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PATTERNS OF FOOD ABUNDANCE FOR BREEDING WATERBIRDS IN THE SAN LUIS VALLEY OF COLORADO

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Abstract: We measured the amount and distribution of macroinvertebrates and seeds in four wetland habitats (short emergent, seasonal open water, semipermanent/permanent open water, and saltgrass [*Distichlis spicata*]) used by breeding ducks and shorebirds at a wetland complex in the San Luis Valley, Colorado, USA. Density of macroinvertebrates did not differ among habitats or sampling periods ($P = 0.45$), but dry mass, crude protein, and gross energy production were greater ($P < 0.05$) in short emergent than in other habitats. These differences were largely due to the greater dry mass of gastropods in short emergent than in other habitats. Total seed density, dry mass, crude protein, and gross energy differed among habitats and periods with interaction effects ($P < 0.01$). Although seed abundance varied among habitats and sampling periods, abundance was greatest in short emergent during all sampling periods. Breeding waterbirds consumed a variety of macroinvertebrates and seeds on the study area. Patterns of abundance among habitats of macroinvertebrates and seeds consumed by six waterbird species were not consistent with patterns of foraging habitat use by most ducks and shorebirds at this wetland complex. Our results indicate that estimates of food or nutrient abundance are useful in assessing the functional role of broad habitat types, but factors other than food abundance also influence avian selection of wetland foraging habitats.

Key Words: American avocet, aquatic macroinvertebrates, cinnamon teal, food abundance, gadwall, killdeer, mallard, San Luis Valley, seeds, Wilson's phalarope

INTRODUCTION

Breeding ducks (Anatidae) and shorebirds (Charadriiformes) have high energetic and nutritional demands (King 1973, Afton and Paulus 1992, Alisauskas and Ankney 1992). Birds may derive fitness-related benefits from foraging in habitats where they can most efficiently obtain required food resources (Stephens and Krebs 1986, Stephens et al. 1986, Lemon and Barth 1992). Breeding shorebirds forage primarily on a variety of aquatic invertebrates (Skagen and Oman 1996), and many breeding dabbling ducks (*Anas* spp.) consume both invertebrates and seeds (Krapu and Reinecke 1992). Differences among habitats in the abundance of these food resources can influence selection of habitats by foraging waterbirds (Murkin and Kadlec 1986, Colwell and Landrum 1993), although water depth is an important constraint on availability even when food resources are abundant (Baker 1979, Poysa 1983, Safran et al. 1997). However, patterns of foraging habitat selection by eight waterbird species breeding on a wetland complex in the San Luis Valley (SLV) of Colorado, USA were not consistent with estimates of food dry mass, even after adjusting for the influence of water depth on habitat availability (Laubhan and Gammonley 2000).

In addition to the overall quantity of food available, the taxonomic composition of foods in each habitat may contribute to the quality of food resources and influence foraging habitat selection by waterbirds. Prey size and mobility influence foraging success and intake rates (Nudds and Bowlby 1984), so birds may select habitats where prey are more easily captured, even if food abundance is lower than in other habitats. Similarly, food distribution among feeding substrates within a habitat may constrain food availability in relation to morphological and foraging mode adaptations of waterbirds. In addition, food items differ in their nutrient and energy content, and birds may select among foraging habitats based on relative accessibility of specific nutrients, rather than overall food abundance (Anderson and Smith 1998). Habitat variables

such as vegetation composition and structure, hydrologic regime, and water chemistry may influence community composition and abundance of aquatic invertebrates (Neckles et al. 1990, Downing 1991, Batzer and Resh 1992, Beckett and Aartila 1992, Huener and Kadlec 1992, Batzer et al. 1993, Campeau et al. 1994, Balla and Davis 1995, Streever et al. 1995). Hydrologic patterns also influence wetland plant communities and seed production (Fredrickson and Taylor 1982, Mushet et al. 1992).

Here, we further investigate the relationship between food abundance and distribution, and foraging habitat selection by breeding waterbirds in the SLV. We determined the taxonomic composition, and estimated the density, dry mass, total gross energy, and crude protein of macroinvertebrates and seeds in different foraging habitats and over the course of the prenesting and nesting period of locally breeding shorebirds and dabbling ducks. We then obtained species-specific estimates of food availability, based on foods present in the diet of six bird species on our study area. We examined whether these estimates were consistent with observed patterns of foraging habitat use by these species.

STUDY AREA

Russell Lakes State Wildlife Area (RLSWA) is a 1,739-ha wetland complex located in the SLV, a high (2,286–2,438 m elevation), arid (<20 cm annual precipitation), intermountain basin in southern Colorado, USA. RLSWA is composed of lacustrine and palustrine wetlands with hydroperiods ranging from permanent to intermittently flooded. We examined food abundance in four habitats where surveys indicated >80% of common breeding waterbirds foraged at RLSWA (Laubhan and Gammonley 2000). Short emergent (628 ha) habitats were generally flooded throughout April–June with waters of mean ± standard error specific conductance = 986 ± 150 μS cm^{-1} and were dominated by emergent vegetation <40 cm (visual obstruction reading [VOR; Robel et al. 1970] = 12.8 ± 0.5 cm) including baltic rush (*Juncus balticus* Willdenow), spikerushes (*Eleocharis* spp.), sedges (*Carex* spp.), and various grasses. Seasonal open wetlands (72 ha) were generally flooded <90 days (6,771 ± 1,463 μS cm^{-1}) and were devoid of emergent vegetation (0.4 ± 0.3 cm VOR) but occasionally supported submerged stands of horned pondweed (*Zannichellia palustris* L.). Semipermanent and permanent open habitats (231 ha) were flooded (542 ± 69 μS cm^{-1}) throughout the study, were commonly bordered by softstem bulrush (*Schoenoplectus tabernaemontani* ((Gmel.) Palla) and cattail (*Typha* spp.), and supported submergent pondweeds (*Potamogeton* spp.), milfoil (*Myriophyllum sibiricum* Komarov), and common marestail (*Hippuris vulgaris* L.) (0.2 ± 0.2 cm VOR). Saltgrass (74 ha) habitats typically were flooded <30 days (7,299 ± 1,413 μS cm^{-1}) and were dominated by inland saltgrass (*Distichlis spicata* (L.) Greene) or occasionally Nevada bulrush (*Scirpus nevadensis* Watson) (6.1 ± 0.2 cm VOR).

METHODS

During 1995 and 1996, we collected macroinvertebrate and seed samples at randomly selected sites in each habitat during four intervals (24–28 April, 17–21 May, 5–9 June, and 24–28 June) that spanned the period of arrival through egg-laying for breeding ducks and shorebirds at RLSWA (Laubhan and Gammonley 2000). We combined data from both years for a total of 232 sampled sites (n = 51 in saltgrass, 61 in short emergent, 60 in seasonal open, and 60 in semi/permanent). At each site, we collected food samples using three techniques (Merritt and Cummins 1984, Murkin et al. 1994). First, we pulled a sweep net (25 × 25-cm frame, 0.5-mm mesh) vertically from the bottom substrate to the water surface to sample the water column (Murkin et al. 1983). Next, we clipped all vegetation within a 25 × 25-cm sample frame. Following removal of vegetation, we collected a benthic sample using a 4 × 4 × 4 cm core sampler (Swanson 1983) with 0.5-mm mesh. At each sampling site, we collected three replicate water column, vegetation, and benthos subsamples. We preserved water column and vegetation subsamples in 80% ethanol and stored vegetation and core subsamples in a freezer. We later identified seeds and macroinvertebrates using standard references (Martin and Barkley 1961, Pennak 1978, Merritt and Cummins 1984) and reference collections. Samples stored in ethanol were rehydrated with distilled water, and vegetation and core samples were washed through a 0.5-mm sieve to facilitate sorting. Each food item in each subsample was then enumerated, dried to constant mass at 80 C, and weighed to the nearest 0.1 mg. We summed numbers and dry mass of each food item across the three replicate subsamples from each sampling site.

We calculated density and dry mass for each food item at each sampling site. We obtained values for percent crude protein and gross energy for each food item or for closely related taxa from available references (Kendeigh and West 1965, Calvert et al. 1969, Cummins and Wuycheck 1971, Driver et al. 1974, Norberg 1978, Driver 1981, Haukos and Smith 1995, Rohel et al. 1995, Anderson and Smith 1998). We multiplied dry mass estimates for each food item by its percent crude protein or gross energy values to ob-

tain estimates of protein and energy abundance for each habitat and sampling interval.

We used chi-square tests of independence to compare occurrences of food items among habitats. We compared density, dry mass, crude protein, and crude energy abundance among habitats and sampling periods using analysis of variance (ANOVA) (PROC GLM; SAS Institute Inc. 1985). Following a significant ($P < 0.05$) ANOVA, we used Fisher's LSD to separate means. Prior to ANOVAs, we square-root-transformed data to stabilize variances (Sokal and Rohlf 1981). We present back-transformed means and confidence intervals (Fowler and Witter 1982).

To examine the taxonomic composition of breeding waterbird diets, we shot foraging American avocets (*Recurvirostra americana* Gmelin), killdeers (*Charadrius vociferus* L.), Wilson's phalaropes (*Phalaropus tricolor* Vieillot), mallards (*Anas platyrhynchos* L.), gadwalls (*A. strepera* L.), and cinnamon teal (*A. cyanoptera* Vieillot) at RLSWA during April–July, 1994–1996. We attempted to collect samples of each species in each of the four major habitat types, but most birds were collected in shallow open and short emergent because these habitats received 56–89% of foraging use among species (Laubhan and Gammonley 2000). We removed the esophagus from each bird and stored its contents in 80% ethanol immediately after collection. We identified seeds and macroinvertebrates in esophageal contents using standard references (Martin and Barkley 1961, Pennak 1978, Merritt and Cummins 1984) and reference collections. Each food item from each bird was then enumerated, dried to constant mass at 80 C, and weighed to the nearest 0.1 mg. All birds used in our analyses were of known reproductive status (i.e., members of pairs that were pre-laying, laying, or incubating), observed foraging for >10 minutes before collection, and contained >0.001 g (dry mass) of food in their esophageal contents.

We used distance sampling methods (Buckland et al. 1993) to estimate densities of foraging waterbirds in each habitat during each sampling period (Laubhan and Gammonley 2000). We measured water depth in randomly placed permanent plots in each habitat and used TOPOGRID (Environmental Systems Research Institute 1996) to generate a bathymetric grid of the study area for each period. These maps of surface water depth were then overlaid on a habitat map to estimate the depth of flooding (5-cm increments) in each habitat type (Laubhan and Gammonley 2000). We then multiplied the total area of each habitat by the estimated period-specific proportion of the habitat flooded at depths used during foraging by American avocets (0.1–30.0 cm), killdeer (0.1–10.0 cm), Wilson's phalarope (>5.0 cm), and dabbling ducks (>0.1 cm), to account for the influence of water depth on habitat availability (Laubhan and Gammonley 2000).

We assumed shorebirds consumed seeds incidentally (Skagen and Oman 1996), and dabbling ducks consumed all of the seed taxa present in the habitats we sampled (see Results). Thus, we focused on macroinvertebrates in subsequent analyses. For each waterbird species, we calculated the total dry mass of macroinvertebrates available in each habitat during each sampling period by multiplying the sum of the mean dry mass of all taxa occurring in the diet by the total area of the habitat available (adjusted for water depth). For each species, we compared estimates of the percentage of total birds present in each habitat to estimates of the percentage of total available dry mass of macroinvertebrates (and seeds for dabbling ducks) in each habitat. Estimates of percent bird use differ from those reported in Laubhan and Gammonley (2000) in that we only considered bird use in the four habitats we sampled.

RESULTS

Macroinvertebrates and seeds were present in 230 (99%) and 206 (88%), respectively, of the 232 sampled sites. We identified macroinvertebrates from 18 orders and 51 families and seeds from 12 families and 17 genera in our samples, of which 14 groups of invertebrates and three groups of seeds occurred in >20% of samples from at least one habitat (Table 1). These more common taxa comprised 89–100% of total individuals and 90–100% of total dry mass of macroinvertebrates and seeds in our samples. Crustaceans (including Cladocera, Copepoda, and Ostracoda) and midge (Chironomidae) larvae were most widespread, occurring at 57–70% and 75–97% of sites in each habitat, respectively. Dipterans comprised 39% (semi/permanent) to 56% (short emergent) of total individuals and 28% (short emergent) to 68% (seasonal open) of total dry mass of invertebrates. Snails (Gastropoda), soldier fly (Stratiomyidae) larvae, and spikerush seeds occurred more frequently in short emergent than in other habitats; mayflies (Ephemoroptera) occurred more frequently and beetle (Coleoptera) larvae occurred less frequently in semi/permanent than other habitats; moss beetle (Hydraenidae) adults and shore fly (Ephydridae) larvae occurred more frequently in SG than in other habitats ($X^2 \geq 31.4$, df 1, $P < 0.001$).

The percentage of total dry mass of most common macroinvertebrates was greater in benthic subsamples than in other substrates; water-column subsamples contained the highest proportion of crustaceans and hemipterans, and vegetation samples contained most of the dry mass of mayflies (Figure 1a). Among periods, benthic samples contained >70% of total mac-

Table 1. Frequency of occurrence, and mean (standard error) density and dry mass of invertebrates and seeds collected from short emergent (SE, n = 61), seasonal open water (SW, n = 60), semipermanent open water (SP, n = 60), and saltgrass (SW, n = 51) habitats at Russell Lakes State Wildlife Area. Taxa that were present at >20% of sampling sites in at least one habitat are presented.

	Frequency (%)				Density (individuals/m²)				Dry mass (mg/m²)			
	SE	SW	SP	SG	SE	SW	SP	SG	SE	SW	SP	SG
INVERTEBRATES												
Oligochaeta	52	12	45	4	122	208	279	7	12.6	33.3	76.9	0.7
					(35)	(108)	(86)	(5)	(5.2)	(17.0)	(29.1)	(0.5)
Crustacea[1]	57	65	70	69	1,182	2,570	2,132	2,449	36.2	161.2	65.4	105.2
					(665)	(544)	(569)	(553)	(13.9)	(55.2)	(20.9)	(41.5)
Gastropoda total	66	7	18	22	415	8	103	30	1,489	3.2	210.1	50.3
					(88)	(5)	(41)	(14)	(471.5)	(2.8)	(121.0)	(26.9)
Lymnaeidae	57	5	8	16	211	4	25	14	982.4	2.8	68.9	22.9
					(62)	(4)	(16)	(7)	(328.0)	(2.7)	(43.6)	(9.3)
Physidae	35	2	15	2	53	1	15	1	378.7	0.0	20.9	0.0
					(20)	(1)	(9)	(1)	(288.3)		(11.5)	
Planorbidae	44	2	15	4	150	3	63	16	128.3	0.3	120.2	27.4
					(38)	(3)	(33)	(13)	(35.3)	(0.3)	(89.6)	(25.8)
Ephemeroptera[2]	5	8	40	4	22	42	155	1	0.9	1.5	31.7	0.5
					(11)	(20)	(39)	(1)	(0.6)	(0.9)	(11.6)	(0.4)
Hemiptera[3]	33	38	25	37	12	32	11	22	3.0	17.9	2.7	5.9
					(5)	(16)	(3)	(11)	(1.3)	(11.3)	(0.9)	(2.3)
Coleoptera total	82	47	18	94	357	148	13	935	97.6	60.7	3.3	144.8
					(134)	(54)	(8)	(200)	(32.7)	(22.1)	(2.0)	(34.3)
Dytiscidae larva	57	32	10	61	65	80	8	85	51.7	39.0	1.9	45.7
					(21)	(40)	(7)	(24)	(29.7)	(17.5)	(1.8)	(20.4)
Hydraenidae adults	44	20	5	80	240	64	4	744	24.1	7.5	1.1	66.5
					(132)	(28)	(3)	(199)	(12.9)	(3.5)	(1.0)	(24.3)
Hydrophilidae larva	54	7	2	39	31	1	1	38	14.8	0.3	0.2	23.5
					(12)	(1)	(1)	(18)	(7.3)	(0.2)	(0.2)	(14.6)
Diptera total	100	90	93	98	3,385	2,575	1,724	2,878	690.2	614.3	242.9	462.2
					(758)	(434)	(362)	(631)	(141.9)	(138.2)	(71.4)	(91.6)
Ceratopogonidae larva	54	13	5	45	872	28	1	165	51.1	3.2	3.2	12.8
					(560)	(10)	(1)	(70)	(26.2)	(1.2)	(3.1)	(4.9)
Chironomidae larva	97	75	93	82	2,661	2,422	1,639	2,459	292.0	525.4	234.1	305.5
					(510)	(438)	(363)	(645)	(63.8)	(137.4)	(71.1)	(92.9)
Ephydridae larva	13	13	2	43	22	42	1	155	4.0	21.2	0.0	81.5
					(11)	(20)	(1)	(39)	(3.1)	(14.5)		(21.9)
Stratiomyidae larva	34	3	0	16	35	7	0	9	186.4	39.2	0.0	10.8
					(15)	(5)		(6)	(96.9)	(29.9)		(7.2)
SEEDS												
Chenopodiaceae[4]	36	50	18	73	1,236	6,417	1,817	4,165	227.3	1,046	223.7	717.0
					(358)	(2,066)	(1,074)	(1,378)	(64.4)	(303.6)	(131.9)	(250.6)
Eleocharis spp.	87	22	25	35	48,856	524	163	186	21,585	70.1	58.7	31.2
					(11,498)	(282)	(64)	(66)	(5,136)	(22.7)	(22.1)	(9.0)
Scirpus spp.	72	30	65	25	5,740	167	4,246	374	5,209	134.5	3,193	329.0
					(2,278)	(46)	(1,176)	(206)	(2,005)	(42.3)	(861.4)	(187.7)

[1] Includes the Orders Cladocera, Copepoda, and Ostracoda.
[2] Includes the families Baetidae (primarily *Callibaetis americana*) and Caenidae (primarily *Caenis amica*).
[3] Family Corixidae (primarily the genera *Callicorixa* and *Trichocorixa*).
[4] Primarily *Chenopodium* and *Kochia*.

roinvertebrate dry mass in short emergent, >75% in seasonal open, >40% in semi/permanent, and >50% in saltgrass (Figure 1b). Benthic samples accounted for >98% of seed numbers and dry mass in all habitats and periods.

Total macroinvertebrate density did not differ among habitats or periods ($F_{15,216}$ = 1.29, P = 0.2127). Total macroinvertebrate dry mass ($F_{15,216}$ = 2.84, P <0.0004), crude protein content ($F_{15,216}$ = 2.79, P = 0.0006), and gross energy content ($F_{15,216}$ = 2.52, P =

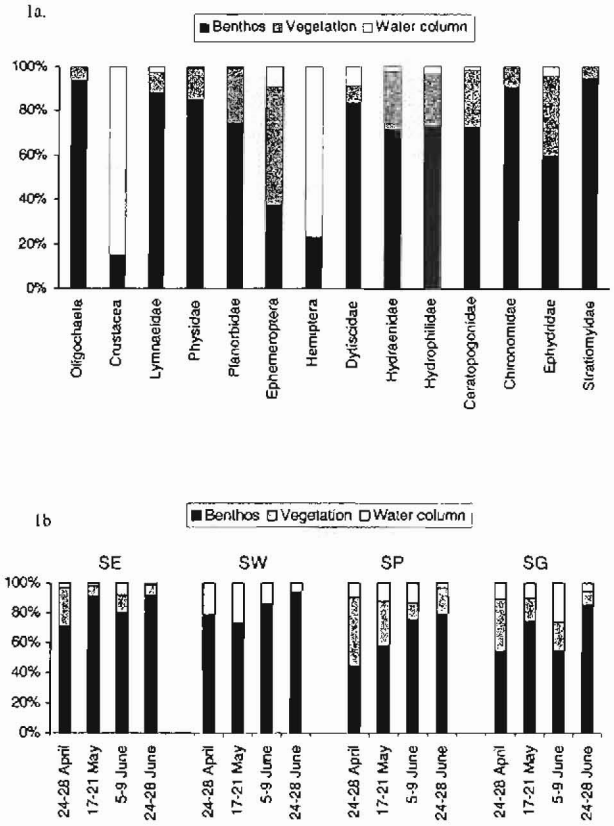

Figure 1. Percentage of total dry mass (all habitats combined) of common invertebrate taxa located in benthic, vegetation, and water-column substrates (a) and percentage of total invertebrate dry mass located in each substrate during four sampling periods in short emergent (SE), seasonal open water (SW), semipermanent and permanent open water (SP), and saltgrass (SG) habitats (b) at Russell Lakes State Wildlife Area, Colorado.

0.0019) differed among habitats (dry mass: $F_{3,228}$ = 9.43, P <0.0001; protein: $F_{3,228}$ = 8.92, P <0.0001; energy: $F_{3,228}$ = 7.64, P <0.0001), with no period ($F_{3,228}$ <1.8, P >0.20) or interaction effects ($F_{9,222}$ <1.4, P >0.18). Total macroinvertebrate dry mass, protein content, and energy content were greater in short emergent than in all other habitats and did not differ among other habitats (Table 2). This result was largely due to the greater dry mass of snails in short emergent than in other habitats; snails accounted for 61% of mean invertebrate dry mass in short emergent and <30% in other habitats (Table 1). When snails were excluded from estimates, 95% confidence intervals for invertebrate dry mass, crude protein content, and gross energy content overlapped in all habitats.

Total seed density ($F_{15,216}$ = 9.08, P <0.0001), dry mass ($F_{15,216}$ = 10.94, P <0.0001), crude protein content ($F_{15,216}$ = 8.52, P < 0.0001), and gross energy content ($F_{15,216}$= 10.99, P < 0.0001) differed among habitats (density: $F_{3,228}$ = 33.60, P <0.0001; dry mass: $F_{3,228}$ = 41.31, P <0.0001; protein: $F_{3,228}$ = 30.74, P <0.0001; energy: $F_{3,228}$ = 41.59, P <0.0001) and periods (density:$F_{3,228}$ = 4.60, P = 0.0038; dry mass:$F_{3,228}$ = 5.06, P = 0.0021; protein:$F_{3,228}$ = 5.03, P = 0.0022; energy:$F_{3,228}$ = 4.99, P = 0.0023), with significant interaction effects (density: $F_{9,222}$ = 2.52, P = 0.0093; dry mass: $F_{9,222}$ = 2.89, P = 0.0030; protein: $F_{9,222}$ = 2.36, P = 0.0145; energy: $F_{9,222}$= 2.90, P = 0.0029). Seed abundance in short emergent was greater than in other habitats during all sampling periods but varied among other habitats across periods and among periods in each habitat (Table 2).

We identified macroinvertebrates from 12 orders and 40 families and seeds from 11 families and 16 genera consumed by dabbling duck and shorebird species we collected. The 14 groups of invertebrates and three groups of seeds that were most common in our habitat sampling comprised ≥86% of the dry mass in the diet of all bird species except gadwalls, which consumed 41% other plant matter (Table 3). Dipterans, coleopterans, and snails comprised >81% of the diets of shorebird species, and dipterans were the most dominant macroinvertebrates in dabbling duck diets. Crustaceans seemed to be a significant food source for Wilson's phalaropes and gadwalls. Seeds were common in duck diets, and comprised 62% of the dry mass of mallard foods (Table 3).

Using only those taxa present in esophageal contents of birds collected at RLSWA, total macroinvertebrate density was similar among habitats for all waterbird species, whereas total dry mass, crude protein content, and gross energy content were greater in short emergent than in other habitats for all species except gadwall (Table 4). This, combined with more hectares of short emergent available (i.e., flooded at accessible depths) to all species than any other habitat, resulted in >64% of available dry mass and nutrients of available macroinvertebrates (i.e., consumed taxa) being located in short emergent for all species except gadwall (Figure 2).

Patterns of habitat use by shorebirds and ducks at RLSWA were not consistent with patterns of macroinvertebrate dry mass and nutrient distribution among the habitats (Figure 2). Percentage use (95% confidence intervals) of seasonal open was much greater than percent availability of macroinvertebrates for all species. Use of short emergent was lower than macroinvertebrate availability for all shorebirds and prenesting cinnamon teal; other dabbling ducks used short emergent in proportion to macroinvertebrate availability. Percent use of semi/permanent was similar to percent macroinvertebrate availability for all species. Percent use of saltgrass was greater than percent avail-

Table 2. Estimated means (95% confidence intervals) of density, dry mass, crude protein content, and gross energy content of macroinvertebrates and seeds in wetland habitats at Russell Lakes State Wildlife Area.

	Invertebrates Combined periods	Seeds			
		24–28 April	17–21 May	5–9 June	24–28 June
Density (individuals/m²)					
Short emergent	6,041 (1,316)	56,823 (7,938)	111,937 (7,832)	17,578 (1,132)	44,961 (3,552)
Shallow open	5,581 (1,253)	7,035 (1,446)	12,049 (1,898)	4,667 (768)	7,903 (1,553)
Semipermanent open	4,483 (1,176)	1,918 (310)	6,310 (894)	9,222 (1,370)	9,931 (1,287)
Saltgrass	6,609 (1,506)	3,667 (594)	8,834 (1,106)	4,305 (518)	2,877 (392)
Dry mass (g/m²)					
Short emergent	2.451 (0.827)	18.491 (2.794)	53.590 (4.196)	8.535 (0.616)	30.537 (2.906)
Shallow open	0.898 (0.335)	0.904 (0.184)	1.899 (0.262)	0.907 (0.158)	2.036 (0.296)
Semipermanent open	0.707 (0.294)	1.138 (0.198)	3.419 (0.530)	4.998 (0.656)	5.437 (0.726)
Saltgrass	0.776 (0.207)	1.033 (0.206)	2.249 (0.248)	0.901 (0.092)	0.473 (0.070)
Crude protein (g/m²)					
Short emergent	1.165 (0.361)	1.259 (0.172)	3.495 (0.266)	0.597 (0.040)	2.048 (0.184)
Shallow open	0.467 (0.151)	0.167 (0.034)	0.301 (0.046)	0.152 (0.026)	0.361 (0.054)
Semipermanent open	0.361 (0.120)	0.079 (0.014)	0.261 (0.038)	0.365 (0.048)	0.432 (0.058)
Saltgrass	0.379 (0.108)	0.213 (0.026)	0.315 (0.040)	0.143 (0.018)	0.080 (0.012)
Gross energy (kcal/m²)					
Short emergent	8.778 (2.830)	91.861 (1.400)	266.507 (21.051)	44.407 (3.104)	151.835 (14.514)
Shallow open	3.906 (1.213)	4.396 (0.897)	9.174 (1.280)	4.426 (0.767)	9.591 (1.394)
Semipermanent open	2.946 (0.906)	5.554 (0.959)	16.372 (2.607)	24.215 (3.148)	25.972 (3.504)
Saltgrass	3.435 (0.910)	5.056 (0.997)	11.024 (1.209)	4.308 (0.443)	2.418 (0.340)

ability of macroinvertebrates for killdeer, but use was less than availability for dabbling ducks. Patterns of foraging habitat use by dabbling ducks were also not consistent with the distribution of seeds among habitats; >90% and <4% of dry mass, protein, and energy from seeds consumed by dabbling ducks were located in short emergent and seasonal open, respectively.

DISCUSSION

Results of our habitat sampling indicate that wetlands at RLSWA support diverse and abundant macroinvertebrate communities, and seeds are also abundant in these wetlands during the breeding period of many waterbirds in the SLV. All devices used to sample aquatic invertebrates have associated biases (Resh 1979, Murkin et al. 1994), and we likely underestimated the abundance of more mobile taxa and life stages with our sampling methods. In addition, some invertebrates from the water column or vegetation may have been included in benthic samples, and some individuals from the water column taxa may have been included in vegetation samples, or vice versa. However, we believe these potential biases were relatively insignificant, or at least consistent among habitats, and our comparisons of macroinvertebrate abundance among habitats and substrates are valid. Potential biases caused by our sampling methods in estimating seed abundance were likely much smaller than those for invertebrates.

The diet composition of breeding waterbirds we collected at RLSWA indicated that the species we examined were diet generalists (see also Krapu and Reinecke 1992, Colwell and Jehl 1994, Gammonley 1995, Skagen and Oman 1996, Robinson et al. 1997, Jackson and Jackson 2000). Shorebird diets were restricted primarily to invertebrates, but a wide diversity of taxa were consumed. Ducks consumed a variety of macroinvertebrates and seeds. Determining the food items in habitats that are actually available to foraging waterbirds is problematic. We adjusted the amount of food in each habitat based on water depths used by each species. We also assumed that only those macroinvertebrate and seed taxa that were present in esophageal contents of birds we collected at RLSWA were "available." This approach is conservative, in that there may have been taxa that a bird could consume (the bird's morphology and feeding behavior did not preclude capture and handling of the food item) but were not consumed by the birds we collected. Hence, our estimates of food "availability" for each waterbird species are likely biased low.

Mallards preferred short emergent and seasonal open over other habitats, and other breeding dabbling

Table 3. Mean percent dry mass (frequency of occurrence) of food items in the diets of 6 breeding waterbird species at Russell Lakes State Wildlife Area.

Food item	American avocet (n = 52)		Killdeer (n = 45)		Wilson's phalarope (n = 50)		Mallard (n = 35)		Gadwall (n = 20)		Cinnamon teal (n = 54)	
INVERTEBRATES												
Oligochaeta	0.0	(0)	0.0	(0)	tr	(4)	tr	(6)	tr	(5)	tr	(4)
Crustacea[1]	0.0	(0)	0.0	(0)	7.7	(14)	0.3	(11)	13.5	(50)	1.7	(22)
Gastropoda total	6.0	(8)	3.8	(16)	6.4	(4)	2.5	(31)	0.2	(10)	13.0	(44)
Lymnaeidae	5.8	(8)	2.6	(16)	0.1	(2)	1.7	(17)	0.0	(0)	10.4	(37)
Physidae	0.2	(2)	1.2	(2)	0.0	(0)	0.4	(11)	0.0	(0)	0.6	(7)
Planorbidae	0.0	(0)	0.0	(0)	1.6	(2)	0.4	(14)	0.2	(10)	2.0	(33)
Ephemeroptera	3.5	(8)	0.6	(13)	tr	(4)	tr	(6)	0.4	(10)	2.4	(9)
Hemiptera	4.5	(21)	1.0	(7)	9.1	(32)	0.5	(14)	tr	(10)	0.8	(9)
Coleoptera total	17.4	(44)	46.3	(89)	36.6	(66)	2.8	(34)	1.6	(30)	6.9	(39)
Dytiscidae larva	10.4	(40)	28.4	(71)	27.4	(54)	1.9	(31)	0.3	(15)	6.2	(37)
Hydraenidae adults	0.0	(0)	0.1	(11)	0.1	(4)	0.0	(0)	tr	(0)	0.2	(13)
Hydrophilidae larva	3.9	(13)	3.0	(29)	5.8	(18)	0.9	(14)	0.2	(15)	0.4	(17)
Diptera total	59.4	(77)	42.8	(76)	38.1	(64)	17.8	(51)	23.9	(65)	26.7	(76)
Certopogonidae larvae	0.2	(6)	tr	(4)	2.2	(6)	0.1	(11)	0.0	(0)	0.2	(15)
Chironomidae larva	52.4	(77)	17.4	(38)	26.0	(50)	17.6	(43)	21.6	(65)	17.5	(54)
Ephydridae larva	3.5	(8)	4.7	(13)	0.4	(4)	0.0	(0)	tr	(5)	5.4	(15)
Stratiomyidae larva	0.4	(2)	8.6	(18)	5.5	(10)	tr	(9)	0.0	(0)	2.5	(9)
Other invertebrates	5.4	(21)	4.7	(27)	0.8	(18)	6.2	(34)	tr	(10)	2.2	(22)
SEEDS												
Chenopodiaceae[2]	0.3	(4)	0.0	(0)	0.0	(0)	5.6	(17)	0.1	(10)	2.2	(13)
Eleocharis spp.	0.6	(4)	0.0	(0)	0.1	(4)	19.3	(63)	4.0	(25)	16.2	(57)
Scirpus spp.	1.0	(4)	0.5	(4)	0.4	(6)	37.2	(83)	13.3	(40)	19.1	(57)
Other seeds	1.9	(12)	0.3	(2)	0.8	(6)	4.4	(43)	1.5	(10)	8.7	(44)
Vegetation[3]	0.0	(0)	0.0	(0)	0.0	(0)	3.4	(9)	41.5	(75)	0.1	(4)

[1] Includes the orders Cladocera, Copepoda, and Ostracoda.
[2] Primarily *Chenopodium* and *Kochia*.
[3] Stems and leaves of *Chara*, *Potamogeton*, and *Zannichellia*.

duck and shorebird species at RLSWA preferred seasonal open over all other foraging habitats, even after controlling for the influence of water depth on habitat availability (Laubhan and Gammonley 2000). Our results indicate that these patterns of foraging habitat selection are not readily explained by differences among habitats in food abundance, taxonomic composition, distribution among foraging substrates, or protein and energy content. Estimates of dry mass, protein, and energy production from invertebrate and seed sources in seasonal open were lower than in short emergent and generally similar to other habitats. All habitats supported a diversity of aquatic macroinvertebrates and several common seeds, and there were no common taxa in seasonal open that were not also common in at least one other habitat. We did not quantify abundance of plant leaves and stems, which comprised a large proportion of gadwall diets. Qualitative assessments suggest that vegetation present in gadwall diets was highly abundant in short emergent and semi/permanent and much less abundant in seasonal open and saltgrass. Thus, percent use of seasonal open by foraging gadwall was likely much greater than the percent availability of vegetative food items, as well as macroinvertebrates and seeds.

Only seasonal open habitats contained little or no vegetation, and food was found primarily in open bottom sediments and, secondarily, within the water column. Given their morphological and feeding behavior adaptations, shorebirds, and to a lesser extent dabbling ducks, likely can locate and capture food items more efficiently in open, unvegetated seasonal open habitats than in other habitats. We speculate that some waterbirds selected seasonal open habitats on our study area because they can forage there more profitably (Stephens and Krebs 1986, Stephens et al. 1986), even though food abundance may be lower than in other habitats. Other factors, such as predation risk, territory defense, and interspecific competition may also impact patterns of foraging habitat selection by breeding waterbirds.

Greater dry mass, energy, and protein availability of

Table 4. Mean (±95% confidence interval) estimates of macroinvertebrate density (individuals/m²), dry mass (g/m²), crude protein (g/m²), and gross energy (kcal/m²) in wetland habitats at Russell Lakes State Wildlife Area. Estimates are based on those invertebrate taxa present in the diet of each waterbird species (see Table 3).

	American avocet	Killdeer	Wilson's phalarope	Mallard	Gadwall	Cinnamon teal
Density						
Short emergent	4,617 (1,458)	4,459 (1,304)	5,856 (1,996)	5,358 (1,728)	5,327 (1,791)	5,640 (1,824)
Shallow open	2,767 (937)	2,761 (1,062)	5,543 (1,619)	5,228 (1,560)	5,280 (1,569)	5,338 (1,567)
Semipermanent open	2,040 (910)	1,957 (706)	4,262 (1,114)	4,184 (1,199)	4,066 (1,198)	4,188 (1,198)
Saltgrass	4,027 (1,025)	3,831 (1,012)	6,303 (1,775)	5,363 (1,572)	6,215 (1,870)	6,296 (1,870)
Dry mass						
Short emergent	2.136 (0.679)	2.154 (0.679)	2.053 (0.525)	2.301 (0.712)	0.620 (0.180)	2.330 (0.715)
Shallow open	0.714 (0.228)	0.699 (0.220)	0.882 (0.256)	0.850 (0.267)	0.814 (0.266)	0.882 (0.266)
Semipermanent open	0.477 (0.180)	0.383 (0.112)	0.622 (0.229)	0.643 (0.229)	0.550 (0.181)	0.676 (0.231)
Saltgrass	0.573 (0.193)	0.638 (0.196)	0.766 (0.223)	0.613 (0.225)	0.678 (0.220)	0.764 (0.224)
Protein						
Short emergent	0.966 (0.352)	0.976 (0.352)	0.956 (0.325)	1.0143 (0.393)	0.330 (0.100)	1.059 (0.369)
Shallow open	0.373 (0.121)	0.363 (0.104)	0.460 (0.151)	0.444 (0.140)	0.420 (0.141)	0.453 (0.140)
Semipermanent open	0.246 (0.091)	0.190 (0.054)	0.321 (0.109)	0.322 (0.106)	0.285 (0.084)	0.338 (0.108)
Saltgrass	0.281 (0.104)	0.320 (0.105)	0.380 (0.117)	0.323 (0.118)	0.335 (0.114)	0.379 (0.117)
Energy						
Short emergent	7.3 (2.8)	7.4 (2.6)	7.2 (2.4)	8.0 (3.2)	2.6 (0.8)	8.1 (3.0)
Shallow open	2.9 (1.1)	2.8 (1.1)	3.9 (1.5)	3.7 (1.4)	3.6 (1.4)	3.8 (1.4)
Semipermanent open	1.9 (0.7)	1.5 (0.6)	2.5 (1.0)	2.6 (1.0)	2.3 (0.9)	2.8 (1.1)
Saltgrass	2.3 (0.8)	2.7 (0.8)	3.4 (0.9)	2.7 (0.9)	3.0 (0.9)	3.4 (1.0)

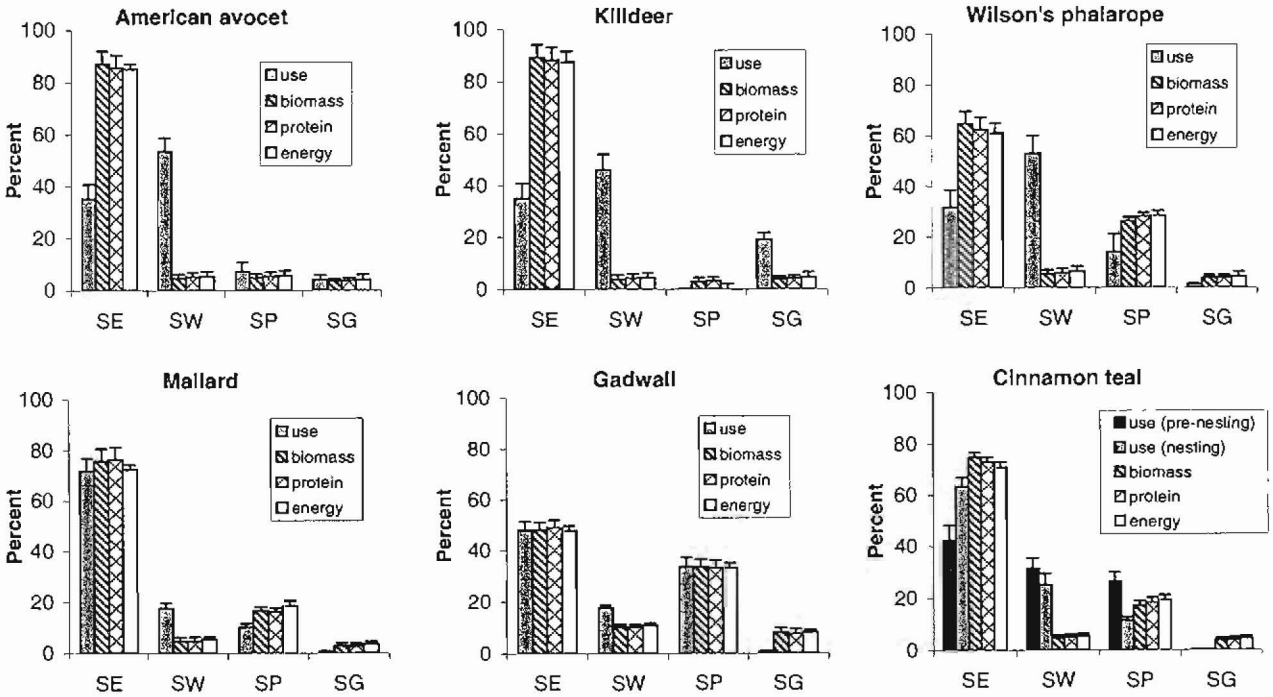

Figure 2. Percent ± standard error use by foraging waterbirds and availability of dry mass, crude protein, and gross energy from invertebrate foods in short emergent (SE), seasonal open water (SW), semipermanent and permanent open water (SP), and saltgrass (SG) habitats at Russell Lakes State Wildlife Area, Colorado.

invertebrates in short emergent than in other habitats could largely be accounted for by the large snails that occupied short emergent. When snails were discounted, all habitats contained similar invertebrate dry mass, protein, and energy. As an individual food item, snails are lower in protein and energy content than most other common invertebrate taxa (37.9–45.9% crude protein and 2.7–3.9 kcal/g gross energy; Anderson and Smith 1998). However, snails are an important food for breeding dabbling ducks because they provide high levels of calcium (26% of dry weight: Sugden 1973), which is required by females during egg formation (Krapu and Swanson 1975, Krapu and Reinecke 1992). Snails occurred frequently in the diet contents of cinnamon teal and, to a lesser extent, mallards at RLSWA. The morphological and foraging mode adaptations of dabbling ducks likely allow them to obtain snails efficiently, even in more densely vegetated short emergent habitats. Shorebirds likely acquire sufficient calcium from snails located in sparsely vegetated sites, and Wilson's phalaropes and gadwalls may also rely on crustaceans such as cladocerans (calcium 12% of dry weight; Sugden 1973) (Serie and Swanson 1976).

Seeds are typically a minor component of the diet of breeding shorebirds (Skagen and Oman 1996), and they comprised <4% of the diets of breeding shorebirds at RLSWA. Female dabbling ducks typically shift from a plant-dominated, non-breeding diet to forage intensively on protein-rich aquatic invertebrates prior to and during egg laying (Krapu and Reinecke 1992, Gammonley 1995). However, seeds may be an important component of the diets of male and prenesting and incubating female dabbling ducks in the SLV (this study; J.H. Gammonley, unpublished data). Plant communities in SLV wetlands are dominated by perennial species, and spikerushes and bulrushes seem to be important seed sources in this landscape. Annual species in the family Chenopodiaceae also provide abundant seed sources. Management techniques that promote seed production by these species may enhance foraging habitats for some species of waterbirds.

Wetland conservation and management efforts in the SLV have emphasized short emergent habitats. Although we examined only one wetland complex, our results indicate that other wetland habitats may have importanr values for foraging waterbirds in the SLV. In particular, sparsely vegetated, typically alkali, wetlands that are shallowly flooded for short periods support diverse assemblages of abundant invertebrates in an environment where they can be efficiently captured and consumed. Conservation approaches that sustain a variety of productive wetland types in close proximity may be particularly beneficial for meeting the diverse life history requisites of breeding waterbird communities (Fredrickson and Laubhan 1994, Laubhan and Gammonley 2000).

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