

Waterbird responses to experimental drawdown: implications for the multispecies management of wetland mosaics

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Summary

1. The loss and human modification of wetlands world-wide underscores the importance of efficient management. For wetlands that provide habitats for non-breeding waterbirds, such management often aims to support a rich and abundant waterbird community.

2. Among the world's many seasonal, moist-soil managed wetlands, annual winter flooding is followed by spring drawdown to encourage germination of waterfowl food plants. Recommendations on how best to maintain flooded wetlands for multiple species are mostly theoretical, and drawdown management typically focuses on spring for migrating shorebirds. The benefits and drawbacks of shallow-water management in winter have not been examined, especially where sizeable populations of wintering shorebirds and waterfowl occur together.

3. We considered The Grasslands Ecological Area in California's Central Valley, USA, as a model wetland complex in which to assess optimal winter flood-depth for multi-species use. We also examined the relative benefits for each waterbird group (e.g. shorebirds and waterfowl) of drawdowns conducted in winter and spring. We experimentally dewatered wetlands of measured topography in the winter and spring of 1994–95, documenting changes in waterbird species richness and abundance associated with daily changes in habitat diversity and availability.

4. Results indicated limited regional availability of shallow-water habitat across the landscape in winter but not spring, as use by shorebirds and teal increased on drawdown wetlands in winter only. Use by deeper-water dabbling ducks and diving waterbirds declined during the later stages of drawdown in both seasons, but not until use by shorebirds and teal had peaked. The maximum diversity and abundance of waterbirds occurred at average depths of 10–20 cm on wetlands with topographic gradients of 30–40 cm.

5. This study has important implications for the winter management of seasonal wetland complexes, especially moist-soil systems where managers provide habitat for different waterbird groups (from shorebirds to diving waterbirds) simultaneously. In general, where topography is variable (e.g. a difference of 30–40 cm between the deepest and shallowest zones), wetlands flooded to average depths of 15–20 cm should accommodate the greatest richness and abundance of waterbirds.

Key-words: diving waterbirds, habitat use, moist-soil management, non-breeding season, shorebirds, water depth, waterfowl.

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Introduction

The severe world-wide loss of wetlands (Mitsch & Gosselink 2000) has significantly increased the importance of those that remain to wetland-dependent organisms such as waterbirds (e.g. Podicipediformes, Ciconiiformes, Anseriformes, Gruiformes and Charadriiformes). For managed wetlands, this importance has led to the goal of attracting diverse and abundant waterbird communities by providing a diversity of foraging habitats (Fredrickson & Reid 1986; Velasquez 1992; Laubhan & Fredrickson 1993; Reid 1993). The distribution and abundance of resources such as seeds, tubers and invertebrates are critical to this end (Krapu & Reinecke 1992; Davis & Smith 1998; Sanders 2000). However, for waterbirds, access to these resources is constrained by water depth (Velasquez 1992; Nagarajan & Thiyagesan 1996; Elphick & Oring 1998; Isola *et al.* 2000) and required foraging depths vary widely among species (Baker 1979; Pöysä 1983). Consequently, the manipulation of a wetland's water depth can be a valuable tool in providing habitat for multiple species.

For many impounded seasonal wetlands, management for waterbirds involves maintaining a stable flooded state (flooded phase) during winter, then dewatering (drawdown phase) in late winter/early spring to germinate the moist-soil plants on which waterfowl feed (Fredrickson & Taylor 1982). Strategies to accommodate multiple waterbird species have been developed for both phases of this drawdown cycle. However, optimal average depths for the flooded phase are mostly supported by either correlational studies (Colwell & Taft 2000) or from observations of overlap among preferred foraging depths (Fredrickson & Reid 1986; Fredrickson 1991; Elphick & Oring 1998). A rich literature has focused on the merits of spring drawdowns for migrant shorebirds (Rundle & Fredrickson 1981; Fredrickson & Taylor 1982; Hands, Ryan & Smith 1991; Velasquez 1992; Weber & Haig 1996) but the relative benefits of drawdown to different waterbird groups have not been contrasted among seasons (winter vs. spring), when resident communities and regional availability of shallow and deep habitats may vary.

The Grasslands Ecological Area (hereafter The Grasslands) of the Central Valley of California, USA, is an ideal wetland complex for assessing the optimal flood depths and seasonal management of drawdowns. Water manipulation is an integral aspect of wetland management in this region. Moreover, in addition to waterfowl, the region attracts a large number of shorebirds during winter and spring (Shuford, Page & Hickey 1998), warranting consideration of optimum depth management in winter. Wetland topography is variable enough to provide a diversity of foraging depths within individual wetlands (Colwell & Taft 2000). Finally, current allocation of habitat via water manipulations may not adequately meet the needs of the differing waterbird communities each season.

We used The Grasslands as a model to examine and refine strategies for multispecies water management. Our objectives were to (i) use drawdowns to identify the average depth at which communities are most diverse and abundant during the flooded phase of wetlands, and (ii) examine the benefits to each waterbird group (e.g. shorebirds and waterfowl) of drawdowns conducted in winter relative to spring, given different seasonal patterns of habitat availability and regional community composition. We examined the effect of drawdown on waterbird communities by prescribing controlled experiments that compared replicated treatments of 'drawdown' to 'no drawdown' in winter and spring. For each experiment, we tested the hypothesis that the species richness and the abundance of different waterbird groups increased or decreased over time in response to drawdown, but remained unchanged on flooded wetlands. We then compared drawdown effects among waterbird groups within and among seasons, addressing whether (i) different taxa temporally overlapped in their use of draining wetlands, and (ii) responses depended on season of drawdown.

Study area

The Grasslands of Merced County, California, USA, is situated in the southern portion of California's Central Valley (37°00'00", 120°45'00") and consists of about 47 000 ha of private, state and federally managed native uplands and palustrine emergent wetlands. The largest continuous area of wetland habitat in the Central Valley (Fredrickson & Laubhan 1995), this area is important for wintering waterbirds (Heitmeyer, Connelly & Pederson 1989; Hunter *et al.* 1991), providing habitat to 800 000 ducks, geese and swans in mid-winter (California Department of Fish & Game 1987–1996) and 60 000–200 000 shorebirds, depending on the season (Shuford, Page & Hickey 1998).

Wetlands in this area are primarily managed under one of four drawdown regimes for annual grasses or waterfowl food plants. Management for cattle pasture requires drawdown in January/February, followed by drawdowns to encourage growth of waterfowl food plants such as nodding smartweed *Polygonum lapathifolium* L. (late February drawdown), swamp timothy *Heleochoa schoenoides* L. (March/April), and water-grass *Echinochloa* spp. (April/May). In addition, each year a small number of seasonal wetlands undergo partial dewatering (flushing) in the winter in an effort to improve water quality. Most wetlands (*c.* 80%) are dewatered in spring for swamp timothy. Descriptions of the study area may be found in Fredrickson & Laubhan (1995) and Williams (1996).

Methods

We conducted four experiments simulating drawdown regimes practised by Grasslands managers: two during late winter (1–21 February 1994; 7–20 February 1995)

and two during early spring (26 March–8 April 1994; 30 March–13 April 1995). The winter 1994 drawdown consisted of partial drainage to mimic flushing to a maximum of 30% mudflat exposure. To minimize confounding effects due to water quality, we conducted this experiment on swamp timothy-managed wetlands with low salt and selenium loads. For winter 1995, we conducted a complete drawdown on impoundments managed for cattle pasture. We dewatered swamp timothy wetlands for both spring drawdowns.

To assess drawdown effects, we compared waterbird use of experimentally drawdown wetlands with flooded wetlands held as controls. Constraints on access and water control prevented complete randomization in wetland selection and assignment of treatments. However, we interspersed sites spatially to minimize confounding environmental factors. For three experiments we replicated treatments on four wetlands; for the spring 1995 experiment, drainage difficulties on one wetland limited sample size to three.

Replicate wetlands were similar in size, topography and dominant plant communities. We chose only wetlands that had retained their natural topography. All had an emergent edge of cattail *Typha* spp., hardstem bulrush *Scirpus acutus* Bigelow, alkali bulrush *Scirpus robustus* Pursh and an interior moist-soil plant community dominated by swamp timothy (winter 1994, spring 1994 and spring 1995 experiments) or mixed annual grasses (winter 1995). Swamp timothy units were irrigated throughout the summer (Heitmeyer, Connelly & Pederson 1989). We presumed invertebrate communities were similar among units due to similarity in vegetation management (i.e. plant communities, drawdown dates and irrigation dates). Moist-soil vegetation and grasses had senesced on all wetlands such that mudflats were unvegetated when dewatered.

We dewatered experimental wetlands at a rate of less than 5 cm day⁻¹, achieved by determining the necessary rate of water outflow (ha cm⁻¹ day⁻¹) given the wetland's size (ha). We monitored daily the water outflow at one or more water-control structures at each wetland. We chose these relatively slow rates to provide a sufficient number of days to observe changes in waterbird communities.

Prior to initiating experiments, we estimated the initial depth (mean and variation) of all wetlands. To sample depth variation, we positioned two sampling transects at roughly 45° angles to the slope (shallow to deep areas) of each wetland. Using a centimetre-marked staff, we measured water at systematically spaced points along these transects, beginning at a random location 0–10 m from the wetland edge. Wetland edge was defined as the area where moist substrate bordered standing water, hence some samples occurred in unflooded habitats. We obtained at least 25 point samples from each wetland to determine initial average water depths with an absolute error of 3 cm. We estimated topographic variation by calculating the difference between the deepest and shallowest depth measurements.

As drawdowns progressed, we monitored changes in depth and amount of available habitat using a gauge placed in the deepest portion of each wetland. For each survey, we estimated the depth at each sample point using the equation $D_n = D_0 - (G_0 - G_n)$, where D_n = point estimate of water depth at survey n , D_0 = initial depth measured at the sample point, G_0 = initial depth reading at gauge, and G_n = gauge reading at survey n . We then calculated the average D for each survey n . On control wetlands in 1994, we coarsely monitored changes in water levels by estimating, with the aid of aerial photographs showing prominent wetland features, changes in the percentages of unflooded habitat.

We surveyed waterbirds during daylight hours (06:00–17:50), each site at roughly the same time of day to reduce noise from systematic patterns (e.g. regular diurnal bird movements) obscuring trends observed within wetlands. Using 22× spotting's copes and 8× binoculars, we counted and identified all waterbirds from fixed locations that maximized observations. For several wetlands, we conducted surveys from a hide. All counts required 1–2 h. We combined observations for species that were difficult to distinguish from a distance or that were indistinguishable except by call (Table 1). We obtained multiple counts of species exceeding 1000 individuals to improve accuracy of estimates.

We surveyed waterbirds once on each wetland before drawdown (survey 0). Thereafter, we conducted surveys coincident with a 2–5 cm decrease in water depth on experimental wetlands between successive visits. Thus we matched waterbird-use data by drainage interval since drawdown initiation, and referred to the time variable as survey instead of day. Owing to differences in drawdown extent among experiments, we conducted 7–10 surveys per wetland during winter experiments, and 11–12 surveys per wetland for spring experiments.

Mean (\pm SD) areas (ha) of experimental and control wetlands, respectively, were 47.2 (\pm 15.3) and 47.7 (\pm 21.5) in winter 1994, 14.4 (\pm 10.1) and 14.5 (\pm 9.7) in winter 1995, 31.8 (\pm 5.7) and 32.1 (\pm 9.4) in spring 1994, and 30.2 (\pm 5.9) and 35.0 (\pm 19.1) in spring 1995. Although we positioned all survey locations to guarantee observing shallow habitats exposed by drawdown, we could rarely observe an entire wetland. We therefore estimated the visible percentage of each wetland to calculate the actual observed wetland area. Thus, mean (\pm SD) observed areas (ha) of experimental and control wetlands, respectively, were 39.9 (\pm 15.5) and 30.7 (\pm 11.6) in winter 1994, 9.7 (\pm 3.2) and 8.8 (\pm 3.6) in winter 1995, 24.4 (\pm 3.8) and 27.4 (\pm 7.7) in spring 1994, and 25.2 (\pm 3.3) and 27.2 (\pm 10.3) in spring 1995.

DATA SUMMARY

To classify community structure, we quantified the temporal variation in species richness (number of species) for the entire community (all waterbirds), and of three foraging groups: waders, dabbling ducks and diving waterbirds (Table 1). We included all waterbird

Table 1. Species observed on wetlands during drawdown experiments conducted in The Grasslands in the winter and spring of 1994 and 1995, including waterbird group and foraging habitat with which each species is affiliated. Common species included in guild abundance analyses in bold. See American Ornithologists' Union (1998) for taxonomic authorities

Dividing waterbirds (> 25 cm)	Dabbling ducks (5–25 cm)	Waders (< 15 cm)	Other waterbirds (unclear, variable)
Clark's grebe <i>Aechmophorus clarkii</i>	Mallard <i>Anas platyrhynchos</i>	Greater white-fronted goose <i>Anser albifrons</i>	American white pelican <i>Pelecanus erythrorhynchos</i>
Western grebe <i>Aechmophorus occidentalis</i>	Gadwall <i>Mareca strepera</i>	Lesser snow goose <i>Chen c. caerulescens</i>	Bonaparte's gull <i>Larus philadelphia</i>
Eared grebe <i>Podiceps nigricollis</i>	American green-winged teal <i>Anas carolinensis</i>	Black-crowned night-heron <i>Nycticorax nycticorax</i>	Ring-billed gull <i>Larus delawarensis</i>
Pied-billed grebe <i>Podilymbus podiceps</i>	American wigeon <i>Mareca americana</i>	Snowy egret <i>Egretta thula</i>	Mew gull <i>Larus canus</i>
Double-crested cormorant <i>Phalacrocorax auritus</i>	Eurasian wigeon <i>Mareca penelope</i>	Great egret <i>Casmerodius albus</i>	Herring gull <i>Larus argentatus</i>
Ruddy duck <i>Oxyura jamaicensis</i>	Northern pintail <i>Anas acuta</i>	Cattle egret <i>Bubulcus ibis</i>	California gull <i>Larus californicus</i>
Canvasback <i>Aythya valisineria</i>	Northern shoveler <i>Anas clypeata</i>	Great blue heron <i>Ardea herodias</i>	Forster's tern <i>Sterna forsteri</i>
Redhead <i>Aythya americana</i>	Blue-winged teal <i>Anas discors</i>	White-faced ibis <i>Plegadis chihi</i>	
Ring-necked duck <i>Aythya collaris</i>	Cinnamon teal <i>Anas cyanoptera</i>	American avocet <i>Recurvirostra americana</i>	
Scaup spp.* <i>Aythya marilaffinis</i>		Black-necked stilt <i>Himantopus mexicanus</i>	
Common goldeneye <i>Bucephala clangula</i>		Semipalmated plover <i>Charadrius semipalmatus</i>	
Bufflehead <i>Bucephala albeola</i>		Snowy plover <i>Charadrius alexandrinus</i>	
Common merganser <i>Mergus merganser</i>		Killdeer <i>Charadrius vociferus</i>	
American coot <i>Fulica americana</i>		Black-bellied plover <i>Pluvialis squatarola</i>	
		Marbled godwit <i>Limosa fedoa</i>	
		Whimbrel <i>Numenius phaeopus</i>	
		Long-billed curlew <i>Numenius americanus</i>	
		Yellowleg spp.* <i>Tringa melanoleuca/flavipes</i>	
		Dowitcher spp.* <i>Limnodromus scolopaceus/griseus</i>	
		Dunlin <i>Calidris alpina</i>	
		Western sandpiper <i>Calidris mauri</i>	
		Least sandpiper <i>Calidris minutilla</i>	

*Species pairs treated as one because they were too difficult to distinguish reliably at great distances (greater and lesser scaup, greater and lesser yellowlegs) or were indistinguishable except by call (long-billed and short-billed dowitcher).

species in analyses of total waterbird richness, but omitted species of variable or uncertain depth preferences (e.g. gulls, terns and pelicans) from group richness analyses. We examined changes in the abundance of the 14 most common waterbird species, grouped into four foraging guilds: calidridine sandpipers (dunlin *Calidris alpina*, western sandpiper *Calidris mauri* and least sandpiper *Calidris minutilla*) associated with water > 0–5 cm deep; large shorebirds (black-necked stilt *Himantopus mexicanus*, American avocet *Recurvirostra americana*, yellowleg *Tringa* spp. and dowitcher *Limnodromus* spp.) associated with water 5–15 cm deep;

teal (cinnamon teal *Anas cyanoptera* and American green-winged teal *Anas carolinensis*) associated with water 5–20 cm deep; and large dabbling ducks (northern pintail *Anas acuta*, mallard *Anas platyrhynchos*, gadwall *Mareca strepera*, American wigeon *Mareca americana* and northern shoveler *Anas clypeata*) associated with water 5–25 cm deep (Baker 1979; Pöysä 1983; Baldassarre & Fischer 1984; Skagen & Knopf 1994; Elphick & Oring 1998; Isola *et al.* 2000).

We summarized changes in water depth resulting from drawdown into two predictors of waterbird responses: depth diversity and habitat availability. We

used depth diversity to predict changes in the species richness of waterbird groups and entire communities, and used habitat availability to predict changes in guild abundances. For depth diversity, we quantified the percentage cover of water at six 5-cm depth intervals (0–5 cm, 6–10 cm, 11–15 cm, 16–20 cm, 21–25 cm, > 25 cm) and calculated a Brillouin Index (Krebs 1989) describing the diversity of depths on each wetland at each survey. A wetland with a low index is either predominantly deep or shallow, whereas a high index indicates even availability of deep and shallow habitats. To quantify changes in habitat availability resulting from drawdown, we calculated the area of foraging habitat within the different depth zones (> 25 cm, 5–25 cm, 5–20 cm, 5–15 cm and > 0–5 cm). From depth data, we estimated the proportions of total point samples in each foraging zone at the time of each survey. From the area of wetlands, we estimated the surface area of each foraging zone within wetlands.

STATISTICAL ANALYSES

For each experiment, with PROC GLM (SAS Institute 1995) we used analysis of covariance (ANCOVA) to compare cumulative (total over time) square-root transformed waterbird richness among treatments while controlling for wetland size (covariate). When wetland size was not a significant covariate, we compared cumulative waterbird richness among treatments using two-tailed *t*-tests.

We compared temporal changes in waterbird richness and abundances (standardized into birds observed area⁻¹) among treatments using repeated measures ANOVA (ANOVAR; Stevens 1992). To normalize count distributions, we square-root or log₁₀-transformed data. We conducted separate ANOVARS for each response variable, with treatment (drawdown or control) and time (survey) as main effects, and the interaction term (survey × drawdown/control) included in each analysis. For species richness analyses, we included actual wetland area as a covariate to adjust for sampling effort due to differences in wetland size. However, when the effect of area was not significant, we made no covariate adjustment in order to retain error degrees of freedom. To maintain balanced ANOVARS with no missing cells, we included only surveys 0–6 in analyses of winter drawdowns, and surveys 0–10 in spring drawdowns. When *F*-tests were significant at $P \leq 0.05$, we complied to the Huynh–Feldt ϵ -adjusted *P*-values (to control for type I error when the variance–covariance matrix deviates from sphericity; Stevens 1992). We considered model terms for interactions significant only if ϵ -adjusted *P*-values were ≤ 0.05 . We used PROC GLM (SAS Institute 1995) to run all ANOVARS.

We considered a significant interaction as sufficient evidence that drawdown wetlands differed from control wetlands in waterbird response over time (i.e. differences between treatment and control increased or decreased over time), and did not conduct the high

number of multiple comparisons required to determine pairwise differences between surveys. Instead, we plotted survey means ($\pm 95\%$ confidence interval; CI) to interpret the results. Because experimental wetlands could have differed from control wetlands prior to treatment, we considered significant treatment effects meaningful only if survey 0 values were similar (initial means lay within each other's SE). If experiments resulted in a significant main effect of treatment in addition to a significant interaction, we interpreted the effect of drawdown as particularly strong.

We used linear regression to assess whether temporal patterns of waterbird responses were associated with drawdown habitat changes. To control for non-independence of successive surveys (Hurlbert 1984), we considered wetland replicates as experimental units. Additionally, because wetland replicates may have differed in the timing and extent of habitat changes, analyses on individual wetlands could reveal trends otherwise obscured in ANOVARS. Consequently, we analysed each wetland separately, using depth diversity to predict total waterbird richness, and square-root or log₁₀-transformed habitat availability to predict guild abundances. For each regression, we included all surveys for each wetland, giving sample sizes of 7–10. Predicting that richness or abundance would increase/decrease with an increase/decrease in predictor variables, we determined if these relationships were positive by testing if mean correlation coefficients were significantly greater than zero (one-tailed, one-sample *t*-test for mean coefficients > 0). We only conducted *t*-tests when at least two of 3–4 regressions gave correlation coefficients ≥ 0.60 . We conducted correlations and *t*-tests using SAS (SAS Institute 1995) and considered tests significant at $P \leq 0.05$.

Results

DEPTH DIVERSITY AND HABITAT AVAILABILITY

Rates of drawdown were similar among experiments, but patterns of change in predictor variables varied by season (Table 2). For all drawdowns, wetlands reached maximum depth diversity (Brillouin Index) at 10–20 cm average depth and mudflat exposure from 2% to 20%. However, while winter wetlands reached these peaks mid-way during drawdowns, spring wetlands were already at maximum diversity at the onset of manipulations. Experiments fell into the following order from most to least complete in extent of drainage: spring 1994, spring 1995, winter 1995, winter 1994.

Dewatering substantially changed the amount of foraging habitat in each depth category used by waterbirds (Table 2). Habitat available to diving waterbirds (> 25 cm) declined precipitously in all four experiments. The availability of habitat for larger dabbling ducks (5–25 cm) followed a curvilinear pattern (increase followed by decrease) throughout

Table 2. Changes in water depth (cm), mean depth diversity (Brillouin Index) and waterbird habitats on Grasslands wetlands during drawdowns in 1994–95. Maximum depth diversity and habitat amounts on drawdown wetlands in bold. $n = 4$ wetlands for winter 1994, winter 1995, spring 1994; $n = 3$ wetlands for spring 1995

Experiment	Survey (time)	Grand mean depth (\pm SD) on treatments	Grand mean depth (\pm SD) on controls	Mean (\pm SD) Depth diversity (Brillouin Index) on experimental wetlands	Habitat availability (mean \pm SD percentage on experimental wetlands) for					
					Diving waterbirds (> 25 cm)	Large dabbler (5–25 cm)	Teal (5–20 cm)	Large shorebird (5–15 cm)	Calidridine sandpiper (> 0–5 cm)	Mudflat
Winter 1994	0*	27 \pm 4	29 \pm 4	1.0 \pm 0.3	63 \pm 17	35 \pm 16	19 \pm 12	12 \pm 7	0 \pm 0	0 \pm 0
	1	25 \pm 3		1.2 \pm 0.2	47 \pm 20	49 \pm 16	23 \pm 10	13 \pm 6	2 \pm 2	0 \pm 0
	2	21 \pm 3		1.4 \pm 0.3	33 \pm 20	60 \pm 20	35 \pm 14	17 \pm 11	5 \pm 1	1 \pm 0
	3	18 \pm 5		1.5 \pm 0.2	21 \pm 26	66 \pm 21	46 \pm 19	24 \pm 11	6 \pm 6	5 \pm 1
	4	15 \pm 4		1.5 \pm 0.1	10 \pm 7	74 \pm 10	53 \pm 11	26 \pm 11	8 \pm 9	8 \pm 5
	5	12 \pm 3		1.5 \pm 0.1	5 \pm 2	70 \pm 14	59 \pm 13	41 \pm 9	11 \pm 6	13 \pm 6
Winter 1995	0*	25 \pm 3	39 \pm 12	1.2 \pm 0.2	49 \pm 18	48 \pm 20	18 \pm 8	8 \pm 6	2 \pm 2	2 \pm 3
	1	20 \pm 3	39 \pm 12	1.4 \pm 0.2	27 \pm 21	67 \pm 24	39 \pm 25	23 \pm 20	3 \pm 4	4 \pm 5
	2	18 \pm 2	39 \pm 12	1.5 \pm 0.1	14 \pm 16	79 \pm 21	50 \pm 21	20 \pm 11	2 \pm 3	5 \pm 6
	3	13 \pm 3	39 \pm 12	1.5 \pm 0.1	1 \pm 1	83 \pm 12	63 \pm 17	35 \pm 20	6 \pm 2	10 \pm 14
	4	9 \pm 1	39 \pm 12	1.3 \pm 0.1	0 \pm 0	74 \pm 13	72 \pm 12	57 \pm 20	11 \pm 4	15 \pm 14
	5	7 \pm 2	40 \pm 12	1.2 \pm 0.2	0 \pm 0	64 \pm 15	62 \pm 14	56 \pm 17	17 \pm 6	19 \pm 17
Spring 1994	0*	18 \pm 2	20 \pm 3	1.3 \pm 0.2	20 \pm 6	74 \pm 6	57 \pm 5	30 \pm 5	5 \pm 9	1 \pm 2
	1	13 \pm 2		1.5 \pm 0.0	6 \pm 5	81 \pm 14	67 \pm 7	44 \pm 7	7 \pm 5	6 \pm 5
	2	12 \pm 2		1.4 \pm 0.0	4 \pm 5	72 \pm 16	64 \pm 10	42 \pm 10	16 \pm 10	7 \pm 8
	3	10 \pm 3		1.4 \pm 0.1	2 \pm 7	69 \pm 15	62 \pm 13	43 \pm 13	15 \pm 9	14 \pm 12
	4	7 \pm 1		1.3 \pm 0.1	1 \pm 2	54 \pm 14	51 \pm 15	42 \pm 15	22 \pm 13	24 \pm 9
	5	5 \pm 1		1.0 \pm 0.2	0 \pm 0	42 \pm 18	41 \pm 17	37 \pm 17	22 \pm 8	36 \pm 13
	6	4 \pm 1		0.9 \pm 0.2	0 \pm 0	35 \pm 20	35 \pm 20	32 \pm 20	18 \pm 4	47 \pm 20
	7	3 \pm 1		0.7 \pm 0.2	0 \pm 0	25 \pm 13	25 \pm 15	24 \pm 16	17 \pm 11	57 \pm 24
	8	2 \pm 1		0.5 \pm 0.2	0 \pm 0	16 \pm 14	16 \pm 14	16 \pm 14	19 \pm 14	64 \pm 24
	9	2 \pm 1		0.4 \pm 0.2	0 \pm 0	12 \pm 12	12 \pm 12	12 \pm 12	18 \pm 14	69 \pm 22
Spring 1995	0*	16 \pm 2	25 \pm 6	1.7 \pm 0.1	14 \pm 9	76 \pm 6	57 \pm 4	29 \pm 4	8 \pm 3	2 \pm 2
	1	14 \pm 2	26 \pm 8	1.7 \pm 0.1	6 \pm 6	81 \pm 7	61 \pm 6	39 \pm 6	9 \pm 3	5 \pm 4
	2	12 \pm 2	25 \pm 6	1.6 \pm 0.1	3 \pm 6	80 \pm 8	66 \pm 4	47 \pm 5	9 \pm 4	9 \pm 4
	3	10 \pm 2	25 \pm 7	1.5 \pm 0.1	1 \pm 1	74 \pm 12	64 \pm 8	47 \pm 9	12 \pm 6	14 \pm 7
	4	7 \pm 2	26 \pm 7	1.4 \pm 0.2	0 \pm 0	60 \pm 5	56 \pm 3	44 \pm 10	21 \pm 11	20 \pm 8
	5	6 \pm 1	26 \pm 8	1.1 \pm 0.1	0 \pm 0	46 \pm 2	45 \pm 2	38 \pm 5	25 \pm 8	29 \pm 9
	6	5 \pm 1	24 \pm 7	1.1 \pm 0.2	0 \pm 0	42 \pm 5	41 \pm 5	36 \pm 3	24 \pm 4	35 \pm 2
	7	4 \pm 1	24 \pm 6	0.8 \pm 0.1	0 \pm 0	32 \pm 5	32 \pm 5	31 \pm 4	25 \pm 11	43 \pm 8
	8	2 \pm 1	21 \pm 6	0.6 \pm 0.2	0 \pm 0	22 \pm 10	22 \pm 10	22 \pm 10	20 \pm 14	58 \pm 18
	9	2 \pm 1	20 \pm 7	0.5 \pm 0.2	0 \pm 0	20 \pm 9	20 \pm 9	20 \pm 9	17 \pm 12	63 \pm 19
10	2 \pm 1	20 \pm 7	0.4 \pm 0.3	0 \pm 0	17 \pm 14	17 \pm 14	17 \pm 14	18 \pm 10	65 \pm 21	

*Survey 0 represents the day on which we initiated drawdowns.

Table 3. Results from ANOVARS comparing changes in waterbird species richness and density (birds per ha) among treatments (drawdown and control) during four drawdown experiments conducted in The Grasslands in the winter and spring of 1994–95. Results focus on significant trend responses (interactions; in bold) and significant treatment effects (see Figs 1–4 for effect size)

	Winter 1994†		Winter 1995†		Spring 1994‡		Spring 1995§	
	Trend	Treatment	Trend	Treatment	Trend	Treatment	Trend	Treatment
Richness§								
Waders	$F = 3.01$ $P = 0.02^*$	$F = 39.31$ $P < 0.01^*$	$F = 5.86$ $P < 0.01^*$	$F = 6.83$ $P = 0.04^*$	$F = 1.75$ $P = 0.09$	$F = 4.96$ $P = 0.07$	$F = 1.31^{\dagger\dagger}$ $P = 0.27$	$F = 52.36^{\dagger\dagger}$ $P < 0.01^*$
Dabbling ducks	$F = 0.20$ $P = 0.97$	$F = 1.80$ $P = 0.23$	$F = 3.97$ $P = 0.02^*$	$F = 0.73$ $P = 0.43$	$F = 2.09$ $P = 0.12$	$F = 0.68$ $P = 0.44$	$F = 1.15$ $P = 0.35$	$F = 2.64$ $P = 0.22$
Diving waterbirds	$F = 0.25$ $P = 0.95$	$F = 0.42$ $P = 0.54$	$F = 2.37$ $P = 0.05^*$	$F = 5.69$ $P = 0.05^*$	$F = 4.88$ $P < 0.01^*$	$F = 2.91$ $P = 0.14$	$F = 1.11$ $P = 0.39$	$F = 25.35^{\dagger\dagger}$ $P = 0.10$
All waterbirds	$F = 2.01$ $P = 0.09$	$F = 14.58$ $P < 0.01^*$	$F = 1.42$ $P = 0.23$	$F = 1.59$ $P = 0.25$	$F = 1.21$ $P = 0.30$	$F = 1.02$ $P = 0.35$	$F = 1.86$ $P = 0.08$	$F = 3.48$ $P = 0.14$
Density¶								
Large Dabbling ducks	$F = 1.68$ $P = 0.16$	$F = 0.15$ $P = 0.71$	$F = 4.94$ $P < 0.01^*$	$F = 0.11$ $P = 0.75$	$F = 1.98$ $P = 0.05^*$	$F = 1.26$ $P = 0.30$	$F = 2.79$ $P = 0.04^*$	$F = 0.07$ $P = 0.80$
Teal	$F = 5.66$ $P < 0.01^*$	$F = 4.74$ $P = 0.07$	$F = 3.11$ $P = 0.05^*$	$F = 3.19$ $P = 0.12$	$F = 0.86$ $P = 0.57$	$F = 0.00$ $P = 0.99$	$F = 1.68$ $P = 0.12$	$F = 3.97$ $P = 0.12$
Large shorebirds	$F = 4.09$ $P = 0.02^*$	$F = 47.28$ $P < 0.01^*$	$F = 2.79$ $P = 0.04^*$	$F = 12.43$ $P = 0.01^*$	$F = 0.59$ $P = 0.82$	$F = 2.36$ $P = 0.17$	$F = 0.63$ $P = 0.78$	$F = 10.81$ $P = 0.03^*$
Calidridine Sandpipers	$F = 4.04$ $P = 0.04^*$	$F = 32.27$ $P < 0.01^*$	$F = 19.14$ $P < 0.01^*$	$F = 20.97$ $P < 0.01^*$	$F = 1.71$ $P = 0.10$	$F = 13.39$ $P = 0.01^*$	$F = 2.06$ $P = 0.11$	$F = 3.84$ $P = 0.12$

†Seven time periods for analyses. Treatment degrees of freedom (d.f.) = 1, error (subject) d.f. = 6, trend d.f. = 6, error (time) d.f. = 36.

‡Eleven time periods for analyses. Treatment d.f. = 1, error (subject) d.f. = 6, trend d.f. = 10, error (time) d.f. = 60.

§Eleven time periods for analyses. Treatment d.f. = 1, error (subject) d.f. = 4, trend d.f. = 10, error (time) d.f. = 40.

¶All response variables square-root transformed except densities of large shorebirds and calidridine sandpipers in winter (\log_{10} -transformed).

††Equals trend and treatment model terms adjusted for significant effect of wetland area: $F = 9.89$, $P = 0.005$ for wader richness; $F = 11.31$, $P = 0.04$ for diving waterbird richness. For both tests, treatment d.f. = 1, area d.f. = 1, error (subject) d.f. = 3, trend d.f. = 10, error (time) d.f. = 30.

winter drawdowns, but declined on wetlands in spring soon after drawdown began. Teal habitat (5–20 cm) followed a curvilinear pattern for all drawdowns, except winter 1994 when habitat area steadily increased. Because wetlands in winter held little shallow water (< 15 cm) at the start of drawdown, increases in the amount of shorebird habitat were dramatic. Estimated mean (\pm SD) topographic variation among drawdown wetlands was 42 cm (\pm 1 cm) in winter 1994, and 30 cm (\pm 4 cm) in winter 1995.

RICHNESS OF WATERBIRD GUILDS

Wetland area was not a significant covariate of cumulative waterbird richness in any experiment. During both winter experiments, more waterbird species used wetlands undergoing drawdown than control wetlands (1994: 27 ± 2 species on drawdown wetlands vs. 18 ± 3 on controls, $t = 4.37$, $P = 0.007$; 1995: 21 ± 2 species vs. 17 ± 2 species, $t = 2.60$, $P = 0.04$). In contrast, during spring the total number of species that used drawdown wetlands was just as high as in winter, but no different from controls (1994: 26 ± 3 species vs. 22 ± 8 species, $t = 0.91$, $P = 0.39$; 1995: 23 ± 1 species vs. 19 ± 3 species, $t = 2.00$, $P = 0.12$).

Temporal trends in species richness differed among waterbird groups and seasons, and wetland area was

not a significant covariate of drawdown response for most (14 of 16) analyses (Table 3 and Figs 1 and 2). Wader richness increased dramatically during drawdowns in winter (time–treatment interaction) but not spring. Winter trends resulted in treatment effects of greater richness of waders using drawdown wetlands than controls. In contrast, during winter 1995 and spring 1994 richness of dabbling ducks and diving waterbirds declined in the latter half of drawdowns while remaining unchanged on controls. Changes in richness of all waterbird species combined were not significant for any experiment, although increases approached significance in winter 1994 ($P < 0.10$), resulting in a significant overall treatment effect. None the less, we detected positive relationships between total species richness and wetland depth diversity (Table 2) during both winter experiments (1994: two of four wetland regressions significant, mean $r = 0.55$, SE = 0.22, $t = 2.52$, d.f. = 3, $P = 0.04$; 1995: two of four regressions significant, mean $r = 0.69$, SE = 0.05, $t = 13.54$, d.f. = 3, $P < 0.001$).

WATERBIRD GUILD DENSITIES

Compared with control sites, densities of shorebird guilds increased markedly on experimental wetlands during winter (Fig. 3), resulting in overall treatment

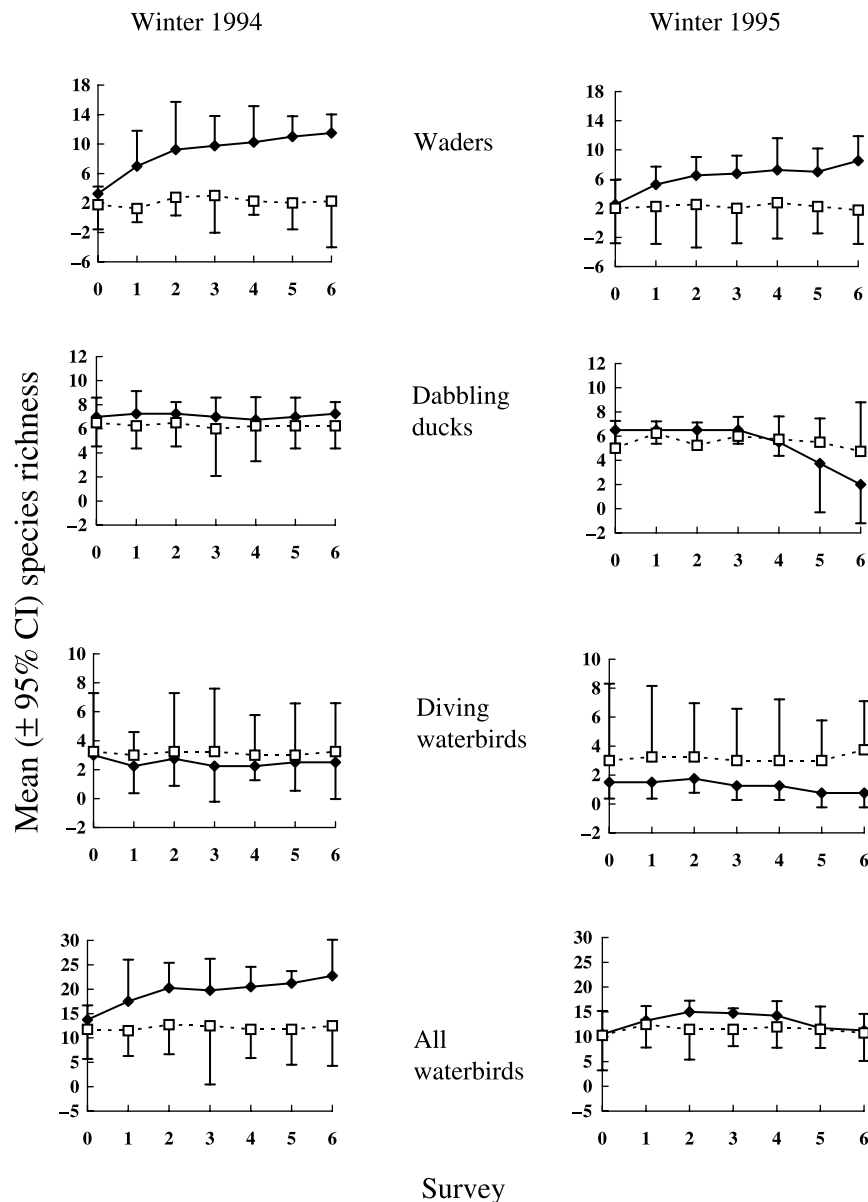


Fig. 1. Mean (\pm 95% CI) species richness of waterbirds on drawdown (solid; $n = 4$) and control (dotted; $n = 4$) wetlands during winter drawdown experiments conducted in The Grasslands in 1994 and 1995.

effects (Table 3). Moreover, large shorebird densities were positively correlated with habitat 5–15 cm deep (winter 1994: two of four regressions significant, mean $r = 0.64$, $SE = 0.15$, $t = 4.24$, $d.f. = 3$, $P = 0.012$; winter 1995: two of four regressions significant, mean $r = 0.48$, $SE = 0.19$, $t = 2.47$, $d.f. = 3$, $P = 0.045$) and calidridine sandpiper densities were positively correlated with availability of habitat > 0–5 cm deep (winter 1994: two of four regressions significant, mean $r = 0.67$, $SE = 0.08$, $t = 8.39$, $d.f. = 3$, $P = 0.002$; winter 1995: two of four regressions significant, mean $r = 0.57$, $SE = 0.10$, $t = 5.86$, $d.f. = 3$, $P = 0.005$). In spring, large daily variation in shorebird densities within and among experimental wetlands produced no significant temporal trends (Fig. 4). However, spring drawdowns attracted more large shorebirds and calidridine sandpipers to dewatering wetlands in 1994 and 1995, respectively (significant treatment effects).

Teal densities increased during winter experiments, declining only in the latter half of the 1995 experiment (Table 3 and Fig. 3). During spring drawdowns, however, trends in teal densities were no different from controls (Fig. 4). Teal densities and availability of habitat 5–20 cm deep were positively correlated during the 1994 winter drawdown (four of four regressions significant, mean $r = 0.80$, $SE = 0.07$, $t = 11.24$, $d.f. = 3$, $P < 0.001$) and marginally related in winter 1995 (two of four regressions significant, mean $r = 0.40$, $SE = 0.23$, $t = 1.75$, $d.f. = 3$, $P = 0.089$).

Densities of large dabbling ducks did not change during winter 1994, but declined steadily on experimental wetlands during the remaining three drawdowns, especially in the latter stages of dewatering (Table 3 and Figs 3 and 4). Likewise, positive relationships between large dabbling densities and the availability of habitat 5–25 cm deep (Table 2) were strong for spring

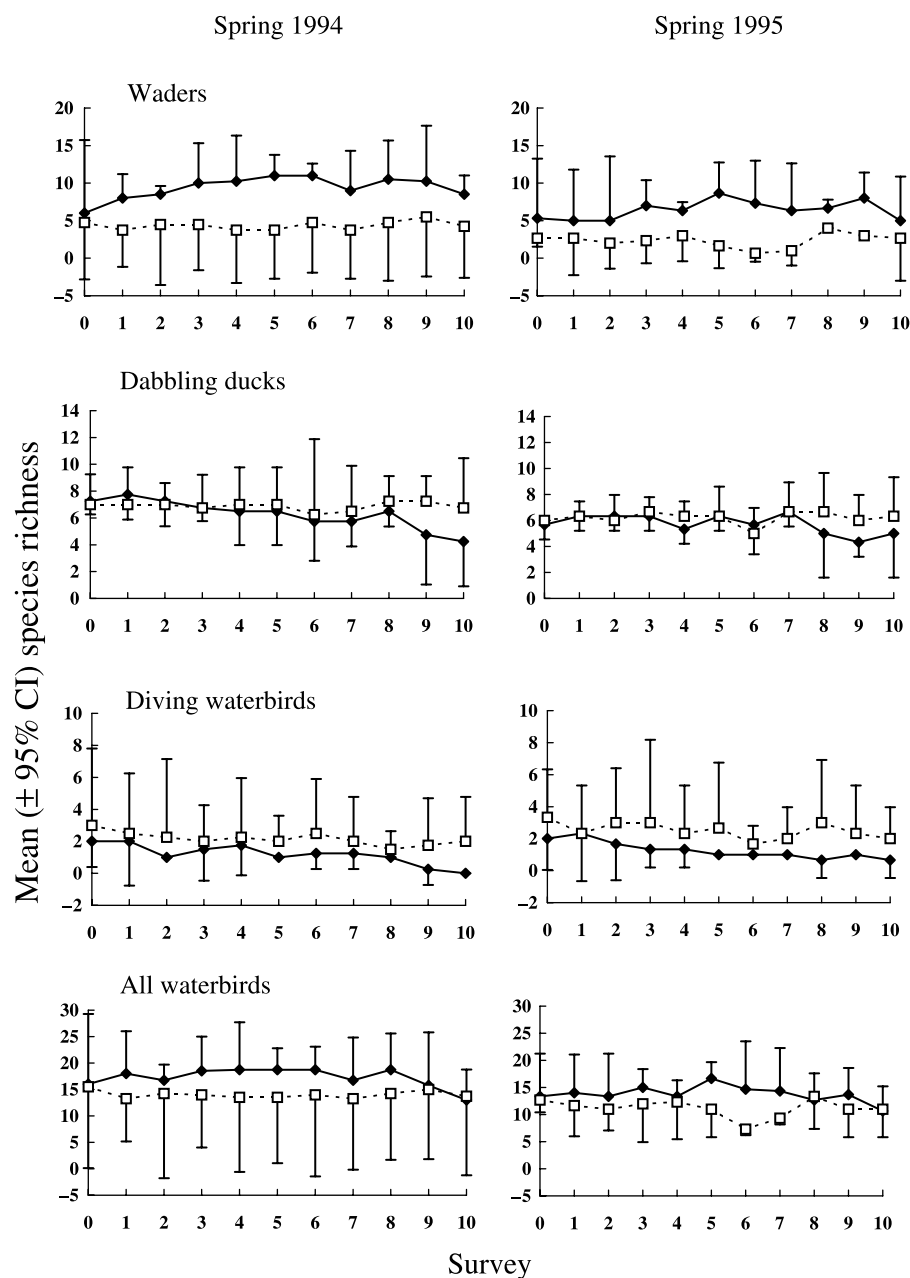


Fig. 2. Mean (\pm 95% CI) species richness of waterbirds on drawdown (solid; $n = 4$ in 1994, $n = 3$ in 1995) and control (dotted; $n = 4$ in 1994, $n = 3$ in 1995) wetlands during spring drawdown experiments conducted in The Grasslands in 1994 and 1995.

experiments (1994: three of four wetland regressions significant, mean $r = 0.68$, SE = 0.06, $t = 11.29$, d.f. = 3, $P < 0.001$; 1995: two of three regressions significant, mean $r = 0.63$, SE = 0.13, $t = 5.00$, d.f. = 2, $P = 0.019$) and approached significance in winter 1995 (two of four regressions significant, mean $r = 0.46$, SE = 0.22, $t = 2.08$, d.f. = 3, $P = 0.064$).

Discussion

Drawdowns influenced waterbird community structure on managed wetlands during all four experiments (Table 4). Overall, dewatering wetlands provided greater diversity and habitat amount to more species and numbers of waterbirds than did flooded wetlands.

Shorebirds responded to drawdowns most dramatically in winter. Dabblers and divers, however, ceased using wetlands towards the end of dewatering, regardless of season. Finally, teal responses were intermediate between shorebirds and the deeper-water species, increasing in abundance on wetlands in winter but decreasing in abundance towards the end of the complete drawdown in winter 1995.

Experimental approaches to evaluating land management are relatively rare in wildlife research (Elphick 1997; Erwin *et al.* 2000), primarily because rigorous experimentation with sufficient statistical power is difficult at large spatial scales. None the less, results from experiments hold greater inferential and predictive power, despite the challenges. We acknowledge

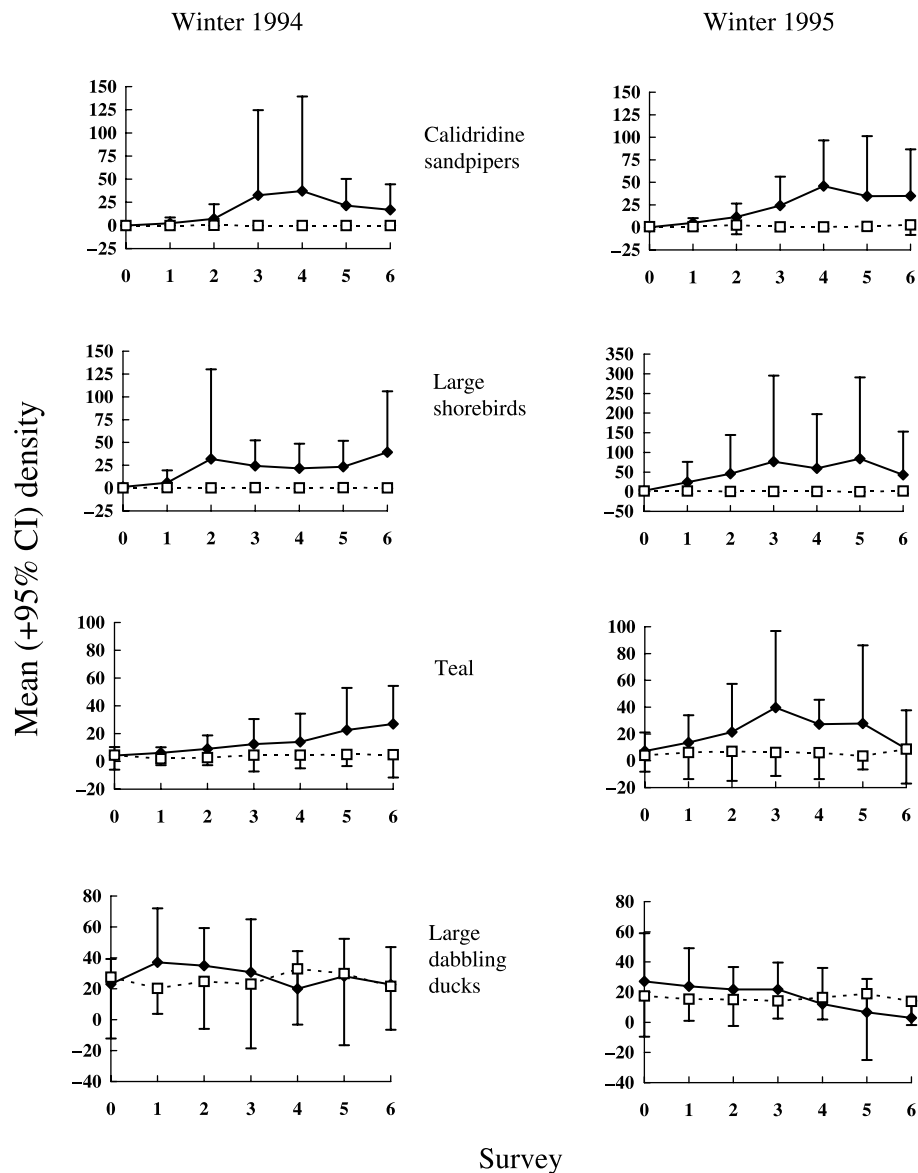


Fig. 3. Mean (\pm 95% CI) density of waterbirds on drawdown (solid; $n = 4$) and control (dotted; $n = 4$) wetlands during winter drawdown experiments conducted in The Grasslands in 1994 and 1995.

that other unmeasured variables (e.g. differences in invertebrate communities and vegetation structure among replicates) might have confounded treatments. However, the risk of such was minimized by using an experimental approach. Further, although sample sizes were small, we believe that a sizeable number of responses to drawdown were not spurious. Significant trends were consistent among experiments of the same magnitude or the same season (Table 4), indicating that the trends detected were not artefacts of the number of tests. Moreover, the correlations corroborated ANOVA, as changes in habitat availability explained most significant changes in waterbird use of wetlands.

TEMPORAL OVERLAP IN PEAK USE AMONG WATERBIRDS

By observing the structure of waterbird communities after each reduction in depth, we determined the depth

range at which managed wetlands in the flooded phase supported the richest and most abundant bird assemblage. In winter, wetlands supported the richest assemblage and greatest numbers of waterbirds when they were 10–20 cm in average depth (Figs 1 and 3 and Table 2). Within this interval, communities were represented by species from all three waterbird groups, and shorebird densities peaked before dabbling ducks began to decline in abundance. The 10–20 cm depth interval also coincided with greatest habitat diversity, when all habitats were simultaneously available, and in most cases when no more than 5% of a wetland's mudflat was exposed (Table 2; Williams 1996). In particular, the winter 1994 partial drawdown illustrated that lowering water levels merely 10 cm below traditional levels can substantially increase use by more species and individuals. Weber & Haig (1996) evaluated response to extremely slow (10 cm month⁻¹) winter drawdowns, and found that large numbers of shorebirds

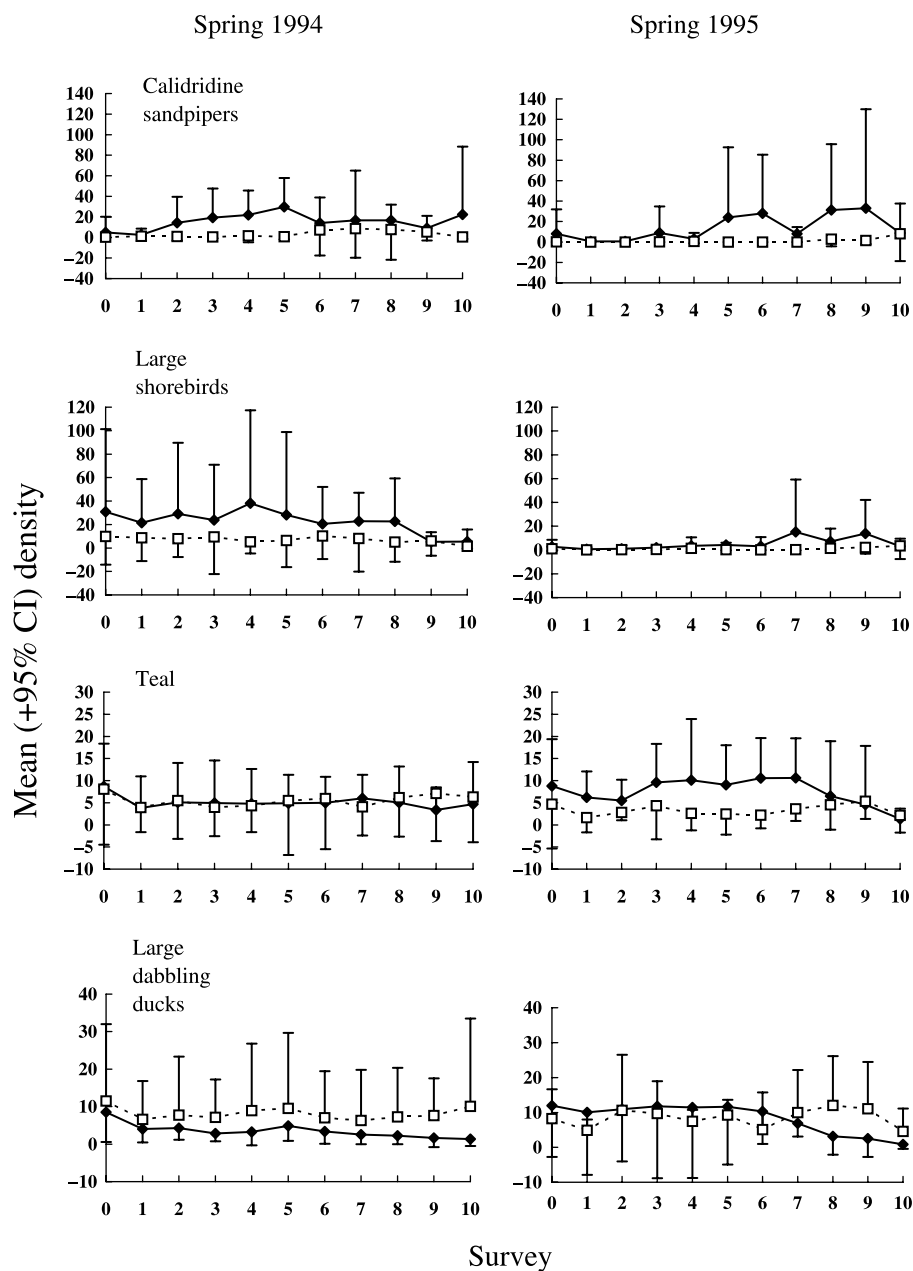


Fig. 4. Mean (\pm 95% CI) density of waterbirds on drawdown (solid; $n = 4$ in 1994, $n = 3$ in 1995) and control (dotted; $n = 4$ in 1994, $n = 3$ in 1995) wetlands during spring drawdown experiments conducted in The Grasslands in 1994 and 1995.

used wetlands whereas waterfowl numbers appeared unaffected. Similarly, Rundle & Fredrickson (1981) observed that teal and geese were attracted to wetlands managed for shorebirds, and Bird, Pettygrove & Eadie (2000) observed wintering waterfowl using shallow flooded (< 10 cm) rice fields.

It is important to emphasize that habitat diversity at a given average depth of a wetland depends on the underlying topography (Fredrickson & Taylor 1982; Skagen & Knopf 1994; Colwell & Taft 2000). Transposing this relationship, greater topographic variation in a wetland will broaden the range of average depths over which multiple habitats will be available to birds. For The Grasslands, where topographic variation was 30–42 cm on average, wetlands provided maximum diversity of foraging depths in the relatively wide

average depth range of 10–20 cm. From experimental manipulations of wetlands of known topography, our data corroborate and refine most assertions regarding depth ranges for optimal waterbird use (e.g. 15–20 cm for relatively level flooded rice fields, Elphick & Oring 1998; < 20 cm for wetlands with variable topography, Colwell & Taft 2000; < 25 cm for wetlands of unknown topography, Fredrickson & Taylor 1982; Fredrickson & Reid 1986; Fredrickson 1991).

SEASONAL DIFFERENCES IN RESPONSE TO DRAWDOWN

Birds respond to the heterogeneity of habitats at several spatial scales (Wiens 1985), from the landscape (e.g. a mosaic of wetlands), to the site (e.g. individual wetlands),

Table 4. Summary of waterbird responses to experimental drawdowns conducted in The Grasslands in winter and spring of 1994–95. Arrows signify significant increasing (↑) or decreasing (↓) trend response (ANOVAR interaction); ‘Yes’ indicates significant positive relationship between group species richness and habitat diversity (Brillouin Index) or between guild density and habitat availability; ‘–’ signifies no significant trend or association; ‘(0·10)’ indicates a trend or relationship that approached formal significant ($P < 0·10$)

	Drawdown experiment			
	Winter 1994*	Winter 1995	Spring 1994	Spring 1995
Richness				
Waders				
Trend	↑	↑	↑ (0·10)	–
Dabbling ducks				
Trend	–	↓	↓	–
Diving waterbirds				
Trend	–	↓	↓	–
All waterbirds				
Trend	↑ (0·10)	–	–	↑ (0·10)
Relationship	Yes	Yes	–	–
Density				
Calidridine sandpipers				
Trend	↑	↑	–	–
Relationship	Yes	Yes	–	–
Large shorebirds				
Trend	↑	↑	–	–
Relationship	Yes	Yes	–	–
Teal				
Trend	↑	↑, ↓	–	–
Relationship	Yes	Yes (0·10)	–	–
Large dabbling ducks				
Trend	–	↓	↓	↓
Relationship	–	Yes (0·10)	Yes	Yes

*Partial drawdown.

to the microsite scale (e.g. foraging areas within wetlands). Accordingly, scale of investigation may influence the patterns detected (Wiens, Rotenbery & Van Horne 1987). Because ephemerality is a dominant characteristic of natural wetlands (Fredrickson & Reid 1990), waterbirds have evolved flexible behaviour to take advantage of water level fluctuations at a variety of scales (Kushlan 1989; Skagen & Knopf 1993, 1994). As it is unlikely that all resource needs can be indefinitely met by one wetland patch, aquatic birds probably supplement their resource intake by using multiple wetlands within a mosaic (*sensu* Dunning, Danielson & Pulliam 1992; Farmer & Parent 1997). Indeed, non-breeding shorebirds move frequently among individual wetlands in the winter, enabling them to find suitable habitat on a landscape scale (Skagen & Knopf 1993; Warnock, Page & Stenzel 1995; Warnock & Takekawa 1996). Although we only observed habitat use at one spatial scale (individual wetlands), responses may have been mediated by regional habitat availability each season.

Our results suggest that the regional availability of shallow water (< 20 cm) in winter may be limiting for shallow-water species. Before winter drawdowns, shallow habitat was scarce on flooded wetlands, whereas in spring evaporation resulted in roughly 40% of wetland areas having habitat less than 15 cm deep (Table 2).

Seasonal differences in shorebird numbers observed on survey 0 mirrored this contrast. While spring wetlands supported a sizeable number of large shorebirds before experiments began, there were few shorebirds on wetlands at drawdown initiation in winter. Significant parallel increases in the abundance of shorebirds and their habitats in winter suggest that individuals tracked habitat within wetlands. We expected to see greater densities of shorebirds on dewatering wetlands during spring migration. However, while maximum densities of calidridine sandpipers were high and comparable to peak densities in winter, abundances varied greatly among surveys within wetlands. These patterns suggest that shorebirds were distributed across the many dewatering wetlands in spring. Such transitory use of wetlands by migrating shorebirds occurs elsewhere (Velasquez 1992).

Teal exhibited patterns similar to shorebirds. In fact, Isola *et al.* (2000) observed that the American green-winged teal in The Grasslands foraged in habitats less than 15 cm deep (95% CI of 11·4–14·6 cm). Thus teal also may have been constrained to find shallow habitat in winter, indicated by their strong increase with the availability of habitat on dewatering wetlands in winter but not in spring. Although this pattern may be explained partly by more teal residing in the region in winter, we suspect that teal did not respond to spring drawdowns

because habitat was widely available in the region during spring.

For dabbling ducks and diving waterbirds, data suggest that regional availability of deep-water habitats in spring influenced birds in a converse manner to that observed for shorebirds and teal. These species left dewatering wetlands as soon as their habitats began to decline in availability in winter (usually mid-drawdown), whereas they remained on wetlands for longer periods in spring despite losses of habitat. Such seasonal differences in wetland departures may indicate that individuals could find preferred flooded foraging habitats nearby in winter but not in spring. Similar declines in dabbler abundance have been linked to regional availability of flooded habitat elsewhere (Duncan *et al.* 1999). That large dabblers did not respond to the winter 1994 drawdown despite an initial increase in hectares at intermediate depths (5–25 cm) further implies that their habitat was not regionally limiting in winter.

Limitation of shallow habitats in winter may be cause for concern, as access to food during the non-breeding season can be a significant density-dependent cause of mortality in shorebirds (Goss-Custard 1979). During winter experiments, mean shorebird densities reached 200 birds ha⁻¹, exceeding responses to drawdowns elsewhere (Rundle & Fredrickson 1981; Hands, Ryan & Smith 1991) and comparable to densities observed where only one wetland was dewatered amidst a flooded landscape (Velasquez 1992). Such sustained high densities may ultimately depress the overwinter survival of individuals via competition or invertebrate food depletion (Goss-Custard 1979; Van Horne 1983). Additionally, peak teal densities on dewatering winter wetlands were twice those at any time in spring. The Grasslands teal potentially competes for the same resources as shorebirds in winter, as invertebrates are important prey for ducks especially when protein demands increase for egg-laying and moult (Miller 1987).

Our data indicate that Grassland managers should provide more shallow habitat during the winter. Winter wetlands dewatered for cattle pasture are typically completed in a few days and collectively occur only for a few weeks. These drawdowns may not provide shallow-water species with enough time to exploit available resources fully (Eldridge 1992; Helmers 1992) and may not support the shallow-water bird community through a 5-month winter. Shallow habitat can be increased either by conducting more winter drawdowns or managing winter water levels at shallower overall depths. Because increasing the number of winter drawdowns in The Grasslands would adversely affect moist-soil management by dewatering wetlands prematurely (Connelly 1979), we suggest that managers maintain flooded wetlands in winter at intermediate (e.g. 10–20 cm) average depths until ready for drawdown. However, with evaporation at 1.5 cm day⁻¹ towards spring, such wetlands may still expose mudflats earlier than is optimal. Thus, we suggest wetlands

maintained at the upper end of 10–20 cm (i.e. 15–20 cm) should provide sufficient habitat while also minimizing premature mudflat exposure; managers should periodically raise water levels to keep wetlands dynamically flooded around this average (Fredrickson & Reid 1990). This scheme enables managers to sustain habitat for waterfowl in winter, and to complete drawdowns in spring when large numbers of shorebirds are migrating.

In this study, wetlands at intermediate depths (10–20 cm) still provided diving waterbird habitat (> 25 cm deep; Table 2) but diving waterbird richness declined when wetlands reached average depths below 15 cm (complete winter 1995 drawdown). Such a response further supports maintaining wetlands at average depths of 15–20 cm. However, a more conservative approach would be to maintain a small number of wetlands within a given wetland complex exclusively for divers.

Irrespective of depth management, invertebrate resources must be abundant and periodically replenished if habitats are to function for extended periods (Miller 1987; Krapu & Reinecke 1992; Rehfish 1994; Davis & Smith 1998). Invertebrate productivity is influenced by wetland plant composition, organic debris, temperature, substrate manipulations and flooding regimes (Neckles, Murkin & Cooper 1990; Rehfish 1994; Batzer, De Szalay & Resh 1997; Sanders 2000; Ausden, Sutherland & James 2001). Cycles of rainfall and evaporation should provide temporary refuge for invertebrates, but if water levels remain constant shorebirds may deplete resources (Eldridge 1992; Helmers 1992). Further data are required on the effects of fluctuating water levels on invertebrate recruitment and depletion by birds (Piersma 1987).

MANAGEMENT IMPLICATIONS

Responses of waterbird communities to depth manipulations in The Grasslands provide an example for multispecies management on other wetlands. Our recommendations particularly apply to other locations where waterbird communities, basin topographies, vegetation structure, management capabilities and goals are similar. For complexes that primarily support dabblers and shorebirds, the following recommendations should lead to efficient management for a diverse community. We hope that these will be incorporated where appropriate by practitioners and agencies involved in wetland management and policy (Ormerod *et al.* 2002).

1. Knowledge of local topography will help to determine the average depths necessary to provide a diversity of waterbird habitats. While a wetland is flooded, topography (range of depths) can be estimated from water depths measured along two transects at roughly 45° to the prevailing slope of the underlying wetland bottom. Wetland restoration to create gentle slopes and undulating bottom topographies will broaden the average depth range at which multiple habitats will become available.

2. For many managed wetlands, spring is considered the most important season in which to provide habitat for migrant shorebirds. For locales with a sizeable population of wintering shorebirds in addition to spring migrants, our data indicate that it may be appropriate to shift some of the management focus from spring drawdowns to greater availability of shallow water in winter. This can generally be achieved by increasing the number of winter drawdowns or by lowering winter water levels. For such locales, winter drawdowns or lowered water levels may be a more effective and efficient use of resources (personnel, time, funding) than more spring drawdowns when there is a regional excess of shallow water.

3. For complexes managed for moist-soil plants and thus where winter drawdowns are not feasible, managers can maintain winter water levels at low average depths to accommodate a diverse regional community without depreciating waterfowl habitat. We recommend average depths between 15 and 20 cm, or 10–25 cm where topography is more variable than in The Grasslands. In localities where the management focuses on waterfowl, managing for deeper average depths will be satisfactory (20–25 cm); if few diving species winter in an area, shallower depths will suffice (10–15 cm). It may be necessary to manage individual wetlands exclusively for species associated with the extreme ends of the depth spectrum (e.g. diving waterbirds and shorebirds), especially where they comprise a large component of the winter community.

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References

- American Ornithologists' Union (1998) *Check-list of North American Birds: The Species of Birds of North America from the Arctic Through Panama, Including the West Indies and Hawaiian Islands*. American Ornithologists' Union, Washington, DC.
- Ausden, M., Sutherland, W.J. & James, R. (2001) The effects of flooding lowland wet grassland on soil macroinvertebrate prey of breeding wading birds. *Journal of Applied Ecology*, **38**, 320–338.

- Baker, M.C. (1979) Morphological correlates of habitat selection in a community of shorebirds (Charadriiformes). *Oikos*, **33**, 121–126.
- Baldassarre, G.A. & Fischer, D.H. (1984) Food habits of fall migrant shorebirds on the Texas High Plains. *Journal of Field Ornithology*, **55**, 220–229.
- Batzer, D.P., De Szalay, F. & Resh, V.H. (1997) Opportunistic response of a benthic midge (Diptera: Chironomidae) to management of California seasonal wetlands. *Environmental Entomology*, **26**, 215–222.
- Bird, J.A., Pettygrove, G.S. & Eadie, J.M. (2000) The impact of waterfowl foraging on the decomposition of rice straw: mutual benefits for rice growers and waterfowl. *Journal of Applied Ecology*, **37**, 728–741.
- California Department of Fish and Game (1987–96) *Periodic Waterfowl Survey*. California Department of Fish and Game, Sacramento, CA.
- Colwell, M.A. & Taft, O.W. (2000) Waterbird communities in managed wetlands of varying water depth. *Waterbirds*, **23**, 45–55.
- Connelly, D.P. (1979) *Propagation of Selected Native Marsh Plants in the San Joaquin Valley*. Wildlife Management Leaflet 15. California Department of Fish and Game, Sacramento, CA.
- Davis, C.A. & Smith, L.M. (1998) Ecology and management of migrant shorebirds in the Playa Lakes region of Texas. *Wildlife Monographs*, **140**, 1–45.
- Duncan, P., Hewison, A.J.M., Houte, S., Rosoux, R., Tournebize, T., Dubs, F., Burel, F. & Bretagnolle, V. (1999) Long-term changes in agricultural practices and wildfowling in an internationally important wetland, and their effects on the guild of wintering ducks. *Journal of Applied Ecology*, **36**, 11–23.
- Dunning, J.B., Danielson, B.J. & Pulliam, H.R. (1992) Ecological processes that affect populations in complex landscapes. *Oikos*, **65**, 169–175.
- Eldridge, J. (1992) *Management of Habitat for Breeding and Migrating Shorebirds in the Midwest*. Leaflet 13.2.14. US Fish and Wildlife Service, Washington, DC.
- Elphick, C.S. (1997) Experimental approaches to shorebird habitat management. *International Wader Studies*, **9**, 20–28.
- Elphick, C.S. & Oring, L.W. (1998) Winter management of Californian rice fields for waterbirds. *Journal of Applied Ecology*, **35**, 95–108.
- Erwin, R.M., Laubhan, M.K., Cornely, J.E. & Bradshaw, D.M. (2000) Managing wetlands for waterbirds: how managers can make a difference in improving habitat to support a North American bird conservation plan. *Strategies for Bird Conservation: The Partners in Flight Planning Process* (eds R. Bonney, D.N. Pashley, R.J. Cooper & L. Niles), pp. 82–87. US Dept of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, CO.
- Farmer, A.H. & Parent, A.H. (1997) Effects of the landscape on shorebird movements at spring migration stopovers. *Condor*, **99**, 698–707.
- Fredrickson, L.H. (1991) *Strategies for Water Level Manipulations in Moist-Soil Systems*. Leaflet 13.4.6. US Fish and Wildlife Service, Washington, DC.
- Fredrickson, L.H. & Laubhan, M.K. (1995) *Land Use Impacts and Habitat Preservation in the Grasslands of Western Merced County, California*. Grassland Water District, Los Banos, CA.
- Fredrickson, L.H. & Reid, F.A. (1986) Wetland and riparian habitats: a nongame management overview. *Management of Nongame Wildlife in the Midwest: A Developing Art* (eds J.B. Hale, L.B. Best & R.L. Clawson), pp. 59–96. The Wildlife Society, Grand Rapids, MI.
- Fredrickson, L.H. & Reid, F.A. (1990) Impacts of hydrologic alteration on management of freshwater wetlands. *Management of Dynamic Ecosystems* (ed. J.M. Sweeney), pp. 71–90. The Wildlife Society, West Lafayette, IN.

- Fredrickson, L.H. & Taylor, T.S. (1982) *Management of Seasonally Flooded Impoundments for Wildlife*. Resource Publication 148. US Fish and Wildlife Service, Washington, DC.
- Goss-Custard, J.D. (1979) Effect of habitat loss on the numbers of overwintering shorebirds. *Shorebirds in Marine Environments* (ed. F.A. Pitelka), pp. 167–177. Cooper Ornithological Society, Berkeley, CA.
- Hands, H.M., Ryan, M.R. & Smith, J.W. (1991) Migrant shorebird use of marsh, moist-soil, and flooded agricultural habitats. *Wildlife Society Bulletin*, **19**, 457–464.
- Heitmeyer, M.E., Connelly, D.P. & Pederson, R.L. (1989) The Central, Imperial, and Coachella Valleys of California. *Habitat Management for Migrating and Wintering Waterfowl in North America* (eds L.M. Smith, R.L. Pederson & R.M. Kaminski), pp. 475–505. Texas Tech University Press, Lubbock, TX.
- Helmets, D.L. (1992) *Shorebird Management Manual*. Western Hemisphere Shorebird Reserve Network, Manomet, MA.
- Hunter, L., Canevari, P., Myers, J.P. & Payne, L.X. (1991) *Shorebird and Wetland Conservation in the Western Hemisphere*. Technical Publication 12. International Council for Bird Preservation, Cambridge, UK.
- Hurlbert, S.H. (1984) Pseudoreplication and the design of ecological field experiments. *Ecological Monographs*, **54**, 187–211.
- Isola, C.R., Colwell, M.A., Taft, O.W. & Safran, R.J. (2000) Interspecific differences in habitat use of shorebirds and waterfowl foraging in managed wetlands of California's San Joaquin Valley. *Waterbirds*, **23**, 196–203.
- Krapu, G.L. & Reinecke, K.J. (1992) Foraging ecology and nutrition. *Ecology and Management of Breeding Waterfowl* (eds B.D.J. Batt, A.D. Afton, M.G. Anderson, C.D. Ankney, D.H. Johnson, J.A. Kadlec & G.L. Krapu), pp. 1–29. University of Minnesota Press, Minneapolis, MN.
- Krebs, C.J. (1989) *Ecological Methodology*. Harper Collins Publishers, New York, NY.
- Kushlan, J.A. (1989) Avian use of fluctuating wetlands. *Freshwater Wetlands and Wildlife, CONF-8603101, DOE Symposium Series No. 61* (eds R.R. Sharitz & J.W. Gibbons), pp. 593–604. USDOE Office of Scientific and Technical Information, Oak Ridge, TN.
- Laubhan, M.K. & Fredrickson, L.H. (1993) Integrated wetland management: concepts and opportunities. *Transactions of the North American Wildlife and Natural Resources Conference*, **58**, 323–334.
- Miller, M.R. (1987) Fall and winter foods of northern pintails in the Sacramento Valley, California. *Journal of Wildlife Management*, **51**, 405–414.
- Mitsch, W.J. & Gosselink, J.G. (2000) *Wetlands*, 3rd edn. Elsevier Science, New York, NY.
- Nagarajan, R. & Thiyagesan, K. (1996) Waterbirds and substrate quality of the Pichavaram wetlands, southern India. *Ibis*, **138**, 710–721.
- Neckles, H.A., Murkin, H.R. & Cooper, J.A. (1990) Influences of seasonal flooding on macroinvertebrate abundance in wetland habitats. *Freshwater Biology*, **23**, 311–322.
- Ormerod, S.J., Barlow, N.D., Marshall, E.J.P. & Kerby, G. (2002) The uptake of applied ecology. *Journal of Applied Ecology*, **39**, 1–7.
- Piersma, T. (1987) Production by intertidal benthic animals and limits to their predation by shorebirds: a heuristic model. *Marine Ecology Progress Series*, **38**, 187–196.
- Pöysä, H. (1983) Resource utilization pattern and guild structure in a waterfowl community. *Oikos*, **40**, 295–307.
- Rehfishch, M.M. (1994) Man-made lagoons and how their attractiveness to waders might be increased by manipulating the biomass of an insect benthos. *Journal of Applied Ecology*, **31**, 383–401.
- Reid, F.A. (1993) Managing wetlands for waterbirds. *Transactions of the North American Wildlife and Natural Resources Conference*, **58**, 345–350.
- Rundle, W.D. & Fredrickson, L.H. (1981) Managing seasonally flooded impoundments for migrant rails and shorebirds. *Wildlife Society Bulletin*, **9**, 80–87.
- SAS Institute (1995) *SAS/STAT User's Guide, Version 6-11*. SAS Institute Inc., Cary, NC.
- Sanders, M.D. (2000) Enhancing food supplies for waders: inconsistent effects of substratum manipulations on aquatic invertebrate biomass. *Journal of Applied Ecology*, **37**, 66–76.
- Shuford, W.D., Page, G.P. & Hickey, C.M. (1998) Patterns and dynamics of shorebird use of California's Central Valley. *Condor*, **100**, 227–244.
- Skagen, S.K. & Knopf, F.L. (1993) Toward conservation of midcontinental shorebird migrations. *Conservation Biology*, **7**, 533–541.
- Skagen, S.K. & Knopf, F.L. (1994) Migrating shorebirds and habitat dynamics at a prairie wetland complex. *Wilson Bulletin*, **106**, 91–105.
- Stevens, J. (1992) *Applied Multivariate Statistics for the Social Sciences*, 2nd edn. L. Erlbaum Associates, Hillsdale, NJ.
- Van Horne, B. (1983) Density as a misleading indicator of habitat quality. *Journal of Wildlife Management*, **47**, 893–901.
- Velasquez, C.R. (1992) Managing artificial saltpans as waterbird habitat: species' responses to water level manipulation. *Colonial Waterbirds*, **15**, 43–55.
- Warnock, N., Page, G.W. & Stenzel, L.E. (1995) Non-migratory movements of dunlins on their California wintering grounds. *Wilson Bulletin*, **107**, 131–139.
- Warnock, S.E. & 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.
- Weber, L.M. & Haig, S.M. (1996) Shorebird use of South Carolina managed and natural coastal wetlands. *Journal of Wildlife Management*, **60**, 73–82.
- Wiens, J.A. (1985) Vertebrate response to environmental patchiness in arid and semiarid ecosystems. *The Ecology of Natural Disturbance and Patch Dynamics* (eds S.T.A. Pickett & P.S. White), pp. 169–193. Academic Press, Orlando, FL.
- Wiens, J.A., Rotenberry, J.T. & Van Horne, B. (1987) Habitat occupancy patterns of North American shrubsteppe birds: the effects of spatial scale. *Oikos*, **48**, 132–147.
- Williams, O.E. (1996) *Waterbird responses to late winter and early spring drawdowns of moist-soil managed wetlands in California's San Joaquin Valley*. MS Thesis. Humboldt State University, Arcata, CA.

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