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Research article

Importance of wetland landscape structure to shorebirds wintering in an agricultural valley

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Abstract

Only recently has the influence of landscape structure on habitat use been a research focus in wetland systems. During non-breeding periods when food can be locally limited, wetland spatial pattern across a landscape may be of great importance in determining wetland use. We studied the influence of landscape structure on abundances of wintering Dunlin (*Calidris alpina*) and Killdeer (*Charadrius vociferus*) observed on wetlands in the agricultural Willamette Valley of Oregon, USA, during two winters (1999–2000, 2000–2001) of differing rainfall. We examined (1) shorebird use within a sample of 100 km² regions differing in landscape structure (hectares of shorebird habitat [wet, unvegetated]) and (2) use of sites differing in landscape context (area of shorebird habitat within a species-defined radius). For use of sites, we also assessed the influence of two local characteristics: percent of soil exposed and area of wet habitat. We analyzed data using linear regression and information-theoretic modeling. During the dry winter (2000–2001), Dunlin were attracted to regions with more wetland habitat and their abundances at sites increased with greater area of shorebird habitat within both the site and the surrounding landscape. In contrast, Dunlin abundances at sites were related to availability of habitat at only a local scale during the wet winter (1999–2000). Regional habitat availability was of little importance in predicting Killdeer distributions, and Killdeer site use appeared unrelated to habitat distributions at both landscape and local scales. Results suggest prioritizing sites for conservation that are located in areas with high wetland coverage.

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. 1999; Riffell et al. 2003), even though most wetland landscapes are inherently heterogeneous (Skagen and Knopf 1994; Robinson and

Warnock 1997). There is a noticeable paucity of work conducted during non-breeding 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 non-breeding periods account for

the majority of the annual cycle for most wetland birds, the potential influence of landscape structure during these periods has far-reaching implications for conservation.

Shorebirds (Order Charadriiformes) are a likely group to respond to wetland landscape structure, particularly during winter. Because many shorebird species are wetland obligates, shorebirds probably perceive wetlands as patches in a relatively inhospitable matrix. During non-breeding seasons when invertebrate resources can be scarce, dynamic, and easily depleted within wetland patches (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). Shorebirds can opportunistically find available habitat both locally (in meters; e.g., Connors et al. 1981; Warnock and Takekawa 1996) and regionally (in kilometers; Warnock et al. 1995; Roshier et al. 2002; Sanzenbacher and Haig 2002a), which suggests that they respond to habitat availability at large and multiple spatial scales.

It should be energetically favorable for wintering waterbirds such as shorebirds to concentrate in areas with proportionately high wetland densities (Evans 1976; Pyke 1983; Farmer and Parent 1997). Thus, although birds may favor certain local wetland habitat conditions, landscape context (i.e., spatial structure of surrounding habitat) also may 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 (Wu and Hobbs 2002).

The Willamette Valley of western Oregon, USA ('Valley' hereafter) is winter residence to 40,000 or more shorebirds that find accessible foraging habitat primarily on agricultural lands where poorly drained soils facilitate ponding and farming practices provide exposed soil. Aside from regions dominated by flooded rice or soybean fields (e.g., Twedt et al. 1998; Elphick and Oring 2003), agricultural wetland landscapes have received little recognition for their current and potential value to wintering waterbirds. To advance conservation planning for the Valley and other similar landscapes, we investigated associations between the distributions of shorebirds and their habitat

within and between two winters of vastly different rainfall and 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*). Whereas Dunlin favor moist or flooded substrates, Killdeer are considered habitat generalists (Warnock and Gill 1996; Jackson and Jackson 2000). In addition, these two species differ in winter home range size (Sanzenbacher and Haig 2002a, b), which suggests their scales of spatial perception differ (With 1994).

We predicted that attraction to clusters of wetland habitat across the Valley landscape would be reflected in disproportionate use of regions with higher abundance of wetlands, and in greater use of wetland sites located in such regions. Thus, our first objective was twofold: (1) test if regional abundances of Dunlin and Killdeer increased relative and disproportionate to the regional availability of habitat, and (2) examine if species' abundances at sites were related to availability of surrounding habitat (landscape context). We also were interested in understanding the extent to which shorebirds used habitat hierarchically (Kotliar and Wiens 1990). Thus, our second objective was to determine if site use was related to both wetland landscape context and local availability of habitat at the site itself.

Study area

The Valley (approximate lat/long midpoint: 44°40' N, 123°0' W) encompasses 9100 km² 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 distance of roughly 290 km (Figure 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 km² 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 (Taft and Haig 2003). Today, remaining Valley wetlands include small urban remnant wetlands, a few private duck hunting reserves, four larger state and federally protected wildlife refuges, and hundreds of

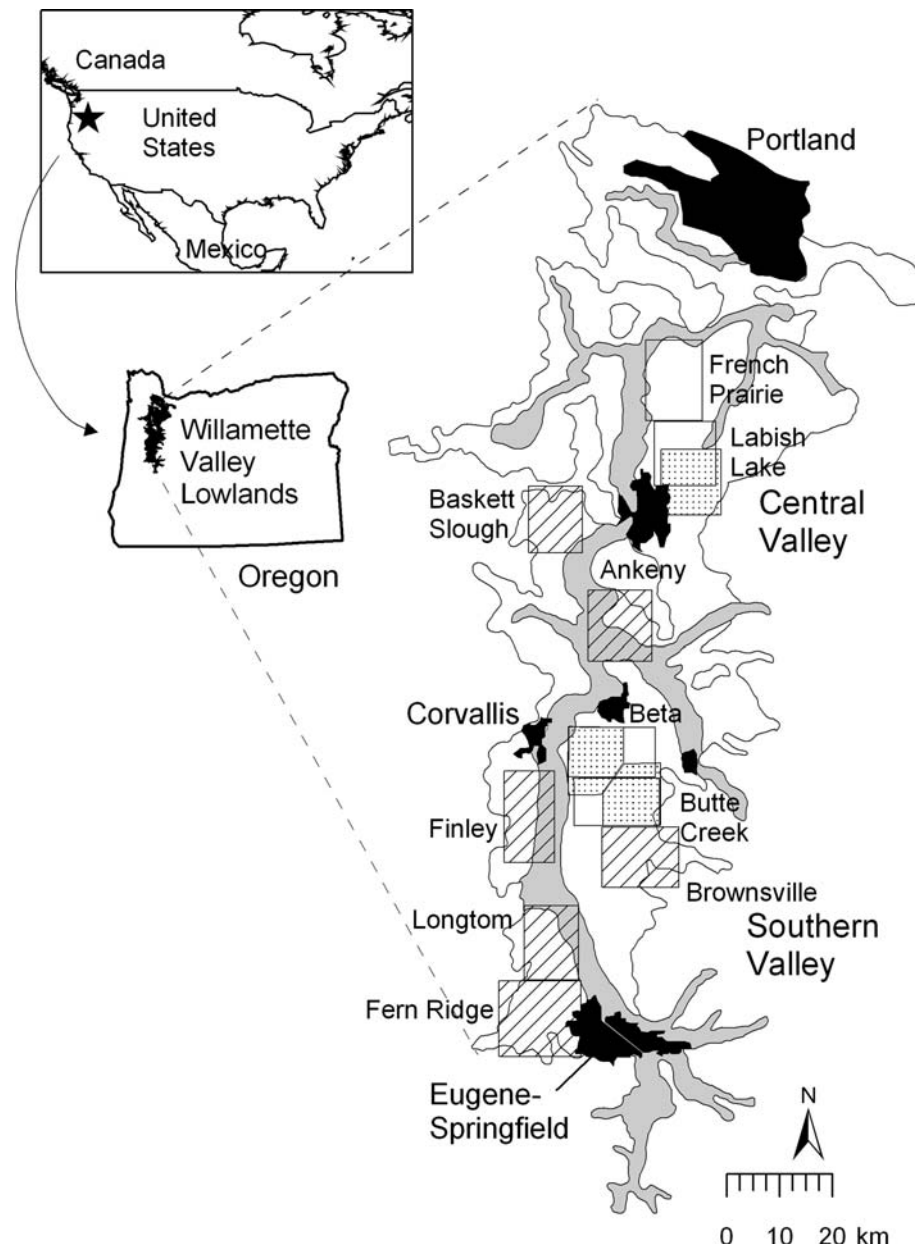


Figure 1. The Willamette Valley lowlands of western Oregon, USA, including locations of the 9 (in 1999–2000) and 10 (in 2000–2001) 100 km² sample regions. Area in gray depicts the Willamette River floodplain, area in white depicts Valley alluvial terraces, and areas in black are urban. Boundaries of regions Beta, Butte Creek, and Labish Lake differed slightly between years. Thatched boxes represent regions studied both years (6 regions), stippled boxes represent additional regions studied in 1999–2000 (3 regions), and open boxes represent additional regions studied in 2000–2001 (4 regions). Three sample regions encompassed the three national wildlife refuges (NWR) with managed impoundments: Basket Slough (encompassing Basket Slough NWR), Ankeny (Ankeny NWR), and Finley (Finley NWR).

scattered privately owned agricultural wetlands ('palustrine emergent-farmed wetlands' of Cowardin et al. 1979). Agricultural wetlands are flooded farmlands that annually develop with the

accumulation of winter rains on native hydric soils (Taft and Haig 2003; Taft et al. 2004).

Common lowland crops include grass seed (most prevalent), vegetables, grains, and pepper-

mint (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 (*L. perenne*) fields have exposed soil between plants throughout the winter. 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: <http://www.ocs.oregonstate.edu/index.html>).

Methods

Spatial and temporal sample design

We examined the influence of landscape structure on shorebird use by collecting and summarizing spatial data simultaneously for patches and landscapes (Tischendorf and Fahrig 2000). We surveyed shorebird use of sites (patches) within 9 (in 1999–2000) and 10 (in 2000–2001) 93–104 km² regions (landscapes) within the central and southern Valley (Figure 1). Based on prior knowledge of the spatial distribution of hydric soils (Daggett et al. 1998), we selected an array of sample regions (REGION) that represented variation in wetland landscape structure in the Valley and at the same time assured a sample of sites with different landscape contexts.

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 to March (Oregon Climate Service: <http://www.ocs.oregonstate.edu/index.html>). Greater rainfall in 1999–2000 led to a more dynamic distribution of wetlands over time compared to 2000–2001: monthly rainfall varied from 7 to 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*).

Land-cover data

Prior to data collection, we observed an association between shorebird use and wet (flooded or saturated), exposed ($\leq 50\%$ vegetation cover) portions of agricultural land ('shorebird habitat' hereafter), particularly for Dunlin and their ecological allies (species in the family Scolopacidae). 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 radar (RADARSAT International, <http://www.rsi.ca>) data at 8-m resolution 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 mapped as shorebird habitat. We considered the mid-winter map to represent maximum availability of habitat for the *Wet Winter*. Taft et al. (2004) provide 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, $\leq 50\%$ vegetation cover) in each sample region by ground mapping visible habitat in February 2001 during and after peak winter wetness. Using visible landmarks that also were 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%); the even distribution and density of roads across the Valley (Hulse et al. 2002) promoted comparable visibility of shorebird habitat among regions.

Bird surveys

Because ponding on agricultural fields tends to occur as widely scattered, irregularly shaped, dynamic areas of shallow (1-cm deep) non-flowing sheetwater, we generally considered entire agricultural fields as sites (SITE). If ponding was clearly concentrated in discrete areas within dry

fields, we considered these concentrated areas as sites. Boundaries of impounded wetland sites were easily discernible.

We surveyed Dunlin and Killdeer weekly within each region, yielding 16 replicate weekly surveys from November to March each winter. By driving all passable roads and observing roadside-visible land with 8× binoculars and 25× 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 survey comprehensively. 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 time-of-day biases. 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. From these GIS data, we calculated the area (ha) of each site. 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.

Data summary

Time periods

To generate *Wet Winter* and *Dry Winter* datasets, we summarized all data collected over each winter, considering surveys 1–16 as temporal replicates ($n = 16$ surveys). The 16 surveys of the *Wet Winter* were partitioned into three sub-seasons, with surveys 1–5 (16 November–1 January) considered replicates within the *Early Winter* period ($n = 5$ surveys), surveys 6–11 (3 January–18 February) replicates for *Mid Winter* ($n = 6$), and surveys 12–16 (21 February–28 March) replicates for *Late Winter* ($n = 5$). Rainfall amounts for survey weeks 5 and 12 were among the lowest

during all weeks (Oregon Climate Service: <http://www.ocs.oregonstate.edu/index.html>) and therefore represented natural breaks for sub-season designations. The three radar images used to produce land-cover data occurred midway in each of these periods.

Regional use

We calculated regional shorebird abundance for each survey by summing counts across sites within regions. For each time period considered, 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.

Site use

For each site, we summarized bird use data into two response variables for each species during each time period: (1) mean abundance (mean bird abundance among surveys), and (2) maximum abundance (maximum bird abundance among surveys). Because shorebirds can sporadically occur in large flocks in the 1000s, maximum abundance among surveys represented information that mean abundance would not have necessarily captured.

We quantified 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 Valley (P. Sanzenbacher, U.S. Geological Survey, personal communication; Sanzenbacher and Haig 2002b).

Local predictors included two independent components describing availability of shorebird

habitat at each site during each time period: (1) mean estimated percent unvegetated substrate (MUD) among surveys, and (2) mean estimated area (ha) of flooded/saturated habitat (WET) among surveys (mean estimated percent of site flooded multiplied by site area [ha]). We used the different measurement units of area (ha) for WET and percentage (%) for MUD to reflect probable nested perception of habitat by shorebirds: individuals likely look for wet agricultural habitat that is relatively unvegetated. Moreover, wet habitat tended to occur in discrete areas of fields whereas amount of exposed soil was uniformly distributed to varying degrees within fields.

Analyses

Analytical methods, assumptions and p-values

We used frequentist methods to compare responses among time periods, and to assess support for relationships modeled with only one predictor. To evaluate support for relationships that could be explained by more than one plausible model, we used information-theoretic modeling (Burnham and Anderson 2002). We used standard methods (Ramsey and Schafer 1997; SAS Institute Inc. 1999) to assess whether statistical assumptions of all techniques used were satisfied. After applying transformations to some variables (details below), all assumptions were adequately met. All reported *p*-values are for the two-sided alternative hypothesis.

Regional use

We compared regional species' abundance (mean and maximum) between the *Wet Winter* and *Dry Winter* using repeated measures ANOVA (PROC MIXED, SAS Institute Inc. 1999) with time (*Wet Winter*, *Dry Winter*) as the main fixed effect, and REGION (subject) as a random effect (Littell et al. 1996). We similarly used repeated measure ANOVA to compare species' abundances between consecutive winter sub-seasons (i.e., *Early* to *Mid Winter*, *Mid* to *Late Winter*). For all comparisons, we \log_{10} transformed mean and maximum species' abundances.

We used simple linear regression (PROC REG, SAS Institute Inc. 1999) to determine whether there was a significant ($p < 0.05$) positive relationship between regional species' abundances or

densities (birds/100 ha habitat) and the regional area of shorebird habitat during each time period. For all regressions, we \log_{10} transformed mean and maximum abundances and densities. 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. Inference from a backtransformed slope estimate concerns a multiplicative (or percent) change in the predicted median response over one unit increase/decrease in the explanatory variable (Ramsey and Schafer 1997). We thus backtransformed slope estimates to interpret how predicted median mean and maximum abundances or densities changed per 1 ha increase in shorebird habitat.

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. To maintain spatial balance in the relative contribution of data from regions, we subdivided sample regions into four quadrants (NW, NE, SE, SW) and systematically chose up to four sites from each region (one per quadrant) for inclusion in analyses.

We compared each species' use of sites between winters (*Dry Winter* vs. *Wet Winter*) using mixed models ANOVA (PROC MIXED; SAS Institute Inc. 1999), with REGION included as a random effect to account for non-independence among sites clustered in the same region (Littell et al. 1996). We compared species' use of sites across consecutive winter sub-seasons (*Early*, *Mid*, and *Late Winter*) using repeated measures ANOVA (PROC MIXED). For sub-season comparisons, some sites used by each species were the same across time periods. Thus, models included time (*Early*, *Mid*, and *Late Winter*) as the main fixed effect, and SITE (subject) and REGION (to account for non-independence among sites clustered in the same region) as random effects. For all comparisons, mean and maximum species' abundances were \log_{10} transformed.

For each species' analysis, we used PROC MIXED (SAS Institute Inc. 1999) to evaluate a set of linear regression models representing plausible hypotheses describing the influence of the three predictors (MUD, WET, HAB) on each response (mean abundance, maximum abundance) during

each time period. To account for potential autocorrelation in observations of the response variables among sites clustered in the same sample region, we included REGION as a random effect in all models (Littell et al. 1996). For all regressions, we transformed species' mean and maximum abundance responses (\log_{10}) and MUD (arcsine square root). We transformed WET (\log_{10}) for all regressions except for the *Dry Winter* analysis for Killdeer, in which WET was a categorical variable (wet or dry) due to the high number of dry sites used. We transformed HAB (\log_{10}) only for *Dry Winter* and *Late Winter* regression analyses.

Potential models represented one of three classes of habitat use hypotheses: bird use was positively related to (1) landscape context (HAB), (2) local availability of habitat (MUD and/or WET), or (3) landscape context 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 alone could influence Killdeer site use. Thus, we considered a set of six biologically plausible *a priori* models explaining 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 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 predictors (all correlation coefficients less than 0.45, most less than 0.30; Cohen 1988) allowed for simultaneous assessment of their influences on bird use (all collinearity diagnostic condition indices < 12; SAS Institute Inc. 1999).

We evaluated relative support for each *a priori* model and relative importance of the three predictors using AIC_c values and information-theoretic modeling (SAS Institute Inc. 1999; Burnham and Anderson 2002). To rank candidate models by level of support, 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 $\Delta \leq 2$ to be plausible competing models explaining the data and worthy of inference. We concluded that predictors were of

little importance when the null model (NONE) was among the set of competing models.

For each analysis, we calculated the Akaike weight (w_i) of each model (weights vary from 0 to 1 with smaller Δ values resulting in higher weights) to assess the strength of evidence in favor of the model under consideration (Burnham and Anderson 2002). In addition, we assessed likelihood of the best model relative to the model under consideration by calculating evidence ratios (i.e., Akaike weight of the model with the lowest AIC_c divided by the weight of the model under consideration). Finally, for those analyses where the null model was not among competing models, 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 2002). Dunlin model sets did not include predictors an equal number of times, but Killdeer model sets were balanced. We ranked importance of predictors by these summed Akaike weights, with 1–3 corresponding to most to least important.

We did not conduct model averaging (see Burnham and Anderson 2002) because we (1) were able to assess the relative usefulness of models by comparing them to the null model, (2) were interested in strength of associations between responses and predictors rather than actual parameter estimates, and (3) were most interested in which of the three classes of habitat-use hypotheses (rather than which actual model) had greatest explanatory power.

Results

Types of sites used

In both winters, Dunlin and Killdeer used hundreds of sites distributed across the Valley (Table 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 between both years) and annual ryegrass (19–29% of sites). Fallow fields accounted for 24–32% of sites between winters (mostly former vegetable crops such as pumpkin, onion, and corn, but also fallow grass seed fields). Of perennial ryegrass fields used

Table 1. Variation in area of shorebird habitat (wet, $\leq 50\%$ vegetated), regional shorebird abundances, and number of sites used by wintering Dunlin and Killdeer among 9 (1999–2000) and 10 (2000–2001) sample regions of the Willamette Valley, Oregon, USA, for five time periods in 1999–2001.

	Wet Winter	Dry Winter	Early Winter	Mid Winter	Late Winter
Number of regions ^a	9	10	9	9	9
Mean area (ha) (range) of shorebird habitat	2040 (828–2815)	148 (33–279)	2258 (1535–3078)	2040 (828–2815)	504 (152–936)
Mean % of region (range) ^b	22 (9–30)	2 (1–3)	24 (15–32)	22 (9–30)	5 (2–10)
Mean (range) mean regional Dunlin abundance ^c	2105 (337–5582)	833 (7–6724)	1222 (391–2606)	2854 (248–10,492)	2078 (2–8284)
Mean (range) maximum regional Dunlin abundance ^d	9207 (1586–22,200)	2674 (75–17,117)	3906 (867–10,005)	6667 (473–22,200)	5018 (9–15,071)
Mean (range) # Dunlin sites	26 (4–49)	20 (5–47)	16 (2–31)	13 (4–31)	6 (1–10)
Mean (range) mean regional Killdeer abundance ^c	529 (220–1455)	582 (253–1227)	694 (264–1337)	703 (294–2473)	155 (44–353)
Mean (range) maximum regional Killdeer abundance ^d	1423 (1768–3404)	1363 (665–2264)	1232 (367–2135)	1169 (545–3404)	339 (84–740)
Mean (range) # Killdeer sites	65 (37–85)	78 (31–133)	38 (17–54)	49 (25–72)	36 (22–52)

^a See Figure 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.

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.

Spatio-temporal distribution of shorebird habitat

Regional area of shorebird habitat differed most between winters, as rainfall and thus habitat was relatively scarce in the *Dry Winter* compared to the *Wet Winter* (Table 1, Figure 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 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 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 $51 \pm 21\%$) to *Mid Winter* ($40 \pm 22\%$ average among sites), and by 9% (± 14) from *Mid* to *Late Winter* ($31 \pm 20\%$ among sites). On newly planted perennial ryegrass fields, percent soil did not change within sites (average difference: $0.5 \pm 11\%$) from *Early Winter* ($80 \pm 13\%$ among sites) to *Mid Winter* ($80 \pm 12\%$ among sites), but it decreased within sites on average by 18% (± 11) from *Mid* to *Late Winter* ($62 \pm 14\%$ among sites). In contrast, percent soil exposed on established perennial ryegrass fields decreased within sites on average by only 4% (± 1) from *Early Winter* ($26 \pm 15\%$ among sites) to *Mid Winter* ($21 \pm 13\%$ among sites), and by only 1% (± 5) from *Mid* to *Late Winter* ($20 \pm 10\%$ among sites). Percent of fields flooded increased on average by 3% (± 9) from *Early* to *Mid Winter*, but it decreased by 3% (± 6) from *Mid* to *Late Winter*.

Regional use

Comparisons between time periods

Regions supported substantially lower Dunlin abundances during the *Dry Winter* than the *Wet Winter* (mean: $F_{1,7.78} = 30.96$, $p = 0.0006$;

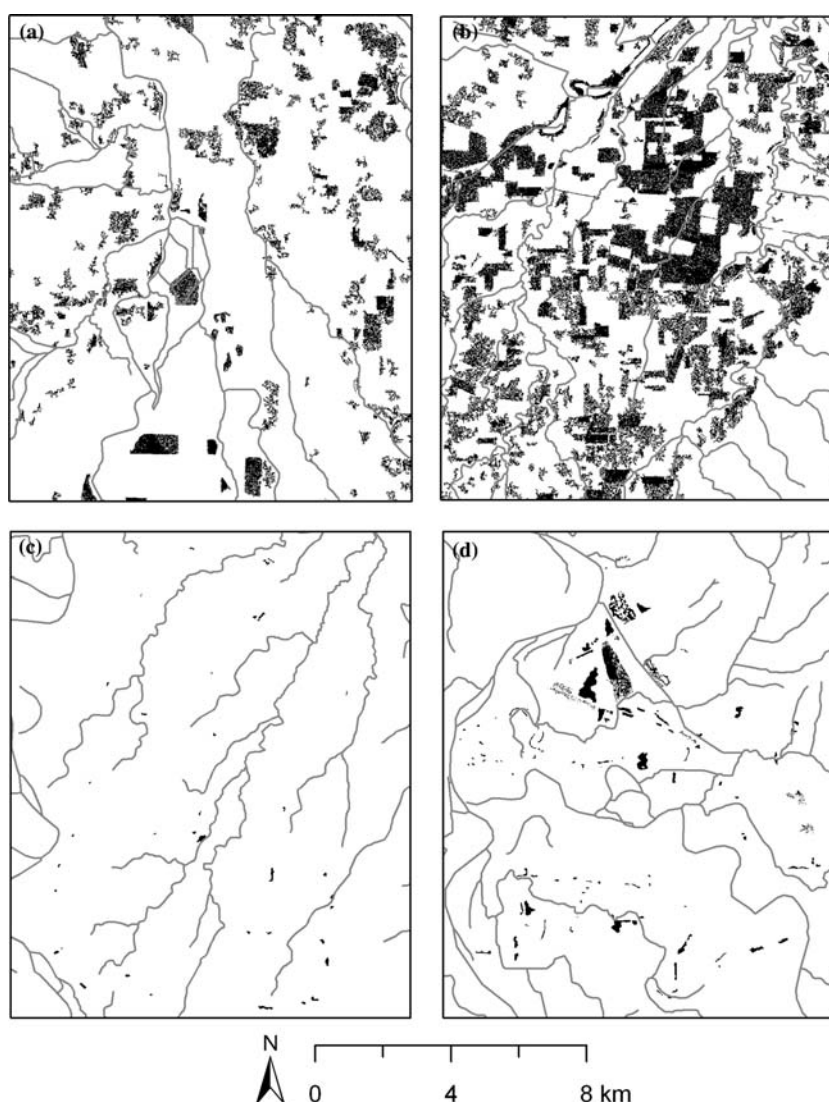


Figure 2. Examples of the range (minimum, maximum) in area (ha) of shorebird habitat (wet, $\leq 50\%$ vegetated; in black) observed among sample regions each year within the Willamette Valley of Oregon, USA: (a) region with the least habitat in the *Wet Winter* of 1999–2000 – Longtom, (b) most habitat 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 1 for sample region locations.

maximum: $F_{1,7.84} = 37.68$, $p = 0.0003$), but number of sites used was only slightly less (by $\sim 20\%$; Table 1). Killdeer regional abundances were not different between winters (mean: $F_{1,8.34} = 2.51$, $p = 0.15$; maximum: $F_{1,8.64} = 0.01$, $p = 0.92$), yet Killdeer used a greater number of sites in the *Dry Winter*.

Regional abundances of Dunlin did not differ between *Early* and *Mid Winter* (mean: $F_{1,8} = 1.50$, $p = 0.26$; maximum: $F_{1,8} = 0.66$, $p = 0.44$) or between *Mid* and *Late Winter* (mean:

$F_{1,8} = 1.03$, $p = 0.34$; maximum: $F_{1,8} = 0.89$, $p = 0.37$). However, total number of sites used by Dunlin declined by $\sim 55\%$ between *Mid* and *Late Winter*. Regional abundances of Killdeer did not differ between *Early* and *Mid Winter* (mean: $F_{1,8} = 1.03$, $p = 0.34$; maximum: $F_{1,8} = 0.75$, $p = 0.41$), but declined from *Mid* to *Late Winter* (mean: $F_{1,8} = 102.70$, $p < 0.0001$; maximum: $F_{1,8} = 62.91$, $p < 0.0001$). Total number of sites used by Killdeer decreased by only $\sim 25\%$ between *Mid* and *Late Winter*.

Influence of regional habitat availability

There were no relationships between regional availability of shorebird habitat and regional abundances of Dunlin in the *Wet Winter*, or during the *Early*, *Mid*, or *Late Winter* periods (Table 2). In the *Dry Winter*, however, regions with more shorebird habitat supported more Dunlin on average. Significant slope estimates backtransformed translated 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 ($0.05 < p < 0.10$) Dunlin abundances increased disproportionate to the availability of habitat in regions, with a 1.3% increase in predicted median mean density of birds, and a 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 ha) regions were each about 120 ha (Figure 1), predicted mean Dunlin abundances increased by 188 birds between the French Prairie and Baskett Slough regions, but by 2182 birds between the Baskett Slough and Ankeny regions.

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

Table 2. Results of regressions between regional Dunlin and Killdeer abundances or densities (birds/100 ha) and regional area (ha) of shorebird habitat 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 are only shown for periods when abundance regressions were significant.

Species	Time Period	Response	Percent Change (Increase/Decrease) in Median Response ^a	95% C.I. ^a	t^b	p	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	
	Early Winter	Max density	+0.99	–0.16 to +2.15	1.99	0.08	0.33	
		Mean abundance	–0.05	–0.15 to +0.06	–0.78	0.46	0.08	
	Mid Winter	Max abundance	–0.05	–0.21 to +0.12	–0.72	0.50	0.07	
		Mean abundance	–0.07	–0.23 to +0.09	–0.90	0.40	0.10	
	Late Winter	Max abundance	–0.09	–0.26 to +0.07	–1.42	0.20	0.22	
		Mean abundance	–0.14	–0.90 to +0.63	–0.41	0.70	0.02	
	Killdeer	Wet Winter	Max abundance	–0.07	–0.77 to +0.64	–0.26	0.80	0.01
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	
Dry Winter		Max density	0.00	–0.05 to +0.05	–0.11	0.91	<0.01	
		Mean abundance	–0.02	–0.55 to +0.51	–0.09	0.93	<0.01	
Early Winter		Max abundance	+0.02	–0.45 to +0.50	0.17	0.87	<0.01	
		Mean abundance	+0.05	–0.01 to +0.10	1.05	0.33	0.14	
Mid Winter		Max abundance	+0.01	–0.10 to +0.12	–0.23	0.82	0.01	
		Mean abundance	+0.07	+0.01 to +0.12	1.96	0.09	0.35	
Late Winter		Max abundance	+0.05	–0.01 to +0.10	1.92	0.10	0.34	
		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 back transformed parameter estimates.

^b Sign of t corresponds to sign of slope.

Site use

Comparisons between time periods

Dunlin were less abundant at sites in the *Dry Winter* than in the *Wet Winter* (mean: $F_{1,175} = 7.28$, $p < 0.01$; maximum: $F_{1,175} = 6.15$, $p = 0.01$), but Killdeer abundances did not differ between winters (mean: $F_{1,281} = 0.00$, $p = 0.96$; maximum: $F_{1,281} = 0.10$, $p = 0.75$; Table 3). Dunlin abundances at sites did not differ from *Early* to *Mid Winter* (mean: $F_{1,98.9} = 1.27$, $p = 0.26$; maximum: $F_{1,103} = 1.30$, $p = 0.26$) or from *Mid* to *Late Winter* (mean: $F_{1,28} = 0.95$, $p = 0.34$; maximum: $F_{1,30.2} = 0.49$, $p = 0.49$). Killdeer were significantly less abundant at sites in *Mid Winter* (mean: $F_{1,133} = 17.69$, $p < 0.0001$; maximum: $F_{1,132} = 10.71$, $p = 0.0014$) and *Late Winter* (mean: $F_{1,138} = 68.46$, $p < 0.0001$; maximum: $F_{1,139} = 64.92$, $p < 0.0001$; Table 3).

Influence of landscape context and local habitat availability

Sites used by both species varied considerably in local characteristics (MUD, WET) and landscape context (HAB; Table 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 by both landscape context (HAB) and local characteristics (MUD, WET) in the *Dry Winter*, but related only to local characteristics in the *Wet Winter* (Table 4). The model MUD + WET was the only model (with $\Delta \leq 2$) explaining variation in mean and maximum abundance of Dunlin among sites in the *Wet Winter*. In the *Dry Winter*, however, models with both landscape and local predictors (HAB + MUD + WET and HAB + WET) were plausible competing models. WET was the most important predictor of Dunlin use for both winters (Table 5). Although HAB was of least importance in the *Wet Winter*, in the *Dry Winter* summed Akaike weights for HAB were comparable to summed weights for WET (Table 5). For analyses of sub-seasons of the *Wet Winter*, there was strong evidence that mean and maximum Dunlin abundances at sites were influenced by local characteristics (MUD, WET) in the *Early Winter* and *Late Winter*, but also possibly related to landscape context (HAB) in the *Late Winter* (Table 4). For all three seasons, however, HAB was least important among predictors (Table 5).

There was little evidence that mean and maximum abundances of Killdeer at sites were related to any of the three predictors during the *Wet* and

Table 3. Mean characteristics and use of analyzed sites by wintering Dunlin and Killdeer during five time periods in 1999–2001 in the Willamette Valley, Oregon, USA.

Species	Time period	n	Site characteristics (mean \pm SD)			Site use (mean \pm SE)	
			HAB ^a (ha)	MUD (%)	WET (ha)	Mean ^c abundance (# birds)	Maximum ^c abundance (# birds)
Dunlin	Wet Winter ^b	95	642 \pm 250	57 \pm 29	3.9 \pm 4.8	340 \pm 97	847 \pm 287
	Dry Winter ^b	87	36 \pm 36	72 \pm 29	2.7 \pm 8.3	232 \pm 92	590 \pm 233
	Early Winter ^b	71	698 \pm 296	59 \pm 29	3.3 \pm 4.2	270 \pm 85	516 \pm 195
	Mid Winter ^b	73	643 \pm 247	60 \pm 30	6.5 \pm 8.4	675 \pm 203	1145 \pm 358
	Late Winter ^b	34	141 \pm 139	55 \pm 37	5.1 \pm 6.6	757 \pm 244	1481 \pm 531
Killdeer	Wet Winter ^b	127	159 \pm 81	49 \pm 29	2.3 \pm 2.3	36 \pm 3	86 \pm 10
	Dry Winter	157	9 \pm 14	64 \pm 29	0.9 \pm 3.3	33 \pm 2	87 \pm 10
	Early Winter ^b	122	176 \pm 102	58 \pm 28	1.9 \pm 2.6	53 \pm 6	78 \pm 10
	Mid Winter	125	160 \pm 82	51 \pm 30	3.1 \pm 3.0	34 \pm 4	59 \pm 7
	Late Winter	117	37 \pm 41	49 \pm 29	2.4 \pm 2.6	11 \pm 1	18 \pm 3

^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 For clarity in presenting central tendency of variables, the mean and SD values shown for WET omit one extreme value originating from one site (Fern Ridge Reservoir). This site was not considered an outlier and was included in regression analyses.

^c Mean and maximum abundance among surveys conducted for the time period.

Table 4. Delta (Δ) values, Akaike weights, and evidence ratios for strongly competing models ($\Delta \leq 2$) explaining influence of three predictors (MUD, WET, HAB) on Dunlin site use (mean abundance, maximum abundance) during five time periods in 1999–2001 in the Willamette Valley, Oregon, USA. Presence of HAB in models is emphasized in bold.

Time period	Response	Models	Δ	w	Evidence ratio
Wet Winter	Mean abundance ^a	MUD + WET	0.00	0.94	1.00
	Maximum abundance ^a	MUD + WET	0.00	0.96	1.00
Dry Winter	Mean abundance	HAB + MUD + WET	0.00	0.67	1.00
		HAB + WET	1.60	0.30	2.23
	Maximum abundance	HAB + MUD + WET	0.00	0.71	1.00
		HAB + WET	1.90	0.28	2.59
Early Winter	Mean abundance	MUD + WET	0.00	0.55	1.00
		WET	0.40	0.45	1.22
	Maximum abundance	MUD + WET	0.00	0.67	1.00
		WET	1.40	0.33	2.01
Mid Winter	Mean abundance	MUD + WET	0.00	0.97	1.00
	Maximum abundance	MUD + WET	0.00	0.98	1.00
Late Winter	Mean abundance	HAB + MUD + WET	0.00	0.63	1.00
		MUD + WET	1.20	0.34	1.82
	Maximum abundance	HAB + MUD + WET	0.00	0.62	1.00
		MUD + WET	1.10	0.36	1.73

^a Mean and maximum bird abundance among surveys conducted for the time period.

Table 5. Summed Akaike weights (and corresponding ranks of importance) for predictors (MUD, WET and HAB) explaining Dunlin site use (mean abundance, maximum abundance) during five time periods in 1999–2001 in the Willamette Valley, Oregon, USA.

Time period	Response	MUD	WET	HAB
Wet Winter	Mean abundance ^a	0.94 (2)	1.00 (1)	0.00 (3)
	Maximum abundance ^a	0.96 (2)	1.00 (1)	0.00 (3)
Dry Winter	Mean abundance	0.69 (3)	1.00 (1)	0.97 (2)
	Maximum abundance	0.72 (3)	1.00 (1)	0.99 (2)
Early Winter	Mean abundance	0.55 (2)	1.00 (1)	0.00 (3)
	Maximum abundance	0.67 (2)	1.00 (1)	0.00 (3)
Mid Winter	Mean abundance	0.97 (2)	1.00 (1)	0.00 (3)
	Maximum abundance	0.98 (2)	1.00 (1)	0.00 (3)
Late Winter	Mean abundance	0.97 (2)	0.99 (1)	0.64 (3)
	Maximum abundance	0.98 (2)	1.00 (1)	0.63 (3)

^a Mean and maximum bird abundance among surveys conducted for the time period.

Dry Winters (Table 6). Similarly, for all three sub-seasons of the *Wet Winter*, the null model (NONE) was among strongly competing models explaining variation in mean and maximum abundances of Killdeer.

Discussion

Influence of landscape structure and context

Our results complement a new but growing recognition of the importance of landscape structure to wetland birds during all phases of their annual

cycle, but particularly during winter. 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 (e.g., Naugle et al. 1999; Calmé and Desrochers 2000; Fairbairn and Dinsmore 2001) or on adjacent habitat affecting the quality of focal breeding patches (Naugle et al. 2000; Milsom et al. 2000; Riffell et al. 2003). In contrast, only a handful of wetland studies have looked at how

Table 6. Delta (Δ) values, Akaike weights, and evidence ratios for strongly competing models ($\Delta \leq 2$) explaining influence of three predictors (MUD, WET, HAB) on Killdeer site use (mean abundance, maximum abundance) during five time periods in 1999–2001 in the Willamette Valley, Oregon, USA. Presence of HAB in models is emphasized in bold.

Time period	Response	Models	Δ	w	Evidence ratio
Wet Winter	Mean abundance ^a	NONE	0.00	0.48	1.00
		MUD	1.10	0.28	1.73
	Maximum abundance ^a	MUD	0.00	0.52	1.00
MUD + WET		0.90	0.33	1.57	
Dry Winter	Mean abundance	NONE	0.00	0.54	1.00
	Maximum abundance	NONE	0.00	0.34	1.00
		HAB	1.30	0.18	1.92
		MUD	1.50	0.16	2.12
		WET	1.80	0.14	2.46
Early Winter	Mean abundance	NONE	0.00	0.48	1.00
	Maximum abundance	NONE	0.00	0.48	1.00
		MUD	1.50	0.23	2.12
		WET	1.70	0.20	2.34
Mid Winter	Mean abundance	NONE	0.00	0.38	1.00
		MUD	0.30	0.33	1.16
		WET	1.90	0.15	2.59
	Maximum abundance	MUD	0.00	0.46	1.00
		NONE	1.40	0.23	2.01
		MUD + WET	1.50	0.21	2.12
Late Winter	Mean abundance	NONE	0.00	0.43	1.00
		WET	2.00	0.16	2.72
		MUD	2.10	0.15	2.86
	Maximum abundance	NONE	0.00	0.38	1.00
		WET	1.70	0.16	2.34
		MUD	1.80	0.15	2.46

^a Mean and maximum bird abundance among surveys conducted for the time period.

landscape context influences foraging waterbirds during non-breeding periods, when birds more typically visit dispersed wetland patches in a landscape (Lovvorn and Baldwin 1996; Farmer and Parent 1997; Elphick 1998; Milsom et al. 1998; Roshier 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*. Results also suggest that the distribution of shorebird habitat was important to Dunlin at both a large and small scale during the *Dry Winter*, suggesting a hierarchical process of habitat use (Kotliar and

Wiens 1990). In contrast, only the distribution of wet, unvegetated habitat at the local scale appeared to influence Dunlin distributions during the *Wet Winter*. Low HAB ranking and thus lack of support for the influence of HAB in the *Wet Winter* is even more pronounced given HAB was included in more models (3) than was MUD (only 2). 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 1, Figure 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 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) also found greater influence of landscape context in the drier breeding season of their study and attributed this to the increased value of surrounding habitat when local wetland food resources were limited.

Dunlin site use patterns for the *Early*, *Mid* and *Late Winter* periods were similar to those during the *Wet Winter*, as illustrated by support for the local habitat models involving MUD and/or WET explaining bird use each season. However, HAB also may have played a role in influencing site use by Dunlin in *Late Winter* after shorebird habitat had undergone a substantial decline in availability since *Mid Winter*. Dunlin used fewer sites (Table 1) and traveled longer distances among sites by *Late Winter* (Sanzenbacher and Haig 2002a), suggesting perception of habitat as relatively limited compared to other sub-seasons. However, unlike in the *Dry Winter*, a model including landscape and local habitat predictors (HAB + MUD + WET) competed with a model with local habitat predictors only (MUD + WET), and HAB ranked third in importance. Indeed, even 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*. These various results suggest that any influence of landscape context in *Late Winter* was not strong.

During all time periods, Killdeer were not influenced by distribution of shorebird habitat 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 wet, unvegetated 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, 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 particular 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 (Taft 2004) and supported by information about movement patterns in the Valley (Sanzenbacher and Haig 2002b), indicates that the cosmopolitan habitat needs of Killdeer are probably met at a local scale.

Implications for wetland landscape planning

Researchers and managers have become increasingly aware that ecological processes occurring within entire wetland landscapes are crucial to consider when strategically conserving wetlands and wetland birds (e.g., Robinson and Warnock 1997; Haig et al. 1998; Roshier et al. 2001). Based on our results, we provide some general recommendations for strategic conservation (protecting, enhancing, and restoring habitat) in our study region.

Our results imply that enhanced or restored sites that are isolated will not benefit birds as much as those that are located near other favorable habitat, especially during dry years. Thus, to benefit birds over the entire range of potential winter conditions, we advocate conserving clusters of dependable habitat that are wet in most years. Potential sites located near reliable wetland habitat in dry years (e.g., refuge impoundments, habitually flooded agricultural sites) should receive conservation priority.

Valley shorebirds (Dunlin) primarily used wet agricultural sites where there also was some exposed soil, regardless of crop type, as the proportions of used sites of each crop type generally corresponded to those for the greater Valley (J. Steiner, USDA-Agricultural Research Service, personal communication). Thus, within prioritized sites of any type (natural or agricultural), managers should promote conserving local features that provide access to invertebrates via wet and relatively unvegetated substrates. For agricultural lands, activities that promote wet habitats (e.g., curtailing installation of new drain tiles, allowing native ponding) will benefit shorebirds, especially where there is some exposed substrate from periodic tillage or new plantings.

Given the number of Valley agricultural sites used (this study) and the impressive numbers of resident Valley wintering shorebirds (Sanzenbacher and Haig 2002a, b), this region is an example of an agricultural landscape of importance to wintering waterbirds. With one-third of the earth's exploitable surface now dominated by agriculture (Ormerod and Watkinson 2000), the importance of agricultural wetland landscapes for conserving shorebirds is likely to increase.

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References

- Benner P.A. and Sedell J.R. 1997. Upper Willamette River landscape: a historic perspective. In: Laenen A. and Dunnette D.A. (eds.), *River Quality: Dynamics and Restoration*. Lewis Publishers, New York, USA, pp. 23–47.
- Best L.B., Bergin T.M. and Freemark K.E. 2001. Influence of landscape composition on bird use of rowcrop fields. *J. Wildlife Manage.* 65: 442–449.
- Burnham K.P. and Anderson D.R. 2002. *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. Springer-Verlag, New York, USA.
- Calmé S. and Desrochers A. 2000. Biogeographic aspects of the distribution of bird species breeding in Quebec's peatlands. *J. Biogeogr.* 27: 725–732.
- Castro G. and Myers J.P. 1989. Flight range estimates for shorebirds. *The Auk* 106: 474–476.
- Clark S.E., White D. and Schaedel A.L. 1991. Oregon, USA, ecological regions and subregions for water quality management. *Environ. Manage.* 15: 847–856.
- Cohen J. 1988. *Statistical Power Analysis for the Behavioral Sciences*, 2nd edn. Lawrence Erlbaum Associates, Hillsdale, NJ, USA.
- Connors P.G., Myers J.P., Connor C.S.W. and Pitelka F.A. 1981. Interhabitat movements by Sanderlings in relation to foraging profitability and the tidal cycle. *The Auk* 98: 49–64.
- Cooke F., Regehr H.M. and Rodway M.S. 2003. Sex and age differences in distribution, abundance, and habitat preferences of wintering Harlequin Ducks: implications for conservation and estimating recruitment rates. *Can. J. Zool.* 81: 492–503.
- Cowardin L.M., Carter V., Golet F.C. and LaRoe E.T. 1979. *Classification of wetlands and deepwater habitats of the United States*. U.S. Fish and Wildlife Service, Washington, DC, USA, 45 pp.
- Daggett S.G., Boulé M.E., Bernert J.A., Eilers J.M., Blok E., Peters D. and Morlan J. 1998. *Wetland and land use changes in the Willamette Valley, Oregon: 1982 to 1994*. Report to the Oregon Division of State Lands. Shapiro and Associates Inc, Portland, Oregon, USA, 38 pp.
- Dunning J.B., Danielson B.J. and Pulliam H.R. 1992. Ecological processes that affect populations in complex landscapes. *Oikos* 65: 169–175.
- Elphick C.S. 1998. *Waterbird conservation and ecology: the role of rice field management in habitat restoration*. PhD Dissertation. University of Nevada, Reno, NV, USA, 162 pp.
- Elphick C.S. and Oring L.W. 2003. Conservation implications of flooding rice fields on winter waterbird communities. *Agricult., Ecosyst. Environ.* 94: 17–29.
- Evans P.R. 1976. Energy balance and optimal foraging strategies in shorebirds: some implications for their distributions and movements in the non-breeding season. *Ardea* 64: 117–139.
- Fairbairn S.E. and Dinsmore J.J. 2001. Local and landscape-level influences on wetland bird communities of the Prairie Pothole Region of Iowa, USA. *Wetlands* 21: 41–47.
- Farmer A.H. and Parent A.H. 1997. Effects of the landscape on shorebird movements at spring migration stopovers. *The Condor* 99: 698–707.
- Goss-Custard J.D., Jenyon R.A., Jones R.E., Newberry P.E. and Williams R.L. 1977. The ecology of the Wash II: seasonal variation in the feeding conditions of wading birds (*Charadrii*). *J. Appl. Ecol.* 14: 701–719.
- Haig S.M., Mehlman D.W. and Oring L.W. 1998. Avian movements and wetland connectivity in landscape conservation. *Conserv. Biol.* 12: 749–758.
- Hulse D., Gregory S. and Baker J. (eds.) 2002. *Willamette River Basin Planning Atlas: Trajectories of Environmental and Ecological Change*. Oregon State University Press, Corvallis, OR, USA.
- Jackson B.J.S. and Jackson J.A. 2000. Killdeer (*Charadrius vociferus*). In: Poole A. and Gill F. (eds.), *The Birds of North America*, No. 517. The Birds of North America Inc, Philadelphia, PA, USA.
- Jackson P.L. and Kimerling A.J. 1993. *Atlas of the Pacific Northwest*. Oregon State University Press, Corvallis, OR, USA.
- Kersten M. and Piersma T. 1987. High levels of energy expenditure in shorebirds: metabolic adaptations to an energetically expensive way of life. *Ardea* 75: 175–187.
- Kotliar N.B. and Wiens J.A. 1990. Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. *Oikos* 59: 253–260.

- Kozakiewicz M. 1995. Resource tracking in space and time. In: Hansson L., Fahrig L. and Merriam G. (eds.), *Mosaic Landscapes and Ecological Processes*. Chapman and Hall, London, UK, pp. 136–148.
- Littell R.C., Milliken G.A., Sroup W.W. and Wolfinger R.D. 1996. *The SAS System for Mixed Models*. SAS Institute Inc., Cary, NC, USA.
- Lovvorn J.R. and Baldwin J.R. 1996. Intertidal and farmland habitats of ducks in the Puget Sound Region: a landscape perspective. *Biol. Conserv.* 77: 97–114.
- Milom T.P., Ennis D.C., Haskell D.J., Langton S.D. and McKay H.V. 1998. Design of grassland feeding areas for waders during winter: the relative importance of sward, landscape factors and human disturbance. *Biol. Conserv.* 84: 119–129.
- Milom T.P., Langton S.D., Parkin W.K., Peel S., Bishop J.D., Hart J.D. and Moore N.P. 2000. Habitat models of bird species' distribution: an aid to the management of coastal grazing marshes. *J. Appl. Ecol.* 37: 706–727.
- Myers J.P. 1983. Conservation of migrating shorebirds: staging areas, geographic bottlenecks, and regional movements. *Am. Birds* 37: 23–25.
- Naugle D.E., Higgins K.F., Estey M.E., Johnson R.R. and Nusser S.M. 2000. Local and landscape-level factors influencing Black Tern habitat suitability. *J. Wildlife Manage.* 64: 253–260.
- Naugle D.E., Higgins K.F., Nusser S.M. and Johnson W.C. 1999. Scale-dependent habitat use in three species of prairie wetland birds. *Landscape Ecol.* 14: 267–276.
- Ormerod S.J. and Watkinson A.R. 2000. Editors' introduction: birds and agriculture. *J. Appl. Ecol.* 37: 699–705.
- Pyke G.H. 1983. Animal movements: an optimal foraging approach. In: Swingland I.R. and Greenwood P.J. (eds.), *The Ecology of Animal Movement*. Clarendon Press, Oxford, UK, pp. 7–31.
- Ramsey F.L. and Schafer D.W. 1997. *The Statistical Sleuth: A Course in Methods of Data Analysis*. Duxbury Press, Belmont, CA, USA.
- Riffell S.K., Keas B.E. and Burton T.M. 2003. Birds in North American Great Lakes coastal wet meadows: is landscape context important? *Landscape Ecol.* 18: 95–111.
- Robinson J.A. and Warnock S.E. 1997. The staging paradigm and wetland conservation in arid environments: shorebirds and wetlands of the North American Great Basin. *Int. Wader Stud.* 9: 37–44.
- Rosenberg D.K. and McKelvey K.S. 1999. Estimation of habitat selection for central-place foraging animals. *J. Wildlife Manage.* 63: 1028–1038.
- Roshier D.A., Robertson A.I., Kingsford R.T. and Green D.G. 2001. Continental-scale interactions with temporary resources may explain the paradox of large populations of desert waterbirds in Australia. *Landscape Ecol.* 16: 547–556.
- Roshier D.A., Robertson A.I. and Kingsford R.T. 2002. Responses of waterbirds to flooding in an arid region of Australia and implications for conservation. *Biol. Conserv.* 106: 399–411.
- SAS Institute Inc. 1999. *The SAS System for Windows Version 8.2*. SAS Institute Inc., Cary, NC, USA.
- Sanzenbacher P.M. and Haig S.M. 2002a. Residency and movement patterns of wintering Dunlin in the Willamette Valley of Oregon. *The Condor* 104: 271–280.
- Sanzenbacher P.M. and Haig S.M. 2002b. Regional fidelity and movement patterns of wintering Killdeer in an agricultural landscape. *Waterbirds* 25: 16–25.
- Skagen S.K. and Knopf F.L. 1994. Migrating shorebirds and habitat dynamics at a prairie wetland complex. *Wilson Bull.* 106: 91–105.
- Szekely T. and Bamberger Z. 1992. Predation of waders (*Charadrii*) on prey populations: an enclosure experiment. *J. Anim. Ecol.* 61: 447–456.
- Taft O.W. 2004. Influence of wetland landscape structure on shorebirds wintering in an agricultural valley. Ph.D. Dissertation. Oregon State University, Corvallis, OR, USA, 233 pp.
- Taft O.W. and Haig S.M. 2003. Historical wetlands in Oregon's Willamette Valley: implications for restoration of winter waterbird habitat. *Wetlands* 23: 51–64.
- Taft O.W., Haig S.M. and Kiilsgaard C. 2004. Use of radar remote sensing (RADARSAT) to map winter wetland habitat for shorebirds in an agricultural landscape. *Environ. Manage.* 33: 749–762.
- Tischendorf L. and Fahrig L. 2000. How should we measure landscape connectivity? *Landscape Ecol.* 15: 633–641.
- Twedt D.J., Nelms C.O., Rettig V.E. and Aycock S.R. 1998. Shorebird use of managed wetlands in the Mississippi Alluvial Valley. *Am. Midland Natural.* 140: 140–152.
- Warnock N.D. and Gill R.E. 1996. Dunlin (*Calidris alpina*). In: Poole A. and Gill F. (eds.), *The Birds of North America*, No. 203. The Birds of North America Inc, Philadelphia, PA, USA.
- Warnock N., Page G.W. and Stenzel L.E. 1995. Non-migratory movements of Dunlins on their California wintering grounds. *Wilson Bull.* 107: 131–139.
- Warnock S.E. and Takekawa J.Y. 1995. Habitat preferences of wintering shorebirds in a temporally changing environment: Western Sandpipers in the San Francisco Bay estuary. *The Auk* 112: 920–930.
- Warnock S.E. and Takekawa J.Y. 1996. Wintering site fidelity and movement patterns of Western Sandpipers *Calidris mauri* in the San Francisco Bay estuary. *Ibis* 138: 160–167.
- With K.A. 1994. Using fractal analysis to assess how species perceive landscape structure. *Landscape Ecol.* 9: 25–36.
- Wu J. and Hobbs R. 2002. Key issues and research priorities in landscape ecology: an idiosyncratic synthesis. *Landscape Ecol.* 17: 355–365.