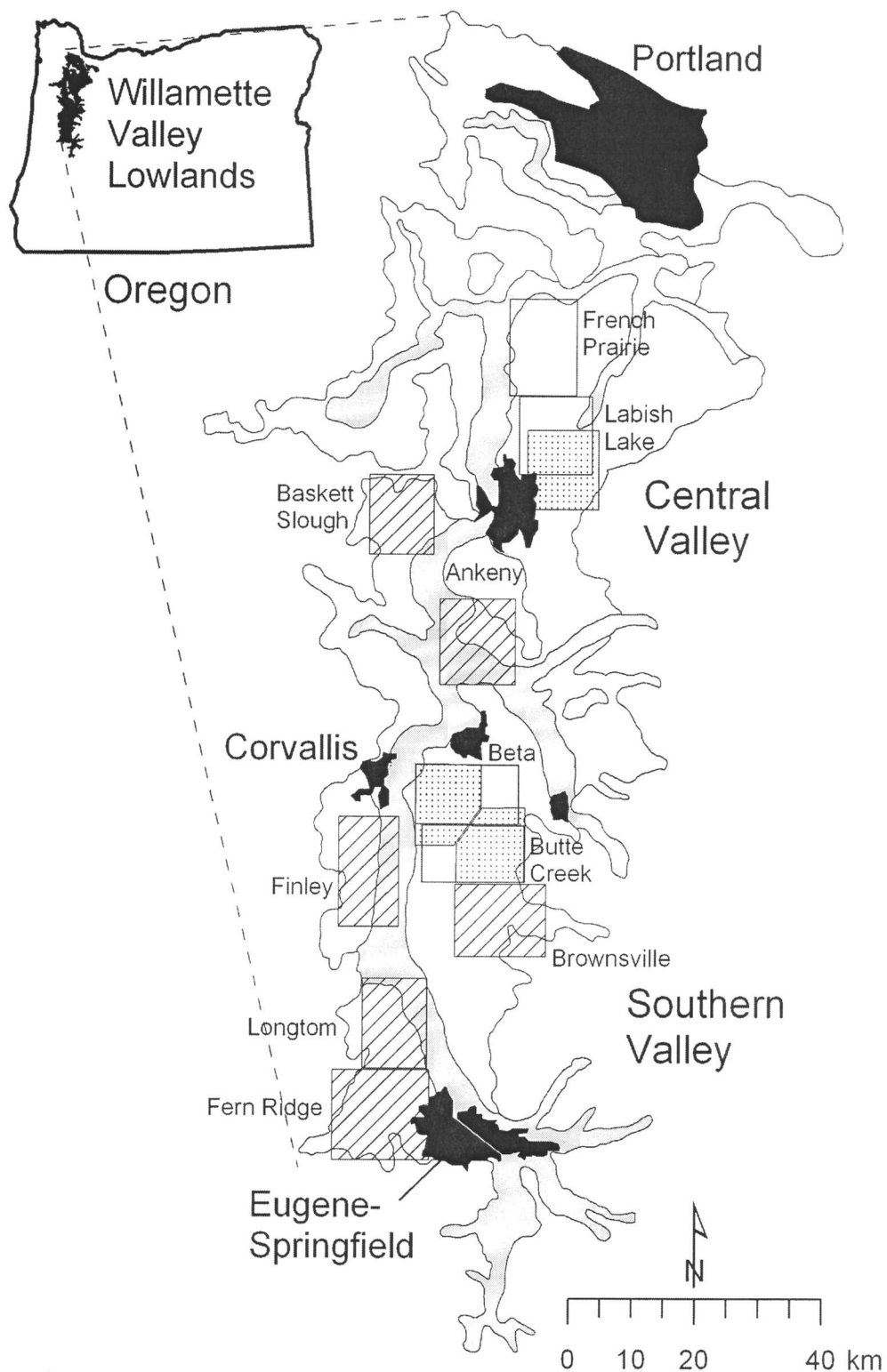
Figure 4.1

Cowardin et al. 1979). Representing the legacy of historical Valley wetlands, agricultural wetlands are flooded farmlands that annually emerge with the accumulation of winter rains on native hydric soils (chapter 2: Taft and Haig 2003; chapter 3: Taft et al. 2004).

Common lowland crops include grass seed (most prevalent), vegetables, grains, and peppermint (Hulse et al. 2002). Grass seed crops are planted in autumn. Whereas annual ryegrass (*Lolium multiflorum*) fields are covered fully (100%) with vegetation by mid to late winter, newly-planted perennial ryegrass fields (*Lolium perenne*) provide exposed soil between plants throughout the winter. Annual ryegrass is replanted every year, but perennial ryegrass and other perennial stocks are replanted on a 3-5 year cycle. Thus location of newly-planted fields shifts annually. Vegetable crops are left fallow through the winter and replanted in spring.

The climate of the Valley is cool Mediterranean, with an average annual rainfall of 100-125 cm, 75% of it falling between October and March (Jackson and Kimerling 1993). Average temperatures range from 1° C in January to 30° C in July (data from Oregon Climate Service).

4.4. Methods

4.4.1. Temporal and Spatial Sample Design

We conducted our study from November to March of 1999-2000 and 2000-2001, two winters that differed dramatically in rainfall: 91 cm in 1999-2000 vs. 40 cm in 2000-2001 from October-March (Oregon Climate Service). Moreover, greater rainfall in

1999-2000 led to a more dynamic distribution of wetlands over time compared to 2000-2001: monthly rainfall varied from 7-23 cm in 1999-2000 compared to only 3-11 cm in 2000-2001. Such dynamics facilitated comparing the influence of landscape structure on bird use between *Wet Winter* and *Dry Winter*, and among three seasons within the wet winter of 1999-2000 (*Early Winter* vs. *Mid Winter* vs. *Late Winter*). We accordingly collected and summarized data to generate datasets for these five time periods.

We took a combined patch/landscape-based approach (*sensu* Tischendorf and Fahrig 2000) to collecting and summarizing spatial data. We surveyed shorebird use of sites (patch-based) within nine (in 1999-2000) and ten (in 2000-2001) 93-104 km^2 regions (landscape-based) within the central and southern Valley (Figure 4.1). Based on prior knowledge of the spatial distribution of hydric soils (Daggett et al. 1998), we selected an array of sample regions representing variation in wetland landscape structure in the Valley and that simultaneously assured a sample of sites with different landscape contexts.

4.4.2. Land Cover Data

Prior to data collection, we observed an association between shorebird use and wet (flooded or saturated), exposed (<50% vegetation cover) portions of agricultural land (hereafter *shorebird habitat*), particularly for Dunlin and their ecological allies (species in the family Scolopacidae). Thus, for both winters, we mapped the distribution of shorebird habitat using a combination of remotely sensed imagery and

data acquired in the field. In 1999-2000, we used remotely sensed radar (RADARSAT) data to produce a series of geographic information system (GIS) layers (Erdas Imagine 8.6, Erdas, Inc., Atlanta, GA) depicting the distribution of shorebird habitat in early (imagery taken 10 December), mid (28 January), and late winter (15 March). Shallow water within impounded semi-natural wetlands on refuges or rice fields was included and mapped as shorebird habitat. Accuracies among maps ranged from 72-80%. We considered the mid-winter map to represent maximum availability of habitat during winter 1999-2000. See chapter 3 (Taft et al. 2004) for further details on creation of land cover maps from radar data.

Analogous satellite imagery was not available to produce a map for winter 2000-2001. Instead, we produced a mid-winter land cover layer of shorebird habitat (wet, <50% vegetation cover) in each sample region by ground mapping visible habitat in February 2001 during and after peak winter wetness. Using visible landmarks that were also depicted on topographic maps (USGS 7.5 minute), we plotted shorebird habitat on field maps and digitized these into a GIS layer (in Erdas Imagine 8.6). In many cases, we verified estimated area of shorebird habitat using data we had collected during surveys (see below). Percent of regions unobservable did not exceed 10% (range: 5-10%). Moreover, the systematic distribution of roads in the Valley (Hulse et al. 2002) promoted relatively equal visibility of shorebird habitat among regions.

4.4.3. Bird Surveys

Because ponding on agricultural fields tends to occur as widely scattered, irregularly shaped, changeable areas of shallow (1-cm deep) non-flowing sheetwater, we generally considered entire agricultural fields as sites. If ponding was clearly concentrated in discrete area(s) within dry fields, we considered these concentrated areas as sites. Boundaries of impounded wetland sites were easily defined.

We surveyed Dunlin and Killdeer weekly within each region, yielding 16 replicate weekly surveys from November-March each winter. By driving all passable roads and observing roadside-visible land with 8x binoculars and 25x spotting scopes, each region took one day (0730-1800) for one observer (one of two observers on alternate weeks in 1999-2000; the same observer in 2000-2001) to comprehensively survey. We identified and counted all shorebirds present at each site, and noted behavior (proportions of birds foraging and roosting). We varied the location at which we began surveying each region to reduce systematic bias. All sites used during prior surveys were checked for shorebird use.

We used land cover maps and landmarks that were both mapped and visible in the field (e.g., topography, creek-road crossings, railroads) to locate and digitize in a GIS layer (in Erdas Imagine 8.6) the center points and approximate perimeters of all sites. We used a GPS unit to map difficult to locate sites. To characterize and monitor local availability of habitat at a site, at the time of each survey we visually estimated percent of soil that was exposed (uncovered by vegetation) and percent of site with

ponded water or saturated soil. However, each survey often yielded new sites used by shorebirds, and thus we could not collect site data prior to the survey of first use.

4.4.4. Data Summary

4.4.4.1. Time Periods. For each of the five time periods considered, we regarded surveys as temporal replicates of predictors and responses. To generate *Wet Winter* and *Dry Winter* datasets, we summarized all data collected over each winter, considering surveys 1-16 as replicates (n = 16 surveys). The 16 surveys of the *Wet Winter* were then partitioned into three sub-seasons, with surveys 1-5 (16 Nov - 1 Jan) considered replicates within the *Early Winter* period (n = 5 surveys), surveys 6-11 (3 Jan – 18 Feb) replicates for *Mid* Winter (n = 6), and surveys 12-16 (21 Feb – 28 March) replicates for *Late Winter* (n = 5). Rainfall during survey weeks 5 and 12 were among the lowest of all weeks (Oregon Climate Service) and therefore represented natural breaks for subseason designations. The three radar images used to produce land cover data occurred midway in each of these periods.

4.4.4.2. Regional Use. We calculated regional shorebird abundance for each survey by summing counts across sites within regions. For each time period, we then calculated mean and maximum regional species abundance among replicate surveys to represent use of regions during the period. We considered maximum abundance as an index of peak use of regions. With our land cover maps, we quantified area (ha) of shorebird habitat available in regions during each time period using Erdas Imagine 8.6

GIS software. To assess whether birds were attracted to regions disproportionate to regional habitat availability, we generated mean and maximum regional densities of each species by dividing mean and maximum regional abundances by regional area of shorebird habitat.

4.4.4.3. Site Use. For each site, we summarized bird use data into three response variables representing site use intensity by each species during each time period: 1) frequency of occurrence (proportion of surveys included in the time period in which species was present), 2) mean abundance (mean bird abundance among surveys), and 3) maximum abundance (maximum bird abundance among surveys). Since shorebirds can sporadically occur in large flocks in the 1000s, we considered maximum abundance among surveys as an additional index that mean abundance would not have necessarily captured. We normalized frequency of occurrence (a proportion) using the arcsine square root transformation, and mean and maximum abundance responses were $\log_{10}$ transformed.

We quantified the predictor of landscape context as the amount of shorebird habitat surrounding each site. In ArcView 3.2 (ESRI, Inc., Redlands, CA), we used our GIS layers for land cover to quantify for each time period the area (ha) of shorebird habitat within circular buffers of 3 km (for Dunlin) or 1.5 km (Killdeer) of each site's central coordinates (HAB). Species-defined radii were derived from the average size of core use areas used by radio-tagged birds during a concurrent study on shorebird winter home ranges in the Willamette Valley (P. Sanzenbacher, personal

communication; Sanzenbacher and Haig 2002b). We $\log_{10}$ transformed HAB for the *Dry Winter* and for the *Late Winter* datasets.

Local predictors included two components describing availability of shorebird habitat at each site during each time period: 1) mean percent open substrate (MUD) among surveys, and 2) mean estimated area (ha) of flooded/saturated habitat (WET) among surveys [mean percent of site flooded multiplied by site area (ha)]. We normalized MUD (a proportion) using the arcsine square root transformation. For the *Dry Winter* Killdeer analysis, we transformed WET to a categorical variable (wet or dry) due to the high number of dry sites used by Killdeer. WET was $\log_{10}$ transformed for all other analyses.

4.4.5. Analyses

4.4.5.1. Regional Use. We used two-sample t-tests to compare species' abundances between the *Wet Winter* and *Dry Winter*, and paired t-tests to compare species' abundances among consecutive winter sub-seasons (i.e., *Early* to *Mid Winter*, *Mid* to *Late Winter*). All reported P values are for the two-sided alternative hypothesis.

We used simple linear regression (SAS version 8.2, SAS Institute Inc. 1999) to determine whether there was a significant ($P < 0.05$) positive relationship between $\log_{10}$-transformed species' abundances or densities (birds/100 ha habitat) and the regional area of shorebird habitat during each time period. Because a biologically meaningful association between bird densities and habitat availability was predicated

upon bird abundances increasing with habitat area, we only evaluated densities when increases in abundance with habitat were significant.

4.4.5.2. Site Use. For all analyses, we omitted sites used only for roosting and included only those sites that were observed for all surveys in the time period. We ran analyses on subsets of spatially independent sites to minimize autocorrelation in measures of HAB among sites clustered in the same sample region. We allocated sites into each data subset by subdividing sample regions into four quadrants (NW, NE, SE, SW) and systematically choosing up to four sites from each region (one per quadrant) whose circular buffers minimally overlapped. Such constraints resulted in four data subsets for all analyses except Dunlin in *Late Winter* (two subsets).

We used two sample *t*-tests to compare each species' use of sites among time periods. All reported P values are two-sided. We report statistical results assuming unequal variance when variances were clearly unequal among groups. For both the *Dry* and *Wet Winter* datasets, many sites used by Dunlin were also used by Killdeer, and a minority of sites were the same across the *Early*, *Mid* and *Late Winter* time periods for each species. Such non-independence (for all comparisons but *Dry* to *Wet Winter*) may have underestimated differences among groups, increasing only the probability of a type II error.

For each species, we evaluated a set of linear regression models for plausible hypotheses describing the influence of the three predictors (MUD, WET, HAB) on each response (frequency of occurrence, mean abundance, maximum abundance)

during each time period. Potential models represented one of three habitat use

hypotheses: intensity of bird use was positively related to 1) landscape context (HAB),

2) local availability of habitat (MUD and/or WET), or 3) landscape and local

availability of habitat (HAB, and MUD and/or WET). Because Dunlin are wet-habitat

obligates, we included WET in all models that included local predictors. However,

because Killdeer frequently use dry habitat, we felt it was biologically plausible that

MUD could be a characteristic influencing intensity of Killdeer site use by itself.

Thus, we considered a set of six biologically plausible *a priori* models explaining

intensity of site use by Dunlin (model 1: NONE; 2: HAB, 3: WET; 4: MUD/WET; 5:

HAB/WET; 6: HAB/MUD/WET) and eight *a priori* models explaining intensity of

use by Killdeer (model 1: NONE; 2: HAB; 3: MUD; 4: WET; 5: MUD/WET; 6:

HAB/MUD; 7: HAB/WET; 8: HAB/MUD/WET). Weak associations between HAB

and WET (correlation coefficients between 0.1 and 03; Cohen 1988) allowed for

simultaneous assessment of their influences on bird use.

We evaluated relative support for each *a priori* model and relative importance

of three predictors using an information-theoretic approach to model selection

(Burnham and Anderson 1998). For each data subset analysis, we calculated AIC_c

values from the residual sums of squares derived from each model regression (SAS

version 8.2, SAS Institute Inc. 1999). To rank candidate models by level of support,

for each subset we calculated the AIC_c difference (Δ) for each model by subtracting

the lowest AIC_c value (best model) among models from the AIC_c value of the model

under consideration. We considered models with $\Delta < 2$ to be plausible competing

models explaining the data and worthy of inference (Burnham and Anderson 1998). We additionally assessed strength of support for models by observing the consistency with which the same models were strongly competing among data subsets of the same analysis. We concluded that predictors were of little importance when the null (NONE) was among models with $\Delta < 2$ for half of the subsets in the analysis or more.

For each subset analysis, we calculated the Akaike weight (w_i) of each model (weights vary from 0-1 with larger Δ values resulting in higher weights) to assess the strength of evidence in favor of the model under consideration (Burnham and Anderson 1998). In addition, we assessed likelihood of the best model relative to the model under consideration by calculating relative Akaike weights (i.e., Akaike weight of the model with the lowest AIC_c divided by the weight of that model under consideration). Finally, for those analyses where the null was among competing models for less than half of all subsets, for each subset we quantified the relative importance of predictors (MUD, WET, HAB) by summing for each the Akaike weights of the models in which the predictor was included (Burnham and Anderson 1998). We ranked importance of predictors by these summed Akaike weights, with 1 to 3 corresponding to most to least important. Among subset analyses, we then averaged summed parameter Akaike weights and ranks.

4.5. Results

4.5.1. Types of Sites Used

In both winters, Dunlin and Killdeer used hundreds of sites distributed across the Valley (Table 4.1). Most of these (91% in both years for Dunlin; 97% both years for Killdeer) were on agricultural land. The most common agricultural cover types included perennial ryegrass (40-44% of agricultural sites used by each species among both years) and annual ryegrass (19-29% of sites). Fallow fields accounted for 24-32% of sites (mostly former vegetable crops such as pumpkin, onion, and corn, but also fallow grass seed fields). Of perennial ryegrass fields used by Dunlin, 53% (*Wet Winter*) and 68% (*Dry Winter*) were newly-planted. Active grass seed crops collectively accounted for about 70% of sites used by both Dunlin and Killdeer. Other crop types (less than 1%) included winter wheat and nursery flowers/trees. Pastures accounted for 4% (*Dry Winter*) and 8% (*Wet Winter*) of sites used by Killdeer, but only 2% (*Dry Winter*) to 3% (*Wet Winter*) of sites used by Dunlin.

4.5.2. Spatio-temporal Distribution of Shorebird Habitat

Regional area of shorebird habitat differed most among winters, as rainfall and thus habitat was relatively scarce in the *Dry Winter* compared to the *Wet Winter* (Table 4.1, Figure 4.2). For instance, minimum to maximum regional area of habitat differed by a factor of eight in the *Dry Winter* but only by a factor of three in the *Wet Winter*. In most regions, area and proportion of shorebird habitat did not change appreciably

Table 4.1. Area of shorebird habitat (wet, ≤50% vegetated), shorebird abundances, and number of sites used by wintering Dunlin and Killdeer in nine (1999-2000) and ten (2000-2001) sample regions of the Willamette Valley, Oregon, USA, for five time periods in 1999 -2001. Regions are arranged in ascending order by area of habitat.

Time Period	Region [a]	Area (ha)	(%)[b]	Dunlin			Killdeer		
				Mean[c]	Max[d]	# Sites	Mean[c]	Max[d]	# Sites
Wet	Longtom	828	(9)	927	8000	4	220	545	46
Winter	Fern Ridge	1247	(12)	2079	9265	11	237	683	37
	Brownsville	1814	(19)	2496	10005	25	587	1768	53
	Finley	2056	(22)	337	1722	31	325	1066	63
	Ankeny	2069	(22)	5582	22200	21	369	1410	65
	Beta	2217	(23)	3115	12013	49	701	1493	85
	Baskett Slough	2591	(28)	2824	15071	29	431	1491	69
	Butte Creek	2729	(29)	704	1586	40	1455	3404	79
	Labish Lake	2815	(30)	883	3002	21	432	945	84
	Mean[e]			**2105**	**9207**		**529**	**1423**	
	Total	**18366**	**(21)**			**231**			**581**
Dry	French Prairie	33	(<1)	14	102	9	476	1263	86
Winter	Butte Creek	76	(1)	80	291	47	1227	2264	131
	Labish Lake	90	(1)	140	749	19	421	991	77
	Finley	126	(1)	7	75	5	355	1398	50
	Brownsville	139	(1)	251	792	24	632	1229	65
	Longtom	140	(1)	221	2245	19	518	1062	48
	Baskett Slough	159	(1)	218	1543	19	385	752	81
	Fern Ridge	201	(2)	485	3003	6	253	665	31
	Beta	214	(2)	192	818	34	921	2212	133
	Ankeny	279	(3)	6724	17117	20	636	1796	77
	Mean[e]			**833**	**2674**		**582**	**1363**	
	Total	**1457**	**(1)**			**188**			**779**

Table 4.1. (Continued).

Time Period	Region[a]	Area (ha)	(%)[b]	Dunlin Mean[c]	Dunlin Max[d]	Dunlin # Sites	Killdeer Mean[c]	Killdeer Max[d]	Killdeer # Sites
Early Winter	Fern Ridge	1535	(15)	1099	3812	7	352	683	19
	Ankeny	1621	(17)	2287	7252	16	555	1410	43
	Baskett Slough	1785	(19)	456	867	11	504	1491	38
	Brownsville	2118	(22)	2606	10005	15	1029	1768	27
	Finley	2177	(23)	685	1722	25	622	1066	53
	Longtom	2589	(27)	391	1500	2	264	367	17
	Butte Creek	2692	(29)	902	1586	17	1337	2135	42
	Beta	2730	(29)	2068	7020	31	893	1282	49
	Labish Lake	3078	(32)	504	1390	17	694	882	54
	Mean[e]			**1222**	**3906**		**694**	**1232**	
	Total	**20325**	**(24)**			**141**			**342**
Mid Winter	Longtom	828	(9)	1426	8000	4	294	545	34
	Fern Ridge	1247	(12)	4095	9265	5	304	617	25
	Brownsville	1814	(19)	1139	2560	13	630	1325	38
	Finley	2056	(22)	325	931	11	311	580	51
	Ankeny	2069	(22)	10492	22200	8	407	732	54
	Beta	2217	(23)	6245	12013	31	878	1493	72
	Baskett Slough	2591	(28)	248	473	17	598	879	45
	Butte Creek	2729	(29)	878	1560	28	2473	3404	64
	Labish Lake	2815	(30)	842	3002	4	434	945	58
	Mean[e]			**2854**	**6667**		**703**	**1169**	
	Total	**18366**	**(21)**			**121**			**441**

Table 4.1. (Continued).

Time Period	Region[a]	Area (ha)	(%)[b]	Dunlin			Killdeer		
				Mean[c]	Max[d]	# Sites	Mean[c]	Max[d]	# Sites
Late	Longtom	152	(2)	758	1250	2	95	260	25
Winter	Fern Ridge	207	(2)	641	3001	4	44	84	22
	Butte Creek	295	(3)	298	802	8	353	740	43
	Brownsville	314	(3)	4015	7500	8	93	203	30
	Beta	478	(5)	408	1873	10	298	674	52
	Labish Lake	620	(7)	1311	2655	6	167	324	50
	Baskett Slough	714	(8)	8284	15071	9	159	373	46
	Finley	826	(9)	2	9	1	46	119	29
	Ankeny	936	(10)	2985	13000	7	137	271	33
	Mean[e]			**2078**	**5018**		**155**	**339**	
	Total	**4542**	**(5)**			**55**			**330**

[a] See Figure 4.1 for region locations.
[b] Percent of total regional area with shorebird habitat.
[c] Mean regional abundance among surveys conducted for the time period.
[d] Maximum regional abundance among surveys conducted for the time period.
[e] Grand mean among regions of mean and maximum abundances.

Figure 4.2. Examples of the range (minimum, maximum) in area (ha) of shorebird habitat (wet, <50% vegetated; in black) observed among sample regions each year within the Willamette Valley of Oregon: a) region with the least habitat in the *Wet Winter* of 1999-2000 - Longtom, b) most habitat in the *Wet Winter* of 1999-2000 – Labish Lake, c) least habitat in the *Dry Winter* of 2000-2001 - French Prairie, d) most habitat in the *Dry Winter* of 2000-2001 - Ankeny. See Figure 4.1 for sample region locations.
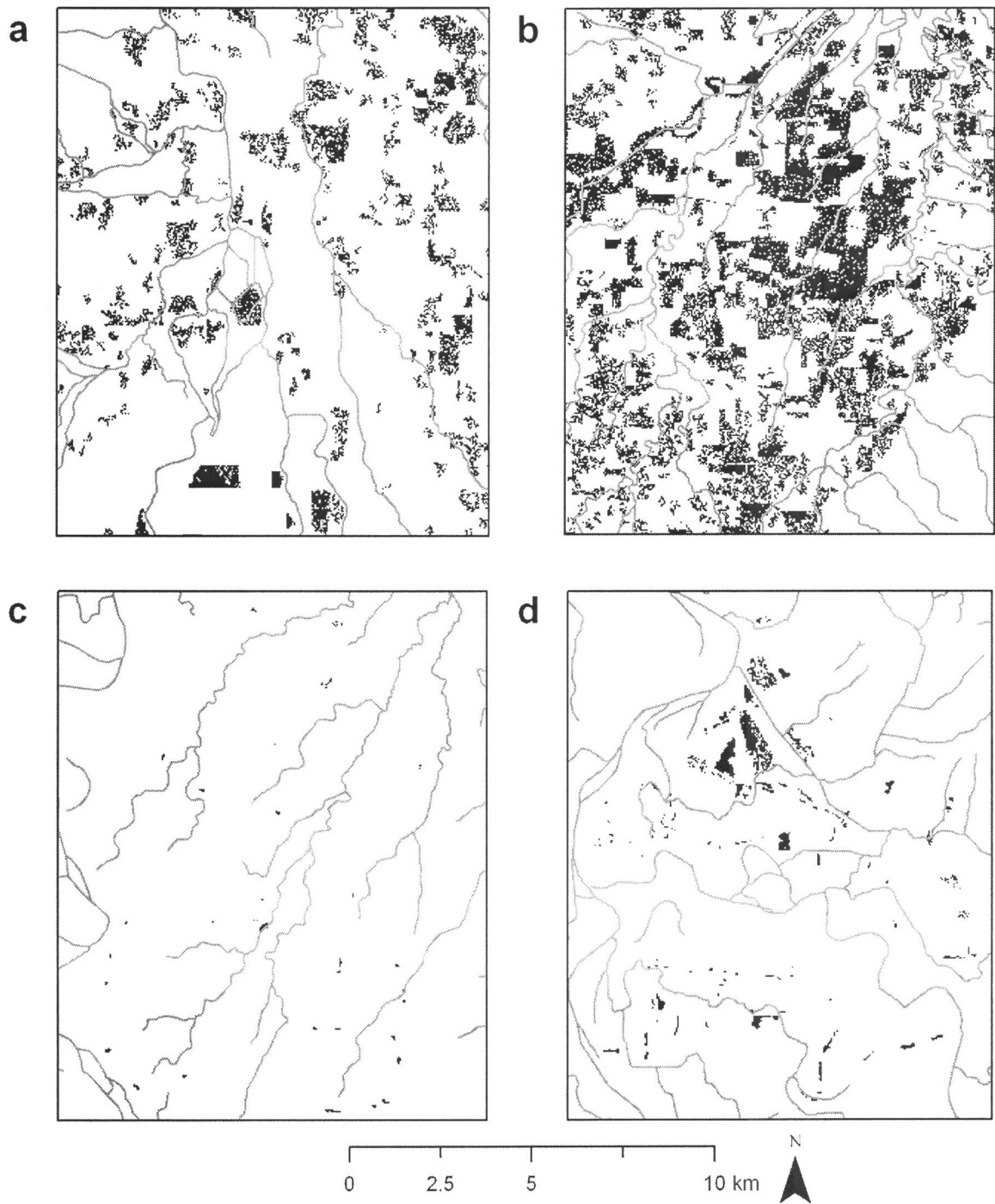
Figure 4.2

between *Early* and *Mid Winter*, but habitat decreased in all regions from *Mid* to *Late Winter* as crop vegetation grew and winter rainfall subsided (Table 4.1). Minimum to maximum regional area of habitat differed by a factor of five by *Late Winter*.

Percent soil exposed on annual ryegrass fields used by either species decreased within sites on average by 11% (+ 15 SD) from *Early Winter* (average percent soil among sites was 51 + 21%) to *Mid Winter* (40 + 22% average among sites), and by 9% (+ 14) from *Mid* to *Late Winter* (31 + 20% among sites). On newly-planted perennial ryegrass fields, percent soil did not change within sites (by only 0.5% + 11) from *Early Winter* (80 + 13% among sites) to *Mid Winter* (80 + 12% among sites), but decreased within sites on average by 18% (+ 11) from *Mid* to *Late Winter* (62 + 14% among sites). In contrast, percent soil exposed on established perennial ryegrass fields decreased within sites on average by only 4% (+ 1) from *Early Winter* (26 + 15% among sites) to *Mid Winter* (21 + 13% among sites), and by only 1% (+ 5) from *Mid* to *Late Winter* (20 + 10% among sites). Percent of fields flooded increased on average by 3% (+ 9) from *Early* to *Mid Winter*, but decreased by 3% (+ 6) from *Mid* to *Late Winter*.

4.5.3. Regional Use

4.5.3.1. Comparisons Among Time Periods. Regions supported substantially fewer Dunlin during the *Dry Winter* than the *Wet Winter* (mean: $t_{17} = 3.33$, $P < 0.01$; maximum: $t_{17} = 3.32$, $P < 0.01$), but number of sites used was only slightly less (by ~20%; Table 4.1). Killdeer regional abundances were no different among winters

(mean: $t_{17} = -0.69$, $P=0.50$; maximum: $t_{17} = -0.07$, $P = 0.95$), yet Killdeer used a greater number of sites in the *Dry Winter*.

Regional abundances of Dunlin were no different between *Early* and *Mid Winter* (mean: $t_8 = 1.62$, $P = 0.07$; maximum: $t_8 = 1.33$, $P = 0.11$) or between *Mid* and *Late Winter* (mean: $t_8 = 0.50$, $P = 0.31$; maximum: $t_8 = 0.63$, $P = 0.27$). However, total number of sites used by Dunlin declined over one-half (~55%) between *Mid* and *Late Winter*. In contrast, Killdeer regional abundances declined from *Mid* to *Late Winter* (mean: $t_8 = 2.72$, $P = 0.01$; maximum: $t_8 = 3.42$, $P < 0.01$) while the number of sites used decreased by only about 25%.

4.5.3.2. Influence of Regional Habitat Availability. There were no relationships between regional availability of shorebird habitat and regional abundances of Dunlin in the *Wet Winter*, nor during the *Early*, *Mid* and *Late Winter* periods (Table 4.2). In the *Dry Winter*, however, regions with more shorebird habitat supported more Dunlin on average (significant slope estimates backtransformed translate to a 2.1% increase in predicted median mean abundance and 1.8% increase in predicted median maximum abundance per 1 ha increase in habitat). Moreover, results for regional densities suggested ($P < 0.10$) Dunlin abundances increased disproportionate to the availability of habitat in regions (1.3% increase in predicted median mean density of birds, and 1.0% increase in predicted median maximum density of birds per 1 ha increase in habitat). Thus, for example, although consecutive increases in area of shorebird habitat between the French Prairie (33 ha), Baskett Slough (159 ha) and Ankeny (279

Table 4.2. Linear regressions between mean and maximum regional Dunlin and Killdeer $\log_{10}$-transformed abundances or densities (birds/100 ha) and regional area (ha) of shorebird habitat (wet, $\leq$50% vegetated) for five time periods in 1999-2001 in the Willamette Valley, Oregon, USA. N = 9 (1999-2000) and 10 (2000-2001) sample regions. Significant relationships (P < 0.05) are in **bold**. Results for regressions of density and habitat only shown when abundance regressions were significant.

Species	Time Period	Response	Percent Change (Increase/Decrease) in Median Response[a]	95% C.I. [a]		b [b]	t-value	P-value	R^2
Dunlin	*Wet Winter*	Mean Abundance	+ 0.01	- 0.10 to	+ 0.12		-0.13	0.90	< 0.01
		Max Abundance	- 0.05	- 0.15 to	+ 0.06		-0.88	0.41	0.10
	Dry Winter	Mean Abundance	**+ 2.08**	**+ 0.72 to**	**+ 3.44**	+	**3.56**	**< 0.01**	**0.61**
		Mean Density	+ 1.26	- 0.13 to	+ 2.67	+	2.09	0.07	0.35
		Max Abundance	**+ 1.80**	**+ 0.68 to**	**+ 2.93**	+	**3.73**	**< 0.01**	**0.63**
		Max Density	+ 0.99	- 0.16 to	+ 2.15	+	1.99	0.08	0.33
	Early Winter	Mean Abundance	- 0.05	- 0.15 to	+ 0.06		-0.78	0.46	0.08
		Max Abundance	- 0.05	- 0.21 to	+ 0.12		-0.72	0.50	0.07
	Mid Winter	Mean Abundance	- 0.07	- 0.23 to	+ 0.09		-0.90	0.40	0.10
		Max Abundance	- 0.09	- 0.26 to	+ 0.07		-1.42	0.20	0.22
	Late Winter	Mean Abundance	- 0.14	- 0.90 to	+ 0.63		-0.41	0.70	0.02
		Max Abundance	- 0.07	- 0.77 to	+ 0.64		-0.26	0.80	0.01

Table 4.2. (Continued).

Species	Time Period	Response	Percent Change (Increase/Decrease) in Median Response[a]	95% C.I.[a]		b[b]	t-value	P-value	R^2
Killdeer	*Wet Winter*	Mean Abundance	+ 0.07	+ 0.01 to	+ 0.12	+	2.51	0.04	0.47
		Mean Density	0.00	- 0.05 to	+ 0.06		0.05	0.96	< 0.01
		Max Abundance	+ 0.05	- 0.01 to	+ 0.10	+	2.55	0.03	0.48
		Max Density	0.00	- 0.05 to	+ 0.05		-0.11	0.91	< 0.01
	Dry Winter	Mean Abundance	- 0.02	- 0.55 to	+ 0.51		-0.09	0.93	< 0.01
		Max Abundance	+ 0.02	- 0.45 to	+ 0.50		0.17	0.87	< 0.01
	Early Winter	Mean Abundance	+ 0.05	- 0.01 to	+ 0.10		1.05	0.33	0.14
		Max Abundance	+ 0.01	- 0.10 to	+ 0.12		-0.23	0.82	0.01
	Mid Winter	Mean Abundance	+ 0.07	+ 0.01 to	+ 0.12	+	1.96	0.09	0.35
		Max Abundance	+ 0.05	- 0.01 to	+ 0.10	+	1.92	0.10	0.34
	Late Winter	Mean Abundance	0.00	- 0.21 to	+ 0.22		0.05	0.96	< 0.01
		Max Abundance	0.00	- 0.22 to	+ 0.22		0.01	0.99	0.00

[a] Percent change in median response per 1 ha increase in shorebird habitat. Figured from backtransformed parameter estimates.
[b] Sign of slope only shown for tests with P < 0.10.

ha) regions were each about 120 ha (Figure 4.1, Table 4.1), predicted mean Dunlin abundances increased by 188 birds between the French Prairie and Baskett Slough regions, but by 2,182 birds between the Baskett Slough and Ankeny regions.

For Killdeer, densities were unrelated to area of habitat in regions in the *Wet Winter*, even though regional abundances of Killdeer significantly increased with area of shorebird habitat (0.05% increase in predicted mean number of birds, and 0.07% increase in maximum number of birds per 1 ha increase in habitat). Regional abundances of Killdeer were unrelated to regional area of habitat in *Early*, *Mid*, and *Late Winter*, and relationships between regional abundance of Killdeer and shorebird habitat in the *Dry Winter* also were not significant.

4.5.4. Site Use

4.5.4.1. Comparisons Among Time Periods. For both species, frequency of occurrence among sampled sites did not differ between the *Dry* and *Wet Winter* (Dunlin: $t_{180} = 0.45$, $P = 0.65$; Killdeer: $t_{282} = 0.55$, $P = 0.59$; Figures 4.3a, 4.4a). Dunlin were less abundant at sites in the *Dry Winter* than in the *Wet Winter* (mean: $t_{180} = 2.37$, $P = 0.01$; maximum: $t_{180} = 2.07$, $P = 0.02$; Figure 4.3c, e), but Killdeer abundances did not differ among winters (mean: $t_{282} = 0.12$, $P = 0.91$; maximum: $t_{282} = 0.13$, $P = 0.89$; Figure 4.4c, e).

Frequency of Dunlin occurrence among sites was no different between *Early* and *Mid Winter* ($t_{142} = 1.08$, $P = 0.28$; Figure 4.3b), but was greater during *Late Winter*
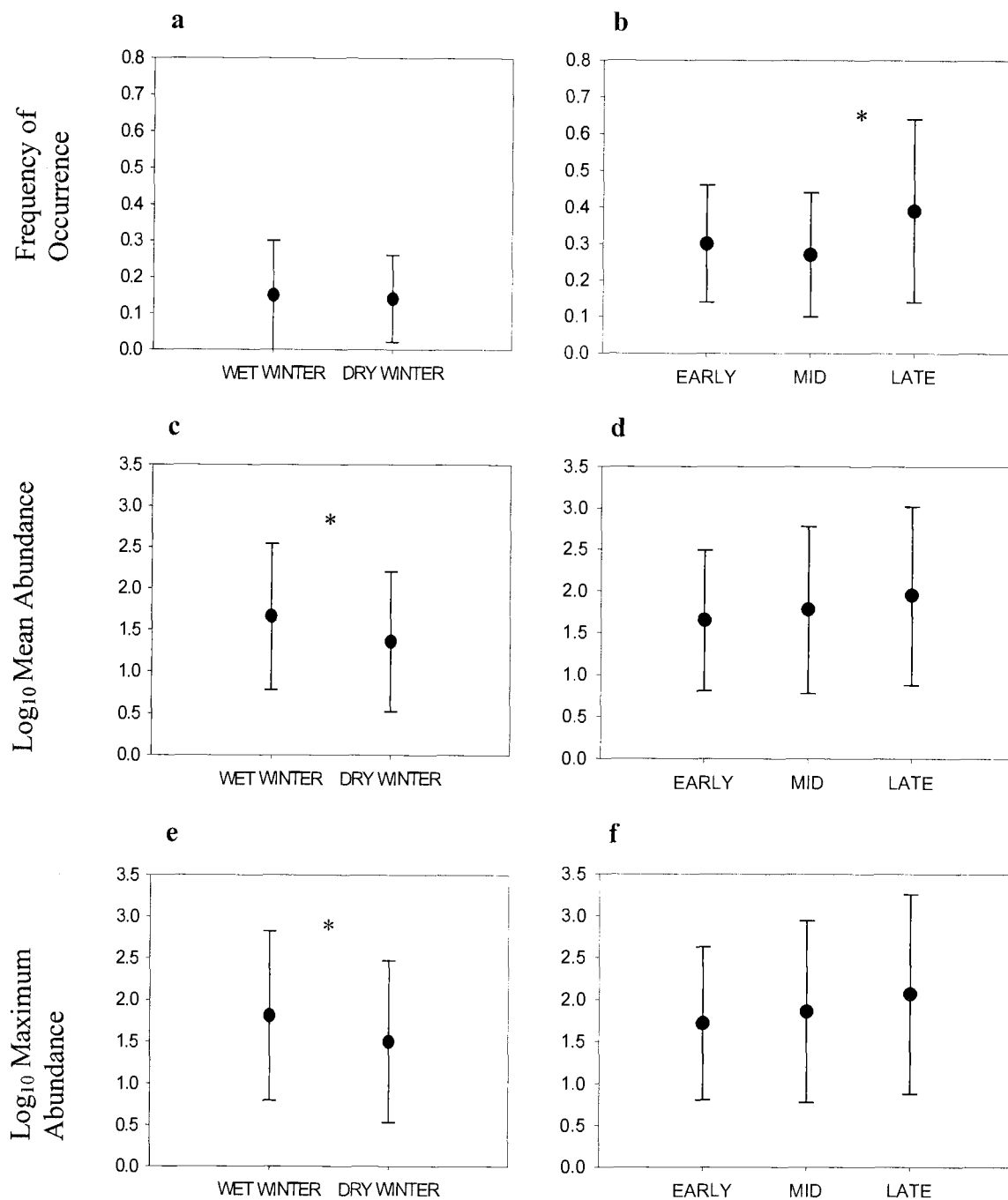
Figure 4.3. Mean frequency of occurrence at sites (a, b), $\log_{10}$ mean abundance (c, d), and $\log_{10}$ maximum abundance (e, f) of Dunlin among surveys conducted in the Willamette Valley, Oregon, during five winter time periods in 1999-2001. Error bars show SD values. Asterisks denote significant differences between time periods.
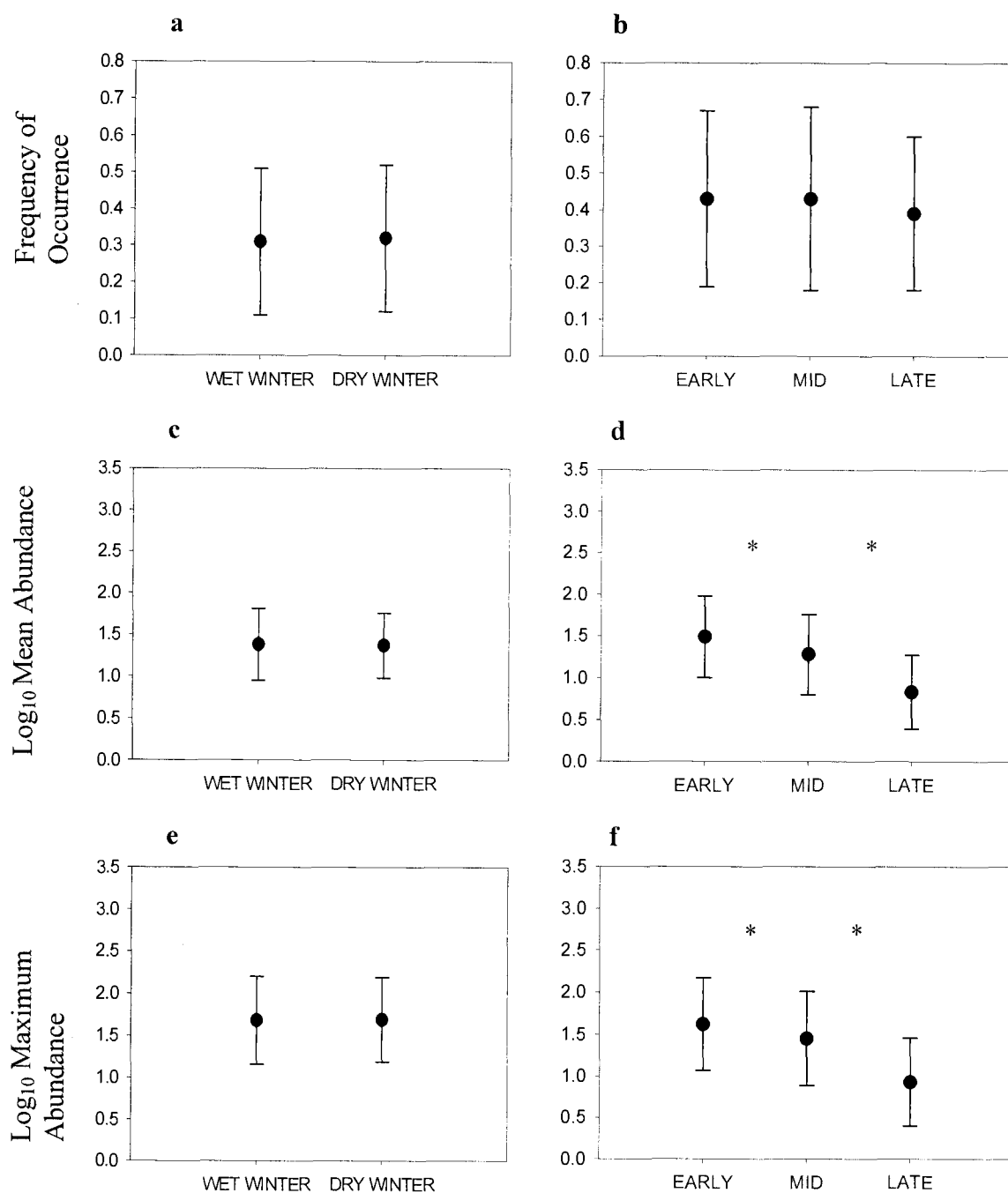
Figure 4.4. Mean frequency of occurrence at sites (a, b), $\log_{10}$ mean abundance (c, d), and $\log_{10}$ maximum abundance (e, f) of Killdeer among surveys conducted in the Willamette Valley, Oregon, during five winter time periods in 1999-2001. Error bars show SD values. Asterisks denote significant differences between time periods.

than during *Mid Winter* (t_{105} = 3.03, P < 0.01; Figure 4.3b). Dunlin abundances at sites did not differ from *Early* to *Mid Winter* (mean: t_{142} = 0.82, P = 0.41; maximum: t_{142} = 0.87, P = 0.39) or from *Mid* to *Late Winter* (mean: t_{105} = 0.83, P = 0.41; maximum: t_{105} = 0.90, P = 0.37; Figure 4.3d, f). While frequency of Killdeer occurrence among sites did not differ among winter sub-seasons (*Early* to *Mid Winter*: t_{245} = 0.03, P = 0.98; *Mid* to *Late Winter*: t_{240} = 1.73, P = 0.08; Figure 4.4b), Killdeer were significantly less abundant at sites in *Mid Winter* (mean: t_{245} = 3.38, P < 0.01; maximum: t_{245} = 2.40, P = 0.02) and *Late Winter* (mean: t_{240} = 7.75, P < 0.01; maximum: t_{240} = 7.43, P < 0.01; Figure 4.4d, f).

4.5.4.2. Influence of Landscape Context and Local Habitat Availability. Sites used by both species ranged considerably in local characteristics (MUD, WET) and landscape context (HAB; Table 4.3). Mean MUD and WET among Dunlin-used sites was higher than among Killdeer-used sites for all time periods. In particular, MUD averaged >50% for Dunlin sites but around 50% for Killdeer sites. Among analyzed Dunlin sites, 78% (*Dry Winter*) to 98% (*Wet Winter*) were wet at some time compared to 46% (*Dry Winter*) to 95% (*Wet Winter*) of sites used by Killdeer.

There was strong evidence that mean and maximum Dunlin abundances at sites were influenced both by landscape context (HAB) and by local characteristics (MUD, WET) in the *Dry Winter*, but related only to local characteristics in the *Wet Winter* (Table 4.4; Figure 4.5). Models MUD/WET and WET consistently (among subset analyses) competed to explain variation in mean and maximum abundance of Dunlin

Table 4.3. Mean (±SD) characteristics and use of analyzed sites by wintering Dunlin and Killdeer during five time periods in 1999-2001 in the Willamette Valley, Oregon, USA.

| | | | Site Characteristics | | | Site Use | | |
| | | | | | | Frequency of Occurrence[c] | Mean[d] Abundance (# Birds) | Maximum[d] Abundance (# Birds) |
Species	Time Period	N	HAB[a] (ha)	MUD[b] (%)	WET[b] (ha)			
Dunlin	*Wet Winter*	95	642 ±250	57 ± 29	3.9 ± 4.8	15 ± 15	340 ± 944	847 ± 2798
	Dry Winter	87	36 ± 36	72 ± 29	2.7 ± 8.3	14 ± 12	232 ± 860	590 ± 2172
	Early Winter	71	698 ±296	59 ± 29	3.3 ± 4.2	29 ± 16	270 ± 715	516 ± 1646
	Mid Winter	73	643 ±247	60 ± 30	6.5 ± 8.4	27 ± 17	675 ± 1738	1145 ± 3061
	Late Winter	34	141 ±139	55 ± 37	5.1 ± 6.6	38 ± 24	757 ± 1422	1481 ± 3096
Killdeer	*Wet Winter*	127	159 ± 81	49 ± 29	2.3 ± 2.3	31 ± 20	36 ± 39	86 ± 113
	Dry Winter	157	9 ± 14	64 ± 29	0.9 ± 3.3	32 ± 20	33 ± 30	87 ± 111
	Early Winter	122	176 ±102	58 ± 28	1.9 ± 2.6	43 ± 24	53 ± 62	78 ± 109
	Mid Winter	125	160 ± 82	51 ± 30	3.1 ± 3.0	43 ± 25	34 ± 46	59 ± 80
	Late Winter	117	37 ± 41	49 ± 29	2.4 ± 2.6	39 ± 21	11 ± 16	18 ± 31

[a] Measured as the amount (ha) of shorebird habitat within 3 km (Dunlin) or 1.5 km (Killdeer) of the central coordinates of the site.
[b] Values shown for MUD and WET are with one outlier removed.
[c] Proportion of surveys in the time period in which species was present at sites.
[d] Mean and maximum abundance among surveys conducted for the time period.

Table 4.4. Delta (Δ) values, Akaike weights, and relative weights for strongly competing models (Δ ≤ 2) explaining influence of three predictors (MUD, WET, HAB) on Dunlin site use (frequency of occurrence, mean abundance, maximum abundance) during the *Wet Winter* of 1999-2000 and the *Dry Winter* of 2000-2001 in the Willamette Valley, Oregon, USA. Presence of HAB in models are emphasized in **bold**.

Time Period	Response	Subset[a]	Models	Δ	w	Relative Weight
Wet Winter	Frequency of Occurrence[b]	1	MUD/WET	0.00	0.37	1.00
			NONE	0.57	0.28	1.33
		2	MUD/WET	0.00	0.35	1.00
			NONE	0.07	0.34	1.04
		3	NONE	0.00	-------	1.00
		4	WET	0.00	0.41	1.00
			MUD/WET	0.05	0.40	1.03
	Mean Abundance[c]	1	MUD/WET	0.00	0.46	1.00
			WET	0.93	0.29	1.60
		2	MUD/WET	0.00	0.28	1.00
			WET	0.21	0.26	1.11
			NONE	0.76	0.19	1.46
		3	WET	0.00	0.46	1.00
			MUD/WET	0.82	0.31	1.50
		4	WET	0.00	0.63	1.00
	Maximum Abundance[c]	1	MUD/WET	0.00	0.55	1.00
			WET	1.89	0.21	2.57
		2	MUD/WET	0.00	0.33	1.00
			WET	0.76	0.23	1.46
			NONE	0.86	0.21	1.54
		3	WET	0.00	0.47	1.00
			MUD/WET	0.86	0.30	1.53
		4	WET	0.00	0.64	1.00

Table 4.4. (Continued).

Time Period	Response	Subset[a]	Models	Δ	w	Relative Weight
Dry Winter	Frequency of Occurrence[b]	1	**HAB**/MUD/WET	0.00	0.40	1.00
			MUD/WET	0.86	0.26	1.54
		2	MUD/WET	0.00	0.42	1.00
			WET	0.15	0.39	1.08
		3	MUD/WET	0.00	0.60	1.00
			WET	2.02	0.22	2.75
		4	WET	0.00	0.63	1.00
	Mean Abundance[c]	1	MUD/WET	0.00	0.52	1.00
			WET	1.74	0.22	2.38
			HAB/MUD/WET	1.96	0.19	2.66
		2	WET	0.00	0.44	1.00
			HAB/WET	0.34	0.37	1.19
		3	WET	0.00	0.36	1.00
			MUD/WET	1.36	0.18	1.97
			HAB/WET	1.67	0.16	2.30
			HAB	1.68	0.15	2.32
		4	**HAB**/MUD/WET	0.00	0.30	1.00
			MUD/WET	0.90	0.19	1.57
			NONE	0.98	0.18	1.63
	Maximum Abundance[c]	1	MUD/WET	0.00	0.51	1.00
			HAB/MUD/WET	1.31	0.27	1.93
		2	WET	0.00	0.46	1.00
			HAB/WET	0.58	0.35	1.33
		3	WET	0.00	0.42	1.00
			HAB/WET	1.45	0.21	2.06
		4	**HAB**/MUD/WET	0.00	0.38	1.00
			MUD/WET	1.58	0.17	2.20
			HAB	1.75	0.16	2.40

[a] Subset sample sizes were 23 (set 1), 25 (set 2), 23 (set 3), 24 (set 4) for winter 99-00; 23 (set 1), 21 (set 2), 23 (set 3), 20 (set 4) for winter 2000-2001. Spatial distribution of sites and an unequal numbers of sites per region yielded slightly different sample sizes among subsets.

[b] Proportion of surveys in the time period in which Dunlin were present at sites.

[c] Mean and maximum bird abundance among surveys conducted for the time period.

Figure 4.5. Scatterplots for mean (among 16 surveys) Dunlin abundance vs. predictors MUD, WET and HAB at sites surveyed during the *Wet Winter* of 1999-2000 and the *Dry Winter* of 2000-2001 in the Willamette Valley, Oregon, USA. MUD was calculated as the mean (among surveys) observed percentage exposed soil, WET as the mean (among surveys) estimated area (ha) of wet habitat, and HAB as the area (ha) of shorebird (wet, <50% vegetated) habitat within 3 km of the site. Data from each subset indicated by symbols: gray diamonds (subset 1), gray triangles (subset 2), crosses (subset 3), black diamonds (subset 4). For purposes of display (but retained in analyses), we omitted one datum with atypically large values for WET (2.47 in 1999-2000, 2.45 in 2000-2001).

Wet Winter 1999-2000

Dry Winter 2000-2001
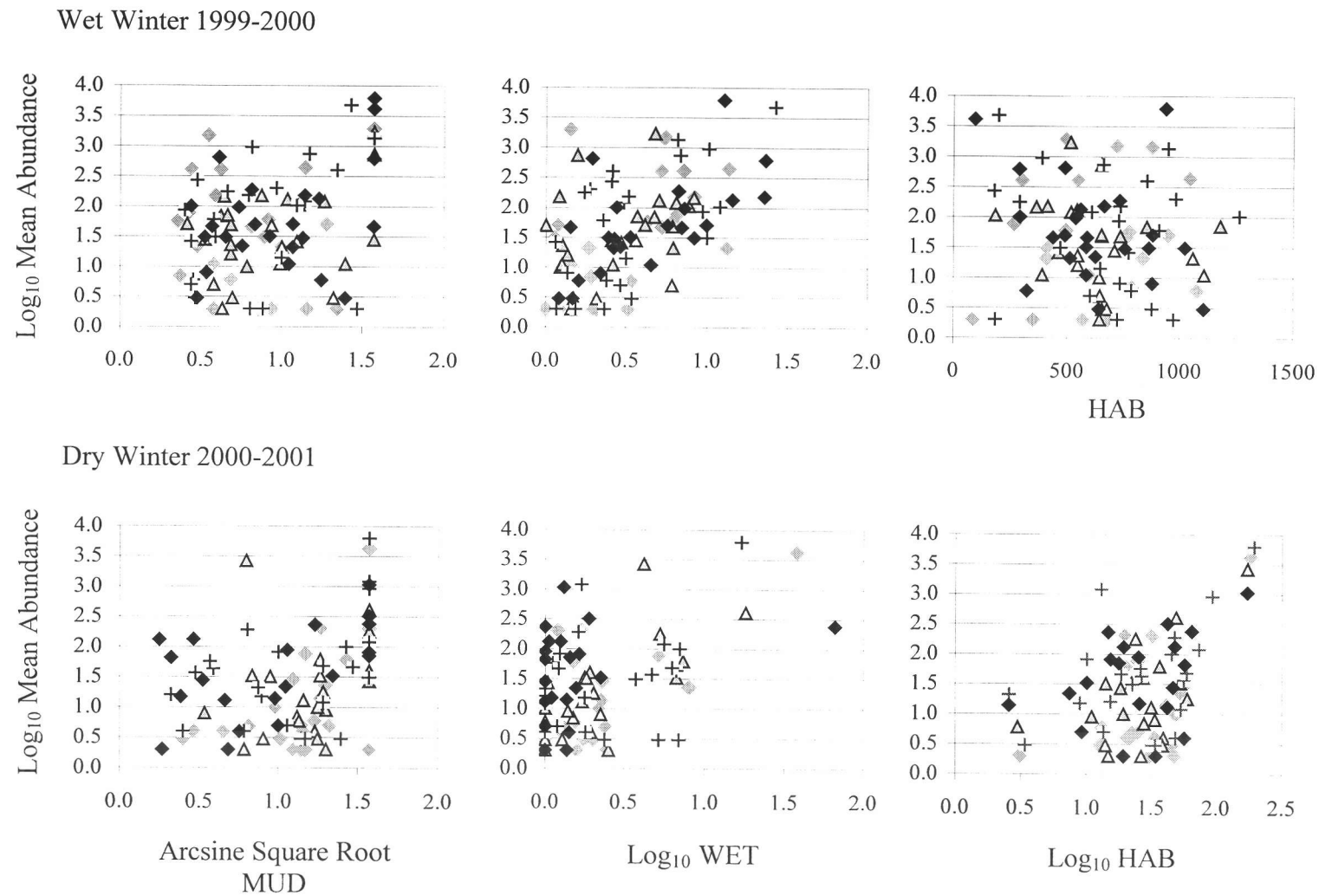
Figure 4.4

among sites in the *Wet Winter*. In the *Dry Winter*, models with both landscape and local predictors (HAB/MUD/WET and HAB/WET) strongly and consistently competed with models containing only local predictors (MUD/WET and WET). For frequency of Dunlin occurrence, competing models contained only local predictors for most subset analyses in the *Dry Winter*. For the *Wet Winter*, however, there was little support for the frequency of Dunlin occurrence at sites relating positively to any of the predictors as the null model (NONE) was among strongly competing models for most subset analyses. Further, responses for Dunlin site use intensity were unrelated to predictors during all winter sub-seasons of the *Wet Winter:* for frequency of occurrence, the null model NONE was strongly competing in 4/4 subsets for *Early Winter*, 3/4 subsets *Mid Winter*, and 2/2 subsets *Late Winter*; for mean abundance and maximum abundance, NONE was strongly competing in 3/4 subsets *Early Winter*, 2/4 subsets *Mid Winter*, and 1/2 subsets *Late Winter*.

For mean and maximum Dunlin abundances, HAB consistently ranked second in importance in the *Dry Winter* (tied with MUD), but of least importance in the *Wet Winter* (third to MUD; Table 4.5, Figure 4.5). Summed Akaike weights for HAB in the *Dry Winter* were roughly twice that in the *Wet Winter*. WET consistently ranked among subset analyses as the most important predictor of Dunlin use for both winters.

For the *Wet* and *Dry Winter*, there was little evidence that the intensity with which Killdeer used sites (all response variables) was related to any of the three predictors analyzed (Table 4.6). Similarly, for analyses of the sub-seasons of the *Wet Winter*, the null model (NONE) was among the strongly competing models explaining

Table 4.5. Summed Akaike weights (and corresponding ranks of importance) for predictors (MUD, WET and HAB) explaining Dunlin site use (frequency of occurrence, mean abundance, maximum abundance) during the *Wet Winter* of 1999-2000 and the *Dry Winter* of 2000-2001 in the Willamette Valley, Oregon, USA. Weights and ranks only calculated for those analyses where the null was among competing models for less than half of all subsets.

Time Period	Response	Subset	MUD	WET	HAB
Wet Winter	Mean Abundance[a]	1	0.56 (2)	0.93 (1)	0.20 (3)
		2	0.36 (2)	0.71 (1)	0.26 (3)
		3	0.40 (2)	0.99 (1)	0.22 (3)
		4	0.21 (2)	1.00 (1)	0.20 (3)
		Mean[b]	**0.38 (2)**	**0.91 (1)**	**0.22 (3)**
	Maximum Abundance[a]	1	0.67 (2)	0.96 (1)	0.21 (3)
		2	0.40 (2)	0.70 (1)	0.23 (3)
		3	0.38 (2)	0.97 (1)	0.21 (3)
		4	0.21 (2)	1.00 (1)	0.19 (3)
		Mean	**0.42 (2)**	**0.91 (1)**	**0.21 (3)**

Table 4.5. (Continued).

Time Period	Response	Subset	MUD	WET	HAB
Dry *Winter*	Frequency of Occurrence[c]	1	0.66 (2)	0.85 (1)	0.61 (3)
		2	0.51 (2)	0.98 (1)	0.18 (3)
		3	0.72 (2)	0.99 (1)	0.17 (3)
		4	0.20 (2)	0.96 (1)	0.17 (3)
		Mean	**0.52 (2)**	**0.94 (1)**	**0.28 (3)**
	Mean Abundance	1	0.71 (2)	0.99 (1)	0.26 (3)
		2	0.17 (3)	0.98 (1)	0.46 (2)
		3	0.25 (3)	0.76 (1)	0.38 (2)
		4	0.48 (3)	0.64 (1)	0.53 (2)
		Mean	**0.40 (3)**	**0.84 (1)**	**0.41 (2)**
	Maximum Abundance	1	0.78 (2)	0.99 (1)	0.33 (3)
		2	0.18 (3)	0.99 (1)	0.44 (2)
		3	0.18 (3)	0.81 (1)	0.40 (2)
		4	0.55 (3)	0.71 (1)	0.61 (2)
		Mean	**0.42 (3)**	**0.87 (1)**	**0.44 (2)**

[a] Mean and maximum bird abundance among surveys conducted for the time period.
[b] Mean summed Akaike weights (and corresponding rank) among subsets.
[c] Proportion of surveys in the time period in which Dunlin were present at sites.

Table 4.6. Delta (Δ) values, Akaike weights, and relative weights for strongly competing models (Δ ≤ 2) explaining influence of three predictors (MUD, WET, HAB) on Killdeer site use (frequency of occurrence, mean abundance, maximum abundance) during the *Wet Winter* of 1999-2000 and the *Dry Winter* of 2000-2001 in the Willamette Valley, Oregon, USA. Presence of HAB in models are emphasized in **bold**.

Time Period	Response	Subset[a]	Models	Δ	w	Relative Weight
Wet Winter	Frequency of Occurrence[b]	1	MUD	0.00	0.20	1.00
			HAB	0.03	0.20	1.02
			NONE	0.67	0.14	1.40
		2	MUD	0.00	0.25	1.00
			NONE	0.27	0.22	1.15
		3	WET	0.00	0.32	1.00
			NONE	1.13	0.18	1.76
		4	MUD	0.00	0.39	1.00
			MUD/WET	0.03	0.38	1.02
			HAB/MUD	2.48	0.11	3.45
			HAB/MUD/WET	2.54	0.11	3.55
	Mean Abundance[c]	1	NONE	0.00	-------	1.00
		2	MUD	0.00	0.30	1.00
			NONE	0.04	0.29	1.02
		3	NONE	0.00	-------	1.00
		4	NONE	0.00	-------	1.00
	Maximum Abundance[c]	1	NONE	0.00	-------	1.00
		2	MUD	0.00	0.44	1.00
			NONE	1.86	0.17	2.53
		3	NONE	0.00	-------	1.00
		4	NONE	0.00	-------	1.00

Table 4.6. (Continued).

Time Period	Response	Subset[a]	Models	Δ	w	Relative Weight
Dry Winter	Frequency of Occurrence[b]	1	MUD	0.00	0.27	1.00
			NONE	0.51	0.21	1.29
		2	WET	0.00	0.48	1.00
			HAB/WET	2.05	0.17	2.79
			MUD/WET	2.45	0.14	3.41
			NONE	3.54	0.08	5.87
		3	WET	0.00	0.30	1.00
			NONE	0.43	0.24	1.24
		4	**HAB**	0.00	0.22	1.00
			HAB/MUD	0.26	0.19	1.14
			MUD	0.70	0.16	1.42
			WET	1.42	0.11	2.04
			HAB/WET	1.68	0.10	2.32
	Mean Abundance[c]	1	NONE	0.00	-------	1.00
		2	NONE	0.00	-------	1.00
		3	NONE	0.00	-------	1.00
		4	NONE	0.00	-------	1.00
	Maximum Abundance[c]	1	NONE	0.00	-------	1.00
		2	NONE	0.00	-------	1.00
		3	NONE	0.00	-------	1.00
		4	NONE	0.00	-------	1.00

[a] Subset sample sizes were 32 (set 1), 32 (set 2), 32 (set 3), 31 (set 4) for winter 99-00; 40 (set 1), 40 (set 2), 39 (set 3), 38 (set 4) for winter 2000-2001. Spatial distribution of sites and an unequal numbers of sites per region yielded slightly different sample sizes among subsets.

[b] Proportion of surveys in the time period in which Killdeer were present at sites.

[c] Mean and maximum bird abundance among surveys conducted for the time period.

intensity of Killdeer use for virtually all subset analyses (frequency of occurrence: 3/4 subsets for *Early* and *Mid Winter*, 4/4 subsets for *Late Winter*; mean abundance: 4/4 subsets for *Early* and *Mid Winter*, 3/4 subsets for *Late Winter*; maximum abundance: 4/4 subsets for all sub-seasons).

4.6. Discussion

4.6.1. Influence of Landscape Structure and Context

Most studies of wetland landscape structure have addressed how context influences the process of settling in a breeding site. Moreover, because foraging movements during breeding periods are usually mediated by a central place (generally a nest; see Rosenberg and McKelvey 1999), these studies have focused on availability of alternative nearby foraging sites (Fasola and Barbieri 1978, Gibbs 1991, Naugle et al. 1999, Calmé and Desrochers 2000, Fairbairn and Dinsmore 2001, Best et al. 2001, Riffell et al. 2003) or on adjacent habitat affecting the quality of focal breeding patches (Naugle et al. 1999, 2000; Milsom et al. 2000, Riffell et al. 2003). In contrast, only a handful of wetland studies have looked at how landscape context influences the process of transient site use, such as mobile birds visiting multiple dispersed wetland patches in a landscape (Lovvorn and Baldwin 1996, Farmer and Parent 1997, Elphick 1998, Haig et al. 1998, Milsom et al. 1998, Roshier et al. 2002). This is likely due to the challenging methodologies required of monitoring a large number of dispersed sites or of radio-tracking birds over great distances (Haig et al. 1998, Webster et al. 2002).

Our results indicate that use of habitat by wintering Dunlin was influenced by wetland landscape structure, but only when shorebird habitat was relatively scarce. Although there were probably fewer Dunlin in the Valley during the *Dry Winter*, regions with more shorebird habitat supported greater abundances of Dunlin, and density results suggested birds disproportionately concentrated in regions with the most habitat. Likewise, there was strong evidence that surrounding habitat (HAB) influenced bird abundances at sites in the *Dry Winter* (Table 4.4, Figure 4.5). We recognize that support for the influence of landscape context on Dunlin numbers was weakened by inconsistent ranking of the best models (lowest AIC_c values) among data subsets and by models with and without HAB competing with each other. However, models with HAB were among the strongly competing models for all subsets in the *Dry Winter* and never among competing models in the *Wet Winter* (Table 4.4). Further, Akaike weights for HAB were twice as large in the *Dry Winter* (Table 4.5). Our dual-level corroborative approach was designed to guard against accepting spurious results potentially arising from the weaknesses of each analysis (i.e., at the regional level: small sample size, coarse scale, disproportionate influence on results of any one region; at the site level: spatial autocorrelation among sites, inappropriate scale for landscape context). Indeed, although regional use results for the *Dry Winter* hinged somewhat on data from the ANK region (see Table 4.1), many high and low use sites associated with high and low HAB, respectively, were in other regions.

That the distribution of wet, unvegetated habitat at both a landscape and local scale influenced use of habitat patches suggests a hierarchical process of habitat use

(*sensu* Kotliar and Wiens 1990). Results suggest that the distribution of shorebird habitat was important to Dunlin at both a large and small scale during the *Dry Winter*, as evidenced by support for two-scale models (HAB and WET and/or MUD; Table 4.4), and by consistent ranking of HAB as tied with MUD and second in importance to WET (Tables 4.5). In contrast, with little support for two-scale models and rankings indicating HAB was of least importance in the *Wet Winter*, only the distribution of wet, unvegetated habitat at the site scale appeared to influence Dunlin distributions during this winter. We are aware of only a few other studies that have investigated hierarchical use of habitat by waterbirds during winter (Warnock and Takekawa 1995, Elphick 1998, Cooke et al. 2003).

Annual differences in habitat availability likely explain why landscape structure was important in the *Dry* but not the *Wet Winter*. Habitat was scarce in the *Dry Winter* relative to the *Wet Winter* (e.g., among regions with the most habitat each winter, area of shorebird habitat differed by a factor of 10; Table 4.1, Figure 4.2). Moreover, availability of shorebird habitat varied among regions by a factor of eight in the *Dry Winter* compared to only three in the *Wet Winter* (Figure 4.2), indicating habitat was regionally more aggregated in the *Dry Winter*. Thus, Dunlin may have been attracted to regional patches of limited habitat in the *Dry Winter*, whereas a relatively abundant and even distribution of shorebird habitat exerted little influence on birds in the *Wet Winter*. Riffell et al. (2003) similarly found greater influence of landscape context in the dry year of their study and attributed this to the increased

value of surrounding supplemental habitat when local wetland food resources were limited.

Surprisingly, we did not find an influence of landscape context on frequency of Dunlin occurrence at sites in the *Dry Winter*. Competing models explaining frequency of occurrence included local habitat predictors (WET and MUD) in the *Dry Winter* and no predictors during the *Wet Winter* (Table 4.4). However, the 16 survey days accounted for only 12% of total possible days (roughly 135 days) birds may have used sites and time spent at each site comprised only a fraction of the day. Moreover, we anecdotally observed sites changing dramatically in wetness (flooding then dissipating) at a finer scale (within a week) than the frequency of our surveys. Shorebirds have been known to opportunistically find newly available habitat within days if not hours of its formation (Skagen and Knopf 1994). Thus, our survey frequency may not have provided us with the ability to detect differences in visitation frequencies among sites.

Killdeer were not influenced by distribution of shorebird habitat (wet, <50% vegetation cover) at any scale. That similar regional abundances of Killdeer were distributed among more sites in the *Dry Winter* further supports their lack of association with shorebird habitat. Although such results would normally call for measuring other explanatory variables and refining our models, we view them as a useful benchmark for evaluating the validity of Dunlin results. As Killdeer are habitat generalists (Jackson and Jackson 2000), we did not expect them to be as responsive to the distribution of shorebird habitat as Dunlin. Other researchers have similarly found

lack of association between use of sites by generalist species and availability of certain habitats in surrounding landscapes (e.g., Yellow-headed Blackbirds *Xanthocephalus xanthocephalus*, Naugle et al. 1999; Brown-headed Cowbird *Molothrus ater*, Best et al. 2001). Compared to Dunlin, the relatively sedentary nature of Killdeer, as implied by a higher frequency of occurrence at sites in both years (Figures 4.3, 4.4) and supported by movement patterns in the Valley (Sanzenbacher and Haig 2002b), indicates that the cosmopolitan habitat needs of Killdeer are probably met at a local scale.

It was surprising we did not detect any relationships for either species during all three winter sub-seasons, particularly for Dunlin in *Late Winter* when shorebird habitat had undergone a substantial decline since *Mid Winter* (Table 4.1). Although Dunlin used fewer sites more frequently (Table 4.1, Figure 4.3) and traveled further distances among sites by *Late Winter* (Sanzenbacher and Haig 2002a), bird abundances at sites were no different than in *Early* or *Mid Winter* (Figure 4.3) and were unrelated to a decreased availability of surrounding habitat (Table 4.4). This suggests that although birds were constrained to fewer sites spaced farther apart, habitat was still too abundant and evenly distributed to concentrate birds at sites in any relationship to availability of habitat in the surrounding landscape. Indeed, those regions with the least shorebird habitat in *Late Winter* of 1999-2000 had as much as those regions with the most habitat in the *Dry Winter* (Table 4.1). Lack of associations between Dunlin abundances and WET and MUD during each time period

can likely be attributed to limited power to detect patterns from small replicate survey sample sizes (i.e., n = 5 or 6).

Overall, our results for Dunlin complement a new but growing recognition of the importance of landscape structure to wetland birds during all phases of their annual cycle. During nonbreeding periods, influence of landscape structure on foraging waterbirds has been demonstrated by only a few other studies in addition to ours. Farmer and Parent (1997) found that migrating Pectoral Sandpipers (*Calidris melanotos*) visiting stopovers moved more within complexes comprised of many wetlands close together and argued such landscapes allow individuals to use more feeding sites with reduced energetic costs. Milsom et al. (1998) found that some coastal wintering shorebirds foraged more frequently in those wet grass fields closest to intertidal feeding areas. Similarly, Lovvorn and Baldwin (1996) documented that coastal wintering dabbling ducks (*Anas* spp.) exhibited greater use of intertidal habitats that were adjacent to farmlands used as supplemental foraging habitat. Elphick (1998) observed a number of positive correlations between the abundance of inland wintering waterbirds (geese, dabbling ducks, wading birds, shorebirds) on flooded rice fields and the amount of supplemental semi-natural wetland or additional flooded rice in the surrounding landscape. Finally, Roshier et al. (2002) illustrated that waterbird use of Australian dryland river valleys was influenced by availability of habitat as far away as adjacent river catchments and surrounding basins (100 to 1000s km).

4.6.2. Implications for Wetland Landscape Planning

Researchers and managers have become increasingly aware that ecological processes occurring within wetland landscapes, rather than only within single sites, are crucial to consider when conserving wetlands and wetland birds (e.g., Robinson and Warnock 1997, Haig et al. 1998, Roshier et al. 2001). Consequently, wetland conservation needs to adopt a broad landscape perspective, and limited conservation resources call for such landscape planning to be strategic. Findings from our study indicate that consideration of wetland location (placement in landscape relative to other habitat) may be the key to such strategic planning. Thus, in regions where wetland location may be an important determinant of wetland choice in dry years, planners should promote conserving clusters of dependable habitat that are wet in most years to guarantee benefiting birds over the entire range of potential winter conditions. Only within those sites of highest conservation priority because of their location should managers then work to enhance local resources such as invertebrates, vegetation structure, water depths, and roosting habitat within wetlands.

The Willamette Valley is an important landscape in which to consider such strategic planning. Many agencies and coalitions are slated to develop strategic wetland conservation plans for the Valley (e.g., Good and Sawyer 1998, Morlan 2000, Brown et al. 2001) and human population growth trends (Hulse et al. 2002) place urgency on establishing such plans before options become spatially restricted. Based on our results, we can provide some general recommendations for such strategic

conservation (i.e., protecting, enhancing and restoring habitat) in this and other similar regions.

The widespread distribution and large numbers of Killdeer illustrate their strong presence in the Valley and in turn the importance of agricultural lands to this species. Killdeer used all types of agricultural fields, including flooded areas with less than 50% vegetation cover (shorebird habitat). Our data indicate that they do not have a great affinity for wet, unvegetated habitat, and are therefore not as restricted in their use of particular agricultural habitats, as is the relatively larger population (in a typical year) of Valley-wintering Dunlin (Table 4.3). Thus, our recommendations are focused on devising conservation measures to conserve wetland habitat on agricultural land, an effort that should most benefit Dunlin and other Scolopacid shorebirds, but also Killdeer.

Especially during a dry year, our results imply that an isolated enhanced or restored site will be used less and thus not as beneficial to birds as one that is located near other favorable habitat. Thus, potential sites located near dependable wetland habitat in dry years (e.g., refuge impoundments, habitually flooded agricultural sites) should receive conservation priority over regularly isolated sites. For example, sites in the Ankeny, Beta, Butte Creek, Finley, and Longtom regions (Figure 4.1) and other Valley regions with high incidence of hydric soils (see Daggett et al. 1998) would be of highest priority to protect, enhance, or restore. Moreover, the Ankeny region (with impounded refuge wetlands) supported the most Dunlin, and impounded sites in the Brownsville, Ankeny, and Baskett Slough regions were used by large numbers of

birds in *Early*, *Mid* and *Late Winter* of 1999-2000, respectively. Because impounded wetlands are assured water each year, agricultural areas encompassing them may be considered strongholds within which conservation of individual sites should focus.

Second, local features that should be promoted within sites spatially prioritized for conservation are a productive food base and access to invertebrates by way of wet (flooded/saturated) and relatively unvegetated substrates. Estimates for invertebrate food abundance in the Valley are at least comparable (per m^2) to that observed in some other important freshwater wintering regions in North America (chapter 5: Taft and Haig *in review b*). As decomposing organic matter and regular fluctuations in flooding regime are crucial to invertebrate productivity (Fredrickson and Laubhan 1994, Rehfisch 1994, Anderson and Smith 2000), agricultural management practices or restoration techniques that promote these will be of foremost importance. Valley shorebirds (Dunlin) did not select certain crop types, but primarily used wet sites where there was also some exposed soil. Indeed, proportions of used sites managed under each crop generally corresponded to that for the greater Valley in a typical year (J. Steiner, USDA-Agricultural Research Service, personal communication), and thus high use of grass fields was only incidental to the fact that ryegrass is typically planted in autumn on poorly-drained soils (Hulse et al. 2002). Thus, amenable farmers can promote wet habitats on fields of any crop type by protecting (e.g., curtailing drainage activities), enhancing (e.g., removing tile drains), or restoring (e.g., re-establishing native ponding) natural flood processes. Farming activities of tilling and newly planting fields every 1-5 years further enhances habitat by periodically mimicking

open substrates attractive to shorebirds. It is important to emphasize, however, that concerns about the detrimental environmental effects of conventional tillage (e.g., Uri et al. 1998) necessitate exploring alternative straw incorporation methods that still promote access to invertebrates.

Conversion of consistently unproductive flooded grass seed fields to wetland impoundments (either to semi-natural wetlands or agricultural wild rice ponds) is another option that may benefit both shorebirds and farmers (e.g., providing waterfowl hunting revenues) in the Valley. Propagation of wild rice may be an economically viable agricultural alternative that has proven benefits to many wintering waterbirds (e.g., Brouder and Hill 1995, Elphick and Oring 1998). However, any such conversion to impounded habitat will require following integrated wetland management protocols (e.g., Laubhan and Fredrickson 1993, Weber and Haig 1996, Taft et al. 2002) to maintain shallow (< 10 cm), unvegetated substrates for foraging shorebirds.

Given the number of agricultural sites used, the impressive numbers of wintering shorebirds, and their resident nature in the Valley (Sanzenbacher and Haig 2002a, b), this region looks to be an important wintering landscape for shorebirds. It is fairly uncommon for a population of shorebirds to rely on the many wetlands of an agriculturally-dominated landscape almost exclusively throughout the winter (Ohmart et al. 1985, Elphick and Oring 1998). Such use supports recognizing the Valley as a wetland complex of at least regional importance (supporting at least 20,000 birds; Myers et al. 1987) within the Western Hemisphere Shorebird Reserve Network

(Brown et al. 2001). Importance of agricultural land to shorebirds has slowly increased in recognition (e.g., Page et al. 1979, Colwell and Dodd 1995, Warnock et al. 1995, Rottenborn 1996, Elphick and Oring 1998, Milsom et al. 1998, Ausden and Hirons 2002; chapter 2: Taft and Haig 2003). With one-third of the earth's exploitable surface now dominated by agriculture (Ormerod and Watkinson 2000), we expect to see even greater future worldwide attention focused on the role of agricultural wetland landscapes in conserving waterbirds.

4.7. Acknowledgements

5. The Value of Agricultural Wetlands as Invertebrate Resources for Wintering Shorebirds

5.1. Abstract

Agricultural landscapes have received little recognition for the food resources they provide to wintering waterbirds. In the Willamette Valley of Oregon, modest yet significant populations of wintering shorebirds (*Charadriiformes*) regularly use hundreds of dispersed wetlands on agricultural lands. Benthic invertebrates are a critical resource for the survival of overwintering shorebirds, yet the abundance of invertebrate resources in agricultural wetlands such as these has not been quantified. To evaluate the importance of agricultural wetlands to a population of wintering shorebirds, we quantified the density (individuals/m^2), biomass (mg/m^2) and general community composition of invertebrates available to birds at a sample of Willamette Valley sites during a wet winter (1999-2000) and a dry winter (2000-2001). Invertebrate densities ranged among wetlands from 173 to 1,925 (mean + SD: 936 + 464) individuals/m^2 in the wet winter, and from 214 to 3,484 (981 + 783) individuals/m^2 in the dry winter. Total invertebrate biomass among wetlands ranged from 35 to 652 (364 + 152) mg/m^2 in the wet winter, and from 85 to 1,405 (422 + 311) mg/m^2 in the dry winter. These estimates for food abundance are comparable (per m^2) to that observed in some other important freshwater wintering regions in North America. Our study provides insight on the relative value of agricultural wetlands to wintering shorebirds, and is a first step towards evaluating the potential carrying

capacity of the Willamette Valley for shorebirds and other waterbirds through restoration and enhancement efforts.

5.2. Introduction

For shorebirds and many other waterbirds, invertebrate food resources provided by a region are critical for overwinter survival (Evans 1976, Goss-Custard 1984, Senner and Howe 1984) and can be an important indicator of landscape quality. Gaining knowledge of typical invertebrate resources available within wetlands is an important first step towards determining potential carrying capacity of a region for waterbirds and for assessing levels of enhancement and restoration needed to support target populations (e.g., Anderson and Smith 1998, 1999, Augustin et al. 1999). However, aside from regions dominated by flooded rice fields (e.g., Fasola and Ruiz 1997, Elphick and Oring 1998, 2003), agricultural wetland landscapes have received little recognition for their current and potential value to wintering waterbirds (e.g., waterfowl, wading birds, shorebirds). Research evaluating invertebrate resources available within flooded agricultural landscapes should undoubtedly provide new perspective on their current importance and future potential as wintering strongholds for waterbirds.

The Willamette Valley of Oregon ("Valley"), USA, is one such agricultural landscape whose current and potential importance to waterbirds has only recently been acknowledged (Sanzenbacher and Haig 2002a, b; chapter 4: Taft and Haig *in review* a). Although most historical wetlands of the Valley have been lost or highly altered

by agriculture (Daggett et al. 1998, Christy et al. 2000, chapter 2: Taft and Haig 2003), current estimates for wintering waterbird populations are nonetheless sizeable (at least 200,000 waterfowl and 40,000 or more shorebirds; Gilligan et al. 1994, Nehls 1994, Sanzenbacher and Haig 2002a, b; chapter 2: Taft and Haig 2003, R. Trost, U.S. Fish and Wildlife Service, pers. comm.). Such numbers support recognizing the Valley as a wetland complex of at least regional importance to shorebirds (supporting at least 20,000 birds; Myers et al. 1987) within the Western Hemisphere Shorebird Reserve Network (Brown et al. 2001). Whereas waterfowl primarily use the few protected refuges of the Valley, shorebirds principally rely on the thousands of hectares of privately-owned agricultural wetlands ('palustrine emergent-farmed wetlands' of Cowardin et al. 1979; Sanzenbacher and Haig 2002a, b; chapter 4: Taft and Haig *in review* a). Representing the legacy of historical Valley wetlands, these are flooded farmlands that annually emerge with the accumulation of winter rains on native hydric soils (chapter 2: Taft and Haig 2003, chapter 3: Taft et al. 2004). As hundreds to thousands of shorebirds have been observed on individual agricultural wetlands at any one time (Sanzenbacher and Haig 2002a, b; chapter 4: Taft and Haig *in review* a), these wetlands are a recent focus of many agencies and coalitions committed to enhancing and restoring Valley habitat (e.g., Good and Sawyer 1998; Morlan 2000; Brown et al. 2001).

The value of agricultural wetlands cannot be fully appreciated, however, without an understanding of the food resources they provide for wintering birds, and how this compares to sites within other significant wetland landscapes. We used the

Valley as a model to explore the relative value of a complex of agricultural wetlands as a wintering landscape for shorebirds and other waterbirds. Our objectives were to quantify benthic invertebrate density and biomass and community composition during two different winters (wet and dry) at a sample of agricultural wetlands potentially used by shorebirds and to assess inter-site variation in these measures. We then evaluate how invertebrate resources of these wetlands compare to other significant wintering regions and assess the potential for augmenting invertebrate productivity in regions like the Valley through local enhancement and restoration.

5.3. Methods and Study Area

5.3.1. Study Area

The greater Willamette Valley encompasses 9,100 km² of lowland plains (Clark et al. 1991, Benner and Sedell 1997) within Oregon's Willamette Basin, a 29,000 km² watershed between Oregon's Cascade and Coast ranges (Figure 5.1; Hulse et al. 2002, Benner and Sedell 1997). The prominent hydrologic feature of the agricultural Valley is the Willamette River and its 13 major tributaries. The Valley climate is cool Mediterranean, with an average annual rainfall of 100-125 cm, 75% of it falling between October and March (Jackson and Kimerling 1993). Average temperatures range from 1° C in January to 30° C in July (Oregon Climate Service; www.ocs.orst.edu). We conducted our study from November – March of 1999-2000 and 2000-2001, two winters that differed dramatically in rainfall [91 cm (1999-2000)
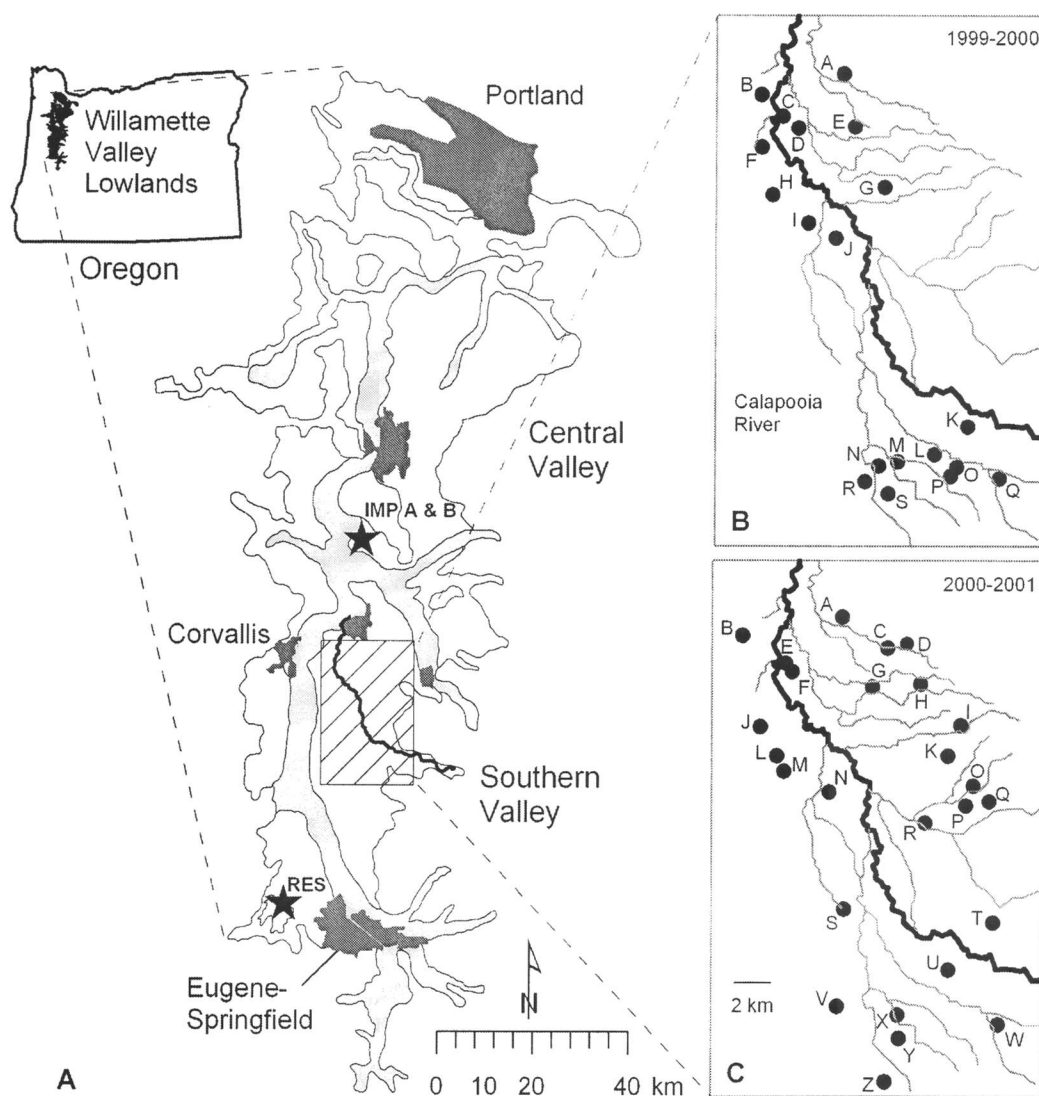
Figure 5.1. Location of wetlands (managed and agricultural) sampled for invertebrates mid-winter during 1999-2000 and 2000-2001 within the Willamette Valley of Oregon. A) Area in gray depicts the Willamette River floodplain, area in white depicts Valley alluvial terraces, and areas in black are urban. Thatched box portrays enlarged study area encompassing alluvial terraces surrounding the Calapooia River: B) Location of 19 agricultural wetlands studied in the wet winter of 1999-2000; C) Location of 26 agricultural wetlands studied in the dry winter of 2000-2001. Stars signify location of sampled impoundments (Imp A, Imp B) and reservoir (Res). Major streams of the Calapooia shown at 1:100,000 scale (Office of Information Resources Management 1994).

vs. 40 cm (2000-2001) precipitation from October-March; Oregon Climate Service]. Consequently, we refer to winter 1999-2000 as the "wet winter," and 2000-2001 as the "dry winter."

Common Valley lowland crops include grass seed (most prevalent), vegetables (e.g., corn, pumpkin, bush beans, cabbage), grains, and peppermint (Hulse et al. 2002). Grass seed crops are planted in autumn, and newly-planted perennial grass fields provide exposed soil between plants throughout the winter. Vegetable crops are left fallow through the winter and replanted in spring. Many of these crops are planted on what were historical wetlands and thus where soils are poorly-drained (chapter 3: Taft et al. 2004). An aquatic invertebrate fauna that can withstand dry periods presumably persists in these soils and flourishes with ponding, although community composition has changed with agriculture (e.g., introduction of nonnative earthworms). Moreover, senescence of crop vegetation (influenced by various tillage methods) provides a steady input of organic matter into the soil and winter ponding boosts decomposition of this plant material and thus the production of invertebrates (e.g., Fredrickson and Laubhan 1994).

Shorebirds find accessible foraging habitat where farming practices provide exposed soil (i.e., newly planted or fallow fields). Of the 40,000 or more wintering Valley shorebird species, Dunlin (*Calidris alpina*) and Killdeer (*Charadrius vociferus*) are the most abundant (Sanzenbacher and Haig 2002a, b; chapter 2: Taft and Haig 2003), but Common Snipe (*Gallinago gallinago*), Long-billed Dowitcher

(*Limnodromus scolopaceus*), Least Sandpiper (*Calidris minutilla*), and Greater
Yellowlegs (*Tringa melanoleuca*) are also fairly common.

We sampled invertebrates in 19 (in the wet winter) and 26 (in the dry winter)
agricultural wetlands in the northeast portion of the southern Willamette Valley, a 480
km^2 area of lowland plain encompassing the Calapooia River, a third to forth order
tributary of the Willamette River (Figure 5.1; Office of Information Resources
Management 1994). This area is characterized by a high incidence of poorly drained
hydric soils interspersed among well-drained areas (Daggett et al. 1998). Because
ponding on agricultural fields tends to occur as widely scattered, irregularly shaped,
changeable areas of shallow (1-cm deep) non-flowing sheetwater, we considered
entire agricultural fields as sites. We chose agricultural fields based on three criteria:
1) access granted by landowners, 2) presence of ponding or saturated soil, and 3)
shorebird access to the wet substrate (vegetation cover < 50% throughout the winter).
Sampled wetlands comprised a diversity of agricultural cover types that generally
represented proportions of the greater Valley in each [wet winter: 72% in grass seed,
16% fallow, 5% pasture, and 5% other (wild rice pond); dry winter: 78% in grass seed,
12% fallow, 4% pasture, and 4% other (wild rice pond); J. Steiner, USDA-
Agricultural Research Service, personal communication]. We also sampled three
impounded wetlands to assess how invertebrates in agricultural wetlands compared to
that in managed wetlands. These sites were two high-use (by shorebirds) wildlife
impoundments (Imp A, Imp B) located in the Ankeny National Wildlife Refuge

(NWR) and the northeastern dewatered shore of Fern Ridge Reservoir (Res; Figure 5.1).

5.3.2. Sampling and Data Summary

We sampled benthic and surface-dwelling invertebrates at each site once during mid winter: between 31 January-15 February in 1999-2000, and between 5 January-5 March in 2000-2001. We collected 15 core samples per site during each sampling event in the wet winter, and 30 samples per site in the dry winter. Each sample was a 5-cm diameter cylindrical core pushed 5 cm (98 cm^3) into the benthos (Sherfy et al. 2000). We sampled invertebrates within an oblong area roughly 150 by 20 meters encompassing concentrated wet areas within sites. Within sample areas, we systematically took one sample every 10 + 2 meters along a linear zig-zagging transect. Half of all samples at each site were collected in flooded habitat (less than 5 cm deep) and half in non-flooded but moist/saturated habitat.

Samples were washed, sieved (500 µm mesh) and preserved in 70% ethanol solution within two days of collecting (kept refrigerated until sieved and fixed). Using a stereomicroscope at 30x, we sorted through sieved debris and identified, counted, and collected all invertebrates of taxonomic groups that have been documented in shorebird diets (Skagen and Oman 1996). We used Pennak (1989) and Merrit and Cummins (1984) to identify these to the level of family for Oligochaeta (Enchitraeidae, Tubificidae, Lumbricidae) and most Insecta larvae (Chironomidae, Empididae, Tipulidae), but identified only to subclass for ostracods (Ostracoda) and

order for haplotaxid worms (Haplotaxida), springtails (Collembola), and caddisfly larvae (Trichoptera). Although shorebirds have been known to take invertebrates (e.g., ostracods) as small as 1.0 mm long (Weber and Haig 1997), we did not feel that we had adequately sampled nektonic and mobile small invertebrates such as ostracods and springtails, respectively, and thus excluded these from abundance measures. We provide information only on presence/absence for these groups.

We observed little inter-site and inter-year variation in body size of individuals of each identified group. Consequently, we estimated dry biomass of samples by drying (at 50°C for 24 hours) and weighing (to nearest 0.0001 g) a random collection of individuals in each group from all sites studied in 2000-2001 (360 small Oligochaetes, 50 Lumbricids, 38 Chironomids, 10 Empids, 23 Tipulids and 20 Trichoptera). We then divided total biomass for each group by the number of collected individuals to generate average biomass multipliers used in conjunction with counts of individuals to calculate estimated total biomass of each sample.

We summarized data for the following numerically dominant taxonomic groups: 1) Aquatic Oligochaetes (small-bodied aquatic worms in the order Haplotaxida and families Enchitraeidae and Tubificidae), 2) Megadrili (large-bodied oligochaetes primarily in the family Lumbricidae), 3) Chironomidae, 4) Empididae, 5) Tipulidae, and 6) Trichoptera. We generated two measures describing the abundance of benthic invertebrates available at each site: 1) invertebrate density (individuals/m^2), calculated as the mean number of invertebrates (total for the six taxonomic groups) among collected core samples; and 2) invertebrate biomass (mg/m^2), calculated as the

mean estimated dry biomass of invertebrates (all six groups) among cores. We assessed differences among sites in log (natural)-transformed invertebrate density and invertebrate biomass using one-way analysis of variance and Bonferroni t-tests for multiple comparisons (Ramsey and Schafer 1997). We also present invertebrate densities for each taxonomic group to assess general trends in community composition.

5.4. Results

In the wet winter of 1999-2000, wetland sites varied in invertebrate density from 173 + 53 (mean + SE among cores) to 1,925 + 428 individuals/m^2, and in invertebrate biomass from 35 + 11 to 652 + 234 mg/m^2 (Figure 5.2). Among sites during the dry winter of 2000-2001, density varied from 214 + 45 to 3,484 + 416 individuals/m^2, and biomass from 85 + 24 to 1,405 + 226 mg/m^2 (Figure 5.3). In the dry winter, impoundments of Ankeny NWR (Imp A and Imp B) ranked among the lowest of sites for density and biomass, and Fern Ridge Reservoir (Res) placed among the highest for both measures. In both winters, sites differed significantly in total invertebrate density (wet winter: $F_{18, 266} = 2.94$, $P < 0.001$; dry winter: $F_{28, 839} = 10.04$, $P < 0.001$) and total invertebrate biomass (dry winter: $F_{18, 266} = 2.30$, $P < 0.01$; dry winter: $F_{28, 839} = 9.04$, $P < 0.001$). Multiple comparisons indicate there were more differences in density and biomass estimates among sites in the dry winter (Figure 5.3) compared to the wet winter (Figure 5.2). However, averaged among all sites, measures for total
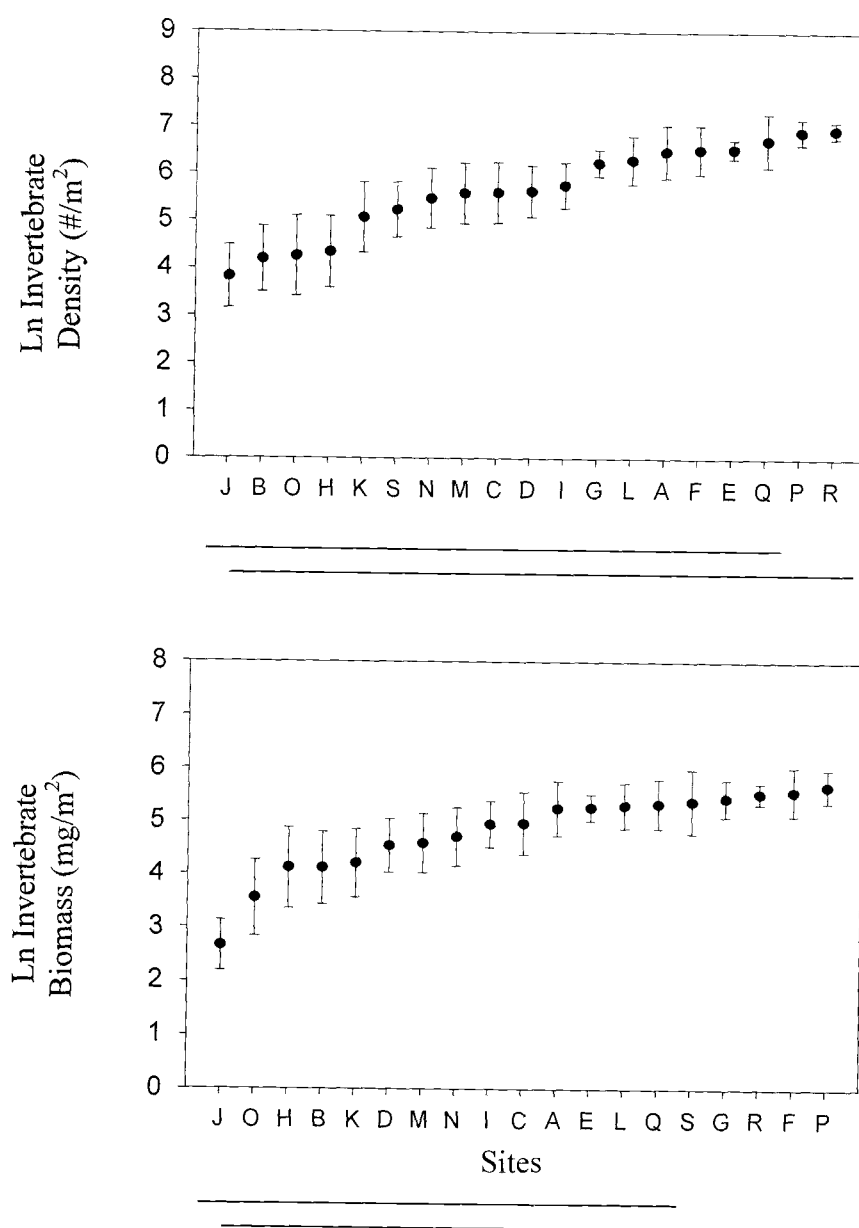
Figure 5.2. Log (natural)-transformed mean (± SE) total invertebrate density (individuals/m²) and biomass (mg/m²) at 19 sites sampled for benthic invertebrate abundance in the Willamette Valley of Oregon during the wet winter of 1999-2000. Lines below bar chart x-axes signify groups of similar sites in density and biomass. Site means spanned by the same line are not significantly different as evaluated using Bonferroni t-tests for multiple comparisons after one-way ANOVA. See Figure 5.1 for locations of sites.

Figure 5.3. Log (natural)-transformed mean (+ SE) total invertebrate density (individuals/m^2) and biomass (mg/m^2) at 29 sites sampled for benthic invertebrate abundance in the Willamette Valley of Oregon during the dry winter of 2000-2001. Bars for managed sites are white, agricultural sites in black. Lines below bar chart x-axes signify groups of similar sites in density and biomass. Site means spanned by the same line are not significantly different as evaluated using Bonferroni t-tests for multiple comparisons after one-way ANOVA. See Figure 5.1 for locations of sites.
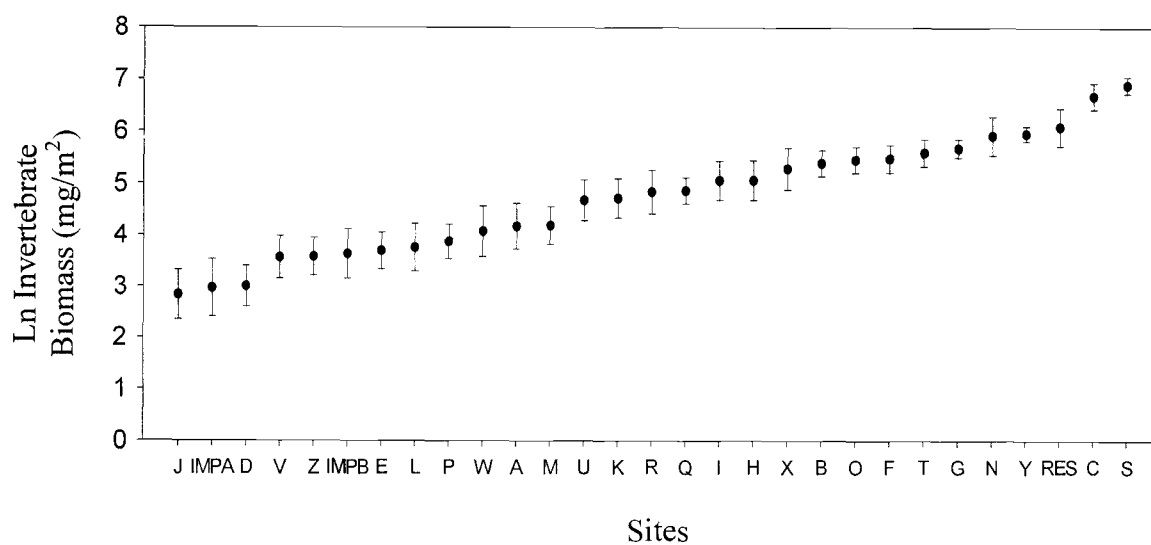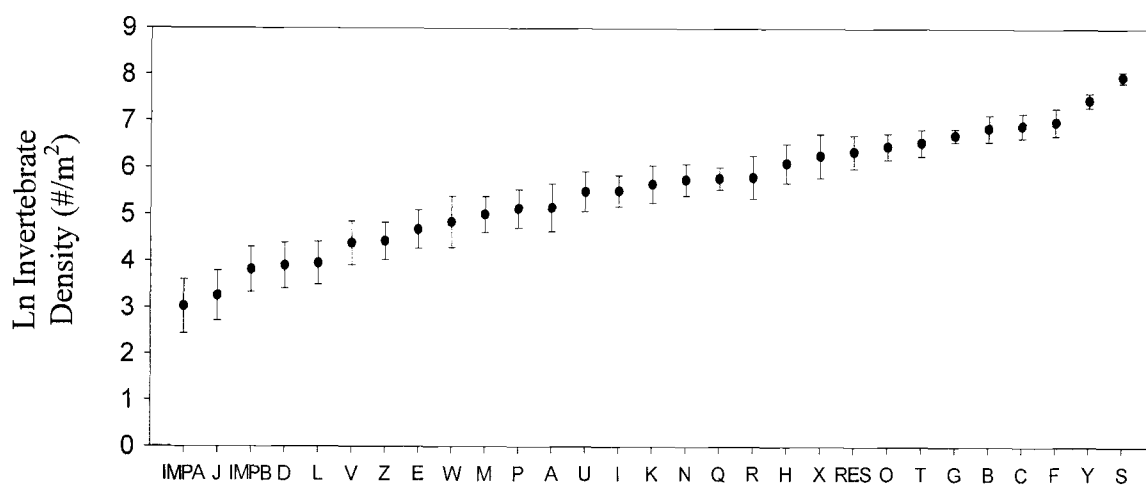
invertebrate density and biomass were similar among years, with 936 + 464 (wet winter) and 981 + 783 (dry winter) individuals/m^2 for density, and 364 + 152 (wet winter) and 422 + 311 (dry winter) mg/m^2 for biomass. In general, given error (i.e., SD around the site mean) in estimated invertebrate abundance of wetlands, most sites could be considered fairly close to the among-site average in both years.

Although community composition varied among sites, most wetlands were dominated by aquatic oligochaetes, with more than 50% of total invertebrates comprised of aquatic oligochaetes in 84% (wet winter) and 93% (dry winter) of sites (Table 5.1). For only a few sites was a relatively significant proportion of the community (e.g., 24-60%) comprised of megadrili (e.g., site H in the wet winter; sites U and C in the dry winter; Table 5.1), chironomids (e.g., site S in the wet winter; sites I, U, Imp B, and Res in the dry winter), tipulids (e.g., site B in the wet winter) or trichoptera (e.g., site M in the wet winter; sites J and V in the dry winter; Table 5.2). For the most part, empids, tipulids, and trichoptera comprised a minority of invertebrate communities. Collembola were present in 10 out of 19 (53%) sites in the wet winter, and 15 of 28 (54%) sites in the dry winter. Ostracods were less common, observed in 5 of 19 (26%) and 9 of 28 (32%) sites in the wet winter and dry winter, respectively (Table 5.2).

Table 5.1. Mean ($\pm$ SE among cores) oligochaete densities (individuals/m^2) observed at 19 (wet winter of 1999-2000) and 29 (dry winter of 2000-2001) sites in the Willamette Valley of Oregon, USA. Sites are arranged in ascending order by total invertebrate density (density of all groups combined).

Site[c]	Aquatic Oligochaetes[a]			Megadrili[b]		
	Density		Proportion of Total[d]	Density		Proportion of Total[d]
-- Wet Winter --						
J	160	$\pm$ 43	92	0	$\pm$ 0	0
B	71	$\pm$ 31	27	10	$\pm$ 10	4
S	224	$\pm$ 80	49	0	$\pm$ 0	0
H	261	$\pm$ 121	46	285	$\pm$ 169	50
I	567	$\pm$ 137	86	58	$\pm$ 23	9
O	686	$\pm$ 279	94	24	$\pm$ 11	3
G	689	$\pm$ 238	84	132	$\pm$ 50	16
N	754	$\pm$ 284	88	0	$\pm$ 0	0
K	801	$\pm$ 297	93	20	$\pm$ 15	2
M	778	$\pm$ 236	89	3	$\pm$ 3	0
C	720	$\pm$ 277	80	10	$\pm$ 10	1
E	842	$\pm$ 178	94	31	$\pm$ 16	3
L	801	$\pm$ 134	88	51	$\pm$ 14	6
D	828	$\pm$ 311	88	10	$\pm$ 7	1
R	1,212	$\pm$ 222	94	7	$\pm$ 7	1
F	1,216	$\pm$ 252	90	14	$\pm$ 9	1
P	1,409	$\pm$ 317	94	92	$\pm$ 28	6
A	1,684	$\pm$ 586	94	48	$\pm$ 27	3
Q	1,874	$\pm$ 421	97	0	$\pm$ 0	0

Table 5.1. (Continued).

Site[c]	Aquatic Oligochaetes[a]		Proportion of Total[d]	Megadrili[b]		Proportion of Total[d]
	Density			Density		
			-- Dry Winter --			
L	115	± 43	54	39	± 11	18
D	228	± 50	93	15	± 11	6
J	129	± 49	49	36	± 15	13
Z	222	± 65	81	3	± 3	1
E	221	± 45	72	10	± 5	3
V	166	± 52	51	0	± 0	0
M	278	± 67	76	70	± 22	19
P	406	± 73	81	58	± 17	12
Q	453	± 102	91	7	± 5	1
I	309	± 67	54	4	± 67	1
N	538	± 97	79	127	± 62	19
U	320	± 96	47	181	± 46	27
K	674	± 137	85	74	± 20	9
A	795	± 216	89	83	± 48	9
G	900	± 121	87	85	± 19	8
O	1,025	± 179	92	53	± 16	5
W	991	± 321	86	53	± 23	5
H	1,109	± 204	91	31	± 11	3
T	1,053	± 210	85	104	± 31	8
R	1,149	± 379	90	0	± 0	0
C	991	± 149	67	475	± 63	32
B	1,584	± 267	98	20	± 11	1
F	1,944	± 326	98	20	± 17	1
X	1,912	± 417	96	0	± 0	0
Y	2,453	± 516	99	8	± 5	0
S	2,828	± 395	81	37	± 13	1
Imp A	166	± 46	71	0	± 0	0
Imp B	443	± 205	89	0	± 0	0
Res	901	± 167	74	0	± 0	0

[a] Small-bodied worms in the order Haplotaxida and families Enchitraeidae and Tubificidae.
[b] Large-bodied oligochaetes, primarily in family Lumbricidae.
[c] See Figure 5.1 for site locations.
[d] Proportion of the density of all tallied invertebrates at each site.

Table 5.2. Mean (± SE among cores) Diptera and Insecta densities (individuals/m^2) and presence (x) of Collembola and Ostracoda observed at 19 (wet winter of 1999-2000) and 29 (dry winter of 2000-2001) sites in the Willamette Valley of Oregon, USA. Sites are arranged in ascending order by total invertebrate density (density of all groups combined).

Site[a]	Chironomidae Density (#/m^2)	Prop. of Total[b]	Empididae Density (#/m^2)	Prop. of Total[b]	Tipulidae Density (#/m^2)	Prop. of Total[b]	Trichoptera Density (#/m^2)	Prop. of Total[b]	Collembola	Ostracoda
				-- *Wet Winter* --						
J	0 ± 0	0	14 ± 14	8	0 ± 0	0	0 ± 0	0		
B	27 ± 16	10	14 ± 14	5	136 ± 49	51	7 ± 7	3		
S	207 ± 84	45	7 ± 7	1	20 ± 11	4	3 ± 3	1		
H	7 ± 7	1	7 ± 7	1	10 ± 7	2	0 ± 0	0		
I	14 ± 9	2	7 ± 7	1	14 ± 9	2	0 ± 0	0	x	
O	7 ± 7	1	0 ± 0	0	7 ± 7	1	7 ± 7	1	x	
G	7 ± 7	1	0 ± 0	0	0 ± 0	0	0 ± 0	0	x	
N	34 ± 28	4	0 ± 0	0	65 ± 25	8	0 ± 0	0		
K	7 ± 7	1	0 ± 0	0	34 ± 24	4	0 ± 0	0	x	x
M	41 ± 28	5	0 ± 0	0	0 ± 0	0	54 ± 36	60		x
C	54 ± 24	6	7 ± 7	1	78 ± 33	9	27 ± 16	3		x
E	20 ± 11	2	0 ± 0	0	7 ± 7	1	0 ± 0	0	x	
L	0 ± 00	0	0 ± 0	0	48 ± 21	5	10 ± 8	1	x	
D	48 ± 34	5	41 ± 17	4	7 ± 7	1	0 ± 0	0	x	
R	7 ± 7	1	0 ± 0	0	48 ± 20	4	24 ± 15	2	x	
F	68 ± 29	5	34 ± 16	3	20 ± 15	2	0 ± 0	0		x
P	0 ± 0	0	0 ± 0	0	0 ± 0	0	0 ± 0	0	x	x
A	44 ± 44	2	0 ± 0	0	7 ± 7	0	7 ± 7	<1	x	
Q	7 ± 7	0	17 ± 17	1	0 ± 0	0	27 ± 16	1		

Table 5.2. (Continued).

Site[a]	Chironomidae Density (#/m²)	Prop. of Total[b]	Empididae Density (#/m²)	Prop. of Total[b]	Tipulidae Density (#/m²)	Prop. of Total[b]	Trichoptera Density (#/m²)	Prop. of Total[b]	Collembola	Ostracoda
					-- Dry Winter --					
L	37 ± 13	17	7 ± 5	3	7 ± 5	3	3 ± 3	2		
D	3 ± 3	1	0 ± 0	0	0 ± 0	0	0 ± 0	0		
J	7 ± 5	3	31 ± 11	12	0 ± 0	0	65 ± 52	24		x
Z	37 ± 27	14	3 ± 3	1	3 ± 3	1	7 ± 5	2	x	x
E	10 ± 6	3	54 ± 19	18	14 ± 6	4	0 ± 0	0	x	x
V	31 ± 16	9	0 ± 0	0	0 ± 0	0	129 ± 52	40		
M	0 ± 0	0	20 ± 8	6	0 ± 0	0	0 ± 0	0	x	
P	10 ± 6	2	14 ± 8	3	7 ± 5	1	0 ± 0	0	x	
Q	7 ± 5	1	14 ± 6	3	0 ± 0	0	17 ± 10	3		
I	228 ± 115	40	21 ± 9	4	0 ± 0	0	4 ± 4	1		
N	3 ± 3	0	10 ± 6	1	3 ± 3	<1	0 ± 0	0	x	
U	165 ± 51	24	14 ± 8	2	0 ± 0	0	0 ± 0	0	x	
K	14 ± 11	2	24 ± 8	3	0 ± 0	0	7 ± 5	1	x	x
A	14 ± 8	2	7 ± 7	1	0 ± 0	0	0 ± 0	0	x	
G	27 ± 19	3	24 ± 8	2	0 ± 0	0	3 ± 3	<1	x	x
O	20 ± 9	2	10 ± 6	1	10 ± 7	1	0 ± 0	0		
W	51 ± 19	4	37 ± 16	3	14 ± 8	1	3 ± 3	<1	x	
H	70 ± 41	6	10 ± 6	1	0 ± 0	0	7 ± 5	1	x	
T	3 ± 3	<1	17 ± 9	1	10 ± 6	1	58 ± 28	5		
R	112 ± 44	9	20 ± 8	2	3 ± 3	<1	0 ± 0	0	x	x

Table 5.2. (Continued).

Site[a]	Chironomidae Density (#/m²)	Prop. of Total[b]	Empididae Density (#/m²)	Prop. of Total[b]	Tipulidae Density (#/m²)	Prop. of Total[b]	Trichoptera Density (#/m²)	Prop. of Total[b]	Collembola	Ostracoda
				-- Dry Winter --						
C	10 ± 7	1	3 ± 3	<1	7 ± 5	<1	3 ± 3	<1		x
B	3 ± 3	<1	3 ± 3	<1	0 ± 0	0	0 ± 0	0	x	
F	3 ± 3	<1	3 ± 3	<1	3 ± 3	<1	10 ± 7	1		
X	54 ± 19	3	10 ± 6	1	20 ± 9	1	0 ± 0	0		
Y	7 ± 5	<1	17 ± 7	1	0 ± 0	0	0 ± 0	0		
S	241 ± 66	7	363 ± 112	10	10 ± 6	<1	7 ± 5	<1	x	x
Imp A	68 ± 20	29	0 ± 0	0	0 ± 0	0	0 ± 0	0		
Imp B	54 ± 15	11	0 ± 0	0	0 ± 0	0	0 ± 0	0	x	x
Res	299 ± 65	25	7 ± 5	1	0 ± 0	0	3 ± 3	<1		x

[a] See Figure 5.1 for site locations.
[b] Proportion of the density of all tallied invertebrates at each site.

141

5.5. Discussion

Given the highly altered state of Valley wetlands, the abundances and composition of invertebrate communities we observed among sampled sites in both years were somewhat surprising. However, a number of features of Valley wetlands render them likely to maintain populations of benthic invertebrates: 1) because these were wetlands historically, invertebrate populations are likely present in wetland soils, 2) senescence and tillage of crop vegetation provides organic material for invertebrates, 3) sites undergo periodic ponding, and 4) herbicides, rather than pesticides, are normally prescribed on fields. Invertebrates were equally (if not more) abundant in agricultural wetlands as in managed wetlands (Imp A, Imp B, and Res) we sampled (Figures 5.2, 5.3). Whether these differences are real or an artifact of our sampling is difficult to say. Impoundments on Ankeny NWR (Imp A and B) were only recently converted from previous farmland and thus management prescriptions to increase their invertebrate productivity are in their infancy. However, two of these managed wetlands (Imp B and Res) were sampled after roughly two months of relatively high use (e.g., 5,000 or more shorebirds) by foraging waterbirds, and thus may have incurred substantial depletion of prey resources (e.g., Székely and Bamberger 1994, Mihuc et al. 1997).

Compared to estimates of invertebrate abundance at inland stopovers in spring and fall (e.g., Farmer and Wiens 1999, Augustin et al. 2000, Ashley et al. 2000), abundance of winter shorebird food among agricultural wetlands of the Valley is relatively low. However, our estimates are comparable to the lower end of the range

of estimates observed during winter in other significant freshwater wintering regions. Moreover, abundance estimates were no different among years, and thus the densities and biomasses we observed are probably reliable assessments of the typical abundance of invertebrates provided by wetlands in any given year. Our estimates are comparable to winter invertebrate abundances observed among brackish managed wetlands in South Carolina (Weber and Haig 1996) where densities range from approximately 250 to 3800 individuals/m^2 and biomass from 250 to 500 mg/m^2. In moist-soil managed playa wetlands of the Southern High Plains of Texas, Anderson and Smith (2000) estimated mean winter total invertebrate (96% benthic) densities among wetlands of only 155 individuals/m^2, but owing to greater presence of large-bodied invertebrates mean biomass estimates were higher than our study (i.e., 3,522 mg/m^2). Among winter wetlands in the Sacramento Valley of California, Elphick (2000) estimated average densities of roughly 2,500 individuals/m^2 among flooded rice fields and approximately 5,500 individuals/m^2 among seminatural wetlands. Finally, moist-soil managed wetlands of the Suisun Marsh (Batzer et al. 1997) and San Joaquin Valley of California (Safran et al. 1997) are highly productive, with high biomass estimates (e.g., on average about 400-1,900 mg/m^2 among foraging sites of five shorebird species; Safran et al. 1997) and densities of chironomids (Batzer et al. 1997) and small oligochaetes (Safran et al. 1997) in the tens of thousands. While we may have sampled sites after shorebirds had depleted prey, thus deflating our estimates of abundance relative to other locales, the confounding influence of prey depletion was a concern among these other studies as well.

Valley wetlands differed relatively little in invertebrate density and biomass,
especially in the wet winter of 1999-2000 (Figure 5.2). This suggests that during a
normal year for rainfall, agricultural wetlands are similar in levels of invertebrate
productivity. Although individual Valley wetlands may provide only moderate
abundances of food resources, such homogeneity would imply that the hundreds of
agricultural wetlands across the landscape (chapter 3: Taft et al. 2004) collectively
provide a notable invertebrate prey base for shorebirds and other waterbirds. We
found greater variation in invertebrate abundance among sites during the dry winter of
2000-2001, and we can only offer some tentative clarifications for this. Mean
minimum and maximum temperatures were no different between winters (Oregon
Climate Service data 1999-2001) discounting the possibility that select sites produced
more invertebrates in the dry winter due to increased temperatures influencing the
vertical distribution of prey or the rate of decomposition of organic matter (e.g.,
Fredrickson and Laubhan 1994, Durell 2000). However, we sampled 25% more sites
in the dry winter, and may have captured more of the inherent variation among
wetlands. In addition, we observed fewer Dunlin at sites in the dry winter (chapters 4,
6: Taft and Haig *in review* a, c), thus invertebrates may not have received the same
predation pressure as in the wet winter.

Agricultural wetlands were dominated numerically by aquatic oligochaetes in
both winters, with earthworms (megadrils) and chironomids comprising the majority
of the remaining community of most sites (Tables 5.1, 5.2). Such composition
contrasts that found in other important wintering wetland locales, namely California

moist-soil managed wetlands where chironomids numerically dominate invertebrate communities (Batzer et al. 1997, Safran et al. 1997). However, caloric content values do not differ greatly between Oligochaeta and Chironomidae (Cummins and Wuycheck 1971). Thus, all else being equal, oligochaete-dominated communities probably energetically benefit Valley wintering shorebirds as much as do chironomid-dominated communities (e.g., biomass of each). As earthworms (Lumbricidae) are common in agricultural lands (Tucker 1992, Ausden et al. 2001), they were present at most Valley sites, comparable in density to that observed in coastal California pastures used by wintering shorebirds (32-176 individuals/m^2; Colwell and Dodd 1995; Table 5.1). Moreover, their contribution to biomass was high in those agricultural wetlands where they were relatively abundant. Earthworms are commonly consumed by plovers (*Charadrius* species; e.g., Bengtson et al. 1976, 1978; Jackson and Jackson 2000) and other waders (Ausden et al. 2001) and we have anecdotally observed Dunlin eating earthworms on a number of occasions (chapter 6: Taft and Haig *in review* c). Earthworms of Valley agricultural wetlands are undoubtedly an important resource for wintering shorebirds.

Our findings provide a first step towards determining either the winter shorebird carrying capacity or the food supply necessary to support a certain target wintering population size for the Valley. With recent attention by various waterbird conservation initiatives to integrate management plans for entire wetland landscapes or complexes (e.g., North American Waterfowl Management Plan, U.S. Fish and Wildlife Service et al. 1994; National Shorebird Plan, Brown et al. 2001; North

American Waterbird Conservation Plan, Kushlan et al. 2002), it has become important to assess the value of regions to nonbreeding waterbirds by quantifying the quality of foraging habitat (e.g., Haukos and Smith 1993, Anderson and Smith 1998, 1999; Augustin et al. 1999). The number of birds that can be supported for a given number of days (i.e., bird use days) can be coarsely predicted with models using parameter values for typical invertebrate biomass (g/m^2) in wetlands, caloric content (kj/g) of taxa comprising invertebrate communities, turnover rates of invertebrates, total hectares of available habitat, diets of target species, and species-specific energetic requirements (Anderson and Smith 1998, 1999, 2000; Augustin et al. 1999; however, see Goss-Custard et al. 2002). For the Valley, we would need to determine the caloric content of Valley invertebrates, their turnover rates, and the particular diets and energy requirement of Valley shorebirds before predictions could be used to set shorebird management goals. However, provided that parameter values for the energetic content of invertebrates and the requirements of wintering shorebirds do not differ dramatically among regions, our findings provide at least a cursory idea of how resource densities in the Valley compare to that in other significant wintering regions.

It is possible that the relatively small wintering population (40,000+) of shorebirds in Oregon's Willamette Valley may reflect the region's present carrying capacity. Indeed, other regions with higher values for invertebrate abundance support more shorebirds (e.g., Sacramento and San Joaquin Valley; Shuford et al. 1994). Thus, if increasing the wintering population of shorebirds is a future goal of managers, our findings suggest enhancing invertebrate productivity at existing agricultural

wetlands. Left in farming, it seems that Valley agricultural wetlands at least have the capacity to produce shorebird food at abundance levels comparable to those sites observed with the greatest abundance of invertebrates (i.e., ~3,000 individuals/m^2; 1,500 mg/m^2). Moreover, active restoration and enhancement of these wetlands and ongoing management of their vegetation and hydrology may boost invertebrate abundances even above these levels. However, even while maximizing all other environmental factors contributing to productivity (e.g., input of detritus, fluctuating water levels), the relatively colder temperatures of the Valley (e.g., on average 6 to 8° Celsius lower than in California; Shuford et al. 1994) may impose an upper bound on the potential productivity of invertebrates. Further study on the production of invertebrates under varying environmental conditions would help to resolve the ultimate resource potential of Valley wetlands.

Drainage for agriculture is responsible in large part for the loss and conversion of wetland landscapes worldwide (e.g., Boulé and Bierly 1987, Wilen 1989, Dahl 1990, Vileisis 1997, Mitsch and Gosselink 2000). Although remaining and relatively intact wetland complexes may be most valuable to waterbirds today, the current and potential future worth of wetland landscapes that have been altered by agriculture should not be overlooked. As exemplified by Valley wetlands, the persistence of invertebrate resources on what were historical wetlands and the exploitation of these resources by a modest population of waterbirds both implore for greater notice of their potential value. Only through committed conservation efforts to restore wetland

habitat and enhance wetland food resources in agricultural landscapes will such potential be realized.

5.6. Acknowledgements

6. Landscape Context Mediates Influence of Local Food Abundance on Wetland Use by Wintering Shorebirds in an Agricultural Valley

6.1. Abstract

While it is widely understood that local abundance of benthic invertebrates can greatly influence the distribution and abundance of wetland birds, no studies have examined if wetland landscape context can mediate this relationship. Such an influence of landscape context is most likely during nonbreeding periods when local invertebrate resources are limited and mobile wetland birds are compelled to interact with the spatial distribution of multiple sites of varying invertebrate productivity across a landscape. We studied the influence of wetland food abundance and landscape context on use of agricultural wetlands by wintering Dunlin (*Calidris alpina*) and Killdeer (*Charadrius vociferus*) in the Willamette Valley of Oregon, USA, over two winters (1999-2000, 2000-2001) of differing rainfall and subsequent habitat distribution. We monitored bird use (frequency of occurrence and abundance) at a sample of wetlands differing in local food abundance (density and biomass) and landscape context [adjacent shorebird habitat (defined as ha of wet habitat with less than 50% vegetative cover and within a 2-km radius) and nearest neighbor distance]. We evaluated predictive models for bird use using all possible subsets regression and the Cp criterion to select the most parsimonious model. During the dry winter (2000-2001), Dunlin exhibited greater use of sites with higher invertebrate density and biomass but also with more adjacent shorebird habitat and closest to a wetland neighbor. Use of sites by Killdeer was unrelated to either local food abundance or

landscape context measures during both winters. Our findings contribute to a growing recognition of the importance of landscape structure to wetland birds and highlight a number of implications for the spatial planning and enhancement of wetlands using a landscape approach.

6.2. Introduction

Only in the last decade have researchers considered landscape-scale influences on use of individual wetlands by wetland birds (e.g., Farmer and Parent 1997, Elphick 1998, Naugle et al. 1999, Calmé and Desrochers 2000, Fairbairn and Dinsmore 2001, Riffell et al. 2003, chapter 4: Taft and Haig *in review* a). In contrast, wetland ecology has a long history of researching the local wetland habitat characteristics that influence the distribution and abundance of wetland birds (e.g., Kadlec 1962; Weller 1978, 1999; Murkin et al. 1997). One tenet that has emerged from this traditional site-based approach is that invertebrate prey resources play a central role in determining waterbird distributions (e.g., wading birds, waterfowl, shorebirds) within and among wetlands during the nonbreeding season (e.g., Evans and Dugan 1984, Goss-Custard 1984, Murkin and Kadlec 1986, Helmers 1991, Krapu and Reinecke 1992, Colwell and Landrum 1993, Kalejta and Hockey 1994, Mercier and McNeil 1994, Safran et al. 1997; Weber and Haig 1996, 1997; Farmer and Wiens 1999, Ashley et al. 2000). However, particularly during nonbreeding periods, many waterbirds are highly mobile (e.g., Haig et al. 1998, Roshier et al. 2002) and thus likely to also interact with the structure of wetland landscapes, or the distribution of wetland resources at larger

spatial scales. How wetland landscape context (i.e., spatial pattern of habitat surrounding wetlands) may mediate correlations between the abundance of waterbirds and their prey is a novel question for wetland ecology, and one whose answers may have significant implications for conservation planning of entire wetland landscapes (*sensu* Wu and Hobbs 2002).

Landscape context likely influences waterbird foraging dynamics during the winter period. For this season in particular, invertebrate resources at temperate latitudes can be scarce and patchily distributed over large distances (e.g., Evans 1976, Myers 1983) and thus waterbirds likely supplement their energy intake by using multiple wetlands within a landscape (*sensu* Dunning et al. 1992). Moreover, the energetic costs of flight, thermoregulation and survival can be high (e.g., Kersten and Piersma 1987, Castro and Myers 1989). Consequently, for wintering waterbirds compelled to forage among multiple patches in a landscape, it should be energetically favorable to concentrate in areas with proportionately high wetland densities (Evans 1976, Pyke 1983, Farmer and Parent 1997). As a result, discovery (and subsequent revisiting) of wetland sites with high food abundance may be influenced by their particular location in the landscape: highly productive sites that are isolated may go unnoticed while those situated in concentrated wetland regions receive greater use, and less productive sites surrounded by much wetland habitat may sustain greater use than if they were isolated.

We examined the influence of wetland food abundance and landscape context on winter use of wetlands by two shorebird species (Dunlin *Calidris alpina* and

Killdeer *Charadrius vociferus*) in the agricultural wetland landscape of the Willamette

Valley ("Valley") in western Oregon, USA. The Valley is winter residence to 40,000

or more shorebirds, of which Dunlin and Killdeer are the most abundant species

(Sanzenbacher and Haig 2002a, b; chapter 2: Taft and Haig 2003). These two species

represent two ends of the spectrum of Valley shorebird ecologies as Dunlin favor

moist or flooded substrates while Killdeer are considered habitat generalists (Warnock

and Gill 1996, Jackson and Jackson 2000). Valley wetlands used by shorebirds are

primarily on converted agricultural lands ("agricultural wetlands" hereafter; these are

"palustrine emergent-farmed wetlands" of Cowardin et al. 1979). Representing the

legacy of historical Valley wetlands, these are flooded farmlands that annually emerge

with the accumulation of winter rains on native hydric soils (chapter 2: Taft and Haig

2003, chapter 3: Taft et al. 2004). Moreover, shorebirds find accessible foraging

habitat where farming practices provide exposed soil. Different management histories

among sites have presumably generated wetlands varying in invertebrate abundance

(chapter 5: Taft and Haig *in review* b). However, in accordance with the variable

distribution of hydric soils, agricultural wetlands also vary considerably in spatial

configuration across the Valley landscape (chapter 3: Taft et al. 2004).

During two winters of differing rainfall and subsequent habitat distribution, our

objectives were to: 1) determine if wetland use (frequency of occurrence and bird

abundances) was related to measures of wetland invertebrate food abundance, and 2)

assess the additional variation in bird use explained by considering wetland landscape

context. We conclude by evaluating implications of our findings to wetland conservation in the Valley and other similar wetland landscapes.

6.3. Study Area

The greater Willamette Valley encompasses 9,100 km^2 of lowland plains (Clark et al. 1991, Benner and Sedell 1997) within Oregon's Willamette Basin, a 29,000 km^2 watershed between Oregon's Cascade and Coast ranges (Figure 6.1; Hulse et al. 2002, Benner and Sedell 1997). The prominent hydrologic feature of the Valley is the Willamette River and its 13 major tributaries. The climate is cool Mediterranean, with an average annual rainfall of 100-125 cm, 75% of it falling between October and March (Jackson and Kimerling 1993); average temperatures range from 1° C in January to 30° C in July (data from Oregon Climate Service). We conducted our study from November – March of 1999-2000 and 2000-2001, two winters that differed dramatically in rainfall [91 cm (1999-2000) vs. 40 cm (2000-2001) precipitation from October-March; Oregon Climate Service data 1999-2001]. Consequently, we refer to winter 1999-2000 as the 'wet winter' and to winter 2000-2001 as the 'dry winter.'

Common Valley lowland crops include grass seed (most prevalent), vegetables (e.g., corn, pumpkin, bush beans, cabbage), grains, and peppermint (Hulse et al. 2002). Grass seed crops are planted in autumn. Whereas annual ryegrass (*Lolium multiflorum*) fields are covered fully with vegetation by mid to late winter, newly-planted perennial ryegrass fields (*Lolium perenne*) provide exposed soil

Figure 6.1. Location of agricultural wetlands studied during the winters of 1999-2000 (wet) and 2000-2001 (dry) within the southern Willamette Valley of Oregon. A) Area in gray depicts the Willamette River floodplain, area in white depicts Valley alluvial terraces, and areas in black are urban. Thatched box portrays enlarged study area encompassing alluvial terraces surrounding the Calapooia River: B) Location of 17 agricultural wetlands studied in the wet winter of 1999-2000. Shorebird habitat is shown in gray; C) Location of 19 agricultural wetlands studied in the dry winter of 2000-2001. Shorebird habitat is shown in black. Major streams of the Calapooia shown at 1:100,000 scale (Office of Information Resources Management 1994).
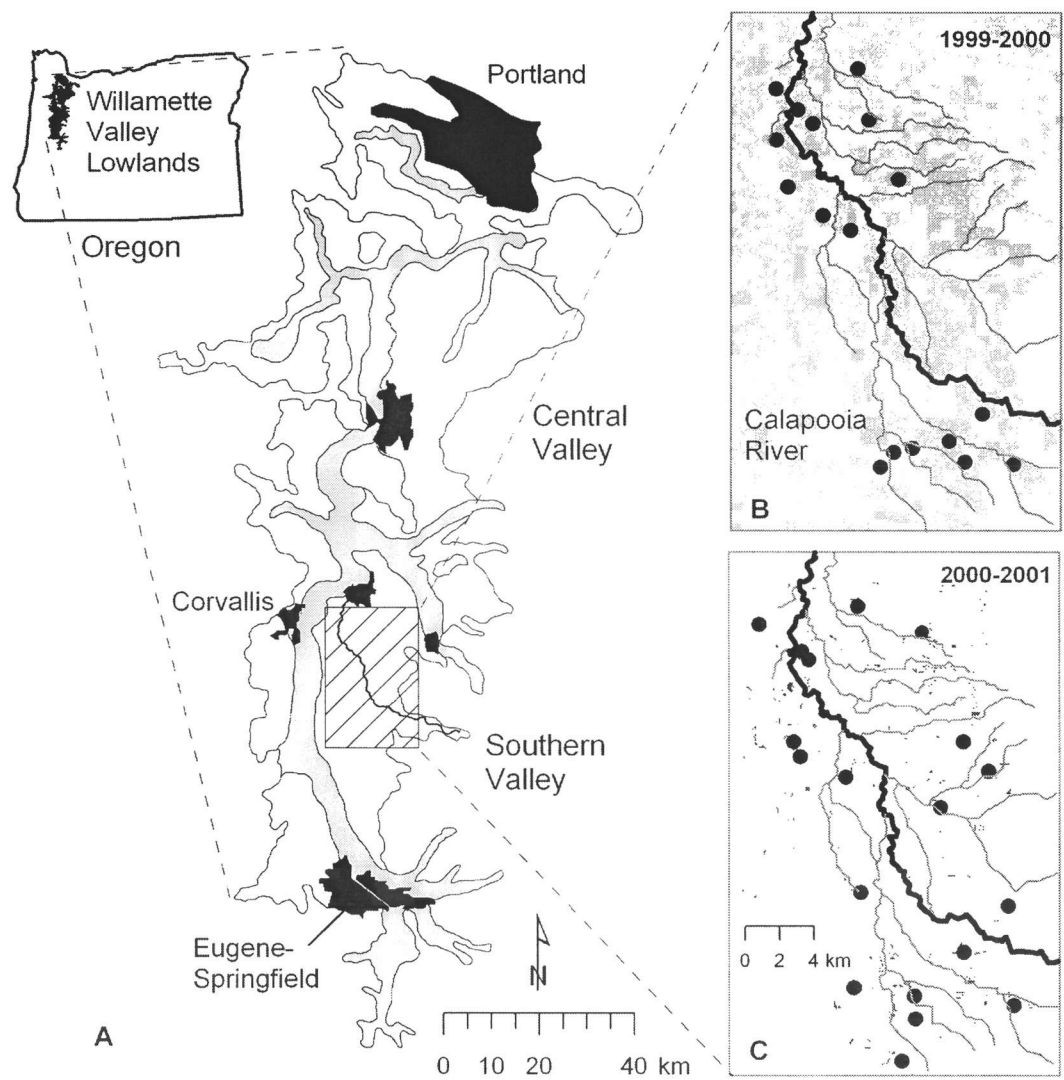
Figure 6.1

between plants throughout the winter. Vegetable crops are left fallow through the winter and replanted in spring. Many of these crops are planted on what were historical wetlands and thus where soils are poorly-drained (chapter 2: Taft and Haig 2003). An aquatic invertebrate fauna that can withstand dry periods presumably persists in these soils and flourishes with ponding, although community composition has changed with agriculture (e.g., introduction of nonnative earthworms). Moreover, senescence of crop vegetation (influenced by various tillage methods) provides a steady input of organic matter into the soil and winter ponding boosts decomposition of this plant material and thus the production of invertebrates (e.g., Fredrickson and Laubhan 1994).

We selected 17 (in the wet winter) and 19 (in the dry winter) study wetlands in the northeast portion of the southern Willamette Valley, a 480 km^2 area of lowland plain encompassing the Calapooia River, a third to fourth order tributary of the Willamette River (Figure 6.1; Office of Information Resources Management 1994). This area is characterized by a high incidence of poorly drained hydric soils interspersed among well-drained areas (Daggett et al. 1998) providing an array of configurations of wetland habitat surrounding sites (variable landscape contexts). Because ponding on agricultural fields tends to occur as widely scattered, irregularly shaped, changeable areas of shallow (1-cm deep) non-flowing sheetwater, we considered entire agricultural fields as sites. We chose sites based on four criteria: 1) access granted by landowners, 2) regular spatial interspersion, 3) presence of ponding or saturated soil, and 4) shorebird access to the wet substrate (vegetation cover < 50%

throughout the winter). Study sites comprised a diversity of agricultural cover types that generally represented proportions of the greater Valley in each [wet winter: 65% in grass seed, 18% fallow, 12% pasture, and 6% other (wild rice pond); dry winter: 62% in grass seed, 16% fallow, 12% pasture, and 5% other (wild rice pond); J. Steiner, USDA-Agricultural Research Service, personal communication].

6.4. Methods

6.4.1. Land Cover Data

Shorebirds prefer moist to flooded foraging substrates that are sparsely vegetated (Rundle and Fredrickson 1981, Fredrickson and Reid 1986, Colwell and Oring 1988, Rottenborn 1996). Moreover, prior to data collection, we observed an association between shorebird use and wet exposed (<50% vegetation cover) portions of agricultural land (hereafter *shorebird habitat*), particularly for Dunlin and their ecological allies (family Scolopacidae). Thus, for both winters, we mapped the distribution of shorebird habitat in our focal study area using a combination of remotely sensed imagery and data acquired in the field (chapter 3: Taft et al. 2004, chapter 4: Taft and Haig *in review* a). For the wet winter of 1999-2000, we used remotely sensed radar (RADARSAT) imagery taken 28 January to produce a layer in a geographic information system (GIS; Erdas Imagine 8.6, Erdas, Inc., Atlanta, GA) depicting the mid-winter distribution of shorebird habitat during peak wetness. Shallow water within impounded semi-natural wetlands was considered shorebird

habitat. See chapter 3 (Taft et al. 2004) for further details on 1999-2000 land cover data.

Because analogous satellite imagery was not available in the dry winter of 2000-2001, we produced a land cover layer of shorebird habitat for mid-winter by ground mapping visible habitat in February 2001 during and after the period of peak winter wetness. Using visible landmarks that were also depicted on topographic maps (USGS 7.5 minute), we plotted areas of shorebird habitat on field maps and digitized these into a GIS layer (in Erdas Imagine 8.6). In many cases, we were able to verify estimated area of shorebird habitat using data we had collected during surveys (see below). Systematic distribution of roads in the Valley (Hulse et al. 2002) promoted relatively consistent visibility of shorebird habitat throughout the study region.

6.4.2. Shorebird Surveys

We surveyed study sites during daylight hours (0730-1800) at weekly intervals and on the days we sampled for invertebrates, yielding 19 (in the wet winter) and 18 (in the dry winter) replicate weekly surveys from November-March. At each survey, we identified and counted all shorebirds present at each site with 8x binoculars and 25x spotting scopes. We assumed that all birds present, whether roosting or foraging at the time, were using the site as foraging habitat. We alternated weekly the survey time of day (morning, afternoon) for each site to reduce systematic bias. We used land cover maps and landmarks that were both mapped and visible in the field (e.g., topography, creek-road crossings, railroads) to locate and digitize in a GIS layer (in Erdas Imagine

8.6) the center points and approximate perimeters of all sites. At the time of each survey, we visually estimated % of site with ponded water or saturated soil.

6.4.3. Invertebrate Sampling

We sampled benthic and surface-dwelling invertebrates at each site once during mid to late winter: between 31 January-15 February in 1999-2000, and between 5 January-5 March in 2000-2001. We collected 15 core samples per site during each sampling event in the wet winter, and 30 samples per site in the dry winter. Each sample was a 5-cm diameter cylindrical core pushed 5 cm (98 cm^3) into the benthos (Sherfy et al. 2000) and retaining any invertebrates present on the soil surface. We sampled invertebrates within an oblong area roughly 150 by 20 meters encompassing concentrated wet areas within sites. Within sample areas, we systematically took one sample every 10+2 meters (+2 meters to prevent sampling in phase with some other environmental variable) along a linear zig-zagging transect. Half of all samples at each site were collected in flooded habitat (less than 5 cm deep) and half in non-flooded but moist/saturated habitat.

Samples were washed, sieved (500 μm mesh), and preserved in 70% ethanol solution within two days of collecting (kept refrigerated until sieved and fixed). Using a stereomicroscope at 30x, we sorted through sieved debris and identified, counted, and collected all invertebrates of taxonomic groups that have been documented in shorebird diets (Skagen and Oman 1996) and that were probable prey items for Dunlin and Killdeer (Warnock and Gill 1996; Jackson and Jackson 2000). We used Pennak

(1989) and Merrit and Cummins (1984) to identify these to the family level for Oligochaeta (Enchitraeidae, Tubificidae, Lumbricidae) and most Insecta larvae (Chironomidae, Empididae, Tipulidae), but identified only to subclass for ostracods (Ostracoda) and order for haplotaxid oligochaetes (Haplotaxida), springtails (Collembola), and caddisfly larvae (Trichoptera).

We observed little inter-site and inter-year variation in body size of individuals in each identified group. Consequently, we estimated dry biomass of samples by drying (at 50°C for 24 hours) and weighing (to nearest 0.0001 g) a random collection of individuals in each group from all sites studied in 2000-2001 (360 small Oligochaetes, 50 Lumbricids, 38 Chironomids, 10 Empids, 23 Tipulids and 20 Trichoptera). We then divided total biomass for each group by the number of collected individuals to generate average biomass multipliers used in conjunction with counts of individuals to calculate estimated total biomass of each sample.

6.4.4. Data Summary and Analyses

We summarized site use data collected across all replicate surveys ($n = 19$ in wet winter, $n = 18$ in dry winter) to generate three response variables for each species: 1) *frequency of occurrence* (proportion of surveys in which species was present), 2) *mean bird abundance* among replicate surveys, and 3) *maximum bird abundance* among surveys. Since shorebirds can sporadically occur in large flocks in the 1000s, we considered maximum abundance among surveys an additional index that mean

abundance would not have necessarily captured. Where necessary, we normalized mean and maximum abundance responses with the natural log (ln) transformation.

We generated four measures indexing local food abundance within sites each winter: 1) *mean invertebrate density* (individuals/m^2), calculated as the mean number of invertebrates among collected core samples at a site; 2) *maximum invertebrate density* (individuals/m^2) revealed by the core sample with greatest number of invertebrates at a site; 3) *mean invertebrate biomass* (mg/m^2), calculated as the mean estimated invertebrate dry biomass among cores in a site; and 4) *maximum invertebrate biomass* (mg/m^2) from the core with the highest estimated dry biomass at a site. Because benthic invertebrates are inherently spatially clumped (Elliott 1977), we considered maximum invertebrate abundance and biomass observed among cores to represent the degree to which sites harbored productivity hotspots. Owing to differences in diet and foraging modes between Dunlin and Killdeer, we calculated the four food abundance measures differently for each species. Although shorebirds have been known to take invertebrates (e.g., ostracods) as small as 1.0 mm long (Weber and Haig 1997), we did not feel that we had adequately sampled nektonic and mobile small invertebrates such as ostracods and springtails, respectively, and thus excluded these from analyses for both species. However, we included all other identified invertebrates in food abundance estimates for Dunlin analyses. For Killdeer analyses, we additionally excluded small oligochaetes (Enchitraeidae, Tubificidae, Haplotaxida) which we regarded as too small and inaccessible to foraging Killdeer.

We defined two predictors describing wetland landscape context: 1) *adjacent shorebird habitat* (ha) and 2) *nearest neighbor distance* (m). We considered *adjacent shorebird habitat* as the amount of shorebird habitat in a 2 km radius surrounding sites each winter, calculated using our GIS layers for land cover in ArcView 3.2 (ESRI, Inc., Redlands, CA) to delineate area of habitat within circular buffers centered on each site's central coordinates. We chose 2 km as an operative radius that would capture variation among sites in amount of adjacent habitat while also minimizing spatial autocorrelation among sites in landscape context measures due to overlapping buffers. Moreover, we considered a 2 km radius as an appropriate average spatial scale at which Dunlin and Killdeer likely interact with the landscape (in a concurrent study of the winter home ranges of radio-tagged individuals, core use areas had roughly a 3 km radius for Dunlin and a 1.5 km radius for Killdeer; Sanzenbacher and Haig, 2002a, b; P. Sanzenbacher, personal communication). Because distance to the closest adjacent habitat could differ for two sites with the same amount of surrounding habitat within 2 km, we included *nearest neighbor distance* as an additional measure quantifying landscape context. We calculated the *nearest neighbor distance* as the Euclidean distance (m) from the midpoint of sample sites to the nearest shorebird habitat edge. Finally, we calculated *wet area* (ha) as the mean % (among surveys) of site flooded/saturated multiplied by the site's area (ha).

For each winter, we used all possible subsets regression to evaluate the influence of one of four food abundance estimates (*mean invertebrate density, maximum invertebrate density, mean invertebrate biomass*, or *maximum invertebrate*

biomass) and both landscape context predictors (*adjacent shorebird habitat* and *nearest neighbor distance*) on each of the three species use response variables (*frequency of occurrence, mean bird abundance,* and *maximum bird abundance*). We adjusted mean and maximum bird abundances for local habitat area by including *wet area* as a covariate in all models. For both winters, weak associations between *wet area* and *adjacent shorebird habitat,* and between *adjacent shorebird habitat* and *nearest neighbor distance* (correlation coefficients between 0.1 and 03; Cohen 1988) allowed for simultaneous assessment of their influences on bird use. We used the Cp criterion to select the most parsimonious regression model (Ramsey and Schafer 1997), and minimized type I error due to violations of independence (from the few sites whose 2 km buffers overlapped) by considering model terms significant only if *P*-values were < 0.01. Partial R^2 values are provided for significant model terms only. All regression analyses were performed using proc REG in SAS version 8.2 (SAS Institute Inc. 1999).

6.5. Results

Study wetlands varied considerably both in estimated local food abundance and measures of landscape context (Table 6.1). Mean and maximum invertebrate densities and biomass varied similarly among sites each year. However, landscape context measures differed more among sites in the dry winter than the wet winter, as illustrated by comparing coefficients of variation (dry vs. wet winter: *adjacent shorebird habitat*: 0.47 vs. 0.26; *nearest neighbor distance*: 0.62 vs. 0.43) and ratios

Table 6.1. Mean (± SD) site features (predictors) and Dunlin and Killdeer use (responses) among 17 (wet winter 1999-2000) and 19 (dry winter 2000-2001) sites monitored throughout the winter (November-March) in the Willamette Valley, Oregon, USA.

Parameters	Wet winter 1999-2000		Dry winter 2000-2001	
	Mean ± SD	Range	Mean ± SD	Range
Site Predictors				
Wet Area (ha)	4.3 ± 3.3	0.4 – 12.4	3.5 ± 2.8	0.5 – 9.3
Mean Invertebrate Density[a] for Dunlin (#/m^2)	976 ± 473	173 – 1,925	1,113 ± 881	208 – 3,487
Mean Invertebrate Density[a] for Killdeer (#/m^2)	113 ± 67	14 – 309	139 ± 148	19 – 659
Maximum Invertebrate Density[a] for Dunlin (#/m^2)	3,613 ± 2,042	764 – 9,524	5,292 ± 4,062	917 – 15,381
Maximum Invertebrate Density[a] for Killdeer (#/m^2)	557 ± 522	204 – 2,496	879 ± 662	204 – 2,801
Mean Invertebrate Biomass[b] for Dunlin (mg/m^2)	356 ± 139	35 – 643	423 ± 306	85 – 1,405
Mean Invertebrate Biomass[b] for Killdeer (mg/m^2)	184 ± 130	3 – 590	228 ± 228	39 – 839
Maximum Invertebrate Biomass[b] for Dunlin (mg/m^2)	1,454 ± 1,074	153 – 4,962	2,193 ± 1,327	384 – 4,964
Maximum Invertebrate Biomass[b] for Killdeer (mg/m^2)	1,087 ± 1,084	41 – 4,850	1,652 ± 1,254	308 – 4,455
Adjacent Shorebird Habitat[c] (ha)	294 ± 76	214 – 486	19 ± 9	5 – 35
Nearest Neighbor Distance[d] (m)	388 ± 168	200 – 815	593 ± 369	150 – 1,602

Table 6.1. (Continued).

Parameters	Wet winter 1999-2000		Dry winter 2000-2001	
	Mean ± SD	Range	Mean ± SD	Range
Bird Use Responses				
Dunlin Frequency of Occurrence[e] (%)	18 ± 13	0 – 47	15 ± 13	0 – 50
Killdeer Frequency of Occurrence[c] (%)	41 ± 26	5 – 84	46 ± 19	17 – 78
Mean Dunlin Abundance[f] (# Birds)	212 ± 390	0 – 1,531	31 ± 26	0 – 98
Mean Killdeer Abundance[f] (# Birds)	39 ± 50	1 – 216	38 ± 23	2 – 102
Max Dunlin Abundance[f] (# Birds)	950 ± 2,223	0 – 9,000	65 ± 70	0 – 260
Max Killdeer Abundance[f] (# Birds)	138 ± 233	1 – 1,000	117 ± 76	2 – 299

[a]   Mean or maximum number of invertebrates (all taxonomic groups combined) per m^2 among collected core samples (n = 15 in 1999-2000, n = 30 in 2000-2001).

[b]   Mean or maximum biomass (mg/m^2; all taxonomic groups combined) among collected core samples (n = 15 in 1999-2000, n = 30 in 2000-2001).

[c]   Amount (ha) of class 1 habitat within 2 km of the central coordinates of the site.

[d]   Euclidean distance (m) from the midpoint of sample sites to the nearest shorebird habitat edge.

[e]   Frequency of occurrence among all surveys conducted (n = 19 in 1999-2000, n = 18 in 2000-2001).

[f]   Mean or maximum bird abundance among all surveys conducted.

of maximum to minimum values (*adjacent shorebird habitat* differed by a factor of 7 in the dry winter but only by a factor of 2 in the wet winter; *nearest neighbor distances* differed by a factor of 11 in the dry winter compared to a factor of 4 in the wet winter). While Killdeer numbers were similar among winters, Dunlin were far less abundant at sites in the dry winter of 2000-2001.

In both winters, local food abundance and both measures of landscape context had low explanatory power in explaining variation in *frequency of occurrences* of Dunlin and Killdeer (Tables 6.2, 6.3). *Wet area* did not account for much variation in Dunlin or Killdeer abundances in either winter (Tables 6.2, 6.3). During the dry winter only, mean and maximum Dunlin abundances were greater at sites with more food (all four measures), but also with more *adjacent shorebird habitat* (Table 6.2). *Adjacent shorebird habitat* accounted for the most variation in Dunlin abundance among sites (R^2 ranging from 0.34-0.43), with food abundance explaining up to half of the remaining variation (R^2 ranging from 0.19-0.34). In addition, *nearest neighbor distance* was an important predictor explaining variation in mean Dunlin abundances in three of four analyses, and was a significant term in one of these. In contrast, during the wet winter, local food abundance and landscape context of sites had low explanatory power in explaining variation in Dunlin abundances at sites. Likewise, variation in Killdeer abundances (mean and maximum) among sites had relatively little to do with local food abundance and the landscape context of sites in both winters (Table 6.3).

Table 6.2. Results of all possible subsets model selection for linear regressions of Dunlin use (frequency of use, mean and maximum bird abundance) on one of four food abundance measures [either mean invertebrate density (individuals/m^2), maximum invertebrate density (individuals/m^2), mean invertebrate biomass (mg/m^2), or max invertebrate biomass (mg/m^2)] and landscape context [adjacent shorebird habitat (ha) and nearest neighbor distance (m)] of wetland sites during two winters in the Willamette Valley, Oregon, USA. Wet area (ha) was forced as a covariate in all models. Statistics are shown for model with lowest Cp. Significant model terms (P<0.01) are highlighted in **bold**, and partial R^2 values are only provided for significant model terms. Seventeen sites (df = 15) in 1999-2000 and 19 sites (df = 17) in 2000-2001 were included in analyses.

Winter	Bird Use Response	Parameters in Model Subset With Lowest Cp	Parameter Estimate (±SE)	t-value	P-value	Partial R^2	F-value	P-value	Model Adj. R^2
Wet 1999-2000[a]	Frequency of Occurrence[b]	Wet Area	1.12 ± 0.99	1.14	0.27	---	1.29	0.27	0.02
	Mean Bird Abundance[c]	Wet Area	0.30 ± 0.15	2.11	0.05	---	4.43	0.05	0.18
	Max Bird Abundance[c]	Wet Area	0.37 ± 0.18	2.05	0.06	---	4.19	0.06	0.17

Table 6.2. (Continued).

Winter	Bird Use Response	Parameters in Model Subset With Lowest Cp	Parameter Estimate (±SE)	t-value	P-value	Partial R^2	F-value	P-value	Model Adj. R^2
Dry 2000-2001	Frequency of Occurrence	Nearest Neighbor Distance[d]	-0.01 ± 0.008	-1.90	0.07	---	3.61	0.07	0.13
	Mean Bird Abundance	Wet Area	0.90 ± 1.45	0.62	0.55	---	8.27	**0.0012**	0.62
		Mean Invertebrate Density[e]	0.02 ± 0.005	3.90	**0.0016**	0.23			
		Adjacent Shorebird Habitat[f]	1.64 ± 0.47	3.51	**0.0035**	0.34			
		Nearest Neighbor Distance	-0.03 ± 0.01	-2.53	0.02	0.14			
		Wet Area	1.39 ± 1.16	1.20	0.25	---	15.23	**< 0.0001**	0.76
		Max Invertebrate Density[e]	0.005 ± 0.0008	5.70	**<0.0001**	0.34			
		Adjacent Shorebird Habitat	1.58 ± 0.37	4.25	**0.0008**	0.34			
		Nearest Neighbor Distance	-0.03 ± 0.009	-3.12	**0.0076**	0.13			
		Wet Area	0.92 ± 1.56	0.59	0.56	---	6.67	**0.0032**	0.56
		Mean Invertebrate Biomass[g]	0.05 ± 0.01	3.35	**0.0047**	0.26			
		Adjacent Shorebird Habitat	2.25 ± 0.54	4.17	**0.0009**	0.34			
		Nearest Neighbor Distance	-0.02 ± 0.01	-1.48	0.16	---			
		Wet Area	0.32 ± 1.18	0.27	0.79	---	17.11	**<0.0001**	0.73
		Max Invertebrate Biomass[g]	0.01 ± 0.003	5.36	**<0.0001**	0.34			
		Adjacent Shorebird Habitat	2.46 ± 0.40	6.20	**<0.0001**	0.43			

Table 6.2. (Continued).

Winter	Bird Use Response	Parameters in Model Subset With Lowest Cp	Parameter Estimate ($\pm$SE)	t-value	P-value	Partial R^2	F-value	P-value	Model Adj. R^2
Dry 2000-2001	Max Bird Abundance	Wet Area	-2.93 $\pm$ 3.79	-0.77	0.45	---	9.89	**0.0008**	0.60
		Mean Invertebrate Density	0.04 $\pm$ 0.01	3.29	**0.0049**	0.24			
		Adjacent Shorebird Habitat	5.71 $\pm$ 1.22	4.69	**0.0003**	0.41			
		Wet Area	-1.68 $\pm$ 3.23	-0.52	0.61	---	15.94	**< 0.0001**	0.71
		Max Invertebrate Density	0.01 $\pm$ 0.002	4.62	**0.0003**	0.34			
		Adjacent Shorebird Habitat	5.55 $\pm$ 1.02	5.43	**< 0.0001**	0.42			
		Wet Area	-2.1 $\pm$ 4.1	-0.51	0.62	---	8.17	**0.0019**	0.54
		Mean Invertebrate Biomass	0.11 $\pm$ 0.04	2.80	0.0134	0.20			
		Adjacent Shorebird Habitat	6.75 $\pm$ 1.40	4.83	**0.0002**	0.42			
		Wet Area	-2.68 $\pm$ 4.07	-0.66	0.52	---	8.02	**0.002**	0.54
		Max Invertebrate Biomass	0.02 $\pm$ 0.009	2.75	0.0148	0.19			
		Adjacent Shorebird Habitat	6.39 $\pm$ 1.36	4.69	**0.0003**	0.42			

[a] Mean and max bird abundance ln transformed.

[b] Frequency of Dunlin occurrence among all surveys conducted (n = 19 in 1999-2000, n = 18 in 2000-2001).

[c] Mean or maximum bird abundance among all surveys conducted.

[d] Euclidean distance (m) from the midpoint of sample sites to the nearest shorebird habitat edge.

[e] Mean or maximum number of invertebrates (all taxonomic groups combined) per m^2 among collected core samples (n = 15 in 1999-2000, n = 30 in 2000-2001).

[f] Amount (ha) of class 1 habitat within 2 km of the central coordinates of the site.

[g] Mean or maximum invertebrate biomass (mg/m^2; all taxonomic groups combined) among collected core samples (n = 15 in 1999-2000, n = 30 in 2000-2001).

Table 6.3. Results of all possible subsets modal selection for linear regressions of Killdeer use (frequency of use, mean and maximum bird abundance) on one of four food abundance measures [either mean invertebrate density (individuals/m²), maximum invertebrate density (individuals/m²), mean invertebrate biomass (mg/m²), or max invertebrate biomass (mg/m²)] and landscape context [adjacent shorebird habitat (ha) and nearest neighbor distance (m)] of wetland sites during two winters in the Willamette Valley, Oregon, USA. Wet area (ha) was forced as a covariate in all models. Statistics are shown for model with lowest Cp. Significant model terms (P<0.01) are highlighted in **bold**. Seventeen sites (df = 15) in 1999-2000 and 19 sites (df = 17) in 2000-2001 were included in analyses.

Winter	Bird Use Response	Parameters in Model Subset With Lowest Cp	Parameter Estimate (±SE)	t-value	P-value	F-value	P-value	Model Adj. R²
Wet 1999-2000[a]	Frequency of Occurrence[b]	Wet Area	2.26 ± 1.99	1.14	0.27	1.29	0.27	0.02
	Mean Bird Abundance[c]	Wet Area	0.07 ± 0.08	0.83	0.42	0.68	0.42	0.00
	Max Bird Abundance[c]	Wet Area	0.10 ± 0.11	0.89	0.39	0.80	0.39	0.00

Table 6.3. (Continued).

Winter	Bird Use Response	Parameters in Model Subset With Lowest Cp	Parameter Estimate ($\pm$SE)	t-value	P-value	F-value	P-value	Model Adj. R^2
Dry 2000-2001	Frequency of Occurrence	Wet Area	-1.51 $\pm$ 1.62	-0.93	0.37	0.86	0.37	0.00
	Mean Bird Abundance	Wet Area	0.96 $\pm$ 1.96	0.49	0.63	0.24	0.63	0.00
	Max Bird Abundance	Wet Area	-1.29 $\pm$ 6.56	-0.20	0.85	0.04	0.85	0.00

[a] Mean and max bird abundance ln transformed.
[b] Frequency of Killdeer occurrence among all surveys conducted (n = 19 in 1999-2000, n = 18 in 2000-2001).
[c] Mean or maximum bird abundance among all surveys conducted.

6.6. Discussion

6.6.1. Influence of Food Abundance and Landscape Context

The strong correspondence we observed between Dunlin numbers (mean and maximum) and all measures of local food abundance during the dry winter (Table 6.2) agrees with the many studies that have documented positive relationships between shorebird abundance and prey density or biomass during the nonbreeding season (reviews by Evans and Dugan 1984, Goss-Custard 1984, Puttick 1984). Dunlin are tactile foragers that probe for invertebrates in the substrate (Warnock and Gill 1996). Although we did not collect the stomach contents of individual Dunlin and therefore do not know with certainty what prey items Dunlin typically consume in the Valley, confirmed Dunlin prey items from studies elsewhere (Skagen and Oman 1996) dominated our measures for total abundance (small oligochaetes) and to some degree biomass (chironomid larvae) (chapter 5: Taft and Haig *in review* b). Moreover, we anecdotally observed Dunlin eating earthworms (Lumbricidae) on a number of occasions, another large-bodied invertebrate group influencing biomass estimates. Thus we believe our measures of food abundance adequately reflected prey items sought by Dunlin, and significant positive associations between Dunlin abundances and both measures of food abundance (invertebrate abundance and biomass) certainly help to support this assertion.

Of perhaps greater ecological significance than the importance of food abundance was that the landscape context of wetlands sites additionally influenced their use during the dry winter. In other words, those productive sites with more

adjacent shorebird habitat and closer to a wetland neighbor attracted the most birds. Not only was habitat scarce in the dry winter, but also variation among sites (min-max) in *adjacent shorebird habitat* (Table 6.1) indicated greater habitat aggregation at the spatial scale we examined (2 km radius). Thus, our results suggest that Dunlin were attracted to clusters of the limited habitat present, and because there were so few sites to choose from, it was important energetically to find the most productive sites within these clusters. As far as we know, no other studies of wetland bird use in relation to food resources have demonstrated the potential mediating role of landscape context. Our study indicates that under certain conditions (i.e., dry years), the spatial distribution of habitat across the landscape may be an important force organizing the distribution of birds at a large scale and thus influencing patterns observed at a smaller wetland patch scale.

Large-scale distribution of habitat may also explain why we did not observe relationships between Dunlin abundances and predictors during the wet winter. Not only was landscape context of wetlands unimportant, but Dunlin numbers varied regardless of local food abundances, even though the range in mean (or maximum) invertebrate density and biomass was just as great as in the dry winter. We believe that the greater availability and widespread distribution of shorebird habitat in the wet winter may be responsible for both of these relationships. In contrast to the dry winter, *adjacent shorebird habitat* varied among sites (min-max) in the wet winter by only a factor of two. Thus, an abundant and relatively even spatial distribution of shorebird habitat likely exerted little influence on bird distributions. Further,

widespread distribution of shorebird habitat during the wet winter may have made discriminating among sites by food abundance alone energetically unnecessary. For example, it was just as efficient (if not more) to forage among a number of sites close together but of moderate quality as to search for the most productive sites within a larger area.

In contrast to Dunlin abundances, in general *frequency of occurrence* at sites was unrelated to either food abundance or landscape context during both winters (Table 6.2). However, the 18-19 survey days accounted for only up to 14% of total possible days (roughly 135) birds may have used sites, and the time we spent at each site comprised only a fraction of the day. Moreover, we anecdotally observed sites changing dramatically in wetness (flooding then dissipating) at a finer scale (less than a week) than the frequency of our surveys. Shorebirds have been known to opportunistically find newly available habitat within days if not hours of its formation (Rundle and Fredrickson 1981; Skagen and Knopf 1994). Thus, our survey frequency may not have provided us with the ability to detect differences in visitation frequencies among sites.

Killdeer use (*frequency of occurrence* and *mean/maximum bird abundance*) was unrelated to both local food abundance and landscape context during both the dry and wet winter. Killdeer, like most plovers, are visual foragers that peck at or immediately below the substrate surface (Baker 1977, Jackson and Jackson 2000). Of the invertebrates we observed among samples, commonly documented Killdeer prey include earthworms (Lumbricidae) and insect larvae (chironomids and tipulids)

(Skagen and Oman 1996, Jackson and Jackson 2000). However, in the winter these may decrease in availability at the surface when cold temperatures cause them to bury more deeply in the substrate (Esselink and Zwarts 1989, Zwarts and Wanink 1993) or become less active and more difficult to detect (Durell 2000). Moreover, in terrestrial settings, Killdeer also eat invertebrates such as grasshoppers (Orthoptera), beetles (Coleoptera) and sod webworms (*Chrysoteuchia topiaria* Zeller) (Kamm 1973, Jackson and Jackson 2000), invertebrates that may have been present but that we did not adequately sample. Thus, our measures for food abundance may not have been a complete reflection of the resources available to Killdeer at these sites, providing one explanation for why our measures for food abundance were of little importance as predictors. Alternatively, the cosmopolitan nature of Killdeer provides another explanation for lack of association with food abundance and landscape context in both winters. Although Killdeer are commonly associated with wetlands, they are also found among a variety of terrestrial habitats (Jackson and Jackson 2000). Thus because potential Killdeer foraging habitat includes more habitat types than shorebird habitat, usable habitat may have been perceived by Killdeer as so widespread that its distribution was inconsequential, and finding the most productive sites was of little importance in surviving the winter. Other researchers have similarly found a lack of association between use of sites by generalist species and landscape context when measured as the availability of specific habitat types in surrounding landscapes (Naugle et al. 1999, Calmé and Desrochers 2000, Best et al. 2001).

Our results for Dunlin complement a new but growing recognition of the importance of landscape context to wetland birds during all phases of their annual cycle. During nonbreeding periods, importance of landscape context to foraging waterbirds has been demonstrated by only a few other studies in addition to ours: for coastal agricultural wet grasslands (Milsom et al. 1998), coastal wetlands (Lovvorn and Baldwin 1996), and inland ricefields (Elphick 1998). If food abundance is a significant determinant of wetland bird use in these systems, landscape context is likely a mediating influence in these landscapes as well. Our findings suggest that at least in the Willamette Valley, there is some limit to the amount of available habitat in the landscape below which landscape context becomes influential and discriminating among sites according to food abundance confers energetic advantages. Above this limit, discerning among sites of variable food abundance becomes less important since habitat is so widely available across the landscape. As we further our understanding of ecological processes in wetland landscapes, it will be of increasing interest to know if similar relationships occur elsewhere. Although a traditional research focus on within-wetland processes will continue to be important, clearly we have more to learn by studying wetlands in the context of the landscapes in which they are found.

6.6.2. Implications for Wetland Landscape Planning

With past and present losses to wetland habitat in the Valley and elsewhere (Dahl 1990, Bernert et al. 1999, chapter 2: Taft and Haig 2003), many agencies and coalitions recognize the need to conserve (i.e., protect, enhance, and restore) wetland

habitat (e.g., National Research Council 1992, Good and Sawyer 1998, Morlan 2000, Brown et al. 2001). While conservation efforts to increase invertebrate abundance within existing or restored wetlands will always be of value to waterbirds, our study indicates that consideration of where to spatially focus these efforts may be of primary importance for wetland landscapes that vary annually in the distribution of habitat.

Especially during a dry year, our results would imply that an enhanced or restored site that is isolated will be used less and thus not as beneficial to birds as one that is located near other favorable habitat. In regions where landscape context may be influential only when overall habitat availability is low (also see Riffell et al. 2003), wetland planners should promote conserving clusters of habitat in order to guarantee benefiting birds over the range of possible winter conditions. Thus, potential sites located near what is fairly dependable wetland habitat in dry years (e.g., managed impoundments or other sites that pond every year) or entire areas of landscapes with high incidence of hydric soils should receive conservation priority over regularly isolated sites. Within these prioritized sites, enhancing invertebrate productivity would then be the next step in conservation planning. A thorough review of techniques developed to augment invertebrates is beyond the scope of this paper. However, the presence of decomposing organic matter and regular fluctuations in flooding regime are two principal features of freshwater wetlands contributing to invertebrate productivity (Fredrickson and Laubhan 1994, Rehfisch 1994, Anderson and Smith 2000). Agricultural management practices or restoration techniques that promote these will be of foremost importance.

For most wetland landscapes, limited resources for conservation (funding, personnel) place a premium on efficient landscape planning (maximizing benefits to species while minimizing costs). Strategic spatial planning is likely to bring greater long-term benefits to wildlife and is thus preferable to a more opportunistic management and restoration approach. Potential for such planning will only increase with further study of wildlife-habitat associations within entire wetland landscapes.

6.7. Acknowledgements

7. Conclusions

7.1. Summary

Results presented in this dissertation provide novel insight for waterbirds in wetland landscapes on the potential influence of landscape structure on habitat use. The study not only provides greater understanding of the importance of the Willamette Valley to shorebirds, but it should heighten awareness of the prospective value of wetland agricultural landscapes to wetland birds in general. Collectively, these advances should provide impetus for landscape planners and managers to assess optimal spatial planning in addition to on-site management in order to benefit waterbirds like shorebirds in wetland landscapes like the Valley.

7.2. Key Findings and Conclusions

7.2.1. Historical Valley

- Land cover data compiled from historical data indicate that historical wetlands in the Valley were of three types valuable to nonbreeding waterbirds (waterfowl, wading birds, shorebirds): emergent wetlands, riverine wetlands, and wetland prairie. Of the three types, wetland prairie was most extensive.

- Historical records indicate that the numbers and diversity of waterbirds using these wetlands was much greater than they are today, although for shorebirds, historical abundances are less clear. Fire management by native Kalapuya and regular flooding of wetland prairie rendered this wetland type of greatest importance to

fall/winter habitat for waterbirds, and historical accounts indicate most intensive use of wetland prairie by all waterbirds.

- Estimates for wetland loss and conversion since Euro-American settlement are as high as ~67% for all three wetland types. By 1880, surface ditching for agriculture and suppression of fire altered much of the wetland prairie. Intensive drainage efforts continue to the present day.

7.2.2. Local and Landscape Scale Influences on Habitat Use

- During both years of the study, invertebrate abundance at sampled sites was comparable to that observed during winter in some other important North American freshwater wintering regions for shorebirds. Moreover, variation among Valley sites in invertebrate abundance was fairly low, suggesting most agricultural wetlands support similar levels of food abundance. Agricultural wetlands were comparable in invertebrate abundance to impounded managed wetlands of the Valley.

- Dunlin use (abundances) of Valley regions and individual sites was related to wetland landscape structure and context (amount of wet, unvegetated habitat within regions and surrounding sites, respectively) during the dry winter of 2000-2001, but not during the wet winter of 1999-2000 or during any of the three 1999-2000 winter sub-seasons. Land cover data suggest habitat was more aggregated across the landscape in the dry winter. Dunlin were likely attracted to these

clusters of limited habitat in the dry winter but influenced little by widespread and even distribution of habitat in the wet winter.

- In addition, local conditions (amount of wet habitat, percent of exposed soil, food abundance within wetlands) were positively related to higher abundances of Dunlin among sites in the dry winter. For the study presented in chapter 4, this suggested hierarchical use of habitat only when wet, unvegetated habitat is spatially aggregated across the landscape. For the study presented in chapter 6, influence of invertebrate abundance during the dry winter implied an energetic need to find the most productive sites only when habitat was generally limited across the landscape. In other words, landscape context mediated the influence of local food abundance when habitat was scarce.

- Wetland landscape structure as measured in this study (distribution of wet, unvegetated habitat) appeared to be of little importance to Killdeer during both winters, regardless of differences in distribution of habitat among periods. This lack of influence was likely due to the generalist nature of Killdeer foraging preferences.

- Killdeer abundances were unrelated to the local conditions measured at sites during both winters. Being habitat generalists, Killdeer were likely as attracted to wet and unvegetated habitat as to other habitat conditions within sites. Moreover, as usable sites for Killdeer were numerous and widely distributed in both winters, finding the most productive sites for food among these would have been unnecessary and thus energetically inefficient.

7.2.3. Conservation Implications

- Agricultural wetland landscapes should not be overlooked as current and potentially important wintering regions for waterbirds. For many wetland landscapes turned agricultural, given historical presence and use of native wetlands by waterbirds, and the disconcerting local, regional, and continental scale declines observed for many waterbird species and their habitats, land managers should work closely with private landowners to conserve (i.e., protect, enhance and restore) wetlands impacted by agriculture wherever possible.

- Agricultural wetlands of the Valley possess great potential for restoration as they represent the formerly vast native wetland prairies and riverine wetlands used by waterbirds in the historic Valley of the early 1800s. Moreover, present-day shorebird use and abundance of invertebrates observed on flooded/saturated regions of Valley agricultural land indicate high probability that such conservation efforts would be successful.

- Results for the importance of landscape structure presented in chapters 4 and 6 encourages a spatially-explicit approach to landscape planning such that clusters of wetlands that pond in dry winters receive conservation priority over sites that are typically isolated.

- Information on the influence of local determinants of habitat use presented in chapters 4 (local habitat availability) and chapter 6 (invertebrate food abundance) supports promoting shallowly-flooded and exposed substrates within agricultural

wetlands wherever possible, and developing wetland management techniques to foster invertebrate productivity of sites.

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