
Functional Equivalency between Rice Fields and Seminatural Wetland Habitats

CHRIS S. ELPHICK*

Ecology, Evolution & Conservation Biology Program/186, University of Nevada, Reno,
1000 Valley Road, Reno, NV 89512, U.S.A.

Abstract: *Evaluating the potential for anthropogenic habitats to act as surrogates for the natural habitats they replace is a key issue in conservation biology. In California, flooded rice fields are used by numerous aquatic birds during winter. If this habitat functions similarly to more natural wetlands, increased flooding may help replace the extensive wetlands that occurred in the region prior to agricultural development. I tested whether food abundance, perceived predation threat, foraging performance, and the way in which birds allocate their time to different behaviors differed between flooded rice fields and seminatural wetlands for several species of aquatic bird. When appropriate, I also compared flooded and unflooded fields. Invertebrate densities did not differ among habitats. Seminatural wetlands had less rice grain but more seeds from other plants than the two rice habitats. The frequency with which predators passed over a feeding area was lower in flooded fields than in unflooded fields or seminatural wetlands. Most differences in feeding performance and time allocation among habitats were small and statistically insignificant. For some species, feeding efficiency was greater in seminatural wetlands than in flooded fields. Increasing attack rates and the amount of time spent feeding when in flooded fields, however, may allow birds to compensate for reduced efficiency. Multivariate analyses showed that group size, predation threat, time of day, date, and water depth often were associated with behaviors, but that these variables rarely accounted for habitat differences. Flooded fields apparently provide equivalent foraging habitat to seminatural wetlands and, because of reduced predation threat, may be a safer habitat for waterbirds. Thus, if managed appropriately, one of the world's dominant forms of agriculture can provide valuable waterbird habitat.*

Equivalencia Funcional entre Hábitats de Arrozales y Humedales Seminaturales

Resumen: *La evaluación del potencial en hábitats antropogénicos para actuar como substitutos de los hábitats naturales que remplazaron es un tema clave en la biología de la conservación. En California, tierras inundadas para cultivo de arroz son utilizadas por numerosas aves acuáticas durante el invierno. Si estos hábitats funcionan en forma similar a humedales más naturales, el incremento de inundaciones podría ayudar a reemplazar los extensos humedales que existieron en la región antes del desarrollo agrícola. Analicé si la abundancia de alimento, la percepción del peligro de depredación, el rendimiento en forrajeo y la forma en que las aves distribuyen su tiempo hacia diferentes conductas difieren entre arrozales inundados y humedales seminaturales para diferentes especies de aves acuáticas. Cuando fue posible, también comparé arrozales inundados contra no inundados. Las densidades de invertebrados no difirieron entre hábitats. Los humedales seminaturales tuvieron menos grano de arroz, pero más semillas de otras plantas que los dos tipos de hábitats de arrozal. La frecuencia con la que los depredadores pasaron sobre un área de alimentación fue menor en los campos inundados que en los campos no inundados o los humedales seminaturales. La mayoría de las diferencias en el rendimiento alimenticio y el tiempo dedicado entre hábitats fue pequeño y estadísticamente insignificante. Para algunas especies, la eficiencia alimenticia fue mayor en humedales seminaturales que en los campos inundados. Sin embargo, el incremento en las tasas de ataque y las cantidades de tiempo utilizado para alimentación cuando los campos estaban inundados podría permitir a las aves compensar por esta reducida eficiencia. Un análisis multivariado mostró que el tamaño de grupo, el pe-*

*Current address: Department of Ecology & Evolutionary Biology, University of Connecticut, 75 North Eagleville Road, U-43, Storrs, CT 06269-3042, U.S.A., email elphick@uconnvm.uconn.edu

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ligro de depredación, hora del día, fecha y profundidad del agua estuvieron frecuentemente asociados con conductas, pero estas variables raramente aportaron elementos para encontrar diferencias entre hábitats. Los arrozales inundados aparentemente proveen un hábitat de forrajeo equivalente a los humedales semi-naturales y debido a la reducida amenaza de depredación, podrían ser un hábitat seguro para aves acuáticas. Por lo tanto, si son manejados adecuadamente, una de las formas más dominantes de agricultura a nivel mundial puede proporcionar hábitat valioso para las aves acuáticas.

Introduction

Evaluating the role of anthropogenic habitats relative to more natural habitats is an important conservation issue 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 & Jensen 1991), and agricultural land currently occupies a third of the Earth's ice-free land surface (Urban & Vollrath 1984).

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 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 it 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 inundated rice fields can act as surrogates for natural wetlands (cf. Fasola & Ruíz 1996), they could double the area of aquatic habitat available.

To improve air quality, the State of California's Rice Straw Burning Act (AB 1378, 1991) requires reductions in the area of rice stubble that can be burned after harvest. To increase straw decomposition rates, many farmers now flood their fields between November and March. This change in rice farming has created an opportunity to increase 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 an opportunity to test whether such management would benefit wildlife.

Little is known about the quality of flooded rice fields compared to natural wetlands. Agricultural fields that are flooded throughout the winter, however, are used by large numbers of waterbirds: 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; flooded fields are clearly beneficial in comparison. Other species (e.g., Great Egret [*Ardea alba*] and 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.

Both empirical and theoretical studies have shown that the highest-quality habitats are not necessarily those that contain the highest animal densities (Fretwell 1972; Van Horne 1981, 1983; Bernstein et al. 1991a, 1991b; Vickery et al. 1992; Sutherland 1996; Purcell & Verner 1998). Consequently, assessing habitat quality requires an examination of measures that are expected to correlate with survival and reproduction. Overwinter survival is likely to be related to the ability to find food and avoid predators, and measures of these activities often are used as indicators of survival rates in waterbirds (e.g., Cresswell & Whitfield 1994; Goss-Custard et al. 1995a, 1995b). I compared the quality of flooded rice fields and more natural wetlands by testing the null hypotheses that the two habitats do not differ in terms of (1) food abundance, (2) perceived predation threat, (3) feeding performance, and (4) time allocated to different behaviors. I also compared the quality of flooded and unflooded rice fields for species that use both habitats.

Methods

Study Area

I conducted field work in the southern Sacramento Valley of California, the portion of the Central Valley where most rice in the western United States is grown. Several field assistants and I sampled rice fields throughout this region and wetlands at the Sacramento National Wildlife Refuge Complex, Gray Lodge Wildlife Management Area, and several private hunting clubs. Due to extensive management of water flows and plant communities, the wetlands remaining in the Central Valley bear little resemblance to historical habitats. Most of these wetlands are flooded seasonally and are managed as tule marshes or "moist soil" habitats dominated by plants that produce food for waterfowl. Nonetheless, these marshes are the nearest approximation to historic wetlands. Heitmeyer et

al. (1989) provide detailed descriptions of these habitats. Throughout, I refer to these wetlands as "seminatural." These marshes cover about 32,000 ha in the Sacramento Valley and vary in size from a few hectares to thousands of hectares (Heitmeyer et al. 1989); the size range of individual management units is similar to that of rice fields.

Between November 1993 and March 1994 we sampled food abundance; other data were collected during the winters between October 1993 and March 1996.

Food Abundance

We sampled food abundance in flooded rice fields, unflooded rice fields, and seminatural wetlands, defining an experimental unit as a wetland management unit or rice paddy surrounded by a raised earthen barrier. Nine replicates of each treatment were selected randomly, from those units to which we had access, and we sampled each once. In each unit, we subsampled the benthos and water column at five randomly selected points and used mean values in analyses.

Subsamples consisted of a sediment core 7.7 cm in diameter taken to a depth of 8 cm. We divided each core into three strata, (1) the water, (2) the top 4 cm of benthos, and (3) the bottom 4 cm of benthos. These subdivisions allowed me to evaluate food availability for different species separately. For each subsample, we measured the water depth and calculated the volume of water sampled. Samples were then sieved through a 500- μm mesh to remove soil, and the remaining material was stored in alcohol. Later, we sorted samples to separate invertebrates and seeds from straw and root material after adding rose bengal to improve sorting efficiency (Mason & Yevich 1967). For each sample, we determined the density of (1) invertebrates $>500 \mu\text{m}$ in size, (2) rice grains, and (3) other seeds.

Predation Threat

We quantified perceived predation threat by recording every potential predator seen crossing wetland units or rice paddies in which waterbirds were present. 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 observation. I pooled predator data in three ways: (1) species that regularly feed on shorebirds and ducks (eagles, harriers, accipiters, and falcons), (2) species likely to attack larger prey such as herons and geese (eagles, dogs, coyotes), and (3) all predators.

Feeding Performance

Foraging observations were made by several people over the course of the study (73% by two people). We collected

data for six species that feed predominantly on animal prey: Great Egret, Black-necked Stilt (*Himantopus mexicanus*), Long-billed Curlew, Greater Yellowlegs (*Tringa melano-leuca*), Long-billed Dowitcher (*Limnodromus scolopaceus*), and Dunlin (*Calidris alpina*). These species were chosen because they are abundant in rice fields, they represent a diversity of foraging behaviors, and their behavior can be sampled easily. Observations of egrets and curlews were made in three habitats: seminatural wetlands, flooded rice fields, and unflooded fields. The remaining species rarely occurred in unflooded fields.

For each management unit, we selected up to five individuals of each species and conducted one 2-minute focal observation on each (5 minutes for Great Egrets, which feed less rapidly). Each unit was sampled only once. For each observation, we recorded the number of pecks (attacks) and the number of successful pecks (feeds). Occasionally birds flew part way through an observation. If the observation was more than half-way through, we recorded the time elapsed and included the observation 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 (1) a prey item was seen to be captured and swallowed, (2) movements of the gular region consistent with swallowing were made, or (3) 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 observation time. In addition, I calculated feeding efficiency by dividing the number of feeds by the number of attacks.

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

Time Allocation

We used scan-sampling (Altmann 1974; P. 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 minutes apart. If a flock was disturbed part way through a scan, we estimated the proportion of the flock that had been sampled; if it was <75%, we discarded the sample.

For each species, I calculated the proportion of the birds engaged in each activity. I defined behaviors as feeding (probing, pecking, or looking at the ground); vigilance (standing still with head up and eyes open but not engaged in preening or obvious interaction with other birds); sleeping (head under wing or eyes closed); preening (preening feathers or stretching); and aggression (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.

Analysis

Initially, I compared food abundance and predation threat in each habitat with multiple regression analysis (SPSS, Inc. 1996). I used date as a covariate because I expected temporal variation in abundance due to invertebrate reproduction and seed depletion. I also expected predation threat to peak in midwinter, when raptors were most abundant, and in the middle of the day, when conditions were more suitable for the soaring flight typical of the most common species. 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 as an independent variable. In all analyses, I examined two measures of perceived predation threat: one excluded predators that were unlikely to prey upon the focal species (measure 1 for shorebirds and 2 for egrets; see above for definitions), and one included all potential predators (measure 3).

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 habitats. First, I compared mean values of each trait using *t* tests or anal-

ysis of variance (ANOVA). 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, and using means would have prevented an examination of this variance. Similarly, observer was a categorical variable for which 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 habitats differed, the issue of interest to managers. The second step provided an exploratory approach to addressing the mechanisms influencing behavior by asking three additional questions: (1) Did covariates affect behavioral traits? (2) Can significant differences among habitats be explained by covariates? (3) Did habitat differences emerge after covariate effects were accounted for?

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 and percent data were transformed to arcsine (square root [*y*]). If transformations failed to equalize variances, I used a nonparametric equivalent to the original test, or I present the results of the original parametric tests and note that assumptions were violated.

I used an alpha 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 >0.80 as evidence that a nonsignificant result meant there was no difference among treatments. For nonparametric tests, I used guidelines given by Siegel and Castellan (1988) to estimate minimum power.

Results

Food Abundance

I found no differences in invertebrate abundance among treatments for any of the strata into which cores were subdivided (*p* > 0.45 in all cases; Fig. 1). Only densities in the water column varied temporally ($F_{1,18} = 5.03$, *p* =

0.037). Variances, were high (Fig. 1), however, 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 nonrice seeds in the water column did not differ among treatments ($p < 0.005$ for all other tests; Fig. 1). Post-hoc tests revealed that these differences were attributable to predictably lower densities of rice grain and higher densities of other seeds in seminatural 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.

Predation Threat

Most (>99%) predators recorded during this study were birds (Falconiformes and Strigiformes). Predators occurred in flooded fields at significantly lower rates than in unflooded fields or seminatural wetlands (Fig. 2a). This pattern was true for species that feed regularly on shorebirds and ducks but not for predators of larger birds (Fig. 2b & 2c). Neither date nor time were significant ($p > 0.3$ for all models) when added as covariates, although variance heterogeneity may have affected this result.

Feeding Performance

Five species attained their highest mean attack rates in flooded rice fields, but in no cases were there statistically significant differences between flooded fields and seminatural wetlands (Table 1, Fig. 3a). Feeding rate did not differ between these treatments for any species (Table 1, Fig. 3b). Great Egrets made significantly fewer attacks and captured fewer prey in unflooded fields than in either flooded habitat (Table 1, Fig. 3a & 3b). On average, all species fed more efficiently in seminatural wetlands than in flooded fields, and in three cases these differences were significant (Table 1, Fig. 3c). Estimates of the statistical power of the nonsignificant 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 >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 were 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 2). Predation threat appeared in 11 of the 18 models. Differences among observers were found in nine models. Effects of water depth and time of day were each found in eight models,

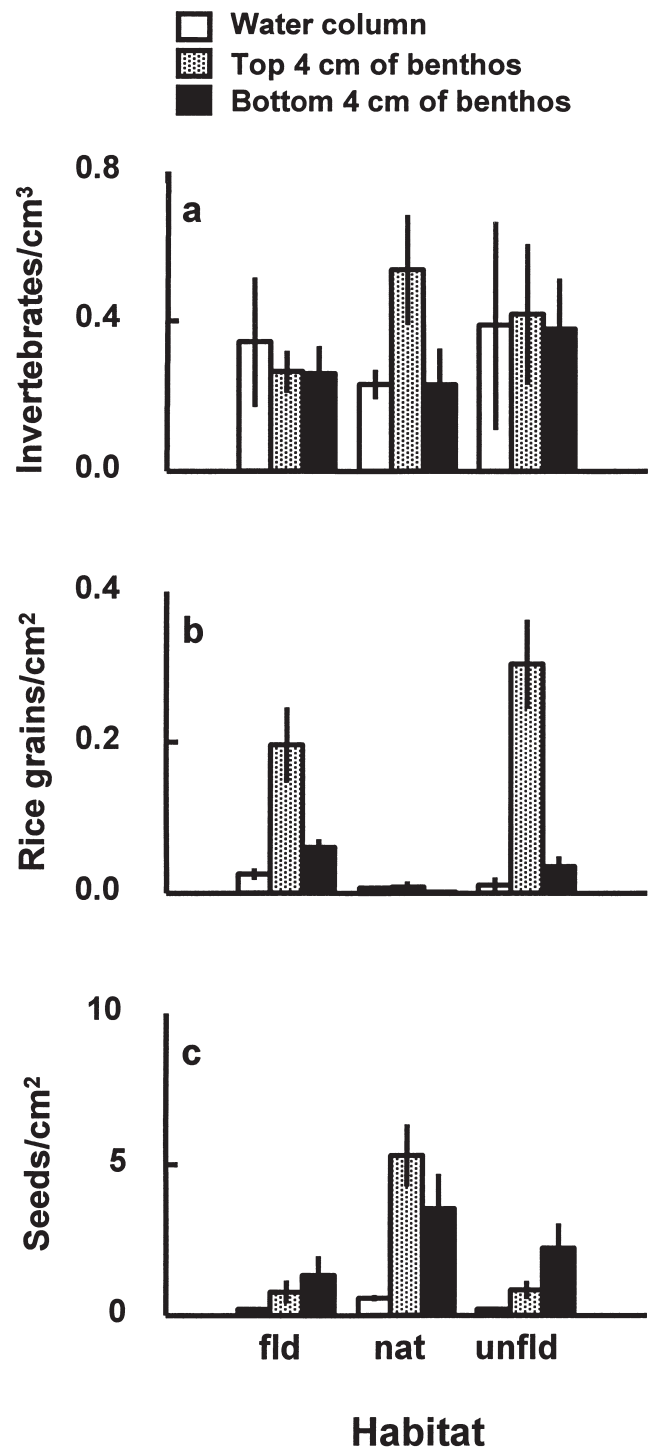


Figure 1. Mean (\pm SE) food abundance in flooded rice fields (fld), seminatural wetlands (nat), and unflooded rice fields (unfld): (a) total invertebrates (>500 μm)/ cm^3 , (b) rice grains/ cm^2 , and (c) all other seeds/ cm^2 .

and date was important in seven models. Finally, each measure of group size appeared in less than half of the models, with the numbers of waterfowl and conspecifics rarely having effects (Table 2). Directions of partial

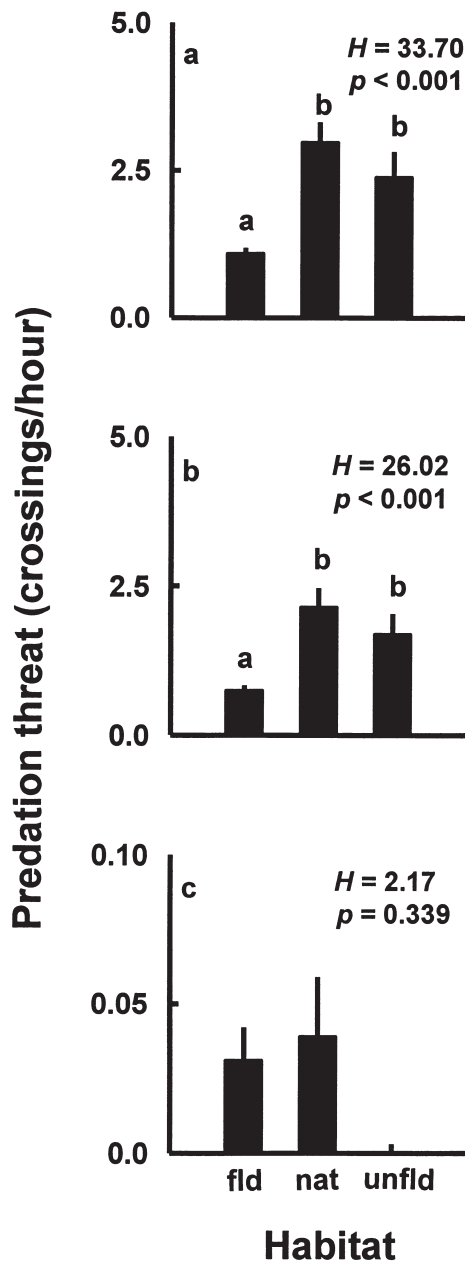


Figure 2. Predation threat in different habitat types measured as the rate at which predators cross the unit: (a) all predators combined, (b) predators that specialize on shorebirds and ducks, and (c) predators that can take larger prey. Statistical comparisons were made with Kruskal-Wallis tests. Habitats with different letters were significantly different according to Dunn's multiple comparison test. Sample sizes for flooded rice fields (fld), seminatural wetlands (nat), and unflooded rice fields (unfld) were 150, 52, and 29, respectively.

correlation coefficients varied among performance measures and species, but no consistent patterns were found.

Many of the covariates considered were correlated

Table 1. Comparisons of foraging performance measures (attack rate, feeding rate, and feeding efficiency) among flooded rice fields (fld), seminatural wetlands (nat), and unflooded rice fields (unfld) for six waterbird species.

	Sample sizes (fld, nat, unfld ^a)	Test statistic ^b	p
Attack rate			
Great Egret	35,11,16	$F_{2,51} = 14.17^c$	<0.001 ^d
Black-necked Stilt	6,20,—	$t_{24} = 1.44$	0.163
Greater Yellowlegs	49,22,—	sep- $t_{28.2} = 0.20$	0.841
Long-billed Curlew	30,2,13	$F_{2,42} = 0.16$	0.854
Dunlin	13,6,—	$t_{17} = 0.08$	0.939
Long-billed Dowitcher	19,11,—	$t_{28} = 1.65^c$	0.109
Feeding rate			
Great Egret	35,11,16	$H = 20.49$	<0.001 ^d
Black-necked Stilt	6,20,—	$t_{24} = 0.84$	0.411
Greater Yellowlegs	49,22,—	$t_{69} = 1.71$	0.091
Long-billed Curlew	27,2,11	$F_{2,37} = 2.02^c$	0.147
Dunlin	13,6,—	$t_{17} = 0.57$	0.575
Long-billed Dowitcher	19,11,—	$t_{28} = 0.52$	0.606
Feeding efficiency			
Great Egret	32,11,11	$H = 6.17$	0.046 ^e
Black-necked Stilt	6,20,—	$t_{24} = 0.42$	0.680
Greater Yellowlegs	49,22,—	$t_{69} = 2.47$	0.016
Long-billed Curlew	30,2,13	$F_{2,42} = 4.11^c$	0.023 ^f
Dunlin	13,6,—	$t_{17} = 1.22$	0.239
Long-billed Dowitcher	19,11,—	$t_{28} = 0.33$	0.745

^aOnly Great Egret and Long-billed Curlew were recorded in unflooded fields.

^bTests used for each variable depended on the number of habitat treatments and results of Levene's variance homogeneity tests. Test statistic F indicates analysis of variance, t indicates a pooled t test, sep-t indicates a separate variance t test, and H indicates a Kruskal-Wallis test. Subscripts give degrees of freedom.

^cData transformed to remove variance heterogeneity.

^dResult of multiple comparison test: (flooded fields = seminatural wetlands) > unflooded fields.

^eResult of multiple comparison test: seminatural wetlands > flooded fields, seminatural wetlands = unflooded fields, flooded fields = unflooded fields.

^fResult of multiple comparison test: seminatural wetlands > (flooded fields = unflooded fields).

with each other, and 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 differences among

Table 2. Summary of the effects of covariates on waterbird behavioral measures.

Behavior ^a	n	Date	Time of day	Predation threat	Group size			Water depth ^b	Observer
					conspecifics	waterfowl	other waterbirds		
Attack rate	6	3	3	5	0	2	1	2	4
Feeding rate	6	1	2	3	1	1	2	3	2
Feeding efficiency	6	3	3	3	1	1	3	3	3
Time allocation	8	4	4	3	6	5	4	—	7

^aFor each behavioral measure the number of species for which there was a significant relationship with a covariate is given.

^bWater depth could not be incorporated in time allocation analyses because depth varied among individual birds.

observers in measuring foraging performance (Table 2; C. S. E., unpublished 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 habitat differences using each observer's data separately. In all cases, significant differences persisted.

The inclusion of covariates in 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 seminatural wetlands ($F_{1,21} = 4.25$, $p = 0.051$). Neither test was significant when covariates were not controlled. A difference in the foraging efficiency of Long-billed Curlews (Table 1) disappeared 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 indicated that the variables I measured did not explain the differences in foraging performance found among habitats and that inherent differences among habitats were not masked by these other variables.

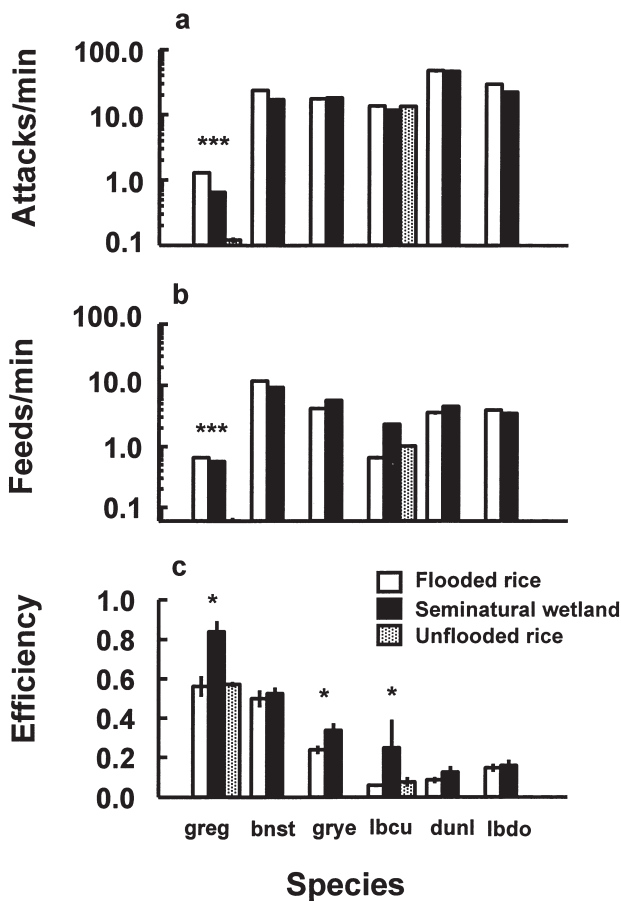


Figure 3. Mean (\pm SE) feeding performance for six waterbird species in different habitat types: (a) attack rate, (b) feeding rate, and (c) feeding efficiency. Only Great Egret and Long-billed Curlew occurred in unflooded fields. Species codes: greg, Great Egret; bnst, Black-necked Stilt; grye, Greater Yellowlegs; lbcu, Long-billed Curlew; dunl, Dunlin; lbdo, Long-billed Dowitcher. Significance tests are given in Table 1; * $0.05 > p \geq 0.01$ and *** $p < 0.001$. A log scale is used for the y-axes of attack rate and feeding rate but not feeding efficiency.

Time Allocation

Few significant differences were found among habitats (Table 3, Fig. 4). 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 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 seminatural wetlands. Dunlins were more aggressive in flooded fields than in seminatural wetlands. Long-billed Curlews were more vigilant in seminatural wetlands than in either rice habitat. Long-billed Dowitchers spent more time sleeping, and Black-necked Stilts spent more time preening in seminatural wetlands than in flooded fields. Finally, Great Egrets spent significantly more time sleeping in unflooded fields than in the other habitats. The time budgets of Killdeers, Greater Yellowlegs, and Least Sandpipers did not differ among habitats. If probabilities are adjusted for multiple comparisons, most of these differences disappear. Only the differences in the amount of time Greater Yellowlegs and Long-billed Dowitchers

Table 3. Results of significance tests comparing the way in which eight waterbird species allocate time to different behaviors in flooded rice fields (fld), seminatural wetlands (nat), and unflooded rice fields (unfld).

Species	Sample sizes (fld, nat, unfld ^a)	Behavior ^b				
		feeding	vigilant	sleeping	preening	aggressive
Great Egret	45,18,10	1.78 ^c (2,70) 0.176	1.78 ^c (2,70) 0.176	8.51 ^{d,e} (—) 0.014	0.11 ^d (—) 0.946	N/A
Killdeer	55,27,10	0.62 ^c (2,89) 0.542	0.42 ^c (2,89) 0.659	3.91 ^d (—) 0.142	0.15 ^c (2,89) 0.861	0.84 ^d (—) 0.658
Black-necked Stilt	8,28,—	0.43 ^f (8.6) 0.678	1.16 ^f (7.2) 0.282	0.44 ^g (34) 0.659	2.58 ^{g,b} (34) 0.014	0.19 ^g (34) 0.850
Greater Yellowlegs	75,28,—	3.01 ^{g,b} (101) 0.003	1.73 ^g (101) 0.087	1.64 ^f (28.0) 0.112	1.77 ^f (30.6) 0.088	1.09 ^f (27.2) 0.284
Long-billed Curlew	31,3,17	1.42 ^d (—) 0.493	3.42 ^{c,b,i} (2,48) 0.041	5.67 ^{d,e} (—) 0.059	0.45 ^c (2,48) 0.784	0.23 ^c (2,48) 0.794
Dunlin	53,18,—	0.65 ^g (69) 0.513	0.55 ^g (69) 0.584	1.31 ^{g,b} (69) 0.196	0.21 ^g (69) 0.833	585 ^j (—) 0.029
Long-billed Dowitcher	29,25,—	2.71 ^f (39.6) 0.010	1.46 ^g (52) 0.152	2.78 ^f (37.1) 0.009	0.37 ^g (52) 0.676	0.37 ^g (52) 0.712
Least Sandpiper	16,7,—	0.75 ^g (21) 0.462	0.35 ^{g,b} (21) 0.732	0.25 ^g (21) 0.804	0.66 ^g (21) 0.517	63 ^d (—) 0.339

^aOnly Great Egret, Killdeer, and Long-billed Curlew were recorded in unflooded fields.

^bTests used for each variable depended on the number of habitat treatments and results of Levene's variance homogeneity tests. In each cell, the test statistic is given first, followed by the degrees of freedom in parentheses where applicable, and the *p* value. Superscripts c to j give the test used and the results of post-hoc tests when applicable. N/A indicates that behavior was never seen.

^cAnalysis of variance.

^dKruskal-Wallis test.

^ePairwise comparisons not significantly different.

^fSeparate-variance *t* test.

^gPooled *t* test.

^hData transformed to remove variance heterogeneity.

ⁱResult of multiple comparison test: seminatural > flooded, seminatural = unflooded, flooded = unflooded.

^jMann-Whitney test.

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 my analysis involved assessing the influence of additional variables on time allocation. All variables played a significant role in at least some models (Table 2). Observer effects were important more frequently than other variables, 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 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 effects.

Time allocation was associated with at least one group size measure 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 (Elphick 1998). Time of day and date each had a significant effect on time allocation by four species. Pre-

ation threat was infrequently associated with time allocation measures (Table 2; Elphick 1998).

Adding covariates to tests of the habitat treatment resulted in different conclusions in only 2 of 40 cases. After controlling for the number of waterfowl and date, the difference in 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 differed between habitats ($F_{1,18} = 5.14$, $p = 0.035$). As was true for foraging performance, these tests suggest that covariates rarely confounded primary tests of habitat differences.

Discussion

Habitat Quality

Flooded rice fields and seminatural wetlands superficially appear to be very different habitats. For example, flooded fields have less surrounding vegetation, less variable water depths, and different nutrient inputs. Furthermore, my study shows that they are not equivalent habitats in terms of variables that may be important to birds (e.g., predation threat was lower in flooded fields than in seminatural wetlands, Fig. 2). Given these differences,

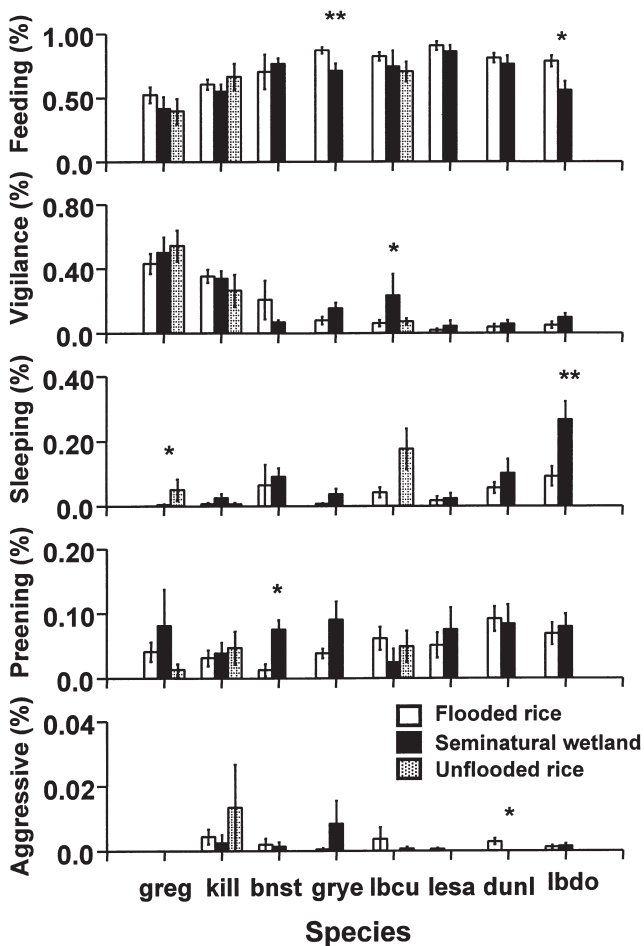


Figure 4. Time allocated to each behavior by eight waterbird species in different habitat types. Each graph gives data for the proportion of time spent doing a particular behavior; bars for each species are grouped vertically. Only Great Egret, Killdeer, and Long-billed Curlew occurred in unflooded fields. Species codes: kill, Killdeer; lesa, Least Sandpiper; see Fig. 3 for others. Significance tests are given in Table 3; * $0.05 > p \geq 0.01$ and ** $0.01 > p \geq 0.001$. To illustrate differences, the y-axis scales for each behavior differ.

one might expect large differences in the behavior of birds using the two habitats, but my results suggest that, to the extent that they exist, differences between 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

species observed attained higher feeding efficiencies in seminatural wetlands than in flooded fields. The three cases for which these differences were not statistically significant were those for which power was lowest. Hence, it is possible that seminatural habitats provide a better foraging habitat than flooded rice fields and that my analyses were unable to detect differences. If this were so, however, there are several ways birds could 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 slightly higher feeding rates for three species (Fig. 3). Birds also may compensate for reduced efficiency by feeding longer (Urft et al. 1996); seven of eight species devoted more time to foraging when in flooded fields than in seminatural wetlands. Given the weak evidence for large behavioral differences between seminatural 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 seminatural wetlands for the species studied.

Incorporating 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 covariates have significant effects on the behavior of the birds studied and that these variables often were more important than habitat per se (Table 2; Elphick 1998). In light of these effects, whatever differences can be attributed to habitat may be trivial. Even though these variables often differed among habitats (e.g., Fig. 2), they did not explain those habitat differences that I did find.

A further issue, not considered here, is that birds may feed on different prey in different habitats. For example, birds in rice fields may feed on larger prey that are less easy to capture but that provide greater nutritional value. Unfortunately, the small size of most prey items prevented the use of noninvasive methods of assessing diet in these birds, and the small behavioral differences found do not seem sufficient to warrant killing the numbers of birds necessary to assess diet differences adequately. Testing the null hypothesis of no difference in diet between habitats (e.g., by stomach flushing captured birds; A. P. 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 (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 seminatural wetlands or flooded fields (Table 1; Fig. 3). The feeding efficiency of both egrets and Long-billed Curlews in unflooded fields also was lower than in

seminatural wetlands, although no different than in flooded fields. These results suggest that unflooded fields may be a low-quality foraging habitat for Great Egrets. An alternative explanation is that prey differed among habitats. The evidence for differences in habitat quality is more equivocal for curlews and lacking for Killdeer.

It is important to consider what these results mean for overwinter survival when the conservation value of the different habitats is assessed. Unfortunately, directly assessing whether survival differs among habitats probably is impossible, especially within the time span over which managers must make decisions. The logistical difficulties of marking and tracking enough birds to estimate survival accurately could be overcome if sufficient resources were available. A more important difficulty is that waterbirds are extremely mobile and use more than one of the habitats available. Consequently, assigning deaths to 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 deaths are a direct result of conditions in the habitat where death occurred or of conditions in other areas the bird used would be more difficult.

Few studies have compared the behavior of birds using rice fields and 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 fields appeared to have deteriorated due to increased pesticide use (Hafner et al. 1986). Variation in feeding conditions for herons also has been found among rice regions in Mediterranean Europe (Hafner & Fasola 1992; Fasola 1994). The quality of rice field habitats clearly varies regionally.

Conservation Implications

My results provide little evidence that the behaviors of the species observed differ between flooded rice fields and seminatural wetlands. If differences exist but could not be detected with my sample sizes, they must be small. Moreover, my data suggest that birds may 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 nongame 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 wa-

terfowl, 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. 1 & 2) and the daily movements of waterfowl to feed in fields (C.S.E., personal observation), however, indicate that flooded fields also are an important habitat for these species (see also Gilmer et al. 1982; Miller et al. 1989; Heitmeyer et al. 1989).

The lack of evidence for differences between seminatural 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 use by waterbirds of other artificial habitats (e.g., sewage ponds, settling beds). Further tests are warranted, however, 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 rice fields results in highly significant increases in waterbird use (Elphick & Oring 1998), these data indicate that winter flooding provides important benefits for waterbirds. 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 that used these seasonally flooded habitats. It appears, however, that flooding could be a valuable contribution to California's wetland resources. In a region where the majority of historic wetlands have been drained (Freyer 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 1991), and these results provide support for the notion that appropriately managed rice fields can contribute to global wetland habitats (Fasola & Ruiz 1996).

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