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University of Nevada

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Waterbird conservation and ecology: the role of rice field management in habitat
restoration

A dissertation submitted in partial fulfillment of the requirements for the degree of
Doctor of Philosophy in Ecology, Evolution, and Conservation Biology

by

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For my parents, Marilyn and Dennis,
who made me play outside.
All those ringing trips finally paid off.

Do different

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ABSTRACT

Agricultural activities occupy a third of the Earth's ice-free land surface and rice farming is a dominant form of agriculture. Flooded rice fields provide a potential surrogate habitat for wetland species, many of which have declined as wetlands around the world are drained. I studied the potential for flooding California rice fields, during winter, to benefit waterbirds. I found that intentionally flooded fields received significantly greater use by most waterbird species than do fields where only passive flooding was possible. Exceptions included geese, which used both habitats equally, and sandhill cranes, which were rarely seen in flooded fields. Different methods of manipulating rice straw in conjunction with flooding had only minor effects on waterbirds. Water depth was associated significantly with the presence of most species considered, but not with bird densities. During much of the winter, average water depths in flooded fields were greater than those for which waterbird use and conservation value of fields were maximized.

Factors other than field management may affect waterbird use of flooded fields. For example, densities of geese, wading birds, and shorebirds were positively related to the proportion of the surrounding landscape that was a wildlife refuge, semi-natural wetland habitat, or both. In contrast, the amount of flooded rice in the landscape was more important for ducks. All relationships depended on the spatial scale at which the landscape was measured.

Finally, I considered whether there were differences in food abundance, predator occurrence, and the behavior of shorebirds and egrets, among semi-natural wetlands, flooded rice fields and unflooded fields. Predators crossed flooded fields less frequently than other habitats. Foraging performance and time allocation varied little among habitats. In general, there was little evidence that flooded fields were inferior to semi-natural wetlands as habitat for the waterbirds studied. In combination, my results suggest that flooded rice fields are an important habitat for most wintering waterbirds, that minor modifications to the way in which fields are managed could increase waterbird use, and that flooded fields provide an important supplement to California's wetland resources. These observations have important implications for waterbird management in rice growing regions worldwide.

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INTRODUCTION

Agricultural habitats dominate the world's land surface. Currently, a third of all ice-free land is used for some form of agriculture, with 11% of this area cultivated each year (Urban & Vollrath 1984). Moreover, agricultural habitats often are concentrated in highly productive and biologically rich parts of the world. Understanding the contribution that farmland can make to the preservation of biological diversity, and developing management techniques that improve the quality of agricultural land in ways that are compatible with continued production, should be important goals for conservation biologists.

Agricultural habitats also provide excellent systems for studying questions of habitat selection and management. Unlike most natural processes, agriculture tends to simplify and homogenize habitats, which means that farmland typically consists of many habitat patches (fields) that are very similar. This combination of uniformity and replication provides a basic requirement for using controlled experimental approaches to test specific hypotheses about the ways in which animals use habitat patches. Despite the similarity of agricultural fields, there usually is variation in the ways in which fields are managed: different crops, different farmers, different field treatments depending on specific needs, etc. In striking contrast to more natural systems, this variation is often characterized by relatively few, discrete, alternatives. When one considers that many agricultural habitats are simplified analogues of natural habitats and that the management techniques used by farmers often mimic natural processes, the potential for exploiting these systems for studying ecological processes becomes apparent. For example, one might hypothesize that in grasslands, vegetation height plays an important role in structuring soil invertebrate communities because it influences environmental conditions at the ground's surface. Wheat fields, which are little more than simplified grasslands, might provide a good system for testing such a hypothesis. Different varieties of wheat could be used to produce fields with different vegetation heights, while controlling for plant species, soil management, plant density, field heterogeneity, etc.

In addition to the potential for using agricultural systems to study ecological processes, often there are similarities among the management options available to farmers and to people involved with conservation and wildlife management. In these cases, agricultural systems can provide opportunities to compare the consequences to wildlife of potential management options at large scales, with reasonable experimental control, and relatively inexpensively.

Rice *Oryza sativa* farming is one of the dominant forms of agriculture worldwide. Originally domesticated over 6,000 years ago somewhere in southeast Asia, rice serves as the main staple food for over half the world's human population. More than 80% of the world's rice production occurs in Asia, but it is also an important crop in the United States, Central and South America, Africa, Mediterranean Europe and parts of the former Soviet Union and Oceania. By the early 1990s, global production was over 500 million tons of rough rice per annum, constituting almost 30% of the world's grain supply. In the late 1980s, more than 145 million ha of rice were planted throughout the world (Lu & Chang 1980; Chang & Luh 1991; Cramer & Jensen 1991; Setia *et al.* 1994; IRRI 1998).

That rice fields offer a potential habitat for waterbirds has been long recognized. Early studies addressed the role that waterfowl, in particular ducks, play as predators of rice plants (Neale 1918; Ellis 1940). These studies soon led to the realization that, in many cases, the damage caused by ducks feeding in rice fields was economically trivial (Frith 1957; Bourne & Osborne 1978) and that the benefits gained from the removal of weed seeds could outweigh any impacts to the harvestable crop (Neale 1918; Jones 1940; Smith & Sullivan 1980). Managers also realized that residual grain left on the fields after harvest was over was eaten readily by game species, so they began managing fields as habitat for geese, ducks, pheasants, etc. (Wright 1959; Harmon *et al.* 1960; McGinn & Glasgow 1963; Forsyth 1965). More recently, biologists have recognized that a much wider variety of bird species may accrue benefits from the use of rice habitats and it has been proposed the rice fields may play an important role in waterbird conservation (Fasola & Barbieri 1978; Fasola 1983; Remsen *et al.* 1991; Pain 1994; Fasola *et al.* 1996; Fasola & Ruíz 1996, 1997; Elphick & Oring 1998; Lane & Fujioka 1998).

Worldwide loss of wetlands to human development have been extensive. In North America, more than half of all wetland habitat south of the Canada-United States border has been drained in the last two centuries (Tiner 1984; Dahl 1990). Similarly, in Asia more than 320,000 km² of wetlands had been drained by 1985 (L'Vovich & White 1990). In particular, the conversion of natural habitats to agricultural land has impacted wetlands because wetlands tend to leave very rich soils when drained. Simultaneously, wetlands are biologically very productive so habitat losses tend to have considerable impact on regional biotas. Rice typically is grown in areas where wetlands formerly occurred and approximately 86% of the land under rice cultivation is inundated for at least part of the year, either through irrigation, rainwater, or deepwater flooding (Chang & Luh 1991). Rice paddies, therefore, offer potential as a surrogate for destroyed wetland habitats.

In Mediterranean Europe, the potential value of rice fields to waterbird conservation has been known for some time. In north-west Italy, the size, number and distribution of heronries is related to the distribution of rice fields (Fasola & Barbieri 1978). At a larger scale, rice fields produced the majority of food taken by six species of breeding herons (Ardeidae) at study sites in Spain, Italy and Greece. Only in the Rhone Delta of France are rice fields not the primary foraging habitat for herons, possibly because there is less food available than in other areas (Fasola *et al.* 1996, Fasola & Ruíz 1997). Less is known about the importance of rice fields to other species in Europe. Recent reviews, however, showed that at least 25 bird species, considered to be of conservation concern in Europe, regularly use rice fields during the nonbreeding season and 16 species use rice fields while breeding (Fasola & Ruíz 1996, 1997). Among the more significant examples of the importance of rice fields are: the use of fields in the Tagus estuary of Portugal by internationally important numbers of black-tailed godwits *Limosa limosa* during winter and by an increasing breeding population of white storks *Ciconia ciconia*; extensive use of fields in the Ebro Delta, Spain, and the Camargue, France, by wintering shorebirds and ducks; and the reliance on rice fields by Audouin's gulls *Larus audouinii*, breeding in the Ebro Delta, during periods when other foods are not available (Fasola & Ruíz 1997 and references therein).

Less research has been done in other parts of the world. The few topics that have been addressed, include: the effects of changing management practices on foraging herons in Japan (Lane & Fujioka 1998), the importance of rice grain in the diet of several bird species using Cuban rice fields (Acosta & Berovides 1982; Acosta Cruz *et al.* 1988), and the feeding ecology of whistling-ducks *Dendrocygna* in South America (Bourne 1981; Bruzual & Bruzual 1983). In addition, the waterbird communities using rice fields in other parts of the world have been described (Hicklin & Spaans 1993; Nagarajan & Thiyagesan 1997).

In North America, rice is grown in California (mostly in the Sacramento Valley; Fig. 1) and throughout the southeastern states (Setia *et al.* 1991). Research on waterbirds has focused on time allocation and foraging ecology of wintering waterfowl, which are regularly hunted in rice fields (Miller 1987; Miller *et al.* 1989; Rave & Cordes 1993); the role of rice fields as breeding habitat for waterbirds, especially rails (Rallidae) and whistling ducks, in the southeastern states (Meanley & Meanley 1959; Helm *et al.* 1987; Turnbull *et al.* 1989a; Hohman *et al.* 1994, 1996); the effects of pesticides on birds that feed in rice fields (Flickinger & King 1972; Turnbull *et al.* 1989b); and the occurrence of shorebirds and other nongame species in rice fields (Sykes & Hunter 1978; Remsen *et al.* 1991; Rettig 1994). Much, however, remains unknown about the role rice agriculture plays in the conservation of waterbird populations in the United States.

Several recent changes in the United States' rice industry have resulted in increased interest in the role of rice fields as wildlife habitat. In California, legislation was introduced in 1991 to restrict the area of harvested rice fields that could be burned during

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Figure 1. Distribution of rice agriculture, by county, in California. Increasing intensity of shading indicates a larger area of rice within a county (after Hill *et al.* 1992).

winter (Rice Straw Burning Act, AB 1378, 1991). Until this time, burning was the preferred method for disposing of residual straw and stubble in preparation for the following year's crop. Introduction of the Act required that farmers seek new ways of removing this material from their fields. Flooding fields soon after harvest, and retaining water on the fields until early spring, increases rates of straw decomposition and effectively removes much of the straw. Moreover, for many years certain farmers had been flooding some of their fields for part of the winter to provide habitat for ducks that could be hunted. Winter flooding, therefore, provides farmers with an alternative to burning, increases opportunities for waterfowl hunting and creates a large area of potential waterbird habitat in central California (Payne & Wentz 1992; Brouder & Hill 1995). This final benefit, is viewed as especially important, given the extensive losses of wetland habitat in the state (Dahl 1990; National Research Council 1992) and the importance of the Central Valley to waterbirds (Heitmeyer, Connelly & Pederson 1989; Reid & Heitmeyer 1995; Shuford, Page & Kjelmlyr 1998).

Two other changes in the United States rice industry occurred at about the same time as the introduction of straw burning restrictions: increased use of "stripper-header" harvesters, which strip the grain off the stalk, and declines in the area of rice farmed in parts of the country. The new harvesters are more efficient than conventional combines, do not cut the rice stalks, and leave less spilled grain and taller stubble in the fields. The abundance and availability of grain in winter rice fields may be reduced as a consequence, raising concerns about the effects on birds that feed on spilled grain (Miller & Wylie 1995; Day & Colwell in review). The declines in rice acreage (Setia *et al.* 1994) have caused rice growers to highlight the potential role of their fields as waterbird habitat to demonstrate supplemental benefits of maintaining a healthy rice industry.

In this study, I investigated the effects of winter flooding of California rice fields on waterbirds. I evaluated the effects of flooding fields on a diverse array of individual waterbird species (Chapter 1) and on the waterbird community as a whole (Chapter 2). In these two chapters, I tested three specific hypotheses. First, I compared bird use of fields that had been intentionally flooded by farmers to fields that were not purposefully inundated. This second group included fields that held standing water due to rainfall or river flooding. The distinction between these two classes is important: the former requires financial input to buy water, whereas the latter does not. If passive flooding alone is sufficient to support waterbird communities, then there would be no conservation benefit to buying water to flood fields. Second, I examined whether different methods of manipulating straw, used in conjunction with flooding, affected bird use of flooded fields. Methods of straw manipulation are used by farmers to enhance decomposition and may influence both food abundance and availability. Finally, I determined what influence water depth has on the waterbird community using flooded fields.

In Chapter 3, I examined the extent to which the densities of waterbirds in a flooded field were influenced by factors other than field management. I used a Geographic Information System to calculate the abundance of various habitats and land uses in the landscape surrounding each study field. I then determined whether the amount of these habitats was related to waterbird abundance. I used this analysis to develop a series of hypotheses describing the ways in which waterbirds may be influenced by the

landscape in which they occur and I elucidated the implications of these hypotheses for management at a regional scale.

Finally, in the last chapter, I examined the question of whether, from the birds' perspective, flooded fields could be considered equivalent to more natural habitats found in the same area. To do this, I measured food abundance, a variety of behavioral traits, and the perceived predation threat in rice fields and semi-natural wetlands found on wildlife refuges and managed hunting clubs.

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CHAPTER ONE

WINTER MANAGEMENT OF CALIFORNIA RICE FIELDS FOR WATERBIRDS

Worldwide, aquatic ecosystems are being destroyed and altered at an increasing rate. In the conterminous United States, more than half of all wetlands have been lost in the last two centuries (Tiner 1984; Dahl 1990; National Research Council 1992), primarily through draining for agriculture (Wilén 1989). Declines in waterfowl populations, and the growing recognition of the biological and economic value of wetlands, have led to concern about these losses (e.g. Canadian Wildlife Service/U.S. Fish and Wildlife Service 1986; Sharitz & Gibbons 1989; Smith, Pederson & Kaminski 1989; Bildstein *et al.* 1991; Finlayson & Moser 1991). This concern has resulted in the creation of various programs to protect extant wetlands, primarily through acquisition by government agencies and nonprofit conservation groups. While these efforts have preserved many sites and enabled restoration at others, they have prevented neither a net loss of wetlands, nor continued declines of wildlife populations (Payne & Wentz 1992). Reversing these trends probably will require providing suitable wetland habitats on privately-owned land (Payne & Wentz 1992). Successful development of such strategies is contingent upon land management practices which maximize benefits for wildlife in ways compatible with the primary use of private lands.

Wetland losses in California have been particularly great, with only 9% of the wetlands that existed in the 1780's remaining (Dahl 1990; National Research Council 1992). The majority of these losses have occurred in the Central Valley of California where over a million hectares of aquatic habitat is estimated to have been drained (Frayer, Peters & Pywell 1989). The Central Valley also is the major wintering area for many North American waterbirds. More than 40 million waterfowl are estimated to have used the region in the past, although numbers now are reduced to 3,000,000 - 6,000,000 birds (Heitmeyer, Connelly & Pederson 1989; Reid & Heitmeyer 1995). Few data exist for other species, although recent surveys have shown there to be 200,000 - 375,000 shorebirds wintering in the Central Valley (Shuford, Page & Kjølmyr 1998).

Rice agriculture has long been recognized as having considerable potential value for waterfowl (e.g. Wright 1959; McGinn & Glasgow 1963; Miller 1987; Miller *et al.* 1989; Brouder & Hill 1995) and more recently for other aquatic birds (Fasola & Barbieri 1978; Fasola 1983; Remsen *et al.* 1991; Pain 1994; Fasola, Canova & Saino 1996; Fasola & Ruíz 1996, 1997; Lane & Fujioka 1998). In the Central Valley, between 140,000 and 180,000 ha of rice are grown annually (Hill *et al.* 1992), predominantly in the Sacramento Valley which comprises its northern half. To improve air quality, recent legislation by the State of California (Rice Straw Burning Act, AB 1378, 1991) mandated that rice farmers phase out their practice of burning rice stubble after harvest. In response to this legislation, many growers flood fields during winter to enhance straw decomposition. This flooding has potential not only to provide farmers with a means of straw disposal, but simultaneously to recreate, albeit in a very artificial manner, some of the region's lost wetland habitat (Brouder & Hill 1995).

Many rice growers use some form of straw manipulation in conjunction with flooding, to increase decomposition rates. These methods increase contact between the

soil and straw through compaction or partial burial, increase the straw's surface area by chopping it up, or both. Methods similar to these have been advocated as ways of increasing invertebrate densities and benefiting waterbirds in managed wetlands (especially shorebirds; e.g. Helmers 1992). The logistical difficulties associated with conducting land-use experiments have limited tests of the efficacy of such methods to studies involving few replicates, little experimental control and comparisons of only a small subset of the management options. These studies generally indicate that management actions that increase the rate of vegetation decomposition lead to increased shorebird use (e.g. Rundle & Fredrickson 1981).

Water depth also has been considered a major factor determining the abundance of waterbird species in wetlands (e.g. Boshoff, Palmer & Piper 1991a,b,c; Fredrickson 1991; Helmers 1992; Velasquez 1992). The variation in depth in most wetlands, however, has prevented rigorous tests of the impact of small depth differences. California rice fields provide an ideal setting for conducting such tests because they are laser-leveled to create uniform water depths.

My goal in this study was to evaluate how rice fields might be managed during winter to maximize their potential as surrogate wetlands. I tested the hypotheses that densities of individual bird species differ among (1) fields that are flooded by rice growers and those that are not, (2) flooded fields that receive different straw management treatments, and (3) fields that are flooded to different depths. I also compared bird densities during two winters with different weather conditions to see whether rainfall affected field use.

MATERIALS AND METHODS

Data were collected at several sites in the Sacramento Valley, California, during the winters (November - March) of 1993/94 and 1994/95. Sites were grouped into three areas: Richvale-Biggs, Sutter, and Princeton (Fig. 2). I chose these areas to ensure that observations represented the primary region in which rice is grown in California.

Within these three areas, I arbitrarily selected rice fields to census; censuses were conducted by myself and one assistant in each winter. In 1993/94, we censused 53 fields, of which 37 were flooded (total area = 797.2 ha; mean area \pm SE = 21.5 \pm 4.1 ha) and 16 were not (486.5 ha; 30.4 \pm 7.1 ha). In 1994/95, twenty-five flooded fields (699.3 ha; 28.0 \pm 5.4 ha) and 15 unflooded fields (398.3 ha; 26.6 \pm 6.4 ha) were sampled. Fifteen of the flooded fields and five of the unflooded fields were sampled in both years. A flooded field was defined as one that was flooded intentionally to enhance straw decomposition, to attract birds or both. Fields defined as unflooded, therefore, were not necessarily dry and sometimes held standing water due to heavy rain or river flooding. The two years of the study were characterized by very different weather patterns: 1993/94 was much drier than 1994/95. For example, in the center of the study area at U.S. National Weather Service station 041948 in Colusa, California, precipitation was 22.7 cm and 74.9 cm for November - March of 1993/94 and 1994/95, respectively (NCDC 1997). During the second winter, there was deeper flooding (Fig. 3) and more unflooded fields with standing water.

Flooded fields were chosen such that a variety of straw management methods were represented within the sample. Six management methods were sampled during the study.

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Copies are available on request.

(Note, this figure corresponds to Fig. 1 in Elphick & Oring 1988, *J. Appl. Ecol.* 35:97)

Figure 2. Study area, showing Sacramento National Wildlife Refuge (NWR) Complex and Gray Lodge Waterfowl Management Area (WMA). Study sites are marked with asterisks. Geographic blocks of sites are enclosed within ellipses with numbers of flooded and unflooded fields given after block names. Inset shows location of study area in California.

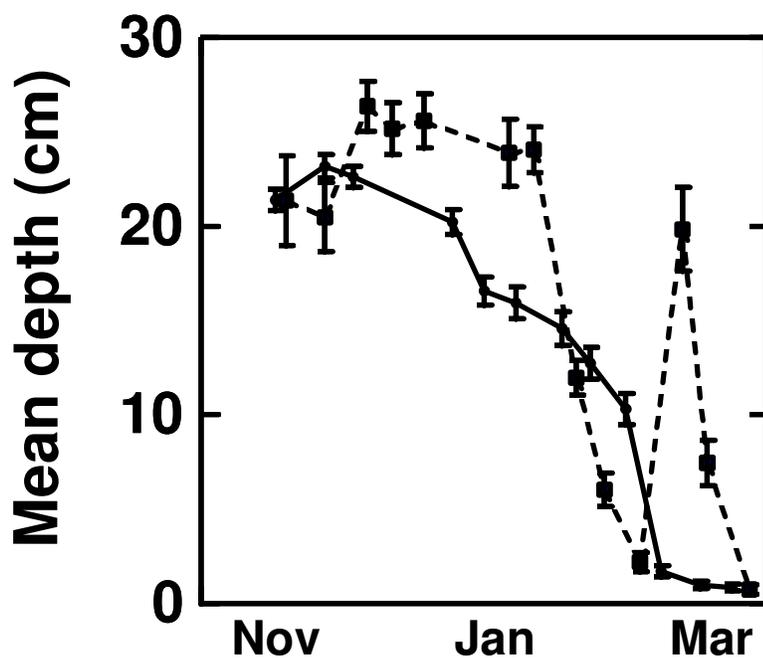


Figure 3. Mean (SE) water depth in flooded rice fields. Solid line = 1993/94, dashed line = 1994/95.

Fields either were (1) flooded without straw management; (2) rolled to flatten the straw and stubble and then flooded; (3) rolled after flooding to increase the extent that straw stuck in the mud; (4) flooded after chopping the straw to increase its surface area; (5) disked or chiseled to both cut up the straw and partially bury it, and then flooded; or (6) flooded after removing the straw either by burning or baling. The first treatment acted as a control for the need to manipulate straw and the last controlled for the presence of straw on the fields.

Logistical and land-access constraints prevented complete randomization in selecting fields and assigning treatments. Consequently, I selected fields such that the various management treatments were spatially interspersed, to reduce the likelihood that unknown factors confounded my experimental design. In addition, I ensured that flooded and unflooded fields were represented in the three geographic areas in similar proportions and that straw treatments occurred in as many of the three areas as possible.

BIRD CENSUSES

We censused fields on foot, counting and identifying all members of the orders Podicipediformes, Ciconiiformes, Anseriformes, Gruiformes, and Charadriiformes (Table 1) seen within the field boundary. Given the open nature of the habitat, these counts were likely to assess abundance accurately for most species. Cryptic species, for which this was not true (e.g. common snipe *Gallinago gallinago*), were not included in the study. Birds disturbed from a field were included in our counts, but birds flying overhead were not. I combined data for snow *Chen caerulescens* and Ross's geese *C. rossii* as accurate species counts were not always possible for large flocks. Hereafter, these species are referred to as "white" geese. Most large flocks of white geese contained a mixture of the two species and it is likely that habitat selection by the two species is similar; this assumption, however, was not tested.

We censused fields at approximately 10-day intervals, except during the hunting season when the spacing between surveys occasionally was altered to accommodate hunting on study fields. The order in which fields were visited was determined arbitrarily and varied among census periods to reduce the likelihood that systematic biases influenced the data (e.g. due to regular movements by the birds, or due to our presence).

In general, we were able to avoid disturbing birds during censuses. Some species (primarily waterfowl), however, occasionally were flushed. Usually we were able to obtain complete counts before the birds flew and often were able to see where they went, thus enabling us to ensure we were not counting birds more than once. In situations where we were uncertain whether a field's count was influenced by our activities I omitted that count from analyses (this happened on seven occasions, each time involving a single field, and affected < 0.1% of observations).

Table 1. Species of waterbirds recorded during surveys of California rice fields 1993-95 (after American Ornithologists' Union 1983, 1995). Four letter acronyms follow U.S. Bird Banding Laboratory. Species that occurred with sufficient frequency to permit statistical analyses are marked in **bold**.

Species	Species
Pied-billed grebe <i>Podilymbus podiceps</i> (PBGR)	Bufflehead <i>Bucephala albeola</i> (BUFF)
American bittern <i>Botaurus lentiginosus</i> (AMBI)	Common merganser <i>Mergus merganser</i> (COME)
Great blue heron <i>Ardea herodias</i> (GBHE)	Ruddy duck <i>Oxyura jamaicensis</i> (RUDU)
Great egret <i>Ardea albus</i> (GREG)	Sora <i>Porzana carolina</i> (SORA)
Snowy egret <i>Egretta thula</i> (SNEG)	Common moorhen <i>Gallinula chloropus</i> (COMO)
Black-crowned night-heron <i>Nycticorax nycticorax</i> (BCNH)	American coot <i>Fulica americana</i> (AMCO)
White-faced ibis <i>Plegadis chihi</i> (WFIB)	Sandhill crane <i>Grus canadensis</i> (SACR)
Tundra swan <i>Cygnus columbianus</i> (WHSW)	Black-bellied plover <i>Pluvialis squatarola</i> (BBPL)
Greater white-fronted goose <i>Anser albifrons</i> (GWFG)	Killdeer <i>Charadrius vociferus</i> (KILL)
“white” goose <i>Chen caerulescens</i> & <i>C. rossii</i> (WHGO)	Black-necked stilt <i>Himantopus mexicanus</i> (BNST)
Canada goose <i>Branta canadensis</i> (CAGO)	American avocet <i>Recurvirostra americana</i> (AMAV)
Wood duck <i>Aix sponsa</i> (WODU)	Greater yellowlegs <i>Tringa melanoleuca</i> (GRYE)
Green-winged teal <i>Anas crecca</i> (AGWT)	Lesser yellowlegs <i>Tringa flavipes</i> (LEYE)
Mallard <i>Anas platyrhynchos</i> (MALL)	Long-billed curlew <i>Numenius americanus</i> (LBCU)
Northern pintail <i>Anas acuta</i> (NOPI)	Western sandpiper <i>Calidris mauri</i> (WESA)
Cinnamon teal <i>Anas cyanoptera</i> (CITE)	Least sandpiper <i>Calidris minutilla</i> (LESA)
Northern shoveler <i>Anas clypeata</i> (NSHO)	Dunlin <i>Calidris alpina</i> (DUNL)
Gadwall <i>Anas strepera</i> (GADW)	Ruff <i>Philomachus pugnax</i> (RUFF)
Eurasian wigeon <i>Anas penelope</i> (EUWI)	Long-billed dowitcher <i>Limnodromus scolopaceus</i> (LBDO)
American wigeon <i>Anas americana</i> (AMWI)	Common snipe <i>Gallinago gallinago</i> (COSN)
Canvasback <i>Aythya valisineria</i> (CANV)	Ring-billed gull <i>Larus delawarensis</i> (RBGU)
Redhead <i>Aythya americana</i> (REDH)	California gull <i>Larus californicus</i> (CAGU)
Ring-necked duck <i>Aythya collaris</i> (RNDU)	Herring gull <i>Larus argentatus</i> (HERG)

COLLECTION OF WATER DEPTH DATA

In California, large rice fields typically are subdivided by narrow earthen levees to provide greater control over water depth; these subdivisions are called “checks”. In my analysis of water depth, I considered each subdivision to be a separate plot because water depth within plots varied by only a few centimeters, while depths of each plot in a field differed considerably. Plot size varied from 0.51 to 19.14 ha (mean area \pm SE: 6.85 ± 0.33 ha, $n = 116$) in 1993/94 and from 0.86 to 19.14 ha (6.55 ± 0.46 ha, $n = 51$) in 1994/95. Depth stakes were placed in each plot and the water depth was read on each census date. These depths were calibrated by taking additional depth measurements at points throughout the plot, and comparing the mean depth to that at the stake. I determined the positions of points by selecting two numbers from a random number table. These determined the number of paces to be made parallel to each edge of the plot. The range of numbers that could be selected was varied depending on the size of the plot, to ensure that any point could be chosen. In 1993/94, twenty-five measurements were made in each plot. Examination of these data indicated that estimates of mean depth could be accurately estimated with fewer points, so in 1994/95 only 15 measurements were made in each plot. I assumed that the difference between the mean depth for the plot and the depth at the stake was constant throughout the winter. During bird censuses, we recorded the number of each species seen in each plot separately, allowing me to subdivide field counts by plot.

DATA ANALYSIS

Prior to analysis, census data were converted to densities to enable comparison among areas of different size. Field areas were either obtained from farmers or calculated from 1:24,000 topographic maps. Tests were conducted on all species that were seen frequently enough to detect significant differences among treatments (Table 1). I used a significance level of $\alpha = 0.10$, set *a priori*. I considered it important to recognize even weak relationships (here defined as $0.05 < P < 0.10$) because logistic constraints limited sample sizes. This problem was especially troublesome considering the high level of variation in abundance typical of flocking species such as those considered. The combination of higher variance and limited sample sizes increased the risk of mistakenly concluding that no treatment effect existed (i.e., making a Type II error). Given the potential management implications of such a mistake (e.g., not implementing management that may be beneficial), I felt it was prudent to raise the α -level, despite the increased risk of concluding a treatment effect where none existed (i.e., making a Type I error).

To allow interpretation of non-significant tests (i.e. $P > 0.1$) I determined power using tables in Cohen (1988). For non-parametric tests, I used guidelines on power-efficiency to adjust sample sizes to their parametric equivalents and obtain conservative power estimates (Siegel & Castellan 1988). In each case, I viewed power greater than 0.8 as evidence for no difference among treatments and determined power for small, medium and large effect sizes following Cohen (1988). Note that quantitative values for these

effect sizes vary among tests. For clarity, I have given these values for each power calculation (see Cohen 1988, for qualitative descriptions of these effect sizes).

Before testing my treatment hypotheses, I determined whether the abundance of each bird species differed between the two years of the study. I used a Wilcoxon signed rank test (Siegal & Castellan 1988) to compare mean densities of each species in the 20 fields censused in both winters. I analyzed each winter's data separately for all species occurring at different densities in the two winters. For the remaining species, I combined data for both winters; in all cases, estimated power was high ($1-\beta > 0.78$) when using a large effect size ($d = 0.8$; Cohen 1988), supporting the conclusion of no difference between years. Fields censused in both winters generated two non-independent data points for each species. To avoid pseudoreplication (Hurlbert 1984) I randomly selected data for one season to use in my analyses. Tests for non-normal distributions and heterogeneous variances indicated a need to use nonparametric tests to compare management treatments. For these tests, I used the mean density for each field. Dunn's multiple comparison test for nonparametric data of unequal sample sizes was used to make *post hoc* comparisons following Kruskal-Wallis tests (Zar 1984).

Differences in species density among the three geographic areas (blocks) studied were a concern because not all straw management treatments were represented in every block; hence, geographic differences could confound these treatments. If treatment differences could be explained simply by correlations between geographic patterns of bird abundance and the distribution of treatments, I viewed the result as confounded. When this occurred, I reanalyzed data from each block separately and only drew conclusions about straw treatment differences based on the results of these supplemental tests.

In all depth analyses, the experimental unit was a single plot on a single date. Consequently, each plot was represented in the data set several times, causing concern that data points may not have been independent. Pooling data for each site, as was done in tests of the flooding and straw manipulation hypotheses, was not possible because water depths fluctuated over time. I believe that non-independence among data points was probably minimal because plots were small relative to the area over which most waterbirds move on a weekly basis (C.S. Elphick, pers. obs.). This difference in scale reduced the degree to which the birds seen in a plot one day were likely to be the same as those seen 10 days later. To determine whether multiple data points for each site were statistically independent, I randomly selected 20 of the plots each species used (10 from each winter) and looked for evidence of autocorrelation. Where fewer than 20 plots were used by a species, I used all plots.

I examined relationships between water depth and species use in three ways. Two methods tested whether "preferred" depths taken from the literature (Fredrickson 1991; Helmers 1992; Table 6) received greater use. For the 14 species considered in the literature, I classified observations according to whether the observed depth lay within the range thought to be favored by the species. These data were first analyzed using log-likelihood ratio tests to determine whether birds were more likely to be present in plots of the "preferred" depths than in other plots (Zar 1984). Second, I used one-tailed separate-variance *t*-tests to determine whether the density of a species, when it was present, was higher at "preferred" depths. These two tests were necessary because the data set

includes many observations when no individuals of a species were seen. These zeros could arise because birds avoided certain plots, or they could simply reflect random site-selection (i.e. birds did not use a suitable plot because they found another one first). This latter explanation is especially likely for species with highly clumped distributions characteristic of many waterbirds. The first test determined whether zeros simply reflect a background level of empty sites (which predicts no difference) or whether active avoidance occurred (which predicts fewer zeros at preferred depths). The second test excluded observations where birds were not present, and determined whether densities were higher at preferred depths for the remaining observations.

Finally, I used regression to model the relationship between water depth and bird density. I tested linear, negative quadratic, and logarithmic models, both with and without date as a covariate, for each species. I considered these models to be descriptive of the likely relationships between depth and bird use.

RESULTS

DIFFERENCES BETWEEN YEARS

There were no significant differences in the densities of most (21/31) species in the two years. For all tests, $1-\beta > 0.78$ (> 0.8 in most cases) when assuming a large effect size ($d = 0.8$). Significant differences were detected for 10 species (Table 2). Five occurred at higher densities in the drier winter of 1993/94 and five at higher densities in the wetter winter of 1994/95. In addition, densities of long-billed curlews *Numenius americanus* using flooded fields were higher in 1993/94 than in 1994/95 ($z = -2.040$; $P = 0.041$).

EFFECTS OF FLOODING

I found differences in density ranks, between flooded and unflooded fields, for 26 species (Table 3). Of these, only great blue herons *Ardea herodias* and sandhill cranes *Grus canadensis* were more common in unflooded fields. Results for species which occurred at different densities in the two winters were generally the same for both winters. Two species, killdeer *Charadrius vociferus* and long-billed curlew, however, were found only to differ in their habitat use in 1993/94, the winter in which they occurred at higher densities.

Table 2. Differences in density between 1993/94 and 1994/95. Wilcoxon's signed rank tests compared mean densities of birds in 20 fields sampled in both winters; only significant differences are given.

Species	Wilcoxon z	P	Winter of higher density
Pied-billed grebe	2.845	0.004	94/95
Green-winged teal	2.542	0.011	94/95
Mallard	-2.277	0.023	93/94
Ring-necked duck	1.826	0.068	94/95
American coot	2.249	0.025	94/95
Killdeer	-3.061	0.002	93/94
American avocet	1.992	0.046	94/95
Greater yellowlegs	-3.516	< 0.001	93/94
Least sandpiper	-2.429	0.015	93/94
Dunlin	-2.134	0.033	93/94

Table 3. Densities of birds in flooded and unflooded rice fields. Test statistics are for Mann-Whitney U-tests. Separate densities and statistical tests are given for species occurring at significantly different densities in the two winters; otherwise data for both winters are combined. Sample sizes for flooded and unflooded fields, respectively, were: 37 and 16 (1993/94), 25 and 15 (1994/95), 47 and 26 (both years combined). Species with significant differences ($P < 0.10$) are marked in **bold**.

Species	Winter	Mean (\pm SE) density (birds km ⁻²)*		U	P
		Flooded	Unflooded		
Pied-billed grebe	1993/94	0.2 (0.1)	0	352.0	0.065
	1994/95	1.5 (0.7)	0.4 (0.3)	252.0	0.038
American bittern	Both	1.2 (0.4)	0.4 (0.2)	767.0	0.049
Great blue heron	Both	0.5 (0.1)	0.9 (0.2)	810.0	0.017
Great egret	Both	2.1 (0.3)	2.0 (0.4)	613.0	0.982
Snowy egret	Both	1.5 (0.5)	0.03 (0.03)	850.5	0.001
White-faced ibis	Both	49.5 (25.1)	0	728.0	0.018
Greater white-fronted goose	Both	32.4 (22.6)	118.6 (53.3)	708.0	0.175
“white” goose	Both	2.2 (1.9)	187.3 (102.6)	643.5	0.658
Canada goose	Both	2.4 (1.7)	1.6 (0.9)	627.0	0.758
Green-winged teal	1993/94	151.8 (58.2)	0	520.0	<0.001
	1994/95	178.2 (79.3)	5.8 (3.1)	258.5	0.043
Mallard	1993/94	110.0 (20.7)	9.1 (5.0)	526.0	<0.001
	1994/95	97.5 (19.4)	22.1 (6.3)	302.0	0.001
Northern pintail	Both	212.9 (53.4)	38.6 (21.2)	1030.0	<0.001
Cinnamon teal	Both	2.6 (1.0)	0.5 (0.3)	781.0	0.011
Northern shoveler	Both	154.5 (27.7)	5.7 (3.0)	1109.0	<0.001
Gadwall	Both	11.9 (4.5)	0.6 (0.4)	916.0	<0.001
Eurasian wigeon	Both	0.1 (0.1)	0.05 (0.04)	654.0	0.386
American wigeon	Both	48.8 (16.4)	8.9 (4.8)	899.0	0.001
Ring-necked duck	1994/95	1.1 (0.7)	0.1 (0.1)	235.0	0.070
American coot	1993/94	445.7 (65.6)	0	576.0	<0.001
	1994/95	651.8 (148.6)	293.7 (225.9)	313.0	<0.001
Sandhill crane	Both	0	0.6 (0.3)	681.5	0.018
Black-bellied plover	Both	1.2 (0.8)	0	715.0	0.027
Killdeer	1993/94	10.1 (2.5)	2.9 (1.2)	434.0	0.007
	1994/95	7.0 (3.0)	1.8 (0.6)	219.0	0.376
Black-necked stilt	Both	3.3 (1.4)	0	728.0	0.018
American avocet	1994/95	6.1 (3.3)	0	255.0	0.010
Greater yellowlegs	1993/94	21.1 (3.9)	0.1 (0.1)	565.5	<0.001
	1994/95	9.3 (5.3)	0.2 (0.2)	332	<0.001
Long-billed curlew	1993/94	11.3 (2.4)	12.1 (6.6)	395.0	0.051
	1994/95	3.3 (1.2)	7.5 (4.5)	189.5	0.950
Least sandpiper	1993/94	6.2 (3.0)	0	424.0	0.002
	1994/95	16.5 (10.7)	0	247.5	0.016
Dunlin	1993/94	80.8 (23.2)	0	472.0	<0.001
	1994/95	93.7 (61.4)	0	270.0	0.003
Long-billed dowitcher	Both	87.3 (39.0)	0	897.0	<0.001
Ring-billed gull	Both	11.3 (2.9)	2.8 (1.5)	903.0	0.001
Herring gull	Both	0.2 (0.1)	0.02 (0.01)	762.0	0.019

* Directions of density and ranking differences concord in all cases except for long-billed curlew (1993/94) where the rank test indicates that birds used flooded fields significantly more than unflooded, contrary to expectation based on examination of densities.

Only great egrets *Ardea albus*, Eurasian wigeon *Anas penelope*, and the geese taxa did not differ significantly between the two treatments. Estimates of statistical power for these tests indicated a high probability ($1-\beta = 0.76-0.93$) of detecting a large treatment effect ($d = 0.8$) if one existed, but much smaller chances of detecting medium ($d = 0.5$; $1-\beta = 0.43-0.63$) or small ($d = 0.2$; $1-\beta = 0.16-0.20$) effects.

EFFECTS OF STRAW MANIPULATION

Differences in the density ranks of birds using flooded fields that had received different straw management treatments were found for 14 species (Table 4). When all tests were considered, a total of 15 out of 39 tests were significant. Given this many tests, four significant results would be expected by chance, suggesting that some, but not all, of the differences may be spurious. Differences among treatments could be attributed to the straw management treatment for only eight of the 14 species. In five cases there was no effect of geographic block, in one there was a block effect but it could not account for the treatment effect, and in two the block effect was potentially confounding but the treatment effects remained after analyses were conducted for each block separately. In the remaining six species, geographic block and straw management treatment were confounded. Four of the species that occurred at different densities in the two winters (mallard *Anas platyrhynchos*, killdeer, least sandpiper *Calidris minutilla*, and dunlin *C. alpina*), showed different patterns in the two years. In all cases, there was a significant difference in 1994/95 only.

Dunn's multiple-comparison test was used to examine pair-wise differences in bird use for all significant differences among treatments (Table 5). Three species (American bittern *Botaurus lentiginosus*, white-faced ibis *Plegadis chihi*, American avocet *Recurvirostra americana*) were most abundant in fields that had been just flooded. These species appeared to avoid fields that had been rolled prior to flooding and, depending on the species, certain other treatments. The four small shorebirds (killdeer, least sandpiper, dunlin, long-billed dowitcher *Limnodromus scolopaceus*) occurred at highest densities in fields where straw had been incorporated into the soil before flooding. These species tended to avoid fields where straw had been chopped or rolled prior to flooding.

I found no evidence of differences for the remaining 16 species, although the power of these tests was low ($1-\beta = 0.34-0.59$, assuming a large effect size: $d = 0.4$). These results, therefore, cannot be taken as evidence that these species were not affected by straw management treatments.

EFFECTS OF WATER DEPTH

I found no evidence that water depths within each plot were temporally autocorrelated. Significant autocorrelation was found in only 3 of 501 tests (Fig. 4). This is far fewer than would be expected by chance (Chatfield 1980).

Most species used a wide range of water depths (Fig. 5), although densities varied considerably among depths. Median water depths for plots in which a species occurred were deepest for diving species (24-33 cm) and most shallow for shorebirds (3-13 cm).

Table 4. Effects of straw management treatments and geographic block on waterbird densities. Test statistics are for Kruskal-Wallis tests. Separate tests were conducted for species occurring at significantly different densities in the two winters; otherwise data for both winters are combined. Treatment sample sizes given in Table 5; block sample sizes given in Fig. 2. Significant differences are marked in **bold**.

Species	Winter	Geographic block effect		Effect of straw management	
		H	P	H	P
Treatment effect					
American bittern	Both	1.10	0.576	15.55	0.008
White-faced ibis*	Both	7.28	0.026	17.22	0.004
Mallard	94/95	0.40	0.820	11.21	0.047
Killdeer	94/95	2.72	0.256	11.44	0.043
American avocet*	94/95	10.10	0.006	11.08	0.050
Least sandpiper	94/95	2.49	0.288	15.58	0.008
Dunlin	94/95	1.44	0.487	13.65	0.018
Long-billed dowitcher	Both	4.68	0.096	11.42	0.044
No treatment effect					
Pied-billed grebe	94/95	0.27	0.875	1.11	0.775
Great egret	Both	1.26	0.533	7.24	0.203
Snowy egret	Both	1.03	0.599	8.03	0.155
Greater white-fronted goose	Both	3.87	0.144	8.14	0.149
“white” goose	Both	2.26	0.323	4.83	0.437
Green-winged teal	93/94	0.91	0.636	2.29	0.514
	94/95	0.05	0.048	8.68	0.123
Mallard	93/94	11.56	0.003	6.04	0.110
Northern pintail	Both	1.81	0.404	7.90	0.162
Cinnamon teal	Both	0.84	0.657	3.77	0.583
Gadwall	Both	3.19	0.203	9.17	0.103
Eurasian wigeon	Both	6.51	0.039	2.95	0.708
American wigeon	Both	9.32	0.009	6.50	0.261
Ring-necked duck	94/95	5.00	0.082	9.07	0.107
American coot	93/94	2.34	0.310	5.20	0.158
	94/95	3.04	0.217	8.48	0.132
Black-bellied plover	Both	1.86	0.395	6.12	0.295
Killdeer	93/94	1.33	0.514	1.37	0.714
Black-necked stilt	Both	4.36	0.113	3.83	0.574
Greater yellowlegs	94/95	0.85	0.655	6.36	0.273
Least sandpiper	93/94	4.86	0.088	4.04	0.257
Dunlin	93/94	0.13	0.935	1.71	0.635
Ring-billed gull	Both	2.17	0.339	6.56	0.256
Herring gull	Both	3.81	0.149	8.60	0.126
Treatment effect confounded by block effect					
Pied-billed grebe	93/94	8.769	0.012	11.96	0.035
Great blue heron	Both	18.71	<0.001	13.18	0.022
Canada goose	Both	6.91	0.032	12.08	0.034
Northern shoveler	Both	10.10	0.006	10.86	0.054
Greater yellowlegs	93/94	8.08	0.018	8.48	0.037
Long-billed curlew	93/94	7.44	0.024	14.35	0.002
	94/95	4.64	0.098	9.89	0.078

*Treatment effect also found within geographic blocks.

Table 5. (a) Results of *post-hoc* comparisons for significant tests of straw management treatments (Table 4). Treatments with different letters were significantly different using Dunn's multiple comparison test. Treatments denoted *a* had higher mean ranks than those denoted *b*. A dash indicates that a treatment was not included in the test that confirmed a treatment effect. Sample sizes are for 1993/94, 1994/95, and both years combined, respectively. (b) Water depths found in each treatment. Treatment means differed significantly ($F_{5,2045} = 11.852, P < 0.001$). Treatments with different letters were significantly different using Tukey's multiple comparison test (in all cases $P < 0.005$ after sequential Bonferroni adjustment). See Methods for detailed treatment descriptions.

		Treatment					
	Winter	Flood only	Roll & Flood	Flood & Roll	Chop & Flood	Incorporate & Flood	Remove & Flood
<u>(a) Species differences</u>							
<i>n</i>		8,7,10	21,4,19	4,4,6	0,4,4	0,3,3	3,3,5
American bittern	Both	<i>a</i>	<i>b</i>	<i>b</i>	<i>b</i>	<i>a,b</i>	<i>a,b</i>
White-faced ibis	Both	<i>a</i>	<i>b</i>	-	-	<i>a,b</i>	<i>b</i>
Mallard	94/95	<i>a</i>	<i>a</i>	<i>a</i>	<i>a</i>	<i>a</i>	<i>a</i>
Killdeer	94/95	<i>b</i>	<i>a,b</i>	<i>a,b</i>	<i>b</i>	<i>a</i>	<i>a,b</i>
American avocet	94/95	<i>a</i>	<i>b</i>	-	-	<i>a,b</i>	-
Least sandpiper	94/95	<i>a,b</i>	<i>b</i>	<i>a,b</i>	<i>a,b</i>	<i>a</i>	<i>a,b</i>
Dunlin	94/95	<i>a,b</i>	<i>b</i>	<i>a,b</i>	<i>b</i>	<i>a</i>	<i>a,b</i>
Long-billed dowitcher	Both	<i>b</i>	<i>b</i>	<i>a,b</i>	<i>b</i>	<i>a</i>	<i>b</i>
<u>(b) Water depths (cm)</u>							
Mean ± SE		16.3 ± 0.7	16.0 ± 0.4	12.6 ± 0.4	16.9 ± 1.1	10.4 ± 1.0	13.9 ± 1.4
<i>n</i>		276	639	683	199	141	113
Pairwise differences		<i>a</i>	<i>a</i>	<i>b</i>	<i>a</i>	<i>b</i>	<i>a,b</i>

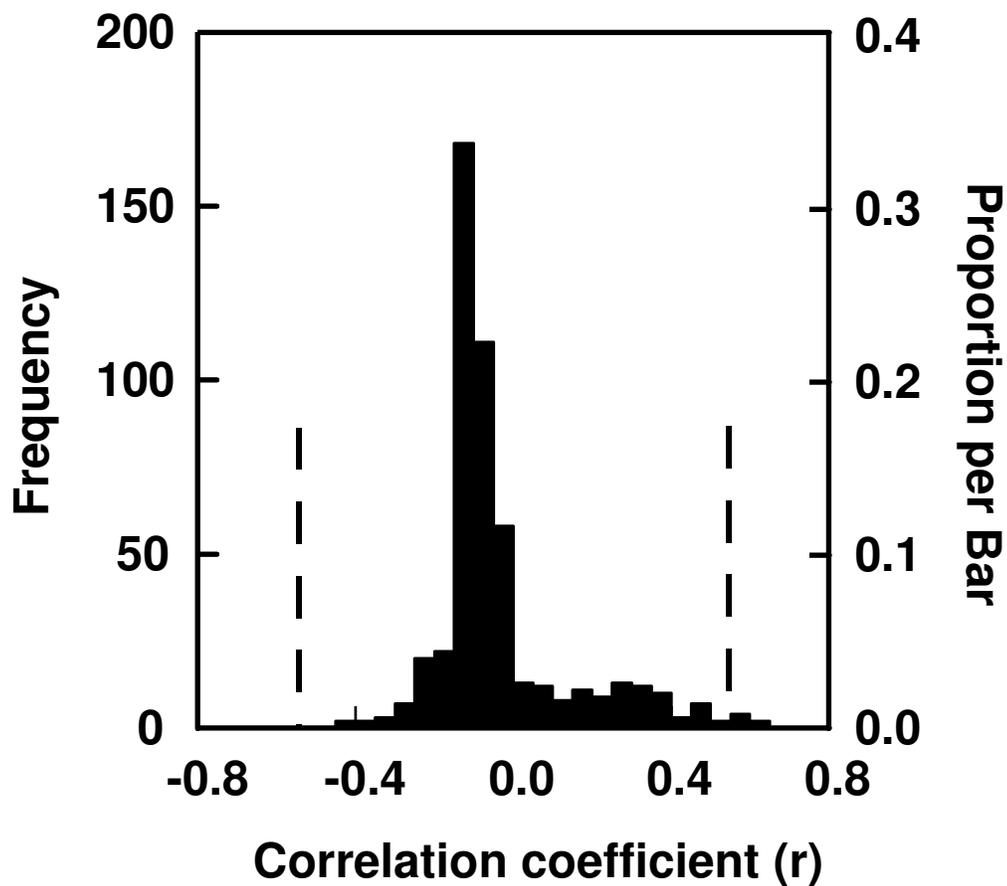


Figure 4. Results of autocorrelation tests to determine whether repeated samples of bird use, in plots used for water depth analyses, were correlated. Figure shows correlation coefficients for 501 tests (all species combined) grouped into 0.05 increments. Only the three coefficients that lie outside the dashed lines were statistically significant.

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(Note, this figure is identical to Fig. 3 in Elphick & Oring 1988, J. Appl. Ecol. 35:104)

Figure 5. Box plots representing the range of water depths used by each species. Boxes represent the interquartile range of depths at which each species was recorded, and are bisected by the median values; whiskers encompass the majority of points; outliers are identified by stars or circles (see SYSTAT 1996 for details). Sample sizes for each species are given above box plots. Four-letter species acronyms are defined in Table 1. Boxes at extreme left of each row give distribution of depths available to birds, for comparison to depths used ($n = 2054$).

Intermediate between these groups were geese (18-26 cm), dabbling ducks (14-22 cm), and herons and ibis (9-20 cm).

My first set of tests determined whether each species was more likely to occur at depths suggested as favored by that species. For 11 of the 14 species, G -tests indicated that occurrence rates within these depth ranges were significantly higher than expected by chance, although for one (least sandpiper) this difference was weak (Table 6). When I looked only at those plots where birds occurred, however, I found that only three species occurred at significantly greater densities at “preferred” depths. At least one significant result would have been expected by chance given the number of tests conducted. Greater yellowlegs *Tringa melanoleuca* was the only species for which the difference was highly significant.

The remaining species (American bittern, great blue heron, and black-necked stilt *Himantopus mexicanus*) were no more likely to occur in plots of “preferred” depths, than in other plots. Nor were there differences in the densities of birds when occupied plots in the two categories were compared (Table 6).

Regression models proved to be poor descriptors of the relationships between depth and bird density. In none of the analyses was more than 10% of the variance explained, probably because of the large number of instances when a species was absent from a plot.

Table 6. The dependence of bird use on water depth. “Preferred” ranges are those hypothesized to be preferred by particular species. Significant *G*-tests show that occurrence rates were higher for depths within these ranges than for other depths. Significant *t*-tests show that when a species was present, densities were higher for these depths. df = degrees of freedom (noninteger values arise from adjustments for unequal variance); *n* = number of observations. Significant *P*-values are marked in **bold**.

Species	“Preferred” range (cm)	<i>G</i> (df, <i>n</i>)	<i>P</i>	<i>t</i> (df)	1-tailed <i>P</i>
American bittern	0-7 ¹	2.20 (1, 2054)	0.138	-0.22 (7.8)	0.415
Great blue heron	10-17 ¹	0.20 (1, 2054)	0.652	2.02 (39.0)	0.975
Green-winged teal	9-20 ¹	45.91 (1, 2038)	<0.001	-0.59 (175.3)	0.280
Mallard	7-14 ¹	35.60 (1, 2038)	<0.001	0.44 (323.7)	0.671
Northern pintail	14-21 ¹	47.72 (1, 2035)	<0.001	-0.93 (213.2)	0.178
Northern shoveler	17-23 ¹	8.57 (1, 2038)	0.003	0.09 (138.2)	0.538
American coot	27-33 ¹	69.38 (1, 2053)	<0.001	-1.80 (120.9)	0.037
Killdeer	0-3 ²	39.69 (1, 2054)	<0.001	0.88 (68.7)	0.810
Black-necked stilt	8-21 ²	2.55 (1, 2054)	0.110	-0.34 (21.0)	0.370
Greater yellowlegs	1-7 ¹	49.90 (1, 2054)	<0.001	-0.99 (116.4)	0.163
	2-12 ²	92.71 (1, 2054)	<0.001	-2.45 (146.4)	0.008
Long-billed curlew	0-16 ²	63.46 (1, 2054)	<0.001	-0.17 (50.7)	0.433
Least sandpiper	0-5 ²	3.18 (1, 2054)	0.075	0.475 (29.2)	0.681
Dunlin	0-10 ²	44.79 (1, 2054)	<0.001	-0.77 (96.9)	0.222
Long-billed dowitcher	2-8 ¹	12.32 (1, 2054)	<0.001	-1.45 (30.0)	0.079
	0-10 ²	24.01 (1, 2054)	<0.001	-1.05 (68.3)	0.149

¹ Depth range taken from Fredrickson (1991).

² Depth range taken from Helmers (1992).

DISCUSSION

EFFECTS OF FLOODING

California rice fields were used by a wide variety of waterbird species during the winter (Table 1). Thirty-one species occurred with sufficient frequency to detect treatment effects. Both flooded and unflooded fields were used by most of these species (Table 3). In general, densities were greater in flooded fields, and several species (mostly shorebirds) never used unflooded fields. Although not intentionally inundated, many unflooded fields did have standing water during some surveys, especially in 1994/95. These fields drained rapidly after heavy rainfall or flood conditions ended and were rarely flooded for long periods. It is, thus, unsurprising that these fields received less waterbird use than intentionally flooded fields. Furthermore, the short periods during which unflooded fields were inundated may have been insufficient to allow invertebrate numbers to increase to levels found in flooded fields.

Several species were less common in flooded fields. Most notable were sandhill cranes and great blue herons, which occurred at significantly higher densities in unflooded fields. I also found no evidence that goose densities differed between flooded and unflooded fields (Table 3). Incidental observations suggest that when geese occurred in flooded fields they tended to be roosting, rather than feeding. This pattern could arise because geese are unable to find spilled grain in flooded fields because it is underwater. Flooded and unflooded habitats, therefore, may be important for geese, though used for different activities.

EFFECTS OF STRAW MANIPULATION

For most species, I found no evidence that the method of straw management used on flooded fields had an effect on density. Given the large number of tests conducted, it is important to examine the likelihood that the differences I did find are spurious. Using an α -level of 0.10, four significant differences would be expected from the 39 tests conducted by chance alone. In fact, I found 15 significant differences, of which eight could be attributed unambiguously to the management treatment. Consequently, I conclude that it was unlikely that all significant results were spurious. Individual test results, however, should be viewed with caution and more detailed studies of the species exhibiting treatment differences are warranted.

Most species for which there was an unambiguous difference fell into one of two groups. The species within each group shared several characteristics supporting the notion that the differences found are real. If the differences were all spurious, coherent grouping of species would be less likely. For this reason, I make no attempt to interpret results for other species (e.g., mallard). Three species were most abundant in fields that had received no treatment other than flooding, and four were most abundant in fields where straw had been incorporated into the soil prior to flooding (Table 5). All of these species feed primarily on invertebrate prey (Ehrlich, Dobkin & Wheye 1988) and were expected *a priori* to prefer fields where straw was heavily manipulated. I also found no evidence that granivorous species avoid fields where straw management was likely to have made grain less available. There are several possible explanations for these results. First, they may indicate that food abundance does not change as expected as a function of straw manipulations. Support for this idea comes from surveys that found higher invertebrate densities in fields that had been just flooded or had straw removed than in fields that were rolled after flooding (D. Loughman & D. Batzer, unpubl. data). An alternative explanation is that, for most species, bird density does not increase with food abundance. This could happen if food was not limiting, or if other factors modified the bird's distributions (e.g. predation, Lima & Dill 1990; disturbance, Gill, Sutherland & Watkinson 1996). A third possibility is that food abundance follows the predicted pattern, but availability does not. The two groups for which straw treatment effects were detected can be separated into long- and short-legged species, suggesting that water depth may be important. In fact, water depth did differ among straw management treatments with shallowest depths found in fields where straw was incorporated into the soil (Table 5). This finding suggests that water depth, rather than straw treatment, may have caused differences for the four short-legged shorebirds that favored this treatment.

EFFECTS OF WATER DEPTH

I found that water depth influenced whether a species was present at a site, but not how abundant it was. I examined the relationship between water depth and bird use of rice fields in two ways. First, I evaluated depth ranges that have been proposed as preferred by certain species. For most of these species, I found evidence for an increased incidence within the proposed range. When I considered only those plots where birds were present, however, I found that densities generally were not greater for these depths. My second approach did not involve an *a priori* prediction as to which depths were preferred. Instead, I tried to describe the relationship between water depth and species densities by fitting various regression models. In all cases, variance was extremely high and I was unable to find any models with high predictive power. These results suggest that birds assessed the suitability of a plot's water depth in a simple yes/no fashion and that there is not a gradation of suitability. Either a depth was suitable, or it was not.

Previous studies have not only demonstrated relationships between water depth and species occurrence, but have been able to explain far more of the variance in the abundance of certain species (Boshoff, Palmer & Piper 1991a,b,c; Velazquez 1992; Colwell & Dodd 1995; Nagarajan & Thiyagesan 1996). Part of this difference may be statistical in nature, arising from differences in the ranges of depths, bird densities, or both, found in the different studies and the extremely high variation in densities found in my study. There may, however, be a qualitative difference in the way birds respond to planned water level drawdowns (e.g. Velazquez 1992) and to uncontrolled depth fluctuations (e.g. this study). The former will gradually concentrate prey, allowing bird densities to build up over time, whereas the latter may not.

Given that birds feeding in rice fields appear to select water depths in a yes/no fashion, it makes sense to identify depth ranges, rather than optimal depths, when designing guidelines for water management for individual species. Support for the hypothesis that a particular depth range is used disproportionately by a species need not mean that bird use will be optimized within that range. Fredrickson (1991) and Helmers (1992) identified different (but overlapping) depth ranges for greater yellowlegs and long-billed dowitchers. For these species, I found increased occurrence rates for both hypothesized ranges. In each case, however, significantly greater densities were found for only one hypothesis (Table 6). For each species, therefore, there may be several depth ranges that would have produced significant results given my analysis. Some of these other ranges could receive greater bird use according to both occurrence and density criteria. A better way to determine which depths receive most use is to examine the distribution of depths a species uses directly (e.g. Fig. 5). Comparing these data across species allows one to evaluate the effects that different flooding regimes will have on the entire community. Examination of the interquartile distances for all species suggests that depths of 15-20 cm will lead to frequent use by the greatest number of species (Fig. 5). In Chapter 2, I show that species richness is highest at depths of 10-15 cm. Currently, most fields are flooded deeper than this during early winter (Fig. 3). Reducing water depths during this period, therefore, can be expected to increase the number of species using each flooded field.

IMPLICATIONS OF THIS STUDY

In general, it seems that flooding rice fields will lead to greater use by most waterbirds. This is not true, however, for all species considered here (Table 3). I also have evidence that increased flooding reduces use of rice fields by certain raptor and passerine species (C.S. Elphick, unpubl. data). Many of the species found at lower densities in flooded fields, however, are among the commonest birds in the Sacramento Valley. In contrast, those that occur at higher densities in flooded fields are species that are likely to have undergone the greatest declines due to wetland destruction. Furthermore, limitations on the availability of water make it unlikely that the extent of winter flooding will increase to the point where all rice fields are submerged in winter. It is, therefore, likely that there will always be a mixture of flooded and unflooded fields. Whether a reduction in unflooded land will have adverse effects on species that use this habitat is unclear and should be examined.

Despite very different weather conditions, most species occurred at similar densities in both years. This result suggests that my general conclusions are robust to a range of rainfall conditions, although testing this hypothesis will require a longer time series. Most of the differences between years can be attributed to differences in water depth (Fig. 3). Species occurring at higher densities in the drier year were predominantly those that prefer shallow conditions, while species more abundant in 1994/95 when there was more flooding tended to be deeper water species (Table 2).

Studies in Europe indicate that rice fields play a vital role in the maintenance of some waterbird populations (Fasola & Barbieri 1978; Fasola, Canova & Saino 1996) and it has been suggested that flooded agriculture can substitute for lost wetland habitat (Fasola & Ruíz 1996, 1997). Evaluating the relative importance of California rice fields is difficult because birds move back and forth between flooded fields and other wetland habitats on a daily basis and because it is not known whether habitat availability currently limits populations. The extent to which waterbirds use flooded fields during winter, however, suggests that rice agriculture also is important in California (Miller 1987; Miller *et al.* 1989; this study). For example, millions of waterfowl winter in the Central Valley and many make daily trips from roost sites in areas protected from hunting to feed in rice fields. Similarly, recent aerial surveys demonstrated that the majority of the wintering shorebirds in the Sacramento Valley occur in rice fields (Point Reyes Bird Observatory, unpubl. data).

Many of the results discussed here may be applicable to other wetland systems. For example, the straw manipulations used by rice farmers could be used by wetland managers doing vegetation control. My results suggest that these methods do not affect bird use and that there would be no advantage to managers using any one in particular. Similarly, my water depth analysis could be used to guide flooding of wetland areas. By studying these issues in an agricultural system, I was able to overcome a number of problems encountered in studies of more natural wetlands. First, rice fields are simpler than most wetland systems. Consequently, many variables which could confound results and increase variability (e.g. vegetation type and structure), were standardized. In addition, I could ensure that management treatments (e.g. water depth) were applied

uniformly across units. The price paid for simplification is a decreased certainty that conclusions will be applicable to more complex situations. Testing the relevance of these results in more natural settings is clearly an important step in assessing the generality of the conclusions.

A second advantage of studying habitat use questions in an agricultural setting is that there are typically many potential sites that can be used. This fact enabled me to obtain fairly large sample sizes, to examine a variety of different treatments, and to select sites such that different treatments were interspersed amongst each other. Consequently, I was able to attain a relatively high level of experimental control, even though I was carrying out a study at a scale where truly controlled experiments were not feasible.

Limited research has been done in rice fields elsewhere in the world (though see references in Fasola & Ruíz 1997). Studies from Europe and the south-eastern United States, however, suggest that shallow flooding of fields in these areas also results in increased use by waterbirds (Remsen *et al.* 1991; Fasola & Ruíz 1996, 1997). Bird communities seem to differ little between these studies and ours. Consequently, the management recommendations listed below may be applicable to other temperate rice-growing regions. If this is the case, improved management of rice paddies for aquatic birds may provide a partial solution to the loss of natural wetland habitats worldwide.

MANAGEMENT RECOMMENDATIONS

1. Increasing the area of winter flooded rice fields is likely to benefit a wide variety of waterbirds, but hurt some others. Most species harmed by flooding fields are of little conservation importance. Possible effects on greater sandhill crane *Grus canadensis tabida*, considered threatened in California, are a concern. How much unflooded rice is necessary to support the crane population is unknown, but is likely to be small relative to the amount of unflooded rice currently available.
2. The method of flooding has little effect on the abundance of most species, and there is no single straw management method that can be recommended for birds in general. Evidence that incorporating straw into the soil (e.g. by disking) leads to increased use by shorebirds was confounded by variation in water depth.
3. In general, water depth affected species occurrence, but not abundance. Reducing depths to a maximum of 20 cm during the entire winter is expected to lead to use by a wider variety of species.

SUMMARY

I investigated the degree to which waterbirds use flooded fields and whether the method of flooding affects their use. Specifically, I tested whether waterbird use (a) was greater in intentionally flooded fields than in unflooded fields, (b) differed among flooded fields receiving different straw manipulations, and (c) varied with water depth.

Intentionally flooded rice fields received significantly greater use by 24 of 31 species studied. Only great blue herons *Ardea herodias* and sandhill cranes *Grus canadensis* were significantly more common in unflooded fields. Goose densities did not

differ between flooded and unflooded fields. Densities of most species did not differ among flooded fields that received different straw manipulations to improve decomposition rates. Species did differ in their use of different water depths. For 14 species I tested whether preferred depths, suggested in the literature, received disproportionately higher use. Most of these species were more likely to be encountered within the suggested depth ranges. Depth, however, was a poor predictor of bird density. Depths of 15-20 cm resulted in frequent use by the greatest number of species.

I conclude that flooding rice fields increased suitable habitat for most, but not all, species studied. Different straw manipulation methods had little effect on most species. Water depth, however, was important in determining species occurrence. During the first half of the winter, water depths were greater than the median depths used by most species. Increasing the area of land flooded and reducing water depths during early winter are expected to benefit waterbirds.

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CHAPTER TWO

EFFECTS OF RICE FIELD MANAGEMENT ON WINTER WATERBIRD COMMUNITIES AND CONSERVATION

One-third of the world's ice-free land area is used for agriculture and 11% is cultivated annually (Urban & Vollrath 1984). Moreover, agricultural habitats often are concentrated in productive and biologically rich areas of the world. To stem the current rapid loss of biological diversity (World Conservation Monitoring Centre 1992), therefore, we need to consider ways in which agricultural land can contribute to the maintenance of plant and animal populations.

The Central Valley of California has undergone great modification over the last two centuries. Prior to extensive human settlement beginning in the mid-1800s, the region contained vast areas of seasonal wetland and riparian forests, and supported a fauna that included grizzly bears *Ursus arctos*, and large herds of tule elk *Cervus elaphus nannodes* and pronghorn *Antilocarpa americana* (Hardwick & Holtgrieve 1996). Today, more than 86% of the wetlands have been drained (Frayer *et al.* 1989), approximately 89% of riparian habitats have been lost (Katibah 1984), most large mammals are extirpated, and the valley has become one of the most productive agricultural regions in the world.

Every year, 140,000 to 180,000 ha of land are planted with rice in California, predominantly in the northern half of the Central Valley (Hill *et al.* 1992). Flooding rice fields offers great potential as surrogate habitat for wetland species and the importance of rice fields to waterbirds has been suggested repeatedly (Wright 1959; McGinn & Glasgow 1963; Fasola & Barbieri 1978; Fasola 1983; Miller 1987; Miller *et al.* 1989; Remsen *et al.* 1991; Pain 1994; Brouder & Hill 1995; Fasola, Canova & Saino 1996; Fasola & Ruíz 1996). The Central Valley is thought to have supported more than 40 million waterfowl historically and, despite substantial declines in waterfowl populations, remains the primary wintering area for 20% of the waterfowl in North America (Heitmeyer, Connelly & Pederson 1989; Banks and Springer 1994; Reid & Heitmeyer 1995). Little is known about other waterbirds, although a minimum of 200,000 to 375,000 shorebirds currently winter in the valley (Shuford, Page & Kjelson 1998).

Recently, legislation was introduced in California to improve air quality by reducing the area of rice stubble burned after harvest (Rice Straw Burning Act, AB 1378, 1991). This legislation has resulted in many rice farmers flooding fields during winter to increase straw decomposition (Brouder & Hill 1995).

In the past, most winter flooding of harvested rice fields was to attract waterbirds for hunting. Previously, I have described the effects of winter flooding on individual waterbird species (Chapter 1; Elphick & Oring 1998). I showed that many species of waterbirds occurred at significantly greater densities in fields that had been flooded intentionally than in fields that had not been flooded. I also found that methods of straw management used by farmers to increase straw decomposition rates in flooded fields had few effects on the densities of individual species, while flooding depth had a significant effect on the occurrence of several species. Here, I consider the waterbird community as a single management unit and examine effects of different flooding regimes on a suite of

community-level variables of interest to managers. My goal was to assess whether an analysis of measures that consider the waterbird community as a single unit leads to the same conclusions as were drawn from examining each species separately. I used a number of variables to describe the waterbird communities found in rice fields and developed a measure that evaluates the contribution of sites to waterbird conservation. For each variable, I tested the three hypotheses used to examine effects on individual species: (1) waterbird use of fields flooded by farmers would differ from fields that were not flooded, (2) flooded fields receiving different straw management treatments would be used differently by waterbirds, and (3) each measure of waterbird use would be affected by water depth. In addition, I examined differences between the two winters of the study, which differed considerably in rainfall (Chapter 1; Elphick & Oring 1998), and among the geographic areas where data were collected.

MATERIALS AND METHODS

STUDY AREA & DATA COLLECTION

I conducted field work in the Sacramento Valley, California during the winters of 1993/94 and 1994/95. Each winter I was aided by one field assistant. The Sacramento drainage, constitutes the northern half of the Central Valley and contains the majority of California's rice lands. Study fields were selected in three representative areas of the California rice-growing region: Richvale-Biggs, Sutter, and Princeton (see Chapter 1: Fig. 2 for map of study area). During the first winter of the study, 37 flooded fields (total area = 797.2 ha; mean area \pm SE = 21.5 ± 4.1 ha) and 16 unflooded fields (486.5 ha; 30.4 ± 7.1 ha) were selected arbitrarily. The following winter, we sampled 25 flooded (699.3 ha; 28.0 ± 5.4 ha) and 15 unflooded fields (398.3 ha; 26.6 ± 6.4 ha). Fifteen flooded fields and 5 unflooded fields were sampled in both winters to test for differences between years. Only fields that were flooded intentionally to enhance straw decomposition, attract waterfowl, or both, were classified as flooded fields. Fields that were not intentionally flooded were defined as unflooded. These fields occasionally held standing water, from rainfall or river flooding, for short periods of time, but were largely dry during most censuses.

Within the sample of flooded fields, six different straw management methods were represented: (1) flooded without straw management; (2) rolled to flatten straw and stubble and then flooded; (3) rolled after flooding to increase the extent that straw stuck in the mud; (4) flooded after chopping the straw to increase its surface area; (5) incorporated by ploughing to both cut straw up and partially bury it, and then flooded; (6) flooded after removing straw either by burning or baling. The first treatment controlled for the need to manipulate straw and the last for the presence of straw. I selected fields such that different straw management treatments were spatially interspersed. Whenever possible, I also chose fields such that treatments were evenly distributed across geographic blocks.

Data collection methods are detailed in Chapter 1. Briefly, we surveyed fields on foot, counting and identifying all birds in the orders Podicipediformes, Ciconiiformes, Anseriformes, Gruiformes, and Charadriiformes seen within the boundary of the field. Surveys were conducted at approximately 10-day intervals from mid-November until the

end of March. Waterfowl hunting occurred throughout the region during the first half of this period. To ensure that samples were representative, we made no attempt to avoid hunted fields during our censuses. To reduce systematic biases, we varied the order in which fields were surveyed among census periods. Rarely, birds were disturbed during censuses and we were unable to obtain accurate counts for certain fields. In these cases, I excluded the field's count from the analyses.

Most California rice fields are subdivided by narrow earthen levees to facilitate water depth management while growing rice; these subdivisions are called "checks". To assess the effects of water depth, I treated each subdivision as a separate plot. These water depth plots were created by farmers to maintain uniform water depths during the growing season. Consequently, levees between plots follow contours in the field and plots varied considerably in size and shape. Plot size ranged from 0.51 - 19.14 ha (mean \pm SE = 6.64 ± 0.28 ha). On any one day, water depth varied little within each plot, but considerably among plots within a single field. On each census, we noted the numbers of birds in each plot separately and recorded the depth at a stake placed in the deepest corner of the plot. Depths measured at these stakes were calibrated using randomly placed measurements taken throughout the plot. Depth measurements were made for 116 plots in 1993/94 and 51 plots in 1994/95.

CALCULATION OF COMMUNITY VARIABLES

Using the census data, I calculated a number of variables that described the waterbird community found in my study fields and tested whether they differed among management treatments. Community variables were calculated as follows:

1. *Waterbird species richness.* I determined the number of waterbird species seen in each field on each census and calculated the mean for each field during a winter.
2. *Total waterbird density.* The mean density of waterbirds (birds/ha) found in each field was calculated as an overall index of the use each treatment received by the waterbird community. Field areas were obtained from farmers or calculated from 1:24,000 topographic maps.
3. *Total densities of specific taxonomic groups.* I estimated the total densities of three taxonomic groups: wading birds (Ciconiiformes plus cranes), waterfowl (Anatidae), and shorebirds (Charadrii and Scolopaci).
4. *Community composition.* I calculated multivariate descriptors of the waterbird communities to determine whether there were differences among fields receiving different management treatments.
5. *Conservation value.* To further evaluate the importance of each habitat to the conservation of waterbirds I calculated a composite measure that reflected the contribution of fields to waterbird conservation. I weighted each species according to its mean density in a particular field (D), its mean relative abundance across its North

American range during winter (A), and its population trend (T). I used estimates of relative abundance and population trends that were calculated from 30 years (1959-1988) of Christmas Bird Count (CBC) data by Sauer, Schwartz and Hoover (1996). These volunteer-based surveys involve counting all birds within a prescribed area, and are conducted during mid-winter across North America (Root 1988, Butcher 1990). Only CBC sites within the usual winter range of a species were used to calculate the relative abundance score for that species. Sauer *et al.* (1996) calculated their population trends with the route-regression method (Geissler and Sauer 1990) using data for all of North America. For my analysis, I transformed trend estimates such that declining populations received large weights and increasing populations received small weights. For each field, I summed values for each species (i) to obtain a single measure of “conservation value”:

$$\sum_{i=1}^x \left[e^{-T(i)} \cdot \frac{D(i)}{A(i)} \right].$$

This value can be interpreted as the sum of species’ densities relative to their distribution-wide abundance, where the value for each species was weighted such that the more positive the population trend the smaller the species’ influence on the summed value.

DATA ANALYSIS

For each of the independent variables described above, I tested three separate null hypotheses: (1) no difference between intentionally flooded and unflooded fields, (2) no difference among flooded fields receiving different straw management treatments, and (3) no relationship with water depth. In general, I used analysis of variance (ANOVA) to examine the first two hypotheses and regression to determine whether there were water depth effects. I used Levene’s test (Levene 1960; Milliken & Johnson 1992) to test for heteroscedacity and, when the assumption of homogeneous variances was violated, I transformed data or used nonparametric tests if an appropriate transformation could not be found.

I present exact P -values for all statistical tests, except in extreme cases ($P > 0.15$ or $P < 0.001$). In interpreting my results, I decided, *a priori*, not to dismiss results where $0.05 < P < 0.10$ because logistic constraints limited sample sizes. Differences with probabilities within this range, however, were given lower weight than those of higher magnitude when interpreting results. This decision decreased the risk of mistakenly concluding that no treatment effect existed (i.e., making a Type II error). Given that such a mistake could mean that beneficial management actions would not be taken, I felt this decision was prudent despite the increased risk of concluding a treatment effect where none existed (i.e., making a Type I error).

I calculated power of non-significant tests using Cohen (1988), with $\alpha = 0.10$. To calculate power for nonparametric tests, I adjusted sample sizes following guidelines on power efficiency (Siegel & Castellan 1988). I considered power greater than 0.8 as evidence for no difference among treatments and determined power for small, medium and large effect sizes. For each calculation, I have given the quantitative values used for these qualitative effect sizes, but note that these values differ among tests (for example, large effect sizes for t -tests and ANOVA are 0.8 and 0.4 respectively; see Cohen 1988 for

detailed descriptions of what these effect sizes signify and justification for specific values).

For tests of flooding and straw manipulation treatments, individual fields were considered experimental units and mean values calculated across dates were used. Analyses of water depth effects differed because depths varied among sampling dates and among different water depth plots within a field. In my depth analyses an experimental unit was a single plot on a single day. To determine whether repeated samples of a plot were statistically independent, I tested for autocorrelation (see also Chapter 1; Elphick & Oring 1998). For each variable, a random sample of 20 sites were tested for autocorrelation. For all variables, the number of sites for which there was significant autocorrelation was less than expected by chance (Chatfield 1980; 2 out of 120 tests when all variables combined; Fig. 6). I, therefore, assumed that samples were statistically independent in subsequent analyses.

For each dependent variable, I tested first for differences between the two winters using data from the 20 fields sampled in both seasons. If there was no difference, I pooled data for subsequent analyses, randomly selecting one winter's data for those fields sampled twice. When the two winters differed significantly, I analyzed data for each year separately. Geographic variation in dependent variables was another potential source of bias in my analysis, because not all straw management methods were represented in all three areas where we collected data. To account for this, I incorporated the geographic area as a blocking factor into all parametric analyses. When I could not test for management treatment and geographic block effects simultaneously, I conducted separate nonparametric tests of geographic differences. If these supplemental tests were significant, I examined data for each block separately to assess whether geographic differences alone could explain differences among treatments.

In addition to linear correlations between dependent variables and water depth, I considered three nonlinear relationships to be possible: an increase to a peak followed by a decline, an increase to a plateau, or a plateau followed by a decrease. To examine these possibilities, I tested for quadratic and asymptotic relationships between each variable and depth after the transformation: $y = \log_{10}(x+1)$. Julian date also was incorporated into these models to control for temporal variation in each measure. Water depth and date were negatively correlated with each other ($r = -0.599$, $P < 0.001$; Chapter 1: Fig. 3) raising concerns about the effects of multicollinearity on my analyses. All regressions were, therefore, repeated with just depth terms to ensure that significant results persisted after the potential for this problem was eliminated.

Most of my variables controlled for differences in the size of fields by dividing bird abundance by area. Species richness, however, does not increase as a linear function of area (Gleason 1922) and estimates cannot be controlled this simply (Elphick 1997). The relationship between species richness (S) and area (A) usually is described by the nonlinear equation $S = cA^z$, where c and z are constants (Preston 1960; Rosenzweig 1995). To test for this nonlinear relationship, I \log_{10} transformed this equation and used linear regression. Tests of management treatment effects, interactions between area and treatment, and differences in species richness among geographic blocks, were conducted by adding these variables to this model.

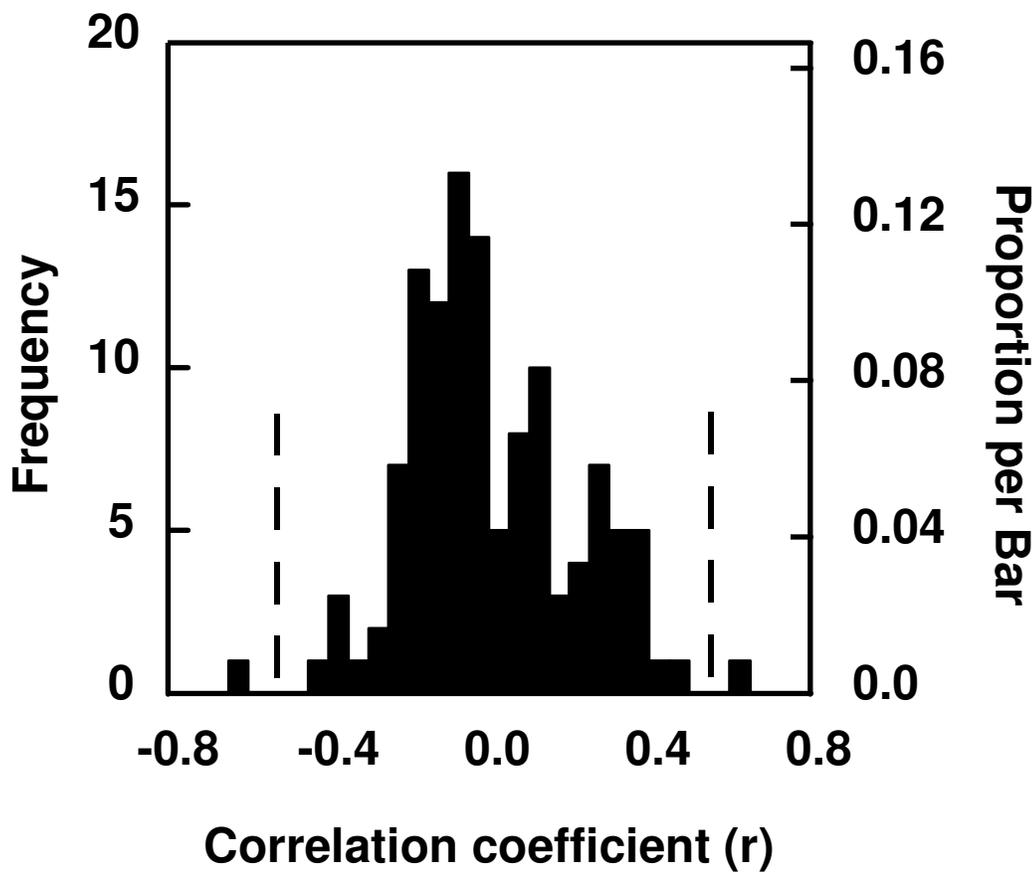


Figure 6. Results of autocorrelation tests to determine whether repeated samples of bird use, in plots used for water depth analyses, were correlated. Figure shows correlation coefficients for 120 tests (all measured combined) grouped into 0.05 increments. Only coefficients that lie outside the dashed lines were statistically significant.

To test for multivariate differences in community composition among treatments, I pooled data for the two years and used randomization tests to examine the significance of three multivariate measures: Romesburg's sum of squares statistic (E), Wilks's lambda (L) and the sum of log (F) statistic. The first of these test statistics determined whether fields within each group were more similar to each other than to the entire population of fields sampled. The other two statistics are based on mean differences among groups (Manly 1991). For each test I used 10,000 randomizations.

RESULTS

WATERBIRD SPECIES RICHNESS

Mean waterbird richness did not differ between years (paired- $t_{19} = 1.09$, $P = 0.291$, $1-\beta > 0.99$ for medium effect size, $d = 0.5$) and data were pooled for all analyses. When all fields were considered, the relationship between the mean number of species using a field and the field's area was highly significant, but left much of the variance unexplained ($t_{73} = 3.38$, $P = 0.001$, $r^2 = 0.124$).

Fields that had been flooded intentionally were used by significantly more waterbird species than fields that were not ($F_{1,70} = 67.23$, $P < 0.001$). On average, flooded fields had three times the waterbird richness of unflooded fields (Fig. 7A). The method of straw management used to aid decomposition in flooded fields also affected waterbird richness ($F_{5,40} = 2.37$, $P = 0.057$), although the difference was not as significant as that between flooded and unflooded fields. Richness was greatest in fields that had been rolled after flooding and lowest in fields where straw had been removed prior to flooding (Fig. 7B). In both cases, field area had a highly significant effect on species richness ($F_{1,70} = 20.63$, $P < 0.001$ and $F_{1,40} = 10.84$, $P = 0.002$, respectively). There was no detectable interaction between area and management method in either model ($P > 0.15$ for both), nor effects of geographic block ($P > 0.45$ for both), so these terms were dropped from the final models. The combination of flooding treatment and field area explained 55.9% of the variance in waterbird richness across all fields. The method of straw manipulation combined with area explained 37.0% of the variability in richness found in flooded fields.

Waterbird richness also varied with water depth, with peaks at depths of 10-15 cm and 35-40 cm (Fig. 8). After controlling for a significant area effect, richness varied as an inverse quadratic function of both water depth and date, with species richness peaking at intermediate depths and mid-winter. All terms were highly significant ($P < 0.001$), although the model explained only 15% of the variance in species richness (Table 7).

TOTAL DENSITIES OF WATERBIRDS AND FOCAL GROUPS

Total waterbird densities did not differ between 1993/94 and 1994/95 (Wilcoxon test, $z = 0.187$, $P = 0.852$). Similarly, there were no differences in the densities of waterfowl or wading birds in the two winters ($z = -0.411$, $P = 0.681$ and $z = -0.448$, $P = 0.654$, respectively). Power for these tests was high for a large effect size ($d = 0.8$; $1-\beta = 0.92 - 0.98$), but not for a medium effect size ($d = 0.5$; $1-\beta = 0.66 - 0.72$). Total shorebird densities did differ, with higher densities in the drier winter of 1993/94 ($z = -2.539$, $P =$

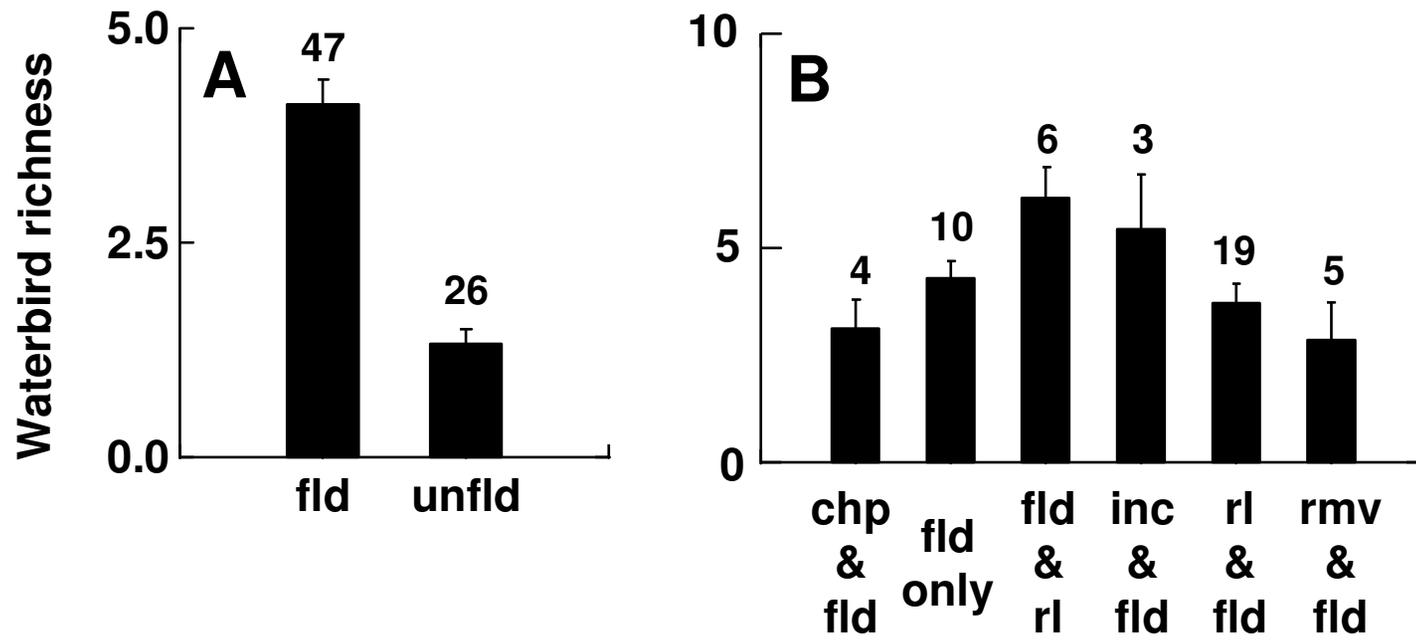


Figure 7. Mean (SE) species richness in different management treatments. A. Flooded (fld) and unflooded (unfld) fields. B. Flooded fields in which straw was: chopped then flooded (chp & fld), just flooded (fld only), flooded then rolled (fld & rl), incorporated into soil then flooded (inc & fld), rolled then flooded (rl & fld), and removed then flooded (rmv & fld). Sample sizes are given above each bar.

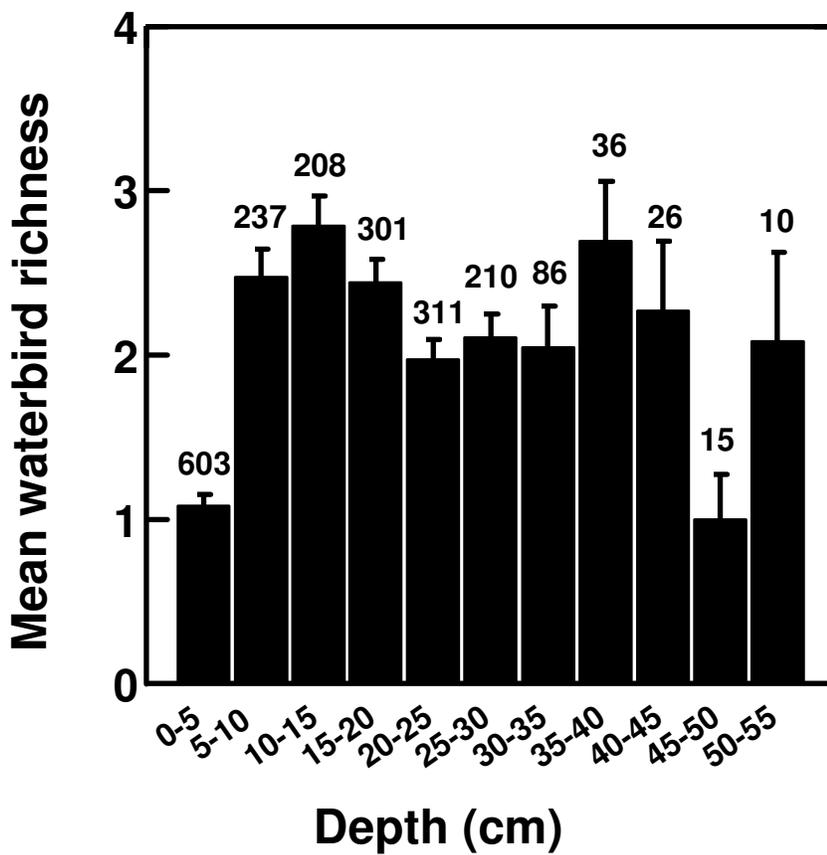


Figure 8. Mean (SE) waterbird richness for 5 cm depth categories. Sample sizes are given above each bar. All depth categories deeper than 55 cm had fewer than 10 observations and were omitted.

Table 7. Results of best fit regression models relating species richness and bird densities to water depths. In each case, I compared models in which the dependent variable was a linear, quadratic, or nonlinear, function of depth. If significant, I also included linear and quadratic date terms. Year was added to the shorebird models because significant differences between winters had been found in earlier analyses (see text). Final models were those with the highest adjusted- R^2 . Significance of depth variables were not affected by the removal of correlated date variables.

Dependent variable	Explanatory variables	Coefficient	P	n	Model adjusted- R^2	Model significance
Richness*	Area*	0.298 ± 0.023	< 0.001	2051	0.150	< 0.001
	Depth	0.013 ± 0.002	< 0.001			
	Depth ²	$-2 \times 10^{-4} \pm 2 \times 10^{-5}$	< 0.001			
	Date	0.025 ± 0.004	< 0.001			
	Date ²	$-3 \times 10^{-5} \pm 5 \times 10^{-6}$	< 0.001			
Wading birds*	Depth*	0.013 ± 0.007	0.063	2051	0.004	0.014
	Date	0.003 ± 0.002	0.055			
	Date ²	$-4 \times 10^{-6} \pm 2 \times 10^{-6}$	0.073			
Waterfowl*	Depth*	0.400 ± 0.029	< 0.001	2035	0.167	< 0.001
	Date	0.057 ± 0.006	< 0.001			
	Date ²	$7 \times 10^{-5} \pm 8 \times 10^{-6}$	< 0.001			
Shorebirds*	Depth*	-0.116 ± 0.018	< 0.001	2051	0.021	< 0.001
	Date	$-0.001 \pm 2 \times 10^{-4}$	< 0.001			
	Year	-0.027 ± 0.015	0.076			
All waterbirds*	Depth*	0.432 ± 0.034	< 0.001	2035	0.156	< 0.001
	Date	0.061 ± 0.007	< 0.001			
	Date ²	$-8 \times 10^{-5} \pm 1 \times 10^{-5}$	< 0.001			
Conservation value*	Depth*	0.254 ± 0.027	< 0.001	2031	0.111	< 0.001
	Date	0.053 ± 0.006	< 0.001			
	Date ²	$7 \times 10^{-5} \pm 8 \times 10^{-6}$	< 0.001			

* Data transformed: $\log_{10}(x + 1)$

0.011). For subsequent analyses of shorebird data, therefore, I conducted separate tests for each winter.

Total densities of waterfowl, shorebirds, and all waterbirds combined were significantly higher in flooded fields than in unflooded fields (Fig. 9). Wading bird density ranks did not differ between the two habitats (Fig. 9A); power was 0.93 for a large effect size ($d = 0.8$; 0.63 for a medium effect size of 0.5). Significant differences among flooding treatments were found for the total numbers of waterbirds and total wading birds (Table 8). When all species were grouped, density ranks were significantly higher in fields that had been either flooded with no straw manipulation or rolled prior to flooding, than in fields where straw had been removed. Wading birds used fields that had been just flooded significantly more than several other treatments (Table 8). In 1994/95, shorebirds used fields where straw had been incorporated by ploughing significantly more than fields where straw was chopped before flooding. These treatments were not present in the 1993/94 sample, when no difference was found (Table 8). Waterfowl use of flooding treatments did not differ significantly. For both of these non-significant results, power was too low to conclude no difference ($1-\beta = 0.57$ and 0.59 , respectively, assuming a large effect size of $d = 0.4$).

Geographic differences were found only in the total numbers of waterbirds and in the numbers of shorebirds in 1994/95 (Kruskal-Wallis tests, $H = 5.39$ $P = 0.068$, and $H = 7.27$, $P = 0.026$, respectively; $P > 0.2$ for all other tests). When all species were pooled, there were significantly more birds at the Princeton sites than the Sutter sites. When shorebirds alone were considered, the difference was driven by greater numbers at Princeton sites than at Richvale-Biggs sites. The geographic and straw treatment differences in shorebird abundance were confounded, because all fields where straw was incorporated by ploughing were in the Princeton area and most fields where straw was chopped were in the Richvale-Biggs area. Differences in total waterbird use of straw treatments were not confounded with geographic differences and persisted when the geographic effect was removed by dropping Sutter sites from the analysis.

Bird densities were related significantly to water depth and date for all groups of waterbirds considered (Table 7). Densities of wading birds, waterfowl, and all waterbirds combined, rose to an asymptote as depth increased, while shorebird densities decreased to an asymptote. None of the models, however, explained more than 17% of the variance in bird densities. Flooded plots that were occupied by waterbirds, waterfowl or wading birds were significantly deeper than sites without these birds. In contrast, sites that were used by shorebirds were significantly shallower than sites that were not used (Fig. 10).

COMMUNITY COMPOSITION

The community composition of flooded and unflooded fields differed significantly according to all three multivariate test statistics (Romesburg's $E = 2362.3$, $P < 0.001$; Wilks's $L = 0.330$, $P = 0.002$; and sum of log (F) = 26.71, $P < 0.001$). Comparisons of straw manipulation treatments were more ambiguous. Values for two test statistics indicated that there were differences (Romesburg's $E = 1264.5$, $P < 0.001$; and sum of log (F) = 14.40, $P = 0.001$). In contrast, the observed value of Wilks's lambda was not significantly different from that expected by chance ($L = 0.001$, $P = 0.799$).

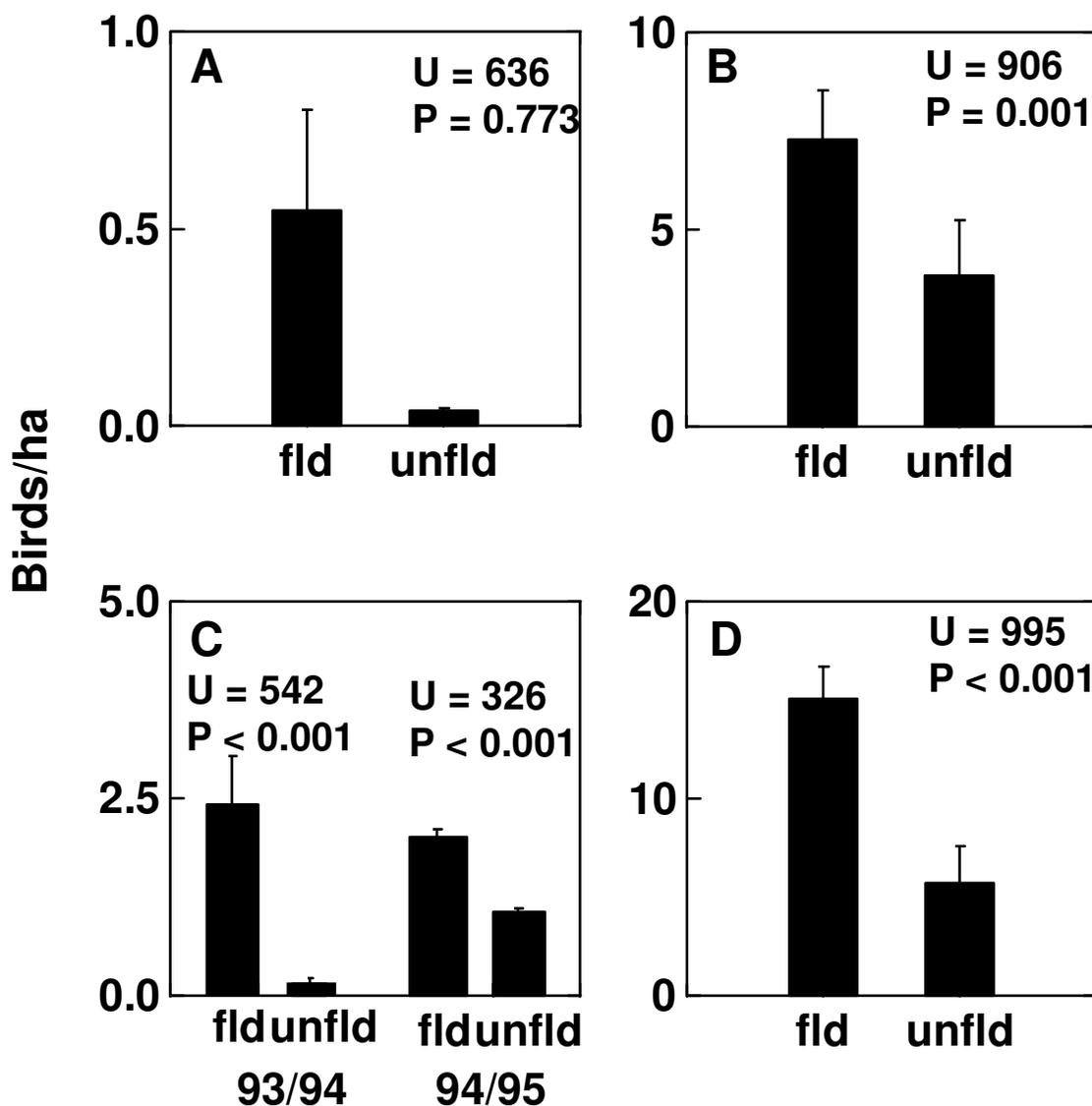


Figure 9. Mean (SE) densities of birds in flooded and unflooded fields (birds/ha). A. Wading birds. B. Waterfowl. C. Shorebirds. D. All waterbirds combined. Significance statistics are for Mann-Whitney tests and, thus, reflect differences in the data after rank transformation rather than differences between means. Shorebird densities differed between winters and data were analyzed separately. Sample sizes for flooded and unflooded fields, respectively, were: 37 and 16 (1993/94), 25 and 15 (1994/95), 47 and 26 (both years combined).

Table 8. Mean (\pm SE) bird densities (birds/ha) in flooded fields receiving different straw management treatments. Significance statistics are from Kruskal-Wallis tests. Superscripts indicate results of Dunn's post-hoc comparisons (Zar 1984): treatments with different letters were significantly different. Shorebird densities differed between winters and separate analyses were conducted for each year. Dashes indicate that a treatment was not present for a particular comparison. Sample sizes are for 1993/94, 1994/95, and both years combined, respectively.

	Treatment						H	P
	Flood only	Roll & Flood	Flood & Roll	Chop & Flood	Incorporate & Flood	Remove & Flood		
<i>n</i>	8,7,10	21,4,19	4,4,6	0,4,4	0,3,3	3,3,5		
Wading birds	2.40 \pm 1.04 ^a	0.05 \pm 0.02 ^b	0.05 \pm 0.02 ^{a,b}	0.02 \pm 0.00 ^b	0.03 \pm 0.03 ^b	0.07 \pm 0.03 ^{a,b}	18.37	0.003
Waterfowl	8.60 \pm 3.22	9.58 \pm 2.29	5.98 \pm 1.86	3.61 \pm 2.07	3.61 \pm 1.46	2.73 \pm 1.34	5.82	0.324
Shorebirds (93/94)	2.54 \pm 0.94	2.67 \pm 0.97	2.22 \pm 1.73	-	-	0.33 \pm 0.02	3.57	0.311
Shorebirds (94/95)	1.01 \pm 0.44 ^{a,b}	0.29 \pm 0.04 ^{a,b}	0.42 \pm 0.10 ^{a,b}	0.18 \pm 0.10 ^b	12.94 \pm 6.60 ^a	0.30 \pm 0.17 ^{a,b}	10.52	0.062
All waterbirds	19.61 \pm 3.86 ^a	17.77 \pm 2.49 ^a	9.05 \pm 2.28 ^{a,b}	9.10 \pm 5.78 ^{a,b}	19.13 \pm 9.48 ^{a,b}	4.98 \pm 1.57 ^b	12.35	0.030

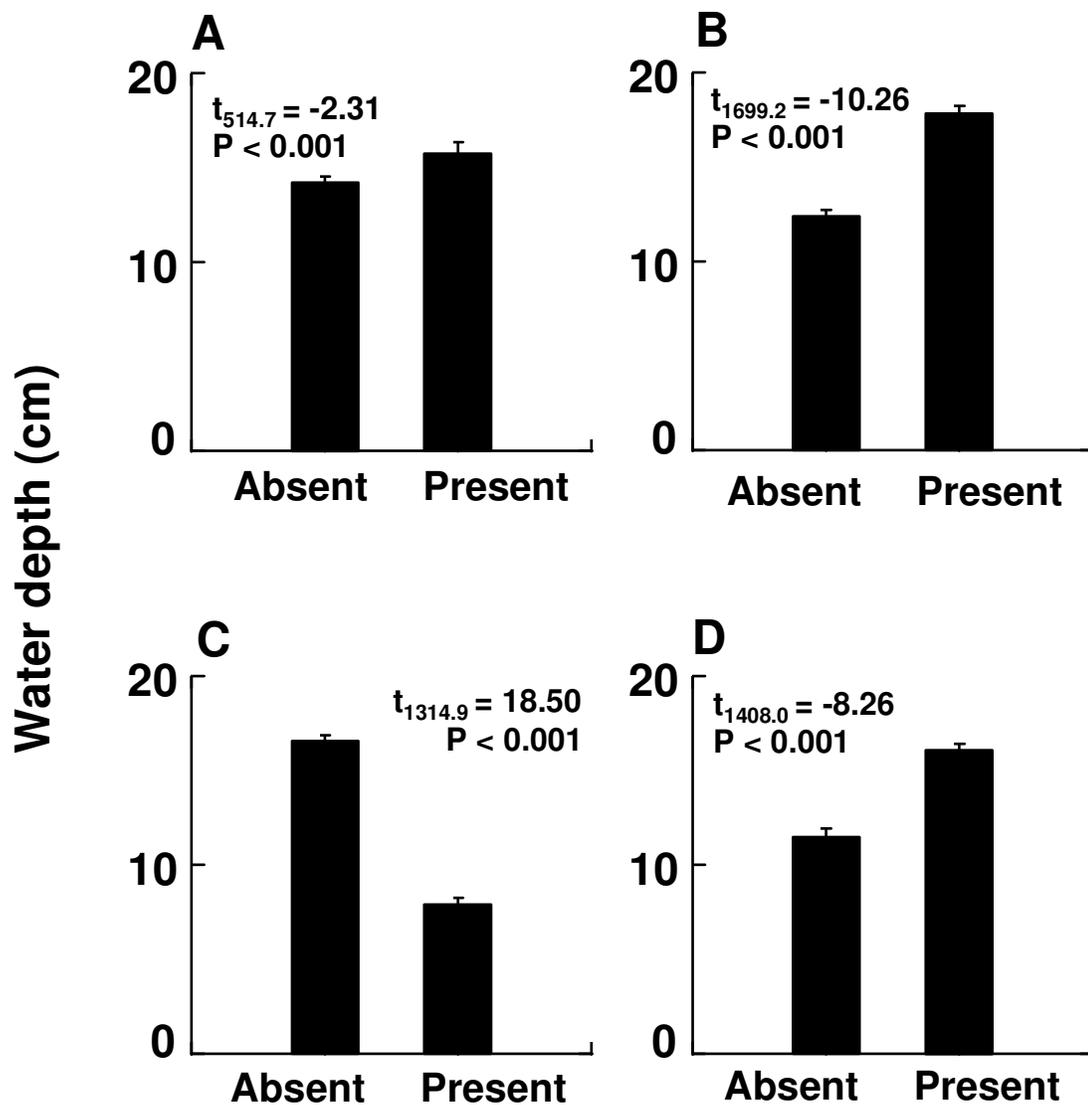


Figure 10. Mean (SE) water depths of plots in which birds were absent and present. A. Wading birds. B. Waterfowl. C. Shorebirds. D. All waterbirds combined. Significance statistics are for separate-variance t -tests.

CONSERVATION VALUE

I found no difference between years in my measure of the conservation value of fields and combined data for the two years in subsequent analyses (Wilcoxon test, $z = 0.485$, $P = 0.627$). Power of this test was 0.98 for a large effect size ($d = 0.8$; 0.74 for a medium effect size of 0.5). Flooded fields received significantly higher conservation value scores than did unflooded fields (Mann-Whitney test, $U = 1079$, $P < 0.001$), but no differences were found among flooded fields receiving different straw manipulations (Kruskal-Wallis test, $H = 8.51$, $P = 0.130$). I could not conclude that there was no difference among straw manipulations in flooded fields, even for a large effect size ($d = 0.4$; $1-\beta = 0.59$). No differences among geographic areas were found ($H = 0.097$, $P = 0.953$).

My conservation value measure increased with water depth to a peak between 10-15 cm, then declined (Fig. 11). In the best regression model, conservation value varied significantly with water depth after $\log(x+1)$ transformation, climbing to an asymptote as depth increased. In addition, there was a quadratic relationship with date, with a peak mid-winter. This model explained 11% of the variance in conservation value (Table 7).

DISCUSSION

EFFECTS OF FLOODING

Flooding harvested rice fields in winter significantly increased waterbird species richness, densities, and the conservation value of fields to waterbirds in winter. Previously, I have shown that significantly greater densities of most waterbird species occurred in fields that had been flooded intentionally than in those that had not (Chapter 1; Elphick & Oring 1998). Given the degree of these differences, it is not surprising that flooded and unflooded fields differed from each other in most of the community measures discussed here. There was no difference in the densities of wading birds, a group for which I found mixed results for individual species. Some wading birds were more common in flooded fields (e.g. white-faced ibis *Plegadis chihi*). In contrast, great blue heron *Ardea herodias* and sandhill crane *Grus canadensis*, were more common in unflooded fields and great egrets *A. albus* were equally abundant in both treatments (Chapter 1; Elphick & Oring 1998).

EFFECTS OF STRAW MANIPULATION

Differences among flooding treatments were less clear-cut. Species richness was greatest in fields that were flooded and then rolled. Total waterbird densities were greatest in fields that were just flooded. Shorebird densities, in contrast, peaked in fields where straw had been incorporated by ploughing before flooding. This final result, however, was confounded with geographic variation in abundance and also may be a consequence of shallower water in incorporated fields, rather than the treatment *per se* (Chapter 1; Elphick & Oring 1998). No single treatment was ranked highest for all measures, although flooding only or flooding in combination with rolling the straw typically were ranked high, while removing or chopping the straw before flooding generally ranked low. Significance tests of pairwise comparisons, however, lacked statistical power and conclusions about the relative value of different flooding methods are tentative.

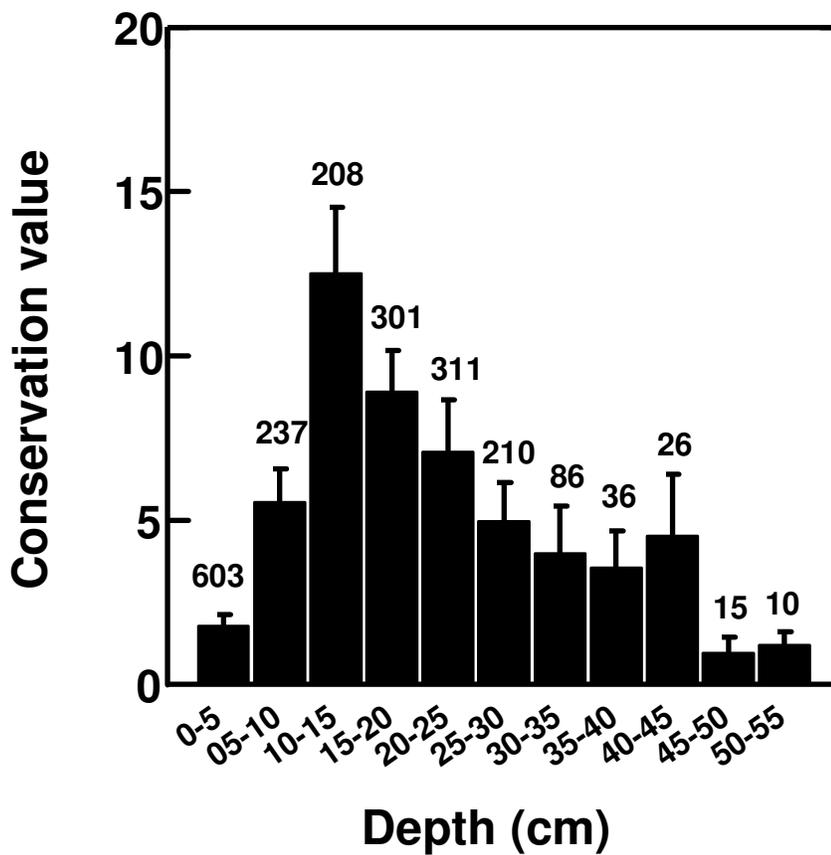


Figure 11. Mean (SE) conservation value scores for 5 cm depth categories. Sample sizes are given above each bar. All depth categories deeper than 55 cm had fewer than 10 observations and were omitted.

Comparisons of straw management treatments for individual species revealed few significant differences (Chapter 1; Elphick & Oring 1998). My multivariate analysis produced ambiguous results. Two of the test statistics suggested that treatments differed significantly, while Wilks's lambda showed no difference. This apparent contradiction may be attributable to poor estimation of the sum of squares and cross-product matrices that are needed to determine Wilks's lambda (Manly 1991).

EFFECTS OF WATER DEPTH

Water depth significantly affected all measures considered, although the nature of the relationships varied. Waterfowl and wading bird densities increased initially with increasing depth, but after a point densities leveled off. The opposite was true for shorebirds and, consequently, waterbird richness peaked at intermediate depths. After correcting for other variables, my measure of conservation value followed the pattern for total waterbird density by increasing with water depth, but at a decreasing rate in deeper conditions. This result suggests that waterfowl, wading birds, or both, influenced my conservation measure more than shorebirds. Two factors contributed to this effect. Waterfowl species tended to have less positive population trends than other species (Sauer *et al.* 1996), and, therefore, contributed more to my measure of conservation value. In addition, there were more species of waterfowl than other groups and their cumulative effect consequently was greater.

I found highly significant relationships between depth and many of the measures considered. Much of the variance in these measures, however, remained unexplained (> 83% in all cases). Determining the cause of the remaining variance would provide greater insight into the relative importance of water depth. The propensity for many waterbird species to flock, creates clumped distributions that inevitably cause high variability in bird densities. Incorporating the effects of individual behavior into explanatory models, therefore, would seem essential. My data support the notion that intermediate depths maximize the value of rice fields to waterbird conservation. Both waterbird richness and conservation value were greatest at depths of 10-15 cm (Fig. 8, 11), with the peak in richness at slightly lower depths than predicted from examination of depths used by individual species (Chapter 1; Elphick & Oring 1998).

Water depth decreased significantly during the winter (Chapter 1: Fig. 3; Elphick & Oring 1998). Additionally, bird use of fields may vary over time due to migratory behavior or food availability. Consequently, it is possible that collinearity between depth and date, influenced my regressions. All significant results between depth and bird use persisted after date was removed from the regressions, verifying that correlations existed. Determining whether these correlations indicate a causal relationship between depth and bird use, however, requires experiments that separate the date and depth variables.

CHOICE OF COMMUNITY MEASURES

I used a number of different measures to describe the waterbird communities of rice fields. These measures were chosen to characterize the community in ways relevant to a diversity of management objectives. Species richness is a standard measure of interest to conservationists. When multiple visits are made to a site, richness can be measured in

two ways. I chose to use the mean number of species found on any particular visit, rather than the accumulated number found when all visits are combined, because the latter measure is more influenced by rarely encountered species. A consequence of this is that in situations such as ours, where species are unlikely to be present but not seen, the cumulative richness is less representative of the community that regularly uses a habitat than the mean richness.

Animal densities also can provide information on the importance of particular sites or habitats. In addition, high waterbird densities may be important to farmers because waterbird activity helps to increase straw decomposition (J. Bird, unpubl. data) and may reduce numbers of weed seeds and crop pests (e.g. Jones 1940; Smith & Sullivan 1980; Fasola & Ruíz 1997). Waterfowl numbers are of particular interest to hunters and to wildlife managers concerned with enhancing populations of game species (Gilmer et al. 1982; Payne & Wentz 1992; Brouder & Hill 1995; Reid & Heitmeyer 1995). Various studies suggest that rice farming can exert considerable influence on the population dynamics of wading birds and that management of rice fields may play an important role in the conservation of these species (Fasola & Barbieri 1978; Hafner, Dugan & Boy 1986; Fasola et al. 1996; Lane & Fujioka 1998). Finally, shorebirds have received attention recently, as a group that could benefit from modifications to current wetland management (Helmers 1992; Streeter, Tome & Weaver 1993). Different types of birds also may have different impacts on straw decomposition and invertebrate populations. For example, waterfowl probably cause more trampling of stubble and have a greater effect on straw decomposition than do other species.

Multivariate comparisons of community composition allowed us to assess the extent to which univariate patterns of species abundance translated into community-scale patterns. Specifically, these analyses allowed us to ask whether the patterns in the abundance of individual species described in Chapter 1 (see also Elphick and Oring 1998) were sufficient to allow treatments to be distinguished? Conversely, these tests examined whether there were subtle community-scale differences in the array of species found in each treatment that could not be detected by univariate tests.

The final measure I used to evaluate treatments, incorporated information on the conservation importance of each species. Weighting species by their probability of extinction provides an objective measure for ensuring that the most vulnerable species receive greatest attention without neglecting other species completely. Unfortunately, extinction probabilities are generally unknown and can be estimated only in rare cases (Boyce 1992). In lieu of this information, surrogate measures that are expected to correlate with extinction probability must be used. Here, I used the abundance of each species in a field relative to other sites they occurred at during winter and population trend to weight each species. As with all indices of conservation value, this one has its limitations. For example, it does not distinguish among species with different total population sizes or life-histories. Unfortunately, adequate data on additional variables are lacking for many species and their relationships with extinction probability are poorly known. My index does, however, incorporate more of the information of interest to conservationists than do common community descriptors such as species richness.

All composite measures are intended to summarize a large number of variables and hence simplify complex situations. By their very nature, however, they result in a loss of information and can fail to capture the idiosyncracities of particular variables. Thus, it is necessary to recognize that management prescriptions based on composite measures relate only to those measures and that certain species may show different responses. I have addressed such individual responses in Chapter 1 and have found general concordance between the responses of individual species and the patterns described here. Nonetheless, no management method will benefit all species and exceptions may need to be catered for separately (e.g., ensuring that sufficient unflooded habitat is available for sandhill cranes). Composite measures, however, can provide information that is not available from a consideration of variables separately. For example, I found little evidence that individual species are affected by straw treatments (Chapter 1, Elphick & Oring 1998). By combining variables, however, small differences among these management methods in species richness and community composition emerged.

IMPLICATIONS OF THIS STUDY

The primary goal in this chapter was to assess whether conclusions drawn from an analysis of measures that consider the waterbird community as a single unit differ from those drawn from examining species separately. To some extent, this assessment depends on the choice of community or conservation measures. For example, a measure that places a lot of influence on small sandpipers would lead to a very different conclusion to one that favors cranes (Chapter 1; Elphick & Oring 1998). My measures were chosen *a priori* with specific goals in mind (e.g. maximizing straw decomposition, waterbird conservation, and hunting value of rice fields). Despite the diversity of these goals, I found similar results for all measures. To some extent, this was not surprising as the broad goal of increasing waterbird numbers was common throughout. Given the number of species involved and the different emphases of each variable, however, the concordance among measures is encouraging because it suggests that similar recommendations will simultaneously create diverse management benefits.

Although I have considered a wide variety of species and management goals, I still anticipate trade-offs from particular management actions. For example, if the primary goal of rice field management was to maximize raptor richness and abundance, then different recommendations would be appropriate (C. S. Elphick unpubl. data). Also, there are limitations to the data presented here. Measures of animal densities need not correlate with habitat quality (van Horne 1983; Sutherland 1996). The mechanism most likely to disrupt this relationship in my study, is the possibility that social interactions among animals restricts access to high quality sites. Of the species that I considered, only shorebirds regularly defend feeding territories in winter. In the Sacramento Valley, aggressive interactions or other indicators of territoriality were rare or absent (Chapter 4, C.S. Elphick unpubl. data). Moreover, the extreme differences between flooded and unflooded fields reduce concern that I may be mistaken in considering flooded fields to be of higher quality than unflooded fields.

My measure of conservation value also has limitations. By weighting species according to population trends, and sites according to their relative importance to

multiple species, it focuses on issues likely to affect population persistence directly. I cannot, however, be certain that these weighting factors produce an index of the contribution of a site to maintaining viable populations, especially as I do not know whether populations are limited by conditions on the wintering grounds. Also, my conservation measure is valid only if there is a relationship between high animal densities and good sites. I believe this is true for this study (see above), however, it may not be true in other situations. Unfortunately, conservation biologists are only just beginning to test predictions about persistence probabilities, even for extremely well known species (Brook *et al.* 1997). It seems likely that it will be some time before we can make accurate predictions for large numbers of species with confidence. There also are limits to the quality of the Christmas Bird Count data that were used to weight species and the inferences that can be drawn from using them. These data, however, give the only long-term, continent-wide, estimates of winter bird abundance and population trends available (Root 1988, Butcher 1990).

My results indicate that flooding rice fields in winter provides feeding habitat for waterbirds. Most flooding in the past was intended to attract waterfowl for hunting and flooded land often was drained as soon as the hunting season was over. Decomposing rice straw, however, requires that land stay wet for several months and many fields now remain flooded until farmers need to start preparing the ground for planting. This change not only has increased the amount of flooded habitat available during the latter half of the winter but allows longer periods over which invertebrate populations can develop.

Additional benefits to waterbirds also may be obtained by developing ways of increasing the area of flooded rice, without using more water. For much of the winter, fields are flooded deeper than is necessary to maximize bird densities (Chapter 1; Elphick & Oring 1998). There is no reason to expect that current depths are necessary to ensure adequate rice straw decomposition. Instead, the presence of deeper water early in the winter may reflect a widespread belief that ducks, which are hunted in many fields, prefer deeper conditions. In addition, in some cases there are constraints on the availability of water during the latter half of the winter, requiring farmers to flood fields deep in order to ensure that they stay inundated until spring (C.S. Elphick pers. obs.). Reducing water depths, therefore, may increase bird use without reducing decomposition rates. Assuming that water is available throughout the winter so that farmers can replace evaporated water, reducing average depths would enable farmers to flood larger areas without needing more water. Another option for increasing the flooded area is to block off field drainage outlets to retain rainwater in fields. Rainfall may not be sufficiently reliable for farmers to use this method alone to dispose of rice straw. It may be helpful, however, in speeding up decomposition in fields where other methods (e.g. ploughing) have been used. Moreover, for very little cost or inconvenience to growers, even very shallow flooding could have considerable benefits for some waterbird species.

Fully evaluating the importance of flooding rice fields to waterbird conservation will require additional information. Flooding rice fields during winter clearly increases their use by waterbirds, but it is less clear that these fields are equivalent to natural, managed, or restored, wetlands. Behavioral studies suggest that differences between semi-natural wetlands and flooded fields in foraging performance and time allocation of

shorebirds and egrets are small. In contrast, predation threat is lower in flooded fields (Chapter 4). Further comparisons of the two habitats are necessary to evaluate the extent to which rice fields can act as surrogates for more natural wetlands (Fasola & Ruíz 1996, 1997). In particular, by comparing the bird communities supported by rice fields and other wetland types it should be possible to identify whether certain habitats are better suited for particular taxa. This information would enhance regional conservation planning by reducing the need to manage for a diverse array of species at single sites (Oring & Elphick 1993). For example, rice fields appear to be well suited for use by species that use shallow conditions because fields cannot hold deep water and growers want to minimize their water costs.

A second important direction for future research should be to evaluate the relevance of my results from California to other regions where rice is grown. The extent of rice agriculture worldwide (Chang & Luh 1991) suggests that there is considerable potential for exploiting rice paddies as surrogate wetland habitat (Fasola & Ruíz 1996, 1997). We need, however, to ask: are waterbird communities in different regions sufficiently similar to that in California to respond in similar ways? Perhaps more important, is whether management changes are politically and logistically feasible? Answering this question will involve resolving issues such as: is water available to flood fields during the non-growing season? Is rainfall sufficient to flood fields without additional water? Is flooding during the non-growing season compatible with other uses of the fields? What are the additional costs to farmers and how can they be offset?

I have focused on the importance of flooding rice fields during the non-growing season. Obviously, there is potential for rice fields to contribute to waterbird conservation during the growing season too (e.g. Fasola & Barbieri 1978; Hafner *et al.* 1986, Hohman *et al.* 1994; Fasola *et al.* 1996; Lane & Fujioka 1998). Indeed, in many parts of the world peak waterbird use of rice fields occurs while rice is being grown because fields are not flooded at other times. During the growing season, ensuring that fields are flooded is less of a problem, although constraints on how fields are managed will be greater. Also, birds are more likely to have adverse effects on rice production at this time (Brouder & Hill 1995) and may be more susceptible to the effects of toxic chemicals (e.g. Flickinger and King 1972). Further quantitative assessments of the role rice fields play as waterbird habitat throughout the year would provide an important addition to our ability to manage waterbird populations.

MANAGEMENT RECOMMENDATIONS

1. Increased flooding of harvested rice fields during the winter is expected to increase habitat for a variety of waterbird species. Whether this rice field habitat simulates historic wetlands is unknown and comparing flooded fields to other wetland habitats should be a research priority. Nevertheless, flooding fields for the entire winter is preferable to leaving them dry or relying on passive flooding.
2. The method of straw manipulation used in conjunction with flooding had small effects on the waterbird community. The existence and type of differences among straw management methods depended upon which aspect of the waterbird community was

measured. Rolling the straw or doing nothing to it, however, appeared to be most beneficial.

3. Flooding fields to depths of 10-15 cm maximized waterbird use according to most criteria considered. At these depths, species that use intermediate depths, including many waterfowl, occur along with species that are restricted to shallower water. I suggest that rice fields can contribute most to waterbird conservation by providing relatively shallow conditions.

4. Managers should investigate methods of increasing the area of flooded rice that do not require increasing water use. Blocking the drains from fields to retain rainwater may be sufficient to increase use by many species, especially shorebirds, and would be inexpensive and easy to do. Reducing water depths from those currently used during the first half of the winter also would increase waterbird use and make water available to flood additional areas. For this to work, however, water must be available to farmers throughout the winter so that they can replace evaporating water continually.

SUMMARY

I studied the effects of flooding harvested rice fields during winter on waterbird communities. I examined variation in waterbird richness; the densities of all waterbirds, wading birds, waterfowl, and shorebirds; and a measure of conservation value that weighted species according to their relative abundance and population trends. For each variable, I tested for differences among (a) flooded and unflooded fields, (b) flooded fields that received different rice straw manipulations, and (c) fields with different water depths. I also used multivariate randomization tests to determine whether the waterbird communities of fields receiving different management treatments were different.

Intentionally flooded fields were used by waterbirds more than unflooded fields according to most criteria considered. Wading bird densities did not differ between flooded and unflooded fields. According to my measure of conservation value, flooded fields contribute considerably more to waterbird conservation than unflooded fields. Waterbird richness, total waterbird density, and the density of wading birds differed significantly among straw management treatments. Shorebird densities differed in one of the two winters, although this may have been caused by geographical variation in shorebird numbers or systematic differences in water depth among treatments. No treatment consistently ranked highest for all measures. Just flooding or flooding combined with rolling the straw, however, typically ranked high, while removing or chopping straw before flooding ranked low.

Water depth was correlated with all aspects of the waterbird community considered and with the importance of a field to waterbird conservation. In all cases, most of the variation in these measures went unexplained. Bird densities were explained best by asymptotic relationships, with shorebird densities greatest in shallow water and waterfowl and wading bird densities greatest in deeper conditions. Waterbird richness and conservation value both peaked at depths of 10-15 cm.

My results demonstrate that intentionally flooding rice fields during winter affected several aspects of the waterbird community. The way that fields were flooded (method of straw manipulation and flooding depth) also influenced the waterbird community, although these effects often were small. These findings support the conclusions of Chapter 1, where effects on individual species were addressed. Furthermore, I obtained consistent results across a suite of measures that emphasized different components of the community. This concordance among measures is encouraging because it suggests that similar recommendations will simultaneously create diverse management benefits.

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CHAPTER THREE

INFLUENCE OF LANDSCAPE FEATURES ON WATERBIRD DENSITIES IN CALIFORNIA RICE FIELDS

Increasingly, biologists recognize the influence of the surrounding landscape on the abundance and variety of species found in habitat patches (Askins 1995). MacArthur and Wilson's (1963, 1967) theory of island biogeography highlighted the role that isolation can play in determining the number of species within a habitat patch. Subsequent studies have identified a variety of other landscape characteristics that can influence the numbers and kinds of species present in a patch, including, the amount of habitat similar to that in the patch in the immediate surroundings (e.g., Askins *et al.* 1987; Carey *et al.* 1992; Hinsley *et al.* 1995; Robinson *et al.* 1995); the types and variety of surrounding habitats (e.g., Strong and Bock 1990; Gibbs 1991; Pearson 1993; Flather & Sauer 1996); the degree of habitat fragmentation (e.g., Hunter *et al.* 1995; Ripple *et al.* 1997); the spatial arrangement of patches (e.g., Dunning *et al.* 1995); the proximity of particular habitat types (e.g., Hinsley *et al.* 1995; Farina 1997); the presence of specific features such as roads and residential areas (e.g., Wilson 1994; Reijnen *et al.* 1995); and the orientation of the patch with respect to migration routes (e.g., Gutzwiller and Anderson 1992).

Despite this rich literature, our knowledge of the role that landscape composition plays in defining animal communities is still immature. Most studies of birds, for example, have focused on species occurring in forested habitats during the breeding season (Pearson 1993). In addition, little is known about the spatial scales at which different species respond to the surrounding landscapes. Landscape characteristics vary depending on the size of the area (i.e., the scale) over which they are measured. For example, the relationship between the amount of forest cover types and fragmentation and the presence of northern spotted owls *Strix occidentalis caurina* appears to exist only at scales of less than 1200m (Hunter *et al.* 1995). Similarly, research on foraging seabirds has shown that patterns between bird abundance and descriptors of their habitat depend on the scales at which variables are measured (Schneider & Piatt 1986; Hunt & Schneider 1987; Logerwell & Hargreaves 1996). Although there is increasing recognition of the need to consider patterns of habitat selection at scales relevant to the organisms of interest (Addicott *et al.* 1987; Wiens 1989; Wiens & Milne 1989), there are relatively few studies that have determined appropriate scales. Information of this type can provide important insight into the ways in which organisms perceive their surroundings and can guide our understanding of the ways in which landscapes affect habitat use.

Waterbirds provide a particularly interesting system for examining the relationship between landscape features and habitat use. Habitat use by waterbirds is likely to be influenced by the surrounding landscape because aquatic birds are extremely mobile at a variety of temporal and spatial scales. At one scale, waterbirds often commute among feeding sites and roosting areas or breeding colonies daily (e.g., Kelly & Cogsworth 1979; Connors *et al.* 1981; Gibbs 1991; Warnock & Takekawa 1996); at another scale, they move among sites within seasons, both locally and regionally (e.g., van Eerden 1984; Warnock & Takekawa 1995; Warnock *et al.* 1995; Ely & Takekawa 1996); and at still larger scales, waterbirds migrate long distances seasonally (e.g.,

Morrison 1984; Ely & Takekawa 1996; Iverson *et al.* 1996). Furthermore, waterbirds generally occur in open habitats and fly among sites at altitudes from which they would be able to see many habitat patches. Consequently, these birds have ample opportunity to learn the characteristics of the surrounding landscape. Many wetland habitats are ephemeral at various time scales, meaning that the locations of suitable habitat are changing constantly (Skagen & Knopf 1993; Warnock & Takekawa 1995; Farmer & Parent 1997; Robinson & Warnock 1997). Simultaneously, the flocking behavior of many aquatic birds makes food depletion, and consequently competition for food, common features of nonbreeding waterbird communities (e.g., van Eerden 1984; Székely & Bamberger 1992). Thus, waterbirds may be expected to benefit from a familiarity with surrounding habitats and from incorporating this knowledge into habitat selection decisions. Moreover, the distances over which waterbirds move suggest that they may be influenced by human land management activities at a regional scale. Consequently, understanding the way in which landscape influences habitat selection by waterbirds may have important applied implications.

Nonetheless, little has been published on the effects of landscape pattern on habitat selection by waterbirds. The spatial arrangement of wetlands influences the movement patterns of individual pectoral sandpipers *Calidris melanotos* during migration (Farmer and Parent 1997). Sandpipers moved more frequently, and over longer distances, in landscapes where wetlands were close together and occupied a large proportion of the surroundings than in landscapes where wetlands were less ubiquitous. Other studies have shown that the location of heronries depends on the proximity and abundance of suitable foraging habitat (Fasola & Barbieri 1978; Gibbs 1991; Hafner & Fasola 1992) and that wintering ducks concentrate in intertidal areas with nearby farmland, where birds can supplement their estuarine diet by feeding on agricultural crops (Lovvorn & Baldwin 1996).

I investigated the relationship between the winter densities of aquatic birds using flooded rice fields in the Sacramento Valley, California, and features of the landscape surrounding these fields. Winter-flooding of rice fields in this region primarily occurs to provide waterfowl habitat for hunting and to facilitate the decomposition of residual rice straw left on the ground after harvest (Payne & Wentz 1992; Brouder & Hill 1995). Little is currently known about the ways in which landscapes influence waterbirds in this region. Consequently, my approach was exploratory (*sensu* James & McCullough 1985); that is, my analysis was intended to be an hypothesis-generating, rather than hypothesis-testing, exercise. My specific goals were to determine: (1) the extent to which waterbird densities are related to the amount of particular habitats and land use types in the surrounding landscape; (2) the extent to which these landscape features had consistent effects on different taxonomic groups of birds; and (3) whether relationships between bird densities and the amount of these land use types depend on the scale at which the landscape was viewed. Finally, I examined the implications of my results to land managers wishing to incorporate ecological processes at a landscape scale into their management decisions.

MATERIALS AND METHODS

STUDY AREAS

Field work was conducted in the southern half of the Sacramento Valley, California, between 15 November 1993 and 31 March 1994. This first half of this time span included periods when waterfowl hunting occurred throughout the region, including some of my study fields. I arbitrarily selected 15 rice fields that had been flooded by farmers to enhance straw decomposition. For this analysis, I considered flooded units that were not separated by a major drainage canal or road to be a single field. Fields were grouped in three areas that I considered to be representative of the rice growing region: Richvale-Biggs in the northeast, Sutter in the south, and Princeton in the northwest (Fig. 12). For each field, I collected data on bird use and determined the abundance of different habitat and land use types in the surrounding landscape.

BIRD DATA

A field assistant and I censused fields by counting and identifying all waterbirds seen within the field boundary. Censuses were conducted at approximately 10-day intervals throughout the survey period. The order in which fields were visited was varied among censuses to reduce the likelihood of systematic biases. The few cases (< 0.1% of all observations) where birds were disturbed from a field during a census before we were able to obtain an accurate count, or where it was possible that disturbed birds moved to another field which had not yet been counted, were excluded from the analysis. Counts for each field were converted into densities and mean bird densities for the entire winter were calculated for each field. I used these mean densities as a measure of bird use in subsequent analyses. Analyses were conducted for four taxonomic groups: geese (Anserinae), ducks (Anatinae), wading birds (Ciconiiformes) and shorebirds (Charadrii and Scolopaci). Species were subdivided in this way to represent the main waterbirds groups that use flooded fields and to separate species that respond to flooding in different ways. Waterfowl were further subdivided because geese and ducks differ in their use of flooded fields; ducks use flooded fields significantly more than unflooded fields, whereas geese do not (Chapter 1; Elphick & Oring 1998). Previous analyses suggested that great blue herons *Ardea herodias* and sandhill cranes *Grus canadensis* avoid using flooded fields (Chapter 1; Elphick & Oring 1998), so these species were excluded from this analysis. Collection of bird data is discussed in more detail in Chapter 1 and in Elphick & Oring 1998.

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Copies are available on request.

(Note, this figure is very similar to Fig. 1 in Elphick & Oring 1988, J. Appl. Ecol. 35:97)

Figure 12. Map showing locations of study fields. For each geographic block the number of fields is shown in parentheses.

LANDSCAPE DATA

We collected landscape data by driving all passable roads within 10 km of each study field and recording the presence of different habitats onto 1:24,000 USGS topographic maps. Land was classified as flooded rice; other flooded agricultural land; semi-natural wetland; unflooded land; or unknown. A field was defined as flooded only if there was evidence that it had been flooded by a farmer (e.g., deep water, flooding early in the season prior to heavy rains, blocked outflows). I excluded fields that contained only standing rain water for several reasons. First, rice fields that are intentionally flooded receive significantly greater waterbird use than other fields and should be viewed as a qualitatively different habitat (Chapters 1 and 2; Elphick & Oring 1998). Second, flooded fields usually held water only for short periods. Consequently, they were only suitable habitat for most waterbirds for a small proportion of the time over which bird use was assessed. Third, a short flooding period also may have reduced the potential for aquatic invertebrate populations to develop in these fields, thereby limiting their value to many waterbird species. In addition to these biological reasons for defining flooded fields in this way, there is an important management distinction between fields that have been flooded intentionally and fields that have flooded passively. The former requires financial input to buy water and labor to maintain conditions, while the latter does not. The “unknown” habitat category referred both to areas where we were uncertain whether land had been flooded intentionally and to areas we were unable to survey.

I digitized landscape features from topographic maps into the Geographic Information System ARC/INFO. Habitat types were based primarily upon ground surveys. I also assigned habitat types to areas that I had not visited, if the habitat could be determined from map features. For example, wetlands shown on the map, but not visited, were recorded as such. Similarly, areas shown as residential, or with a lot of relief, were designated as part of the unflooded matrix. To each habitat patch I assigned information on habitat type, whether the polygon characteristics had been verified, whether it was part of a wildlife refuge, and whether it was one of the fields for which I had data on bird use.

From this habitat map, I defined three zones around each census field corresponding to different scales of analysis. These zones contained all land within 2 km, 5 km, and 10 km, of a field's boundary, respectively. Scales were chosen arbitrarily because I did not know, *a priori*, how birds would respond to the landscape. I then described the landscape within each zone by calculating the proportion of the land that was: (1) flooded rice fields, (2) any flooded agricultural land (including rice), (3) semi-natural wetland, and (4) part of a wildlife refuge. Proportions of flooded land were calculated by dividing the flooded area by the total area where habitats had been verified. Therefore, I assumed that the portion of the zone for which habitat types were known was representative of the entire zone. The extent of semi-natural wetlands and wildlife refuges were marked on maps, providing better information than was available for the amount of flooded agricultural land. Consequently, I calculated the proportion of land that was part of a wetland or refuge by dividing their area by that of the entire zone.

DATA ANALYSIS

I used multiple linear regression to determine relationships between mean bird densities in flooded fields and surrounding landscape features. For each group of birds, I sought to build a model that predicted mean bird density using landscape features. I began by testing all single-factor models using each of the landscape variables in turn. I then examined all multiple-variable models that I considered legitimate to determine whether they improved the significance, or explanatory power, of the model. In this process, I excluded models that contained landscape variables that were significantly correlated with each other to avoid the effects of extreme multicollinearity. Most flooded agricultural fields in the Sacramento Valley were rice fields, consequently the amounts of these two habitat types were highly correlated. Similarly, much of the semi-natural wetland in the region is on wildlife refuges causing correlations among these measures. The next stage of my analysis was to add field area to each of the models considered previously to determine whether additional relationships emerged when controlling for area. Finally, I coded each field by the geographic area in which it occurred and added this variable to each model to test whether differences in abundance within the rice growing region affected the results. This process was repeated for all 12 combinations of different taxa and scales.

Due to the exploratory nature of my analysis and logistical constraints on sample size, I used a liberal interpretation of significance results throughout. I considered all relationships for which $P < 0.10$ to be worthy of discussion in developing hypotheses from my results. I also chose not to adjust significance levels for multiple comparisons. Finally, I examined the effects of removing outliers on my regression models. Outliers were dropped from an analysis only if they improved the predictive power of the model and there was something anomalous about the outlying data point that accounted for its influence.

RESULTS

LANDSCAPE CHARACTERIZATION

It was possible to classify a large proportion of land into habitat categories using data from ground surveys and maps: 79.3% (SE = 3.6%; range = 47.4 - 97.3%), 61.4% (4.5%; 28.3 - 85.0%), and 61.9% (3.2%; 41.3 - 75.4%) of the habitat surrounding each field was classified at the 2 km, 5 km and 10 km scales, respectively. At all three scales, there were significant correlations between the proportions of flooded agricultural land and flooded rice fields in the landscape and between the amount of semi-natural wetland and land in a wildlife refuge (Table 9).

EFFECTS OF LANDSCAPE ON WATERBIRD DENSITIES

At both the 5 km and 10 km scales, goose densities were positively related to the proportion of the surrounding land that was part of a wildlife refuge ($r^2 = 0.24$, $F_{1,13} = 5.39$, $P = 0.037$, and $r^2 = 0.24$, $F_{1,13} = 5.50$, $P = 0.035$, respectively). No improvements could be made to these models by adding other variables and no other variables were significant when considered alone. In contrast, the proportion of land that was flooded rice provided the best explanation of the density of ducks, although this positive

relationship existed only at the 5 km scale ($r^2 = 0.25$, $F_{1,13} = 5.75$, $P = 0.032$). At this scale, the total area of flooded land also was marginally significant but explained less of the variance in duck densities ($r^2 = 0.18$, $F_{1,13} = 4.04$, $P = 0.066$). No other variables were significant and no multivariable models provided a better fit to the data. At the 2 km and 10 km scales, no variables were related significantly to duck densities.

Wading bird densities were not related to any landscape variables at the 2 km scale, but were positively related to the amount of semi-natural wetland in the surrounding landscape at both larger scales ($r^2 = 0.20$, $F_{1,13} = 4.50$, $P = 0.054$ and $r^2 = 0.23$, $F_{1,13} = 5.09$, $P = 0.042$ at 5 km and 10 km scales respectively). At the larger of these scales, the proportion of land in refuges also was marginally significant ($r^2 = 0.18$, $F_{1,13} = 4.06$, $P = 0.065$). At this scale, however, the amount of refuge land and semi-natural wetland were so highly correlated that they were essentially the same variable (Table 9). Altering these models, either by replacing or adding variables failed to provide a better explanation of wading bird densities. Dropping an outlier (Fig. 13), however, altered the results at the 2 km scale. Without this data point, the proportion of land that was part of a wildlife refuge became very important, increasing with bird abundance and explaining more than half the remaining variability in wading bird densities ($r^2 = 0.54$, $F_{1,13} = 16.12$, $P = 0.002$; Fig. 2). I considered the exclusion of this outlier to be justified because it represented the only site where white-faced ibis *Plegadis chihi* occurred regularly. Compared to the other wading birds considered, ibis are much more abundant and congregate in very large flocks. For example, mean densities of ibis in flooded rice fields were at least 20 times greater than mean densities of any other wading species and there was at least a 50-fold difference in standard errors (Chapter 1; Elphick & Oring 1998). Excluding this point, therefore, effectively removed the influence of an anomalous species from the wading bird group.

Finally, shorebirds densities were related positively to the proportion of the surrounding 2 km zone that was part of a wildlife refuge ($r^2 = 0.18$, $F_{1,13} = 4.11$, $P = 0.064$). When field area was included as a covariate in the model the relationship strengthened (multiple- $R^2 = 0.29$, model $F_{2,12} = 3.80$, $P = 0.053$). At the intermediate scale of 5 km, no variables were related significantly to shorebird density, although there may be a weak negative association with the amount of flooded agricultural land ($r^2 = 0.13$, $F_{1,13} = 3.04$, $P = 0.105$). This negative relationship strengthened at the 10 km scale, where the proportion of land that was flooded rice provided the best explanation of shorebird densities ($r^2 = 0.18$, $F_{1,13} = 3.98$, $P = 0.067$).

In no cases did the addition of geographic area as a blocking factor improve a model. In all regression models, the statistical power of tests was low ($1-\beta < 0.58$), even when assuming a large effect size ($f^2 = 0.35$; $\alpha = 0.05$; conventions follow Cohen 1988). Consequently, nonsignificant results could not be taken as evidence that there were no relationships. Adjusting P -values for the number of tests using the sequential Bonferroni technique (Rice 1989) renders all regression results non-significant if $\alpha = 0.10$, except that between the density of wading birds and the amount of refuge at the 2 km scale after removing the outlier. An alternative approach to addressing the potential for spurious relationships, however, suggests that this is overly conservative. Given the 12 possible relationships summarized in Table 10, one would expect only one significant result by

Table 9. Summary of landscape data and correlations among landscape variables. Data describe the landscapes around flooded rice fields, within a 2 km, 5 km, or 10 km zone, measured from the field boundary. n = 15 in all cases.

	Mean \pm SE	Min - Max	Correlation coefficients		
			% flooded farmland	% wetland	% wildlife refuge
<u>2 km</u>					
% flooded rice	19.59 \pm 2.69	7.08 - 35.46	$r = 0.995; P < 0.001$	$r = -0.453; P = 0.090$	$r = -0.337; P = 0.220$
% flooded farmland	20.12 \pm 2.61	7.08 - 35.46	-	$r = -0.400; P = 0.140$	$r = -0.261; P = 0.347$
% wetland	8.51 \pm 3.92	0.00 - 45.36	-	-	$r = 0.691; P = 0.004$
% wildlife refuge	3.95 \pm 1.87	0.00 - 24.41	-	-	-
<u>5 km</u>					
% flooded rice	11.07 \pm 1.59	3.64 - 22.45	$r = 0.971; P < 0.001$	$r = -0.134; P = 0.635$	$r = 0.549; P = 0.034$
% flooded farmland	12.91 \pm 2.20	3.64 - 26.97	-	$r = -0.208; P = 0.458$	$r = 0.564; P = 0.028$
% wetland	9.86 \pm 3.51	0.00 - 38.05	-	-	$r = 0.534; P = 0.040$
% wildlife refuge	10.40 \pm 2.67	0.00 - 25.16	-	-	-
<u>10 km</u>					
% flooded rice	6.80 \pm 1.08	2.65 - 14.38	$r = 0.999; P < 0.001$	$r = -0.360; P = 0.187$	$r = 0.151; P = 0.592$
% flooded farmland	7.38 \pm 1.29	2.65 - 16.25	-	$r = -0.363; P = 0.184$	$r = -0.164; P = 0.558$
% wetland	7.28 \pm 2.35	0.25 - 23.42	-	-	$r = 0.795; P < 0.001$
% wildlife refuge	7.53 \pm 1.86	0.04 - 19.51	-	-	-

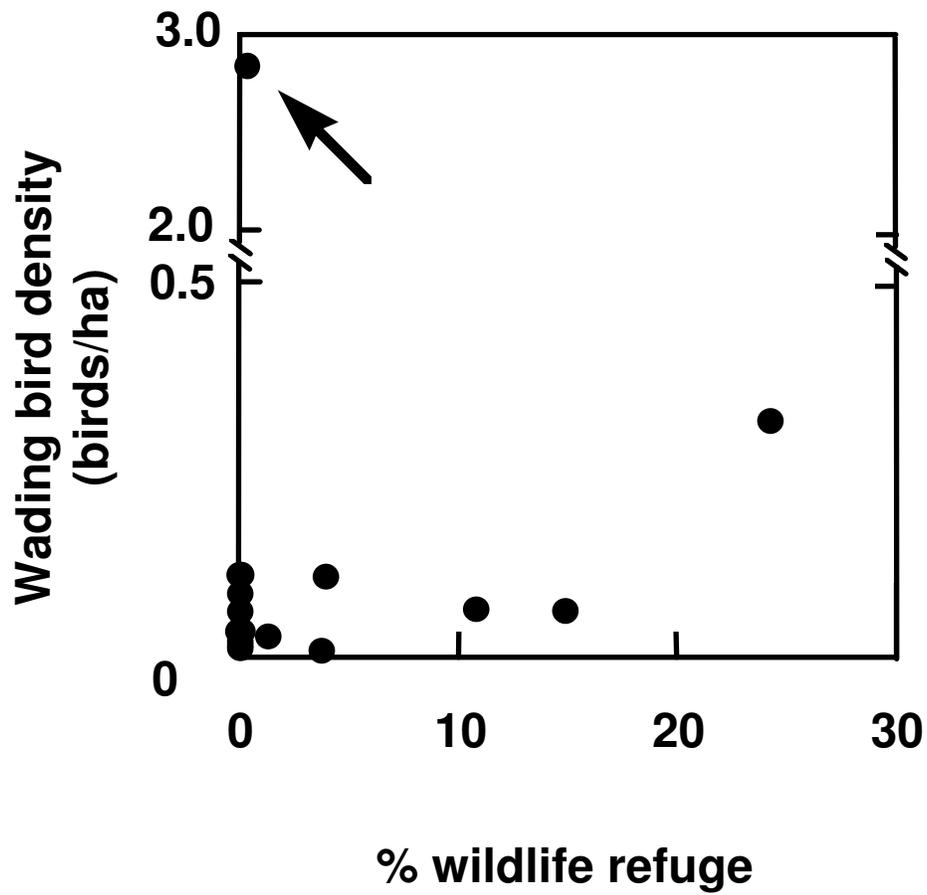


Figure 13. Scatterplot showing the relationship between the density of wading birds and the percentage of land in a wildlife refuge. The point marked by the arrow represents an anomolous field where very large flocks of white-faced ibis occurred regularly. The relationship is highly significant if this outlier is removed from the analysis (see text for details).

chance using either $\alpha = 0.05$ or $\alpha = 0.10$. Instead, I found eight relationships, which is significantly more than expected ($G_1 = 33.1$, $P < 0.001$ and $G_1 = 11.21$, $P < 0.001$ for the two α levels respectively; but, note that initial tests are not independent of each other).

DISCUSSION

Waterbird use of flooded rice fields was related to the relative abundance of features in the surrounding landscape. There were, however, differences among taxa in the landscape variables that were important and the scales at which relationships were found (Table 10). The amount of the surrounding land that was part of a wildlife refuge was related positively to the abundance of geese at scales of 5 km and 10 km. I found, however, no evidence of a relationship with duck densities. At the smallest scale (2 km), refuges also appeared to influence the abundance of shorebirds and, especially, the densities of wading birds other than white-faced ibis (i.e., the Ardeidae). At both larger scales (5 km and 10 km), the amount of semi-natural wetland was most strongly related to wading bird density irrespective of whether ibis were included. High correlations between the amount of wetland and refuge habitat mean that caution should be used when differentiating these habitats. Flooded fields located in areas containing high proportions of these habitats, however, appear to receive greater use by several waterbird groups.

The proportion of intentionally flooded rice land in the surrounding landscape appears to influence the waterbird community less than do the amounts of wetland or refuge habitat. Only two relationships were found between bird abundance and the amount of flooded land, although low statistical power may have contributed to the paucity of significant relationships.

Variation among the responses of different taxa, and at different scales, suggests that various processes may affect waterbird habitat selection. Reliance on wildlife refuges as roost sites would explain the results for geese, with birds concentrating their feeding in areas that are in close proximity to wildlife refuges where they can roost (Ely 1992; Gill 1996). A similar explanation may hold for wading birds and shorebirds. White-faced ibis roost communally in semi-natural wetlands during winter, and leave to forage in flooded fields during the day (Shuford *et al.* 1996; C.S. Elphick pers. obs.). Less information is available about the habitat needs of herons and egrets, although observations of large groups roosting in trees on refuges in the Sacramento Valley suggests that they too may rely on this habitat, and, thus, use fields close to refuges disproportionately (C.S. Elphick pers. obs.). Elsewhere, I have shown that great egrets *Ardea albus* can achieve higher feeding efficiencies (i.e., prey captures per attempt) in semi-natural wetlands than in flooded rice fields (Chapter 4). This suggests another explanation: that these birds differentially occupy areas where there is an abundance of semi-natural wetland and refuge habitat because they can maximize foraging opportunities in such areas.

Little is known about the nocturnal behaviour of shorebirds in the Sacramento Valley. Observations of flocks leaving flooded fields shortly before dusk and returning early the next morning in a predictable fashion, suggests that nocturnal roosts exist (C.S. Elphick pers. obs.). Whether these roosts are located on wildlife refuges, however, is not

Table 10. Summary of relationships between landscape features and waterbird densities. Each box contains the landscape variable that best explained the density of a taxon at a particular scale. Dashes imply no relationships were found. Signs in parentheses show direction of relationships. * $0.10 < P \leq 0.05$; ** $0.05 < P \leq 0.01$; *** $P < 0.01$.

Taxon	Scale		
	2 km	5 km	10 km
Geese	-	% refuge (+)**	% refuge (+)**
Ducks	-	% flooded rice (+)**	-
Wading birds	% refuge (+)***†	% semi-natural wetland (+)*	% semi-natural wetland (+)**
Shorebirds	% refuge (+)*	-	% flooded rice (-)*

† Significant result only found after one extreme outlier was removed.

clear. Alternatively, shorebirds may be attracted initially to wetlands that appear natural and move out into nearby flooded fields from there. Without better information on the movements of individuals, distinguishing among these explanations is impossible.

In contrast to geese, wading birds and shorebirds, ducks do not appear to be affected by the abundance of semi-natural habitat or wildlife refuges. The positive relationship with the abundance of flooded rice fields, however, suggests that ducks may congregate in areas where flooded fields are concentrated. Ducks, therefore, may not rely on more natural habitats for roost sites as do other taxa; rather they may select sections of the landscape with abundant foraging habitat. Evidence for this currently is limited; however, ducks will stay in flooded fields throughout the day and night as long as those fields are not used by hunters. The role that hunting plays in determining distribution patterns throughout the Sacramento Valley also is unclear. It is possible that hunting activities are more dispersed in areas where much land is flooded, allowing ducks to find undisturbed areas. In contrast, isolated fields may receive greater hunting pressure, and, therefore, be avoided. A better understanding of how individual birds move around with respect to these variables is necessary to understand duck use of flooded rice fields.

Variation in the relationships between landscape variables and bird densities at different scales was common to all taxa. Similar changes in the degree of correlation between the abundance of organisms and habitat features at different spatial scales have been noted previously (Hunt & Schneider 1987; Wiens *et al.* 1987; May 1994; Schneider 1994) and can be caused by changes in the scale at which either the organisms or the landscape is sampled. Only the latter was altered in my study. In previous studies, abundance often alternates between being significantly correlated with habitat features or not as the sampling scale changes (e.g., Hunt & Schneider 1987; Wiens *et al.* 1987). An understanding of which scales correlations are found at can provide information about how organisms perceive their surroundings and, hence, how changes in those surroundings may affect populations.

At “small” scales, correlations with landscape features can be unimportant for two reasons. First, organisms may alter the surroundings in ways that overwhelm landscape effects (Logerwell & Hargreaves 1996). Second, the behavioral responses of individuals will have a greater impact on their spacing patterns at small scales than at larger ones. For example, the lack of any relationship between goose densities and landscape features at the 2 km scale may be because food depletion is rapid within such a small area. This would preclude the maintenance of high densities over a long enough time for any relationship to be apparent when considering average use over the entire winter as was done in this study. At larger scales of landscape measurement, habitat area increases geometrically, and the effects of short-term depletion are less likely to swamp any landscape influence. An alternative explanation is that at such a small scale, the distribution of geese is determined primarily by the way in which individuals respond to factors such as the distribution of food, competitors, and predators, and is essentially random with respect to the landscape.

At “large” scales, the landscape also may be unimportant because landscape measures become dominated by areas that have no relevance to the population being studied (e.g., because they do not contain appropriate habitat or because members of the

population cannot, or need not, perceive conditions over such large areas). In between these “small” and “large” scales there may be some intermediate zone in which landscape features are important. Moreover, this alternating of importance may continue as further scales are considered; i.e., correlations may exist at “very large” scales, but not exist at “extremely large” scales (Hunt & Schneider 1987). Determining what is “small” and “large” will depend on the species being studied (With 1994), and possibly on the nature of landscape (Elphick & Hunt 1993). For example, my study suggests that a 2 km scale may be too small for the Sacramento Valley landscape to influence geese and duck densities, but not too small to affect wading birds or shorebirds. Similarly, the range of “intermediate” scales that influence ducks appear to be fairly narrow, somewhere between 2 km and 10 km. In contrast, my results indicate that wading birds are influenced at scales that at least span this range.

When correlations existed between landscape features and waterbird abundance, they tended to be positive (7 out of 8 cases). This result suggests that birds concentrate in areas where there is an abundance of suitable habitat (which I term the attraction hypothesis), rather than simply spreading out more in more habitat (the dilution hypothesis). This pattern applied generally across the taxa and scales considered. Over short time scales, this result is not surprising given the tendency of most waterbirds to aggregate during the nonbreeding season. These aggregations, however, would be expected to move around in the landscape as they deplete patches of food. Evidence for attraction when averaging densities over the entire winter, therefore, suggests that waterbird populations favored certain habitat patches over others. The single exception to this pattern were shorebirds at the largest scale, when densities declined in areas with an abundance of flooded rice fields. This result suggests that something constrained the total number of shorebirds at the 10 km scale, although it is not clear what this might be.

The nonrandom variation in the densities of birds using flooded fields suggests that suitable habitat may not be limiting for waterbirds in the Sacramento Valley. If habitat were limiting, all fields would be used by the same, maximal, density of individuals when densities are averaged across the winter. Hence, there would be no variation in use among suitable patches at this temporal scale. This hypothesis makes two assumptions. First, it assumes that birds are capable of finding all patches. This seems reasonable, given the vagility of the species concerned, but has not been tested. The second assumption is that there are no differences in habitat quality between flooded fields that are surrounded by other flooded habitats, refuges, or both, and those flooded fields that are isolated. Given the apparent uniformity of rice fields, it seems unlikely that food availability varies in this way, although it is possible that farming methods differ (e.g., because isolated fields are in areas less suitable for rice-farming) and this may affect the food supply. Predation risk also may be correlated with the isolation of flooded fields. Unflooded rice fields harbor greater densities of avian predators than do flooded fields (Chapter 4; C.S. Elphick unpubl. data). Whether predator density correlates with predation risk is unknown. If this relationship exists, predation would be expected to be positively correlated with the amount of unflooded land surrounding a flooded field. Raptors also fly over semi-natural wetlands at a high rate (Chapter 4), however, weakening this explanation. Measurements of habitat quality variables in fields with

different surroundings are necessary to address the assumption that quality does not vary as a function of the landscape.

This analysis was conceived as an hypothesis-generating, rather than an hypothesis-testing, exercise (James & McCullough 1985). The relationships reported herein are correlative and based on data collected opportunistically. In some cases, the zones around each field that were used to characterize the landscape overlapped with the zones around other fields, reducing the independence of observations. Moreover, the patterns described herein suggest that no two fields in the entire study area are completely independent of each other. If aspects of the landscape surrounding a site commonly affect the abundance of animals at that site, this lack of independence among replicates could be widespread in ecological studies. In addition, sample sizes were fairly small; the level of statistical significance often was marginal; and there is a risk that a few significant results may be spurious because of the number of tests conducted. As in many studies, the interpretation of nonsignificant results should be tempered by the knowledge that significance tests were conducted with low statistical power. Consequently, all interpretations should be viewed as tentative. Nonetheless, the observed patterns are provocative and provide insights into animal distributions at different spatial scales and their possible ecological bases. Testing the numerous hypotheses discussed herein would greatly enhance our understanding of how waterbirds select habitats.

MANAGEMENT IMPLICATIONS

These results have several important management implications. Flooding rice fields can have important benefits for waterbirds (Chapters 1, 2 and 4; Payne & Wentz 1992, Brouder & Hill 1995; Elphick & Oring 1998). The Central Valley of California is one of the most important areas for wintering waterbirds in North America, but has undergone extensive wetland losses over the last two centuries (Frayer *et al.* 1989). Consequently, the restoration of some form of waterbird habitat could have far-reaching consequences for the conservation of continental waterbird populations. Moreover, the ubiquity of rice agriculture in areas important for waterbirds (e.g., Fasola & Ruíz 1997; Lane & Fujioka 1998) suggests relevance to other parts of the world.

My results suggest three specific hypotheses of relevance to managers. First, the clumping of flooded fields at a 5 km scale is expected to increase the densities of ducks using specific fields. Second, a similar effect on other waterbirds is expected if fields are located in the vicinity of large areas of semi-natural wetland and/or wildlife refuge. Finally, the strength of these effects can be expected to be scale-dependent. For example, flooded fields located with an abundance of wildlife refuge land within 2 km can be expected to receive increased use by shorebirds, but not necessarily by geese. In contrast, the opposite is expected to be true for fields with an abundance of refuge land within 5-10 km. Although these hypotheses require testing, it is clear that they have important implications for decisions about where to concentrate efforts to encourage farmers to flood their fields and where to locate wetland restoration projects.

SUMMARY

Habitat use can be influenced not only by characteristics of the habitat, but also by the nature of the surrounding landscape. Waterbirds have a suite of characters that make them ideal for investigating the influence of the landscape on habitat selection, yet few studies have addressed these species. In this study, I conducted an exploratory analysis of the relationships between the densities of waterbirds using flooded rice fields in winter and characteristics of the surrounding landscape in California's Sacramento Valley. The spatial scale at which the landscape was described was varied by calculating the amount of each habitat type within 2 km, 5 km, and 10 km of each field's boundary. Densities of geese, wading birds, and shorebirds were positively correlated with the amount of wildlife refuge or semi-natural wetland in the vicinity of a flooded field. These two variables were highly correlated with each other and their effects could not be assessed separately. For all species, correlations were scale-dependent. The abundance of flooded rice fields in the landscape was less likely to be related to bird use of flooded fields, but was positively related to duck densities at a 5 km scale and negatively related to shorebird densities at a 10 km scale. Thus, patterns in the landscape were related to waterbird densities in flooded fields. The nature of the relationship differed among taxonomic groups and depended on the scale at which the landscape was characterized. These results suggest a number of hypotheses about the ways in which different waterbirds use landscape features to select habitat patches and lay the groundwork for future studies of waterbird habitat use.

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CHAPTER FOUR
FUNCTIONAL EQUIVALENCY BETWEEN ANTHROPOGENIC AND NATURAL HABITATS?
WATERBIRDS IN CALIFORNIA RICE FIELDS AND WETLANDS

Assessing the quality of different habitats is an important goal for conservation biologists and wildlife managers. High quality habitats contribute more to population persistence than do low quality habitats (Block & Brennan 1993). These good habitats, therefore, should be the first to be preserved and, where possible, their extent should be increased. Evaluating the role of anthropogenic habitats, relative to their natural forebears, is especially important because humans continue to convert lands for their own ends at a considerable rate. For example, the area of land that had been developed for farming in the world increased by 13.5% between 1950 and 1985 (Cramer and Jensen 1991) and agricultural land currently occupies more than a third of the Earth's ice-free land surface (Urban & Vollrath 1984).

Habitats often are considered to be of high quality when they contain high animal densities, but there are several situations when this assumption is not true (Van Horne 1983). Various studies, both empirical (Van Horne 1981; Vickery *et al.* 1992; Purcell & Verner in press) and theoretical (Fretwell 1972; Bernstein 1991a, b; Sutherland 1996), have supported the view that this assumption is not always valid. Van Horne (1983) defined habitat quality explicitly in terms that incorporate information on density, reproductive rate and survival. Using her formula, habitat quality provides a direct measure of the contribution of the habitat to population persistence. As Van Horne (1983) pointed out, however, estimating all the parameters to measure habitat quality is an onerous, if not impossible, task in most cases. This is especially so when the species of interest are long-lived because it may take many years to collect appropriate data to estimate reproduction and survival accurately. Migration also complicates matters, because it makes it necessary to estimate the importance of one habitat (e.g. a wintering site) to processes that occur elsewhere (e.g. reproduction at a breeding site). One solution to this problem is to use surrogate measures that can be expected to correlate with survival and reproduction. For instance, overwinter survival is likely to be related to the ability to find food and avoid predators (Sutherland 1996), and measures of these activities often are used as indicators of survival rates (e.g. Cresswell & Whitfield 1994; Goss-Custard *et al.* 1995a, b).

Worldwide, the extent of natural wetlands continues to decline as land is converted to accommodate increasing human populations. Rice agriculture presents a potential surrogate habitat for species that use natural wetlands (Fasola & Ruíz 1996). Rice fields generally are inundated for long periods and often occur in areas where wetland losses have been greatest. For example, restoring wetland habitats to the Central Valley of California is important because this region is the primary wintering area for many species of migratory waterbirds in western North America (Heitmeyer *et al.* 1989). More than 86% of the Central Valley's historic wetlands have been destroyed and rice agriculture currently occupies as much land as do wetlands (Frayer *et al.* 1989). If, therefore, inundated rice fields can act as surrogates for natural wetlands, they could

double the area of aquatic habitat available and contribute greatly to the conservation of waterbirds.

To improve air quality, the State of California's Rice Straw Burning Act (AB 1378, 1991) has required reductions in the area of rice stubble that can be burned after harvest. To increase straw decomposition rates, many farmers have begun to flood their fields between November and March. This change in the way rice is farmed has created an opportunity to increase considerably the amount of flooded habitat in the region (Payne & Wentz 1992; Brouder & Hill 1995). In addition, passive flooding of fields during the nongrowing season is an option in many parts of the world and the situation in California provides a model for testing whether such management would be effective.

Little is known about the quality of flooded rice fields compared to natural wetlands. Agricultural fields that are flooded throughout the winter, however, can be used by large numbers of many waterbird species. Indeed, densities of 24 waterbird species were significantly greater in flooded rice fields than in unflooded fields (Elphick & Oring 1998). For most of these species, unflooded fields do not appear to constitute habitat and flooded fields are clearly beneficial in comparison. Other species [e.g. great egret *Ardea albus*, long-billed curlew *Numenius americanus*] occurred regularly in both flooded and unflooded fields. For these birds, it is less certain which is the better habitat.

In this paper, I assess the quality of flooded rice fields in comparison to more natural wetlands in the same area. Due to extensive management, none of the wetlands remaining in the Central Valley bear much resemblance to historical habitats. Wetlands on wildlife refuges and hunting clubs are the nearest approximation to historic wetlands (Heitmeyer *et al.* 1989); throughout, I refer to these wetlands as "semi-natural". I also compared the quality of flooded and unflooded rice fields for waterbird species which regularly occur in both habitats. I tested the null hypotheses that (1) food abundance, (2) perceived predation threat, (3) feeding performance, and (4) time allocated to different behaviors, do not differ among habitats. Understanding the relationships between these variables and habitat types is important because they will provide insight into the question of whether habitats created by humans can function in the same way as natural habitats.

METHODS

STUDY AREA

Several field assistants and I conducted field work in the southern Sacramento Valley, California; the portion of the Central Valley where most rice in the western USA is grown. We sampled rice fields throughout this region and semi-natural wetlands at the Gray Lodge Wildlife Management Area, Sacramento National Wildlife Refuge Complex, and at several private hunting clubs. Food abundance samples were collected between November and March, 1993/94; other data were collected over the winters of 1993/94 to 1995/96.

FOOD ABUNDANCE

We sampled food abundance in flooded rice fields, unflooded rice fields and semi-natural wetlands, defining an experimental unit as a wetland management unit or rice paddy that was surrounded by a raised earthen barrier separating it from adjacent areas. Of the sites

to which we had access, I randomly selected nine replicates of each treatment and we sampled each once. In each experimental unit, we sub-sampled the benthos and water column at five randomly selected points and used the mean values in analyses.

Sub-samples consisted of a 7.7 cm diameter core taken to a depth of 8 cm, which is the maximum depth to which birds are likely to probe. We divided each core into three strata (a) the water, (b) the top 4 cm of benthos and (c) the bottom 4 cm of benthos. These subdivisions allowed separate evaluation of food availability for different species. For each sub-sample, we measured the water depth and calculated the volume of water sampled. Each subdivision was sieved with a 500 μm mesh sieve to remove soil and the remaining plant and animal material were stored in alcohol. Later, samples were sorted to separate invertebrates and seeds from straw and root material. Rose bengal, which stains animal protein red, was used to improve sorting efficiency (Mason & Yevich 1967).

Rice fields are commonly used by both predominantly granivorous species (e.g. waterfowl) and invertebrate predators (e.g. shorebirds and herons), so I examined differences in the abundances of both types of food. For each sample, we determined (a) the total density of macroinvertebrates ($>500 \mu\text{m}$), (b) the density of rice grain, and (c) the total density of other seeds. Invertebrate biomasses in our samples were too small to estimate accurately. Composition of the invertebrate communities will be described in detail elsewhere (R. Schroeter, O. Kulkoyluoglu & C. Elphick in prep.).

PREDATION THREAT

During each set of behavioral observations (see below), we quantified the perceived predation threat by recording every potential predator seen crossing the experimental unit being sampled. I assumed that birds would use this same information as an index of the risk of being preyed upon. I divided predator counts by the amount of time spent watching the unit to get an estimate of relative predation threat for each set of observations. I pooled predator data in three ways: (a) species that regularly feed on shorebirds and ducks (eagles, harriers, accipiters, and falcons), (b) species likely to attack larger prey such as herons and geese (eagles, dogs, coyotes), and (c) all predators.

FEEDING PERFORMANCE

Foraging data were collected by several people over the course of the study (73% by two people). We collected foraging data for six species, all of which feed predominantly on invertebrates: great egret, black-necked stilt *Himantopus mexicanus*, long-billed curlew, greater yellowlegs *Tringa melanoleuca*, long-billed dowitcher *Limnodromus scolopaceus* and dunlin *Calidris alpina*. Observations of egrets and curlews were made in three habitats: semi-natural wetlands, flooded rice fields and unflooded rice fields. The remaining species rarely occurred in unflooded rice fields (Chapter 1; Elphick & Oring 1998). For each management unit, we selected up to five individuals of each species and conducted one 2 min focal observation on each (5 min for great egrets, which feed less rapidly). Each unit was sampled on one day only. For each observation, we recorded the number of pecks made (attacks), and the number of pecks that were successful (feeds). Occasionally (7% of all observations) birds flew away part way through an observation.

If the observation was more than half way through, we recorded the time elapsed and the observation was included in the analysis; if not it was discarded.

I defined an attack as any occasion on which the bird's bill entered the water or mud; when multiple probes were made between the bill's entry and exit from the water (e.g. "stitching" by dowitchers) I recorded a single attack. Attacks were deemed successful if one of the following conditions applied: (a) a prey item was seen to be captured and swallowed, (b) movements of the gular region consistent with swallowing were made after the attack, or (c) the bird showed evidence of prey transport either by "head-throwing" (i.e. inertial feeding; Gans 1961) or "mandibular spreading" (i.e. surface tension feeding; Rubega & Obst 1993, Rubega 1997). I converted the numbers of attacks and feeds to rates by dividing by the time spent watching. In addition, I calculated feeding efficiency by dividing the number of feeds by the number of attacks.

During observations, we collected data on a number of variables that may influence feeding performance: date, time of day, perceived predation threat (see above), group size, and water depth. Group size was the number of birds using the experimental unit and was subdivided into the numbers of conspecifics, waterfowl and other waterbirds (including conspecifics), because the effects of each subgroup on foraging performance may differ. I measured water depth, which may influence prey availability, relative to the bird's height by estimating to where the water came on its legs during the observation. Paired observations, conducted by different people watching the same bird simultaneously, revealed significant observer-effects for several performance measures (C.S. Elphick, unpubl. data). To control for these effects, I also recorded the observer for each sample and incorporated this variable into multivariate analyses (see below). When observer effects were confounded with habitat differences, supplemental tests were conducted to examine whether the habitat differences persisted when each persons observations were considered separately.

TIME ALLOCATION

We used scan-sampling (Altmann 1974; Martin & Bateson 1993) to collect time budget data for the six species for which we measured feeding performance, plus killdeer *Charadrius vociferus* and least sandpiper *Calidris minutilla*. Experimental design followed that described for foraging performance. We scanned each unit up to five times to record the behavior of each individual of a species; adjacent scans were at least 30 min apart. If a flock took off part way through a scan-sample, we estimated the proportion of the flock that had been sampled and if it was less than 75%, discarded the sample.

For each species, I calculated the proportion of the birds that were engaged in each activity. This is equal to the time a bird spends on each behavior if birds are assumed to allocate time equally. I defined behaviors as follows: feeding - bird was probing, pecking, or looking at the ground; vigilance - bird was standing still with its head up and eyes open but was not engaged in preening or obvious interaction with other birds; sleeping - bird had its head under its wing or its eyes closed; preening - bird was preening feathers or stretching; aggression - bird was chasing another individual or being chased. Other activities (e.g. copulation, take-off) were combined into a miscellaneous category. For analyses, I used the mean proportion of time spent in each activity for each

experimental unit. Data on potential covariates were collected as described for foraging performance.

DATA ANALYSIS

I tested for gross differences in food abundance and predation threat (hypotheses 1 and 2), without focusing on the portions of these measures for individual taxa. Behavioral differences (hypotheses 3 and 4) were examined only for species that were common, amenable to observations, and representative of the full range of body sizes, foraging behaviors, microhabitat use, and diets found among wading birds that use rice fields.

I compared food abundance and predation threat in each habitat treatment with multiple regression. I used date as a covariate because I expected temporal variation in abundance due to invertebrate reproduction and seed depletion. Additionally, I expected predation threat to peak mid-winter, when predators were most abundant, and in the middle of the day, when conditions were more suitable for soaring flight typical of the most common predators. These expectations predicted negative quadratic relationships between predation threat and both date and time of day, and I included linear and quadratic terms for each predictor variable. Time of day was taken as the midpoint of the observation period. I also incorporated predation threat into analyses of behavioral variables (see below) as an independent variable. In all analyses, I examined two measures of perceived predation threat: one that excluded predators that were unlikely to prey upon the focal species [measures (a) for shorebirds and (b) for egrets; see above for definitions] and one that included all potential predators [measure (c)].

In my analysis of behavioral traits (foraging performance and time allocation), I considered management units, rather than individual birds, to be experimental units and used mean values of each performance and covariate measure. I used a two-step process to examine differences in behavioral traits among habitat treatments. First, I compared mean values of each trait using *t*-tests or analysis of variance (ANOVA) to test for differences among habitats. Second, I conducted a sequential analysis in which I examined the variation in each behavioral measure using general linear models. In each case, I began with a model that included the habitat variable and all potential covariates. I then reduced the model by sequentially dropping the covariate with the largest *p*-value, until only habitat and significant covariates remained. Detecting effects of some covariates may not have been possible using means calculated for each experimental unit. For example, time of day varied among observations made at a single site; using means would have prevented an examination of this variance. Similarly, observer was a categorical variable and no mean could be calculated. Consequently, I conducted supplementary analyses in which I considered each observation as a replicate. These supplementary analyses were not appropriate tests of the habitat effect, because subsamples were not independent, but allowed an exploratory examination of the effects of additional covariates.

The first step of this behavioral analysis addressed whether or not the habitats differed, the issue of most interest to managers. The second step provided an exploratory approach to addressing the mechanisms influencing behavior by asking three additional questions: (1) Did the covariates affect behavioral traits? (2) Can significant differences

among habitats be explained by covariates? (3) Did habitat differences emerge after covariate effects had been accounted for?

Violating the assumption of homoscedacity can affect the results of *t*-tests and ANOVA (Milliken & Johnson 1992). Throughout, I used Levene's tests (Levene 1960) to detect unequal variances in the model residuals. When variances were unequal, I used either separate variance *t*-tests (Zar 1984) or repeated analyses using transformed data. Count data were log transformed; percent data were transformed to arcsine [square root (*y*)]. If transformations failed to equalize variances, I used a nonparametric equivalent to the original test; for multiple regression models, where there was no nonparametric equivalent, I present the results of the original parametric tests and note that assumptions were violated.

Throughout, I used an α -level of 0.05. I calculated the statistical power of tests assuming large and medium effect sizes (see Cohen 1988 for quantitative values and qualitative descriptions of these effect sizes for specific tests). I viewed power greater than 0.80 as evidence that a non-significant result meant there was no difference among treatments. For nonparametric tests, I used guidelines in Siegel & Castellan (1988) to estimate minimum power.

RESULTS

FOOD ABUNDANCE

Despite considerable differences in management and appearance among rice field and semi-natural wetland habitats, invertebrate abundance did not differ among treatments for any of the three strata that core samples were subdivided into ($p > 0.45$ in all cases, Fig. 14). Only densities in the water column varied temporally ($F_{1,18} = 5.03$, $p = 0.037$). Variances, however, were high (Fig. 14) and statistical power to detect even a large effect size was low ($1-\beta = 0.32-0.40$). Densities of rice grain and other seeds differed among treatments when all strata were combined ($F_{2,23} = 68.81$, $p < 0.001$, and $F_{2,21} = 8.78$, $p = 0.002$, respectively). When individual strata were considered separately, only the number of non-rice seeds in the water column did not differ among treatments ($p < 0.005$ for all other tests; Fig. 14). Post-hoc tests revealed that these differences were attributable primarily to predictably lower densities of rice grain and higher densities of other seeds in natural wetlands than in either rice habitat ($p < 0.05$ in all cases). The two rice treatments differed only in the density of seeds in the water column; note that some unflooded fields contained standing water from rainfall or flooding.

PREDATION THREAT

Most (> 99%) of the predators recorded during this study were birds (Falconiformes and Strigiformes). Predators occurred in flooded rice fields at significantly lower rates than in unflooded fields or semi-natural wetlands (Fig. 15A). This pattern also held when I considered only species that feed regularly on shorebirds and ducks, but not when I compared predators of larger birds (Fig. 15B, C). Neither date nor time were significant ($p > 0.3$ for all models) when included as covariates in linear regression models, although variance heterogeneity may have affected this result.

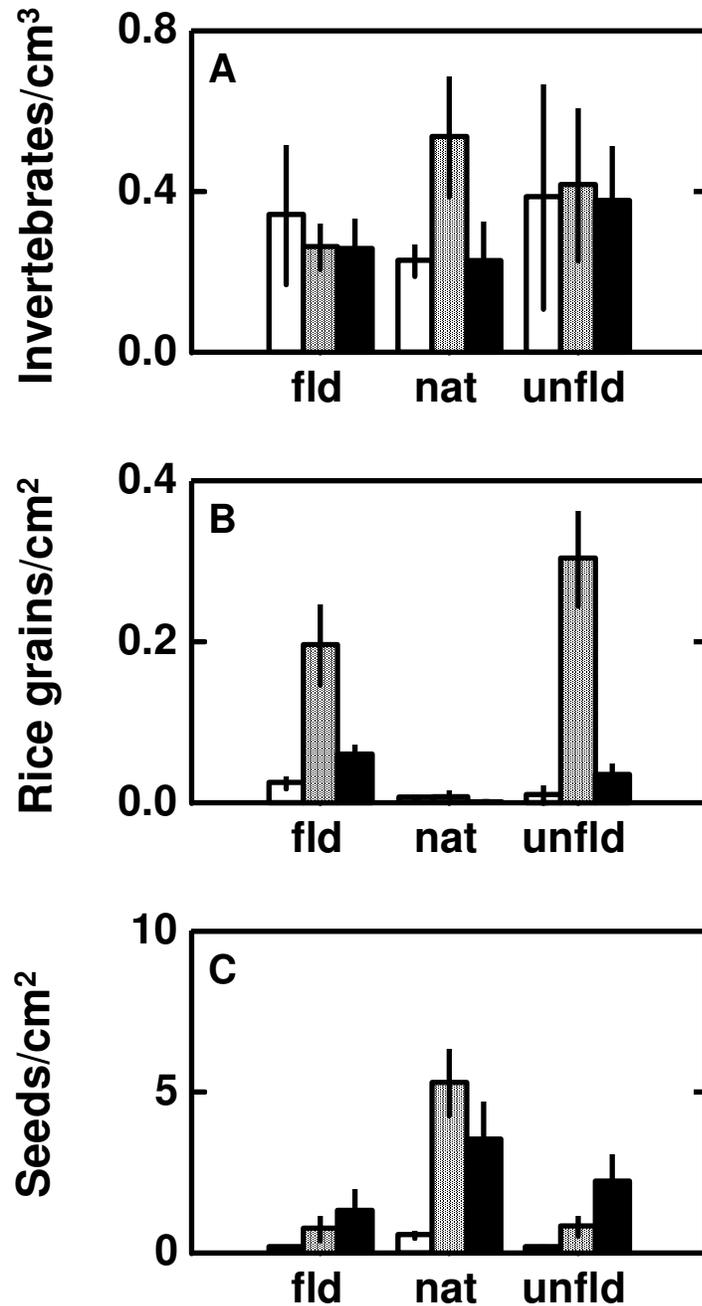


Figure 14. Food abundance in flooded rice fields (fld), semi-natural wetlands (nat) and unflooded rice fields (unfld). A. Total invertebrates (> 500 m)/cm³. B. Rice grains/cm². C. All other seeds/cm². Mean densities (SE) are given for the water column (open), top 4 cm of the benthos (shaded) and bottom 4 cm of the benthos (solid).

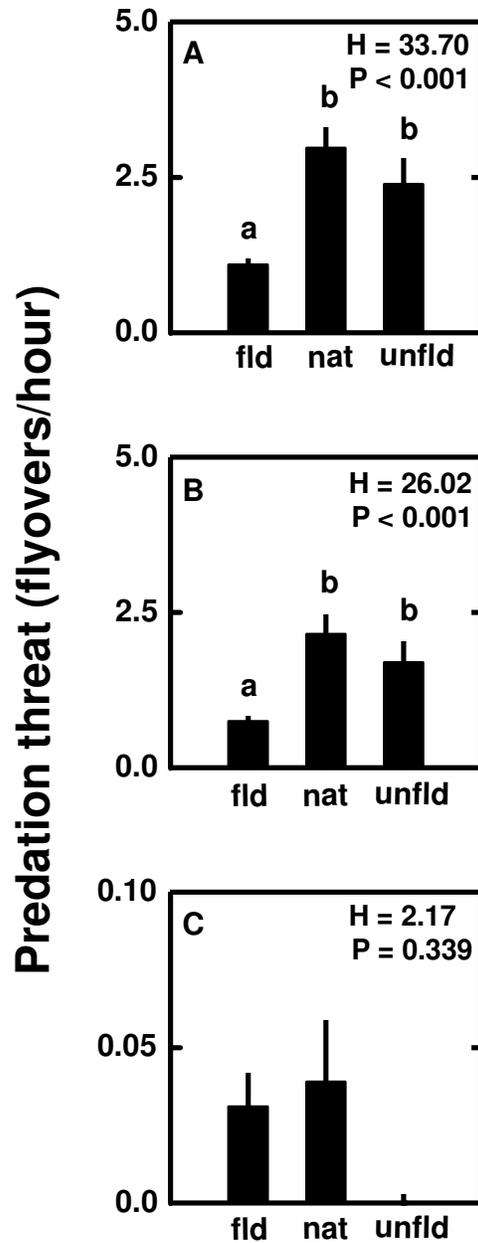


Figure 15. Predation threat in different habitat types, measured as the rate at which predators cross the unit. A. All predators combined. B. Predators that specialize on shorebirds and ducks. C. Predators that can take larger prey. Statistical comparisons were made with Kruskal-Wallis tests. Habitats with different letters were significantly different using Dunn's multiple comparison test. Sample sizes for flooded rice fields (fld), semi-natural wetlands (nat) and unflooded rice fields (unfld) were 150, 52, and 29 respectively.

Table 11. Results of significance tests on foraging performance measures shown in Fig. 16. Tests used for each variable depended on the number of habitat treatments and results of Levene's variance homogeneity tests. Subscripts give degrees of freedom. Sample sizes are for flooded rice fields (fld), semi-natural wetlands (nat) and unflooded rice fields (unfld); only great egret and long-billed curlew were recorded in unflooded fields.

	Sample sizes (fld, nat, unfld)	Test	Test statistic	<i>p</i>
<u>Attack rate</u>				
Great egret	35,11,16	ANOVA ^a	$F_{2,51} = 14.17$	< 0.001 ^b
Black-necked stilt	6,20,-	Pooled <i>t</i> -test	$t_{24} = 1.44$	0.163
Greater yellowlegs	49,22,-	Separate variance <i>t</i> -test	$t_{28.2} = 0.20$	0.841
Long-billed curlew	30,2,13	ANOVA	$F_{2,42} = 0.16$	0.854
Dunlin	13,6,-	Pooled <i>t</i> -test	$t_{17} = 0.08$	0.939
Long-billed dowitcher	19,11,-	Pooled <i>t</i> -test ^a	$t_{28} = 1.65$	0.109
<u>Feeding rate</u>				
Great egret	35,11,16	Kruskal-Wallis	$H = 20.49$	< 0.001 ^b
Black-necked stilt	6,20,-	Pooled <i>t</i> -test	$t_{24} = 0.84$	0.411
Greater yellowlegs	49,22,-	Pooled <i>t</i> -test	$t_{69} = 1.71$	0.091
Long-billed curlew	27,2,11	ANOVA ^a	$F_{2,37} = 2.02$	0.147
Dunlin	13,6,-	Pooled <i>t</i> -test	$t_{17} = 0.57$	0.575
Long-billed dowitcher	19,11,-	Pooled <i>t</i> -test	$t_{28} = 0.52$	0.606
<u>Efficiency</u>				
Great egret	32,11,11	Kruskal-Wallis	$H = 6.17$	0.046 ^c
Black-necked stilt	6,20,-	Pooled <i>t</i> -test	$t_{24} = 0.42$	0.680
Greater yellowlegs	49,22,-	Pooled <i>t</i> -test	$t_{69} = 2.47$	0.016
Long-billed curlew	30,2,13	ANOVA ^a	$F_{2,42} = 4.11$	0.023 ^d
Dunlin	13,6,-	Pooled <i>t</i> -test	$t_{17} = 1.22$	0.239
Long-billed dowitcher	19,11,-	Pooled <i>t</i> -test	$t_{28} = 0.33$	0.745

^a Data transformed to remove variance heterogeneity.

^b Result of multiple comparison test: (fld = nat) > unfld.

^c Result of multiple comparison test: nat > fld, nat = unfld, fld = unfld.

^d Result of multiple comparison test: nat > (fld = unfld).

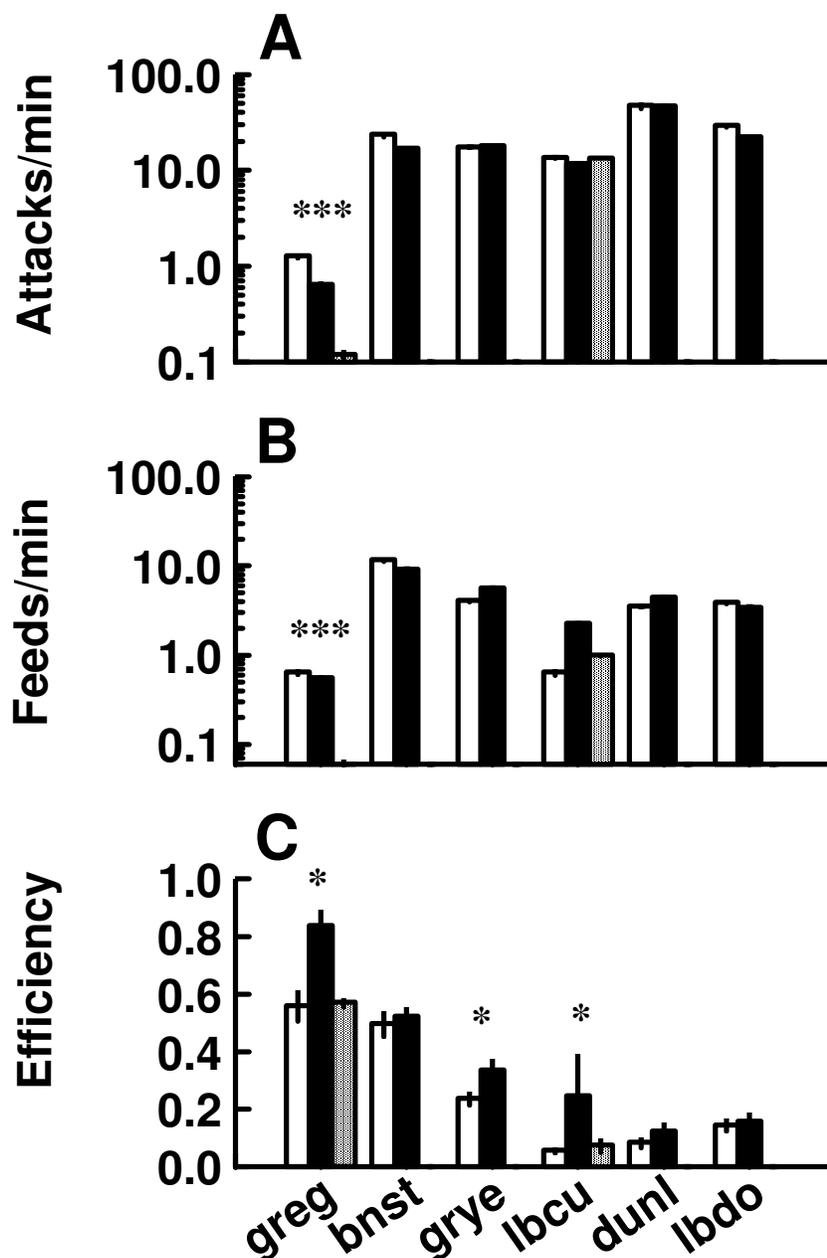


Figure 16. Mean (\pm SE) feeding performance for six waterbird species in different habitat types. A. Attack rate. B. Feeding rate. C. Feeding efficiency. Open bars = flooded rice fields, solid bars = semi-natural wetlands, shaded bars = unflooded rice fields; only great egret and long-billed curlew occurred in unflooded fields. Species codes: greg = great egret, bnst = black-necked stilt, grye = greater yellowlegs, lbcu = long-billed curlew, duml = dunlin, lbdo = long-billed dowitcher. Significance tests are given in Table 11; * $0.05 > p > 0.01$, *** $p < 0.001$. Note that a log scale is used for the y-axes of A and B, but not C.

FORAGING PERFORMANCE

Five species attained their highest mean attack rates in flooded rice fields; however, in no cases were there statistically significant differences between flooded fields and semi-natural wetlands (Table 11, Fig. 16A). Feeding rate also did not differ between these two treatments for any species (Table 11, Fig. 16B). Great egrets made significantly fewer attacks and captured fewer prey in unflooded fields than in either flooded habitat (Table 11, Fig. 16A, B). On average, all species fed more efficiently (i.e. they made more captures per attempt) in semi-natural wetlands than in flooded fields, and in three cases these differences were significant (Table 11, Fig. 16C). Estimates of the statistical power of the non-significant tests, using a large effect size, indicated that sample sizes were not adequate to conclude that there were no differences in most cases ($1-\beta = 0.32-0.86$; only the attack rate and feeding rate tests for greater yellowlegs had power greater than 0.80). Adjusting probabilities for multiple comparisons, using the sequential Bonferroni method, suggested that only the differences in attack and feeding rates found for great egrets are significant at $\alpha = 0.05$ (to do this, my grouping criterion was to combine all tests for a particular measure; i.e. $k = 6$, Rice 1989).

All covariates had a significant effect in at least one feeding performance model (Table 12). At least one measure of predation threat appeared in 10 of the 18 models. Differences among observers and effects of water depth were each found in eight models. The two temporal variables, date and time of day, were detected in seven and eight models respectively. Finally, the three measures of group size all appeared in less than half of the models, with the numbers of waterfowl and conspecifics rarely having a significant effect (Table 12). Directions of partial correlation coefficients varied among performance measures and species but no consistent patterns were found.

Many of the covariates were correlated with each other. Consequently, relationships between covariates and foraging measures should be viewed as tentative in the absence of controlled experiments. There also was a significant association between habitat classes and observers ($\chi^2_8 = 30.76, p < 0.001$, when data for all species were combined), meaning that observer's efforts were not randomly distributed across habitats. This last result, combined with the apparent extent of differences among observers in measuring foraging performance (Table 12, C.S. Elphick unpubl. data), raised the possibility that habitat differences were caused by measurement differences among observers. To control for this possibility, I repeated all those tests that had indicated significant differences among habitats for each observer separately. In all cases, significant differences persisted.

The inclusion of covariates into habitat comparisons resulted only in minor changes in the patterns of significant differences among treatments. After the effects of covariates had been controlled for, long-billed dowitchers had higher attack rates in flooded fields ($F_{1,25} = 5.41, p = 0.029$) and black-necked stilts were somewhat more efficient foragers in semi-natural wetlands ($F_{1,21} = 4.25, p = 0.051$). Also, I failed to find a difference in the foraging efficiency of long-billed curlews when covariates were added to the model ($F_{2,34} = 0.72, p = 0.494$). The overall similarity of significance tests calculated with and without covariates indicates that the variables I measured cannot

Table 12. Significant covariates from exploratory models of the factors affecting foraging performance measures. All models also included habitat type. Italics denote results that should be viewed with caution because model errors did not have equal variances and no suitable transformation could be found. Specific predation threat only included species likely to prey on the focal species.

	Attack rate	Feeding rate	Efficiency
Great egret	specific predation threat* <i>observer***</i> <i>time of day**</i>	<i>observer***</i> <i>time of day**</i>	date**
Black-necked stilt	<i>observer***</i> <i>time of day***</i>	total predation threat* <i>observer***</i> <i>time of day*</i>	specific predation threat** <i>observer***</i> water depth* time of day* # other waterbirds**
Greater yellowlegs	<i>total predation threat*</i> water depth**	water depth* # other waterbirds*	<i>observer***</i>
Long-billed curlew	total predation threat* <i>observer***</i> date** time of day*	date**	date** <i>time of day*</i>
Dunlin	total predation threat*** date*** # other waterbirds* # waterfowl*	specific predation threat* water depth*	total predation threat* date* water depth*** # other waterbirds*** # waterfowl*** # conspecifics*
Long-billed dowitcher	total predation threat* <i>observer***</i> water depth** date** # waterfowl**	total predation threat* water depth* # other waterbirds** # waterfowl** # conspecifics**	total predation threat* <i>observer***</i> water depth** time of day* # other waterbirds*

* $0.05 > p \geq 0.01$, ** $0.01 > p \geq 0.001$, *** $p < 0.001$

explain the differences in foraging performance found among habitats and that inherent differences among habitats are not being masked by these other variables.

TIME ALLOCATION

Few significant differences were found among habitat treatments (Table 13, Fig. 17). The statistical power of these tests indicated that large effects should have been detected if they existed (i.e. $1-\beta > 0.80$) for all species except for black-necked stilt, long-billed curlew and least sandpiper (for these species, $1-\beta \approx 0.36 - 0.70$). Power was low (< 0.80) for medium effect sizes for all species. Both greater yellowlegs and long-billed dowitchers spent more time feeding in flooded rice fields than in semi-natural wetlands. Dunlin were more aggressive in flooded fields than in semi-natural wetlands. Long-billed curlew were more vigilant in semi-natural wetlands than in either rice habitat. Long-billed dowitchers spent more time sleeping and black-necked stilts spent more time preening in natural wetlands compared to flooded rice fields. Finally, great egrets spent significantly more time sleeping in unflooded fields than in the other two habitats. The time budgets of killdeer, greater yellowlegs, and least sandpipers did not differ among habitats. If probabilities are adjusted for multiple comparisons, using the sequential Bonferroni method, most of these differences disappear. Only the differences in the amount of time greater yellowlegs and long-billed dowitchers spent feeding, and the time allocated to sleeping by dowitchers, remained significant (assuming $\alpha = 0.05$ and grouping tests by species; i.e. $k = 5$, Rice 1989).

The second part of this analysis involved assessing the influence of additional variables on time allocation. All variables played a significant role in at least some models (Table 14). Observer effects were found to be important more frequently than any other variable, affecting some aspect of time allocation for seven of eight species. Observer effort was not randomly distributed across habitat types ($\chi^2_8 = 107.36, p < 0.001$, when data for all species were combined). I, therefore, repeated each significant analysis and examined data collected by each observer separately. Differences persisted in four of seven cases where significant differences were found initially, at least for those observers that had conducted sufficient observations to detect differences, and were concordant across observers. Exceptions were the differences found for black-necked stilt, long-billed curlew and dunlin. Only the curlew result was potentially confounded with observer differences.

Time allocation was associated with at least one measure of group size for all species except great egret; the numbers of conspecifics was most likely to be influential. Typically, the proportion of time spent feeding decreased as the number of birds increased, with a concomitant increase in the time allocated to other activities. Time of day and time of year each had a significant effect on the time budgets of four species. In contrast to the foraging performance measures, predation threat was infrequently associated with time allocation (Table 14).

Table 13. Results of significance tests on measures of time allocation shown in Fig. 17. Tests used for each variable depended on the number of habitat treatments and results of Levene's variance homogeneity tests. Superscripts give test used and results of post-hoc tests when applicable; subscripts give degrees of freedom. Sample sizes are for flooded rice fields (fld), semi-natural wetlands (nat) and unflooded rice fields (unfld) respectively: only great egret, killdeer and long-billed curlew were recorded in unflooded fields. N/A Not applicable because behavior was never seen. Significant results are emboldened.

Species	Sample sizes (fld, nat, unfld)	% time feeding	% time vigilant	% time sleeping	% time preening	% time aggressive
Great egret	45,18,10	$F_{2,70} = 1.78^a$ $P = 0.176$	$F_{2,70} = 1.78^a$ $P = 0.176$	$H = 8.51^{d,h}$ $P = 0.014$	$H = 0.11^d$ $P = 0.946$	N/A
Killdeer	55,27,10	$F_{2,89} = 0.62^a$ $P = 0.542$	$F_{2,89} = 0.42^a$ $P = 0.659$	$H = 3.91^d$ $P = 0.142$	$F_{2,89} = 0.15^a$ $P = 0.861$	$H = 0.84^d$ $P = 0.658$
Black-necked stilt	8,28,-	$t_{8,6} = 0.43^b$ $P = 0.678$	$t_{7,2} = 1.16^b$ $P = 0.282$	$t_{34} = 0.44^c$ $P = 0.659$	$t_{34} = 2.58^{c,f}$ $P = 0.014$	$t_{34} = 0.19^c$ $P = 0.850$
Greater yellowlegs	75,28,-	$t_{101} = 3.01^{c,f}$ $P = 0.003$	$t_{101} = 1.73^c$ $P = 0.087$	$t_{28,0} = 1.64^b$ $P = 0.112$	$t_{30,6} = 1.77^b$ $P = 0.088$	$t_{27,2} = 1.09^b$ $P = 0.284$
Long-billed curlew	31,3,17	$H = 1.42^d$ $P = 0.493$	$F_{2,48} = 3.42^{a,f,g}$ $P = 0.041$	$H = 5.67^{d,h}$ $P = 0.059$	$F_{2,48} = 0.45^a$ $P = 0.784$	$F_{2,48} = 0.23^a$ $P = 0.794$
Dunlin	53,18,-	$t_{69} = 0.65^c$ $P = 0.513$	$t_{69} = 0.55^c$ $P = 0.584$	$t_{69} = 1.31^{c,f}$ $P = 0.196$	$t_{69} = 0.21^c$ $P = 0.833$	$U = 585^e$ $P = 0.029$
Long-billed dowitcher	29,25,-	$t_{39,6} = 2.71^b$ $P = 0.010$	$t_{52} = 1.46^c$ $P = 0.152$	$t_{37,1} = 2.78^b$ $P = 0.009$	$t_{52} = 0.37^c$ $P = 0.676$	$t_{52} = 0.37^c$ $P = 0.712$
Least sandpiper	16,7,-	$t_{21} = 0.75^c$ $P = 0.462$	$t_{21} = 0.35^{c,f}$ 0.732	$t_{21} = 0.25^c$ $P = 0.804$	$t_{21} = 0.66^c$ $P = 0.517$	$U = 63^e$ $P = 0.339$

^a Analysis of variance; ^b separate-variance t -test; ^c pooled t -test; ^d Kruskal-Wallis test; ^e Mann-Whitney test; ^f data transformed to remove variance heterogeneity; ^g result of multiple comparison test: nat > fld, nat = unfld, fld = unfld; ^h pairwise comparisons not significantly different

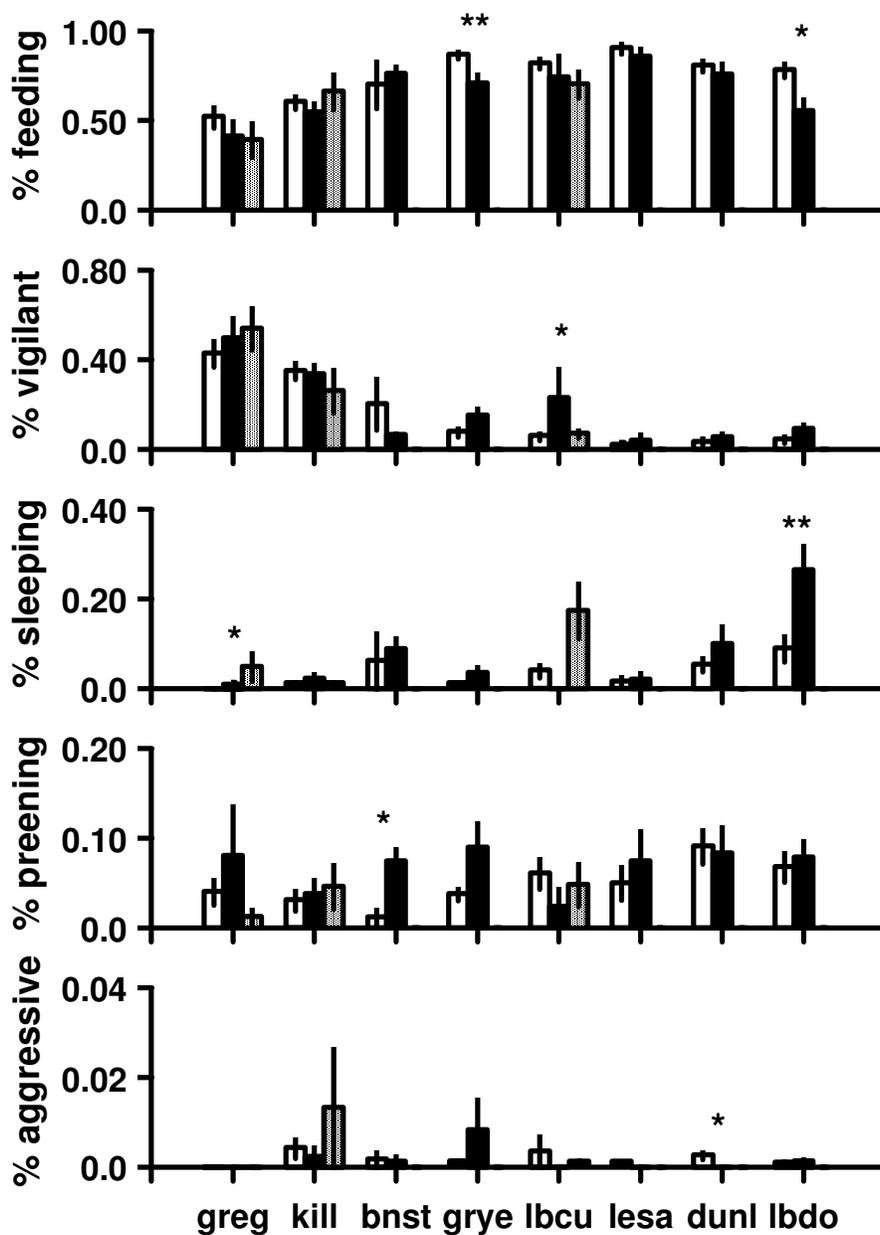


Figure 17. Time allocation by eight waterbird species in different habitat types. Each horizontal graph gives data for the proportion of time spent doing a particular behavior; bars for each species are grouped vertically. Open bars = flooded rice fields, solid bars = semi-natural wetlands, shaded bars = unflooded rice fields; only great egret, killdeer and long-billed curlew occurred in unflooded fields. kill= killdeer, lesa = least sandpiper; see Fig. 3 for other species codes. Significance tests are given in Table 13, * $0.05 > p > 0.01$, ** $0.01 > p > 0.001$. Note that, to illustrate differences, the y-axis scales for each behavior differ.

Table 14. Significant covariates from exploratory models of the factors affecting time allocation by eight waterbird species. All models also included habitat type. Italics denote results that should be viewed with caution because model errors had unequal variances and no suitable transformation could be found. Time allocation variables are not independent, hence, I have made a single list of significant covariates for each species indicating which components of the time budget they affected. + and - give directions of partial correlation coefficients for continuous variables.

Species	Significant covariates	Behaviors affected
Great egret	<i>observer</i> time of day	<i>preening</i> feeding ⁺ , vigilant ⁻
Killdeer	observer date time of day # waterfowl	feeding, vigilant preening ⁺ vigilant ⁺ feeding ⁺
Black-necked stilt	specific predation threat observer date time of day # other waterbirds # conspecifics	aggressive ⁺ feeding, <i>sleeping</i> preening ⁺ feeding ⁺ , <i>sleeping</i> ⁻ , <i>aggressive</i> ⁻ feeding ⁺ , vigilant ⁻ , preening ⁻ feeding ⁻ , <i>sleeping</i> ⁺ , <i>aggressive</i> ⁺
Greater yellowlegs	observer date # waterfowl # conspecifics	feeding, <i>vigilant</i> , <i>sleeping</i> feeding ⁺ , vigilant ⁻ feeding ⁻ , <i>sleeping</i> ⁺ , preening ⁺ , <i>aggressive</i> ⁺ feeding ⁻ , <i>sleeping</i> ⁺ , preening ⁺
Long-billed curlew	observer <i>time of day</i> # waterfowl # conspecifics	feeding, <i>sleeping</i> <i>sleeping</i> ⁺ <i>sleeping</i> ⁻ feeding ⁻ , <i>vigilant</i> ⁺ , preening ⁺ , <i>sleeping</i> ⁺
Least sandpiper	specific predation threat observer date # other waterbirds # conspecifics	aggressive ⁻ aggressive, preening vigilant ⁻ preening ⁺ feeding ⁻ , <i>sleeping</i> ⁺ , preening ⁺ , <i>aggressive</i> ⁺
Dunlin	<i>total predation threat</i> observer # other waterbirds # waterfowl # conspecifics	<i>sleeping</i> ⁻ feeding, <i>vigilant</i> , <i>sleeping</i> feeding ⁻ , <i>sleeping</i> ⁺ feeding ⁻ , <i>sleeping</i> ⁺ <i>sleeping</i> ⁻ , preening ⁺
Long-billed dowitcher	# other waterbirds # waterfowl # conspecifics	aggressive ⁻ feeding ⁻ , <i>sleeping</i> ⁺ , preening ⁺ feeding ⁻ , <i>sleeping</i> ⁺ , preening ⁺ , <i>aggressive</i> ⁺

Adding covariates to tests of the habitat treatment resulted in different conclusions in only two of 40 cases. After controlled for the number of waterfowl and date, the difference in the time allocated to preening by black-necked stilts disappeared ($F_{1,32} = 1.94, p = 0.174$). In addition, once the number of conspecifics was accounted for, the amount of time least sandpipers spent feeding was found to differ between habitats ($F_{1,18} = 5.14, p = 0.035$). As was also true for foraging performance, these additional tests suggest that covariates rarely confounded primary tests of habitat differences.

DISCUSSION

HABITAT QUALITY

Flooded rice fields and semi-natural wetlands superficially appear to be very different habitats. For example, flooded fields have less surrounding vegetation, have less variable water depths, and receive different nutrient inputs (both in terms of fertilizers and dead vegetation). Furthermore, my study shows that they are not equivalent habitats in terms of some variables that may be important to birds (e.g. perceived predation threat was lower in flooded rice fields than in semi-natural wetlands: Fig. 15). Given these differences, one might expect to find large differences in the behavior of birds using the two habitats. This study, however, suggests that, to the extent that they exist, differences between the two habitats are small.

In most cases, I was unable to detect statistically significant differences in behavioral measures among habitats. Moreover, when one considers the large number of tests conducted it becomes apparent that many of the differences found could be explained by chance. At best, my significance tests had high statistical power only for large effect sizes. It is, therefore, possible that differences existed that I could not detect. To explore this possibility, I compared mean values for each measure to see if there were consistent patterns across species. All six bird species observed, attained higher feeding efficiencies in semi-natural wetlands than in flooded fields (Fig. 16). The three cases for which these differences were not statistically significant were those for which sample sizes (and hence power) were lowest. Hence, it is possible that semi-natural habitats provide a better foraging habitat than flooded rice fields and that my analyses were unable to detect differences. Even if this were so, there are a variety of ways in which birds may be able to compensate for a reduced feeding efficiency in flooded fields (cf. Swennen *et al.* 1989). Birds could increase intake rates, and indeed mean attack rates were marginally greater in flooded fields for five of six species resulting in marginally higher feeding rates for three species (Fig. 16). Birds also may compensate for reduced efficiency by spending more time foraging (Urfi *et al.* 1996) and seven of eight species devoted more of their time budget to feeding when in flooded fields than in semi-natural wetlands (Fig. 17). Given the poor evidence for large behavioral differences between semi-natural wetlands and flooded rice fields and the indications that even small, undetectable, differences may be compensated for, current evidence suggests that flooded rice fields can be considered equivalent to semi-natural wetlands for the species studied.

The incorporation of additional variables into tests of behavioral differences among habitats provided further evidence that inherent differences among habitats lacked

biological significance. These models revealed that a number of other variables have significant effects on the behavior of the birds studied and that these variables often were more important than habitat *per se* when significance tests controlled for other variables in the regression model (cf. Tables 11 and 12). In light of these effects, whatever differences can be attributed to habitat may be insignificant. It also is interesting to note that, even though these variables often differed among habitats (e.g. Fig. 15) they did not explain those habitat differences that I did find.

Preliminary analyses suggests that there may be differences in the invertebrate communities of flooded fields and semi-natural wetlands. For example, some chironomids appear more abundant in semi-natural wetlands and some ostracods more abundant in flooded fields (R. Schroeter, O. Kulkoyluoglu & C. Elphick, unpubl. data). Currently there is little information on the diets of birds feeding in the two habitats, however, prey may differ in size, ease of capture, and nutritional value. Unfortunately, the small size of most prey items prevented the use of non-invasive methods of assessing diet in these birds and the limited behavioral differences found do not seem sufficient to warrant killing the large numbers of birds necessary to assess diet differences adequately. Testing the null hypothesis of no difference in diet between the two habitats (e.g. by stomach flushing captured birds, Martin & Hockey 1993) would be a valuable complement to this study.

Most species of waterbirds occur rarely in rice fields that are not intentionally flooded (Chapter 1; Elphick & Oring 1998). Three species considered in this study, however, used unflooded fields with some regularity. Great egrets fed at a significantly lower rate in unflooded fields than in either semi-natural wetlands or flooded fields (Table 11, Fig. 16). My data also indicate that the feeding efficiency of both egrets and long-billed curlews in unflooded fields was lower than in semi-natural wetlands, although no different to flooded fields. These results suggest that unflooded fields may be a low quality foraging habitat for great egrets. The evidence for differences in habitat quality is more equivocal for curlews and completely lacking for killdeer.

Few other studies have compared the behavior of birds using rice fields and more natural habitats. At the Ebro Delta, Spain, dunlin were more vigilant when feeding in rice fields than when using littoral habitats (Barbosa 1997). In this area, predator densities were greater in the rice field habitat. Studies of breeding little egrets *Egretta garzetta* in the Camargue, France, provide mixed results. In the late 1970s, intake rates and feeding efficiency were greater in rice fields than in freshwater marshes. By the early 1980s, however, foraging conditions in the rice fields appeared to have deteriorated as a result of increased pesticide use (Hafner *et al.* 1986). Variation in feeding conditions for herons also has been found among rice regions within the Mediterranean (Hafner & Fasola 1992). The quality of rice field habitats clearly will depend upon specific conditions within a region.

EFFECTS OF OTHER VARIABLES ON BIRD BEHAVIOR

My analysis of the influence of variables other than habitat on bird behavior primarily was intended to control for the potentially confounding effects of additional variables on tests of habitat differences. Similarity between tests of habitat effects with and without

these covariates suggests that habitat results were neither affected, nor caused, by these covariates. A second role for these supplemental tests was to provide insight into which other factors influence the behavior of birds occurring in rice fields. This aspect of the analysis was viewed as exploratory in nature and all results should be considered tentative for two reasons. First, the multitude of models examined and the large number of variables in each model resulted in a considerable number of tests. Consequently, there is a high probability that some of these tests arose simply by chance. Estimating the number of spurious tests was difficult, because tests were not independent of each other (i.e. many models shared both dependent and independent variables). Without independent tests, it is impossible to know the probability of obtaining a significant test by chance. My second concern with the results of the covariate analysis is that many variables were correlated with each. Many of these correlations reflect causal relationships (e.g. between the number of waterfowl and perceived predation threat). This multicollinearity among independent variables may have influenced the accuracy of statistical tests (SAS Institute Inc. 1991). Both of these issues require that individual tests be viewed with caution. Broad patterns across a series of regression models, however, are less likely to be statistical artifacts and should be considered worthy of future testing through controlled experiments.

Measures of predation threat most frequently played a role in predicting feeding performance, while measures of group size were least frequently important. In contrast, time allocation was more likely to be influenced by measures of group size and less likely to be affected by predators. My measure of predation threat may not correlate with the risk of being captured. Nonetheless, predators seemed to influence the performance of individuals while they fed, though not whether the potential prey spent time foraging. Group size variables were most likely to affect feeding performance of small, flocking, species. These are species for which benefits (e.g. protection from predators) and costs (e.g. interference, prey depletion) of group size are most likely. Unlike many studies (reviewed by Barnard & Thompson 1985 and Lima & Dill 1990), group size usually was negatively correlated with the proportion of time spent feeding. Reduced feeding time in large flocks was not associated with an increase in the time devoted to aggressive encounters among individuals (cf. Goss-Custard 1980, Barnard & Thompson 1985). The possibility that there is increased interference in larger groups (Sutherland 1996), however, has not been ruled out.

IMPLICATIONS OF THIS STUDY

My results provide little evidence that the behaviors of the species observed differ between flooded rice fields and semi-natural wetlands. If differences exist, but could not be detected with my sample sizes, they must be relatively small. Moreover, my data suggest that birds may be able to compensate for any reduced efficiency in flooded rice fields. The species considered were chosen because they span the range of foraging behaviors, microhabitat use, and diets, found among non-game birds that prey on invertebrates in these habitats. The similarity of results across an array of species with different life-histories, suggests that it is reasonable to extrapolate this conclusion to other wading birds. The application of my results to waterfowl, which rely more on grain and

use different foraging methods, is less certain. The reduced predation threat and large quantities of spilled grain found in flooded rice fields (Figs. 14 and 15) and the daily movements of waterfowl to feed in them (C.S. Elphick pers. obs.), however, indicate that flooded fields also are an important habitat for these species (see also Gilmer *et al.* 1982, Miller *et al.* 1987, Heitmeyer *et al.* 1989).

It is important to consider what these results mean for overwinter survival when assessing the conservation value of the different habitats. Unfortunately, directly assessing whether or not survival differs among habitats probably is impossible, especially within the time span over which managers need to make decisions. The logistical difficulties of marking and tracking sufficient numbers of individuals to estimate survival accurately could be overcome if sufficient resources were available. A more important difficulty though, is that waterbirds are extremely mobile in winter and appear to use more than one of the habitats available (C.S. Elphick, pers. obs.). Consequently, assigning deaths to particular habitats would be difficult. Determining where deaths occur is feasible, although with the long-lived species included in this study this would require a long-term commitment and large samples of marked birds. Distinguishing whether these deaths are a direct result of conditions in the habitat where death occurred, or due to conditions in other areas where the bird spent time prior to death would be more difficult.

The lack of evidence for differences between semi-natural wetlands and flooded rice fields suggests that even approximate facsimiles of natural wetlands could benefit waterbird populations. Additional support for this hypothesis comes from research on the importance of European rice fields to herons (Fasola *et al.* 1996) and the extensive waterbird use of other artificial habitats (e.g. sewage ponds, settling beds). Further tests, however, are warranted and regional variation in the importance of artificial wetlands is to be expected (e.g., Hafner & Fasola 1992). Unflooded fields were not used by several species and appeared to be an inferior feeding habitat for great egrets. Coupled with evidence that flooding fields results in highly significant increases in waterbird use (Chapters 1 and 2; Elphick & Oring 1998), these data indicate that flooding rice fields during winter should be viewed as an important means of benefiting waterbird populations. Flooding rice fields cannot be considered equivalent to the restoration of historic wetlands, because it fails to provide suitable conditions for the full suite of species (especially plants) that used these seasonally flooded habitats. It appears, however, that flooding could be a valuable contribution to California's wetland resources, particularly as a habitat for wintering waterbirds. In a region where the vast majority of the historic wetlands have been lost (Frayer *et al.* 1989), a method for expanding the amount of flooded habitat, without jeopardizing agricultural interests, is particularly welcome. Moreover, rice is one of the world's most important crops (Chang & Luh 1985) and these results provide support for the notion that appropriately managed rice fields can contribute to global wetland habitats (Fasola & Ruíz 1996).

SUMMARY

Evaluating the potential for anthropogenic habitats to act as surrogates for the natural habitats they replace is a key issue in conservation biology. Agricultural habitats

dominate the world's surface and are, thus, especially important. In central California, many rice growers flood their fields during winter to promote decomposition of straw left on fields after grain harvest. Flooded fields are used by a variety of aquatic birds, and these fields may help replace the extensive seasonal wetlands that occurred in the region prior to agricultural development. Before this hypothesis can be accepted, fields need to be shown to provide equivalent, or better, conditions than more natural habitats. I tested whether measures of food abundance, perceived predation threat, foraging performance, and time allocation differed between flooded rice fields and semi-natural wetlands for a variety of aquatic birds; when appropriate, I also compared flooded fields to unflooded fields.

Invertebrate densities did not differ among habitats. Semi-natural wetlands had fewer rice grains, but more seeds from other plant species, than the two rice habitats. Predation threat was significantly lower in flooded fields than in unflooded fields or semi-natural wetlands. Most differences in feeding performance and time allocation among habitats were statistically insignificant. Examination of the data and the statistical power of tests indicated that any behavioral differences among habitats must be small. Furthermore, there was evidence that small differences in feeding efficiency may be compensated by increases in attack rate and time spent feeding in flooded fields. Multivariate analyses showed that group size, predation threat, time of day, date, and water depth often were associated significantly with the behaviors measured, but that these variables could not account for habitat differences in most cases. These results suggest that flooded fields may provide equivalent foraging habitat to semi-natural wetlands and, because of reduced predation threat, may be a safer habitat for waterbirds. Thus, this study suggests that, if managed appropriately, one of the world's dominant forms of agriculture may provide valuable habitat for a variety of bird species.

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CONCLUSIONS

Flooding rice fields in winter potentially offers considerable benefits for waterbird populations. Fields which are intentionally flooded by farmers receive greater use by a wide variety of waterbird species than are fields where passive flooding alone is possible. Manipulation of water depths in rice fields, especially early in the winter, offers an opportunity to increase the conservation value of flooded fields. Shallower conditions appear to benefit a wider variety of species, particularly those species constrained by short leg-lengths. Maintaining depths of 10-15 cm would seem to minimize the trade-off between these shallow-water species and birds that use deeper conditions, although any depth will exclude some species.

Factors other than the way a field is managed also should be considered when trying to understand the abundance of species using a particular site. The location of a flooded field with respect to other landscape features also was related to the densities of birds using that field. The amount of the surrounding land that was part of a wildlife refuge, a semi-natural wetland, or both, influenced the numbers of geese, wading birds and shorebirds. Similarly, the amount of flooded agricultural land in the surroundings was positively related to the density of ducks found in a flooded rice field. All of these relationships depended on the spatial scale at which the landscape was measured. These results provide insight into the different factors influencing how waterbirds select sites within the landscape. These patterns should help land managers to determine where fields can be flooded most productively and where to site wetland restoration projects.

Whether flooded rice fields can be considered truly equivalent to wetlands occurring in the Central Valley historically can never be known because historic wetlands have been drained or greatly altered. Nonetheless, I found little evidence that flooded fields are an inferior habitat, compared to semi-natural wetlands, for the waterbirds that I considered. In fact, the one variable for which there are clear differences, the rate at which predators cross a habitat patch, suggests that flooded fields may be the safer habitat. A number of other factors must be explored before flooded fields can be considered as valuable as more natural sites. For now, however, flooded fields should not be dismissed as a second-rate habitat.

There is little doubt that flooding fields in winter may have important consequences for waterbird populations. Testing the long-term value of flooding fields to waterbird populations, however, requires more work. For example, currently it is unknown whether waterbird population sizes are limited by conditions on the wintering grounds, or even whether these populations are limited at all. If population sizes are not limited by conditions in California, management changes will not alter total bird numbers. Preliminary modeling suggests that, at a population level, granivorous species are unlikely to deplete the food resource of spilled rice completely (C.S. Elphick unpubl. data.). Whether current levels of food depletion are sufficient to affect population sizes is unknown, however, because we lack information necessary to validate model results and know little about food availability. Determining the relationship between land management and population dynamics is an important goal for the future.

Large-scale increases in the area of flooded rice fields depend upon a number of things other than the biological efficacy of flooding. The single most important factor is agronomic: if flooding harms rice production (e.g. by increasing the incidence of disease) it will not be used by farmers. This issue is currently the subject of much research by agronomists. The availability of sufficient water to flood fields also is important and will be determined politically. It is important to note, however, that some of the management recommendations in this dissertation would enable increased flooding without requiring more water. In addition, the development of less expensive methods of straw disposal will reduce the incentive for farmers to flood their fields. Here, there is opportunity for management agencies and non-governmental organizations to provide farmers with incentives to flood their fields. The more active these bodies are in facilitating flooding (e.g. by helping farmers to buy water), the greater potential there will be for influencing the spatial arrangement of flooded fields and, hence, exploiting the influence of landscape patterns on birds for management purposes.

Finally, it is important to ask, what are the trade-offs associated with increased flooding? In this dissertation, I have focused on species traditionally associated with wetlands. Even among this group, there are some species occurring at higher densities in unflooded fields than in flooded fields, one of which (greater sandhill crane *Grus canadensis tabida*) is considered Threatened in California. There are numerous other species, more typically associated with upland habitats, that use rice fields during winter. These include a variety of raptors and passerine birds. A number of these species occur in unflooded fields at greater densities than in flooded fields and the consequences of flooding for these birds and other taxa should be explored (C.S. Elphick unpubl. data).

Although there is still much to be learned, flooded rice fields should be considered a valuable supplement to California's wetland resources. Rice fields will never replace historic wetlands and cannot provide for the full range of species that occur in more natural habitats. If managed appropriately, however, they can provide habitat that is used by a wide variety of waterbird species. Moreover, if my results are generally applicable, this study has important implications for the management of rice fields and waterbird populations worldwide.