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Diet and Body Mass of Wintering Ducks in Adjacent Brackish and Freshwater Habitats

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Abstract.—Field-collected and hunter-donated ducks obtained during September-January of 1997-98 and 1998-99 were used to determine if food habits and body mass of Northern Pintails (Anas acuta) and Mallards (A. platy-rhynchos) wintering in Suisun Marsh (Suisun), California, a managed estuarine brackish marsh, differed from values in the adjacent Sacramento-San Joaquin River Delta (the Delta), a freshwater region of grain fields flooded after harvest. Ducks in Suisun fed primarily on seeds of Sea Purslane (Sesuvium verrucosum), followed by Alkali Bulrush (Schoenoplectus maritimus) and Wild Millet (Echinochloa crusgalli), together forming 73-90% (aggregate % dry mass) of the diets. Ducks in the Delta fed primarily on seeds of Smartweed (Polygonum spp.), followed by corn (Zea mays) and tomato seeds (Lycopersicon esculentum), together forming 62-88% of the diets. Pintails and Mallards collected in Suisun each had similar (5 of 11 seasonal comparisons) or greater (6 of the 11 comparisons) body mass compared to their conspecifics collected from the Delta (90% confidence interval analyses), despite a composite diet in the Delta having about 39% greater metabolizable energy content (ME) and 24% greater protein content than in Suisun. Therefore, diet quality alone was not a predictor of body mass in these two areas. Other factors must have been involved, such as greater food abundance and density, lower waterfowl abundance and density, or lower daily energy costs in Suisun. Direct measurement of these factors should explain the apparent inconsistencies in body mass relative to food quality in these brackish and freshwater habitats. Received 28 June 2008, accepted 23 February 2009.

Key words.—*Anas acuta, Anas platyrhynchos*, body mass, brackish water, California, diet, food habits, freshwater, Mallard, Northern Pintail.

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The diets of wintering waterfowl using coastal brackish or marine habitats differ from those feeding in nearby freshwater habitats (Beter 1957; Tietje and Teer 1996; Ballard et al. 2004). The respective foods are often not of the same nutritional quality and may not allow accumulation of comparable winter fat and protein reserves (body condition) critical for subsequent breeding success (Krapu 1981; Mann and Sedinger 1993; Esler and Grand 1994), or support survival (Raveling 1979), recovery from food deprivation (Jorde et al. 1995), and migration (Alerstam and Lindström 1990). For example, foods consumed by Northern Shovelers (Anas clypeata) in saline wetlands along the Texas Gulf Coast differed from those in inland freshwater wetlands (Tietje and Teer 1996), and body condition (body mass,

omental-fat, muscle mass) in freshwater generally exceeded that in the saline area (Tietje and Teer 1988). The diets of Northern Pintails (*A. acuta*) in Gulf Coast saline habitats contained less protein and fat and more ash than Pintails feeding inland in flooded rice (*Oryza sativa*) (Ballard *et al.* 2004), and the Pintails in the saline environment had lower body mass. Whether this is a consistent feature of other wintering regions is not known.

In California, the brackish Suisun Marsh (hereafter, Suisun) and the adjacent freshwater Sacramento-San Joaquin River Delta (hereafter, Delta) (Fig. 1) have traditionally supported relatively large wintering populations of waterfowl. However, Pintails, the most abundant duck wintering in Suisun, declined from the 1960s through the 1970s because increased commercial corn (*Zea mays*) produc-

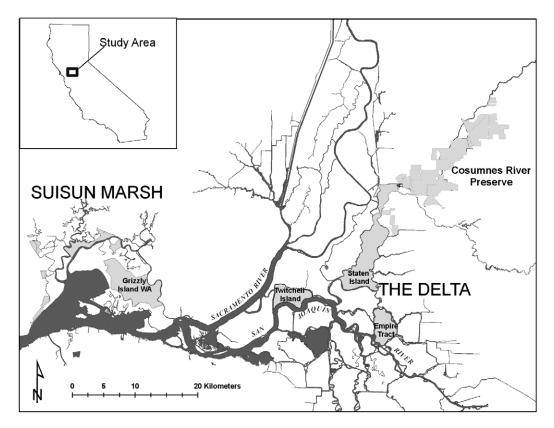


Figure 1. The Suisun Marsh and Sacramento-San Joaquin River Delta, California, study areas, 1997-99.

tion in the adjacent Delta provided easily obtained waste corn in harvested fields (Michny, F. J., unpublished report). Corn, wheat (Triticum aestivum), and rice grains remaining in fields after harvest are important foods for dabbling ducks because of their high metabolizable energy (ME) content (Baldassarre et al. 1983; Jorde et al. 1983; Joyner et al. 1987; Clark and Sugden 1990), and Pintails and Mallards will use agricultural grains even when marsh foods are available (Sugden 1980; Miller 1987). In contrast, Alkali Bulrush (Schoenoplectus maritimus) and many other marsh seeds eaten in Suisun (George et al. 1965; Burns 2003) have limited metabolizable energy (ME) content (Pederson and Pederson 1983; Petrie et al. 1998; Mueller and van der Valk 2002; Dugger et al. 2007).

The contrast in food resources available in Suisun and the Delta led us to suspect that food habits and body mass of these ducks could be different. If true, the results would suggest lower food quality and improved habitat management needs for the area with the lower average body mass. George et al. (1965) and Burns (2003) documented food use for Suisun, but no comparable data were available for the Delta. Therefore, we examined diets and body mass of Mallards and Pintails in the Delta during the fall and winters of 1997-98 and 1998-99, and herein compare our results with those from the Burns (2003) study, which was conducted simultaneously. Based on literature reports of greater quality diets in freshwater habitats, we predicted that body mass of collected ducks in the Delta would be greater than in Suisun.

METHODS

Study Area

Suisun Marsh—Suisun is a brackish estuarine wetland within a tidal zone consisting of 23,000 ha of wetlands managed to control daily tidal influence, reduce salt accumulation in the soil, and promote food production (Rollins 1981). During September to February, when pond water circulates and originates from adjacent delivery canals, the salinity of pond water can be

2.5-14.0 parts per thousand total dissolved solids (ppt TDS), and in marsh soils salinity reaches 6-44 ppt TDS (Mall 1969; Rollins 1973). Suisun supported a complex array of plants during our study, each with different ranges of salt tolerance, such as Alkali Bulrush, Fat-hen (Atriplex triangularis), Brass Buttons (Cotula coronopifolia), Sea Purslane (Sesuvium verrucosum), and Pickleweed (Salicornia virginica), as well as Wild Millet (Echinochloa crusgalli) in the fresher areas (< 3 ppt TDS) (Miller et al. 1975; Rollins 1981).

Wintering duck populations in Suisun had declined before the late 1990s as measured by annual midwinter surveys (M. Wolder, U.S. Fish and Wildlife Service, unpublished midwinter survey data). For example, we compared counts during 1973-1977, when large continental waterfowl populations prevailed in North America (North American Waterfowl Management Plan 2004), with those of 1997-1998, one of our study years. We found that total dabbling ducks (tribe Anatini) declined from 72,000 to 64,000, and Pintails declined from 47,000 to 16,000; however, Mallards increased from 6,000 to 10,000.

The Delta—The Delta is a freshwater system (generally 0 ppt TDS), but water of ≤1 ppt TDS can intrude into the narrow westernmost part of the Delta during drought years (California Department of Water Resources 1987: Fig. 30). High levees separate the Delta into a network of farmed islands isolated by navigable streams, and the primary crops grown included corn, wheat, and tomatoes. Landowners flooded harvested fields to control Johnsongrass (Sorghum vulgane) and leach salts from the soil, and these fields provided habitat used by wintering waterfowl. Isolated managed marsh occurred on some of the islands (e.g., Mandeville, Bract Tract) and on Cosumnes River Preserve (CRP) (Fig. 1).

Duck populations had generally been greater in the Delta than Suisun leading up to our study, but the disparity narrowed after the 1970s. Comparing average midwinter numbers during 1973-1977 with 1997-1998, we found that total dabbling ducks declined from 389,000 to 84,000 because Northern Pintails had declined from 371,000 to 47,000, following a continental trend (Miller and Duncan 1999); Mallards, however, increased from 11,000 to 22,000.

Minimal interchange of ducks occurs between Suisun and the Delta. Food habits studies have documented only small amounts of corn in ducks from Suisun where none is grown (George et al. 1965; Burns 2003). Also, telemetry data for Pintails radio-tagged in Suisun show that frequent and large-scale back-and-forth movements closely linking Suisun and the Delta apparently do not occur (Casazza 1995). Comparable data are not available for Mallards wintering in Suisun or for either species in the Delta.

Location of Duck Collections

The largely private ownership of the Delta and Suisun, wherein most lands served as duck clubs, precluded our collection of feeding ducks randomly during the duck hunting seasons. For example, in Suisun, Burns (2003) collected ducks on private lands only prior to the hunting seasons and on state-owned wildlife areas once the hunting seasons began. In the Delta, which contained few public hunting areas, we limited our work to Staten and Twitchell Islands, Empire Tract, and the CRP (Fig. 1). Further, during October 1998, the land manager at Staten Island denied further access to collect feed-

ing ducks, and instead required that we obtain food samples only from hunter-donated ducks.

Duck Collections

General-Similar field procedures were followed in Suisun and the Delta to obtain samples. Investigators collected ducks by shotgun during autumn and winter 1997-98 (Year 1) and 1998-99 (Year 2). During the hunting seasons, they collected ducks only on non-shoot days (Monday, Tuesday, Thursday, Friday) or in afternoons (late October-January). Both studies used esophageal samples from actively feeding and non-feeding ducks to eliminate bias of hard foods common with gizzard analyses (Swanson and Bartonek 1970). Esophageal samples were obtained from actively feeding Mallards and Pintails (Swanson and Bartonek 1970; Miller 1987), those pass-shot as they transited the areas (Miller 1987; Ely and Raveling 1989), and those donated by private hunting clubs (Delnicki and Reinecke 1986). Body mass was obtained for each collected duck (not hunter-donated ones), and in the Delta we aged them as hatch-year (HY) or after hatch-year (AHY) (Carney 1992). Because hunter-donations and pass-shooting essentially sampled ducks under the same set of circumstances from blinds as the ducks returned to roosting ponds, and because sample sizes of pass-shot birds proved to be inadequate in the Delta (2 Pintails, 5 Mallards) compared to Suisun (35 Pintails, 48 Mallards), we pooled these two sources of ducks and categorized them as non-feeding.

Actively feeding ducks—Burns (2003) first collected actively feeding ducks in Suisun during September and October of both years, when all potential seeds would be present at maximum quantity and variety, and continued through December. In the Delta, we collected actively feeding ducks during December-February (Year 1) or September-February (Year 2). Although Burns (2003) collected benthic samples at feeding sites in Suisun, we obtained these only sporadically in the Delta. As a result, and because it would not be relevant to the point of our study, we do not consider food preference (Johnson 1980).

Non-feeding ducks—Burns (2003) pass-shot ducks in Suisun as they returned to diurnal roosts at dawn during October-December both years, and in the Delta we pass-shot ducks as opportunities arose and only during Year 1. Suisun duck club managers retained intact esophagi (with proventriculi) from ducks shot by members throughout the hunting season (October-January), preserving them in jars of 70% ethanol until retrieved (Burns 2003). In the Delta, during October-December of Year 2, we obtained esophageal contents of ducks directly from hunters on Staten Island and Empire Tract.

Processing Esophageal Contents

Processing of samples followed Miller (1987) in both regions. Esophageal contents (including proventriculus) from feeding and non-feeding ducks were removed after collection, placed in 70% ethanol in plastic bags, stored on ice in coolers, and later frozen for subsequent analyses. Food samples were thawed, washed through 500 µm mesh sieves, then each item was identified and dried to constant dry mass (DM) at 65° C (Reinecke and Owen 1980; Miller 1987). Existing reference samples, known seeds collected from the two study areas, and published sources (Miller 1987) were used to identify seeds. Additionally, the California Department of Food and Agricul-

ture's seed laboratory in Sacramento identified many unknown seeds. Invertebrates were identified using Pennak (1978), Merritt and Cummins (1996), and assistance of the Bohart Museum of Entomology at UC Davis.

Data are presented for each food item as frequency of occurrence (% occ) and aggregate percent dry mass (agg% DM) (Swanson *et al.* 1974; Miller 1987):

- (1) % occ = number of ducks in which the food item occurs ÷ total ducks;
- (2) agg% DM = \sum (percentage DM of the food item in each duck) \div total ducks.

Nutritional Value of Foods

We used literature sources to obtain values of ME (apparent or true) content, as determined directly from feeding trials, of foods (>10.0 agg% DM) consumed in Suisun and the Delta. We also obtained percentages of crude protein (CP), fat (FAT), nitrogen free extract (NFE) (estimates carbohydrate), crude fiber (CF), and ash (ASH) of these foods from the literature. Where we could find no published ME data (one food item), we calculated a predicted value using an equation based on published digestibility and gross energy content of CP (91%, 4.1 kcal/g), NFE (96%, 4.2 kcal/g), and FAT (96%, 9.11 kcal/g), where ME of CF is assumed to be zero (Harris 1966:15; Vohra 1972). However, the method can bias ME high relative to direct feeding trial measures if hard seed coats resist digestion (Pederson and Pederson 1983; Dugger et al. 2007). For example, 50-72% of Alkali Bulrush seeds and 25-50% of Smartweed seeds fed to Mallards and Pintails passed intact in their excreta (Pederson and Pederson 1983; Hoffman and Bookhout 1985; Mueller and van der Valk 2002; Dugger et al. 2007). Therefore, we used published direct values of ME obtained from feeding trials for Alkali Bulrush (Ballard et al. 2004; Dugger et al. 2007), Smartweeds (Hoffman and Bookhout 1985, Petrie et al. 1998, Sherfy et al. 2001, Checkett et al. 2002), and Flatsedges (Sherfy 1999) to compare with predicted values calculated from the equations (Miller 1987: Table 7) (Alkali Bulrush: 3.24 vs. 1.3 kcal/g; Smartweeds: 3.16 vs. 1.4 kcal/g; Flatsedges: 3.08 vs. 2.0 kcal/g). This provided an average correction factor of 0.502 (SE = 0.08), which is the average percentage lower that a direct ME measure is versus the predicted value. Thus, the corrected ME for predicted values is 0.502 x predicted value.

We combined Pintail and Mallard food habits data to construct hypothetical composite diets and their ME (kcal/g) and CP content, each for Suisun and the Delta following Miller and Newton (1999) for ME. To do this, we multiplied aggregate percent dry mass of important food items (>5.0 agg% DM) by the average ME and CP of each, which yielded ME and CP for each food. We then summed these values from all foods to derive total ME and CP of the composite diet. We did not weight the ME or CP of each food by the number of ducks collected by region because we assumed ducks used one or the other region (little or no interchange). Finally, we compared total ME and CP of the composite diets in each region.

Statistical Analysis

Body mass—We combined all body mass estimates of collected ducks by sex to compare body mass of each species by period between the Delta and Suisun Marsh.

We used confidence interval (CI) analyses (Johnson 1999; Anderson et al. 2001; Johnson 2002) for small sample sizes (Zar 1999) to determine if mean body mass could differ between Suisun and the Delta for each species. In the absence of controlled experiments and limited sample sizes resulting from limited areas to work, we adopted 90% CI (Tacha et al. 1982). Overlap of CIs on the means of body mass (CI on the means) and CIs on the difference between the means that include zero (CI on the difference) imply a strong probability of similar body mass between Suisun and Delta ducks. Zero or marginal overlaps are suggestive of different mean body masses. We could not compare body mass by age, because age was not assigned to Suisun ducks. We examined possible biases associated with this limitation by using 90% CI analyses to compare body mass of Delta Mallards and Pintails by age.

Dietary differences.—We did not use hypothesis-testing to detect differences in the diet of ducks between the Delta and Suisun, because differences in foods consumed between the two regions proved to be obvious and distinctive, precluding the necessity of statistical tests (Cherry 1998). Also, sample size was small in some instances in the Delta compared to the number of foods consumed (Miller 1987).

RESULTS

Collections of Ducks

Suisun Marsh—In Year 1, Burns (2003) collected 166 Mallards and 95 Pintails in Suisun from September to January, not all of which contained food items. These included 26 Mallards and 24 Pintails collected as they fed and, respectively, 140 and 71 non-feeding. During Year 2, Burns (2003) collected 159 Mallards and 130 Pintails, and these included 19 Mallards and 19 Pintails collected as they fed and, respectively, 140 and 111 non-feeding.

The Delta—During Year 1 in the Delta, we collected 33 Mallards and 26 Pintails from December to February, not all of which contained food items. These included 27 Mallards and 22 Pintails collected as they fed and, respectively, six and four non-feeding. During Year 2, we collected 46 Mallards and 17 Pintails from September to February, and these included 26 Mallards and ten Pintails taken as they fed and, respectively, 20 and seven non-feeding.

Body Mass in Suisun Marsh versus the Delta

Our data allowed eight direct body mass comparisons between Suisun and Delta Mallards and six comparisons for Pintails (Table 1). Mean body mass of Suisun Mal378 WATERBIRDS

Table 1. Average body mass (g) ± SE, 90% confidence interval (CI) for small samples (Zar 1999), and period sample size (N), and average difference in body mass (g) ± SE and 90% CI on the difference for small samples (Zar 1999) of Mallards and Northern Pintails collected (actively feeding or passing) in Suisun Marsh and the Sacramento-San Joaquin River Delta, California, during September-October-November combined and December-January combined, 1997-98 and 1998-99.

				:
	Mallard	ard	Northern Pintail	n Pintail
	Male	Female	Male	Female
1997-98 collections (Year 1) ^a				
December-January				
Suisun	$1390 \pm 40 (1315, 1465) (7)$	$1210 \pm 25 \ (1160, 1260) \ (7)$	$1055 \pm 25 \ (1010, 1100) \ (12)$	$*1000 \pm 25 (950, 1050) (6)$
Delta	(a1 = 0, t = 1.943) $1370 \pm 35 (1305, 1435) (11)$	(m = 0, t = 1.943) $1180 \pm 55 (1075, 1285) (8)$	(M = 11, t = 1.790) $1020 \pm 35 (985, 1055) (15)$	(a = 5, t = 2.013) $890 \pm 25 (845, 935) (9)$
Difference	(df = 10, $t = 1.812$) $20 \pm 50 \ (-70, 110)$	(dI = 7, t = 1.895) $30 \pm 60 \ (-90, 150)$	(dI = 14, t = 1.761) $35 \pm 35 (-25, 95)$	(d1 = 8, t = 1.860) $110 \pm 35 (50, 170)$
	(df = 13, t = 1.771)	(df = 5, t = 2.015)	(df = 22, t = 1.717)	(df = 12, t = 1.782)
1998-99 collections (Year 2)				
September-October-November				
Suisun	$*1380 \pm 25 (1335, 1425) (21)$	$1160 \pm 25 \ (1115, 1205) \ (10)$	$*1115 \pm 20 (1080, 1150) (18)$	$*985 \pm 35 (920, 1050) (9)$
	(df = 20, t = 1.725)	(df = 9, t = 1.833)	(df = 17, t = 1.740)	(df = 8, t = 1.860)
Delta	$1285 \pm 25 \ (1240, 1330) \ (18)$	$1190 \pm 25 \ (1090, 1290) \ (6)$	$1010 \pm 35 \ (945, 1075) \ (8)$	$825 \pm 40 \ (740, 910) \ (5)$
	(df = 17, t = 1.740)	(df = 5, t = 2.015)	(df = 7, t = 1.895)	(df = 4, t = 2.132)
Difference	$95 \pm 35 (60, 130)$ $(4f = 35 \ t = 1645)$	$30 \pm 55 \ (-75, 135)$ (4f = 7, t = 1.895)	$105 \pm 45 (25, 185)$ (Af = 11 t = 1 796)	$160 \pm 55 (60, 260)$
December-January	(01 - 20) (01 - 10)			
Suisun	$*1440 \pm 25 (1395, 1485) (19)$	$1235 \pm 55 (890, 1580) (2)$	$*1140 \pm 25 (1095, 1185) (9)$	No comparative data
	(df = 18, t = 1.734)	(df = 1, t = 6.314)	(df = 8, t = 1.860)	
Delta	$1330 \pm 55 (1225, 1435) (7)$	$1120 \pm 35 \ (1020, 1220) \ (3)$	$1055 \pm 15 \ (1010, 1100) \ (3)$	No comparative data
	(df = 6, t = 1.943)	(df = 2, t = 2.920)	(df = 2, t = 2.920)	
Difference	$110 \pm 60 \ (0, 220)$	$115 \pm 80 \ (-120, 350)$	$85 \pm 30 \ (30, 140)$	1
	(df = 8, t = 1.860)	(df = 2, t = 2.920)	(df = 9, t = 1.833)	

*Indicates the larger body mass between Suisun and the Delta during each seasonal period as determined with 90% CI analysis. No data obtained in the Delta until December in Year 1, so no comparisons with Suïsun are possible prior to this period.

lards and Pintails exceeded those of Delta Mallards and Pintails, respectively, in 13 of the 14 comparisons. However, not all of these differences were equally probable. For example, 90% CI analyses suggest that body mass of female Pintails was greater in Suisun than the Delta in December-January of Year 1, the only period available, but no other differences occurred for Pintails or Mallards in Year 1. However, during Year 2, body mass in Suisun likely exceeded that in the Delta for male Mallards in October and November, and male and female mallards in December-January, as well as female Pintails in September, and male Pintails in October, November, and December-January (Table 1). The exception occurred in Year 2, in which body mass of male Mallards in the Delta clearly exceeded mass in Suisun during September.

Body Mass Differences by Age in the Delta to Assess Potential Bias

We found mixed results for differences in body mass (years combined) by age for Delta ducks (90% CI on the means). Adult Mallards had larger body mass than HY Mallards, but we found no differences in mass by age for Pintails. Mallard males: AHY mean = 1410g, SE = 20g [N = 26, df = 25, t = 1.708, CI = 1375-1445g] vs. HY mean = 1270g, SE = 30g[N = 25, df = 24, t = 1.711, CI = 1240-1300g]; Mallard females AHY mean = 1240g, SE = 45g [N = 15, df = 14, t = 1.753, CI = 1195-1285g] vs. HY mean = 1150g, SE = 40g [N = 13, df = 12, t = 1.782, CI = 1100-1190g]. Pintail males: Male AHY mean = 1060g, SE = 35g[N = 9, df = 8, t = 1.860, CI = 1025-1095g] vs. HY mean = 1000g, SE = 30g [N = 19, df = 18, t = 1.734, CI = 970-1030g]; Pintail females: AHY mean = 920g, SE = 50g [N = 6, df = 5, t = 2.015, CI = 870-970g] vs. HY mean = 845g, SE = 35g [N = 8, df = 7, t = 1.895, CI = 785-905g].

General Patterns of Food Use

In Suisun, seeds from ten species of plants accounted for >90% of foods consumed for both duck species, and seeds of Sea Purslane, Alkali Bulrush, and Wild Millet

each made up >10% of the diets of Pintails, Mallards, or both, regardless of collection method. Only small numbers of invertebrates occurred in the Suisun diet. In the Delta, seeds from seven species of plants accounted for >90% of foods consumed by Pintails and 14 accounted for >90% for Mallards. Agricultural grains formed a relatively large proportion of the Mallard and Pintail diets in the Delta, consisting of corn and tomato seeds, with some wheat, as well as large amounts of Smartweed seeds. Only Smartweeds (Polygonum spp.), corn, tomatoes, Flatsedge (Cyperus sp.), Wild Millet, and Rabbitsfoot Grass (Polypogon monspeliensis) each made up >10% of the diets of feeding and non-feeding Pintails, Mallards, or both. Ducks consumed measurable amounts of invertebrates in the Delta.

Actively Feeding Ducks

Suisun Marsh—Four food items each accounted for ≥5 agg% DM in feeding ducks (Table 2). Actively feeding Pintails consumed Sea Purslane in the largest quantity and, together with Alkali Bulrush and Wild Millet, most frequently. Actively feeding Mallards consumed these same foods most frequently, and they dominated the diet. Actively feeding ducks consumed few invertebrates, primarily midge larvae and diving beetle larvae. We found no agricultural grain in esophagi of feeding ducks.

The Delta-Seeds of six species of plants and one invertebrate each accounted for ≥5 agg% DM in feeding ducks (Table 3). In combined crop fields and freshwater marsh, actively feeding Pintails consumed Smartweed seeds most frequently, and they dominated Pintail diets, followed distantly by Rabbitsfoot Grass and tomato seeds. Wheat was consumed by only two feeding pintails, in Year 2, forming 9.4 and 17.8 agg% DM of their diets. Segmented worms (Naididae) and midge larvae together formed <1.0 agg% DM of the Pintail diet. Actively feeding Mallards in the Delta consumed Smartweeds most frequently, and this seed predominated in the diet, followed by corn, Flatsedge, and invertebrates (>8.0 agg% DM) (Naididae, Lumbricidae, Chironomidae).

Table 2. Foods of 38 Northern Pintails and 39 Mallards, all of which had ≥ 1 food items, collected while actively feeding in Suisun Marsh, California, during 1997-98 and 1998-99 (only foods ≥ 5.0 aggregate percent dry mass [agg% DM] in ≥ 1 duck species included in table).

	% occi	urrence	agg	% DM
Foods	Pintails	Mallards	Pintails	Mallards
Marsh and grass seeds				
Alkali Bulrush (Schoenoplectus maritimus)	82.9	69.6	8.8	34.1
Italian Ryegrass (Lolium spp.)	0	10.9	0	10.0
Sea Purslane (Sesuvium verrucosum)	85.4	63.0	71.2	27.0
Wild Millet (Echinochloa crusgalli)	29.3	39.1	9.6	23.4
Others ^a	29.3	13.1	9.4	3.8

^aItems with <5 agg% DM, Pintail and Mallard data respectively: Fat hen (*Atriplex triangularis*) agg% DM = 2.5 and 0.3; Pickleweed (*Salicornia virginica*) agg% DM = 1.9 and 0.1; Smartweed (*Polygonum* spp.) agg% DM = <0.1 and 1.4; Swamp Timothy (*Crypsis schoenoides*) agg% DM = 4.9 and 2.0; midge larvae (Chironomidae) % occ. = 24.4 and 32.6; diving beetles (Dytiscidae) % occ. = 4.9 and 13.0; water boatman (Corixidae) % occ. = 0 and 13.0.

Table 3. Foods of 25 Northern Pintails and 39 Mallards, all of which had ≥1 food item, collected while actively feeding in the Sacramento-San Joaquin River Delta, California, during combined 1997-98 and 1998-99 (only foods >5.0 agg% dry mass [agg% DM] in at least 1 duck species included in main table).

	% occ	urrence	agg?	% DM
Foods	Pintails	Mallards	Pintails	Mallards
Commercial grains				
Corn (Zea mays)	4.0	17.9	2.4	17.9
Tomato (Lycopersicon esculentum)	8.0	2.6	8.0	2.6
Marsh and grass seeds				
Flatsedge (Cyperus spp.)	12.0	17.9	0.1	11.0
Rabbitsfoot Grass (Polypogon monspeliensis)	32.0	0	11.8	0
Smartweeds (<i>Polygonum</i> spp.)	76.0	66.7	58.5	41.5
Wild Millet (Echinochloa crusgalli)	12.0	23.1	3.9	6.0
Other seeds ^a	22.0	7.1	13.7	14.1
Invertebrates ^a	36.5	12.8	0.8	8.5
Segmented worms (Naididae)	25.0	17.9	0.4	5.6

[&]quot;Items with <5 agg% DM, Pintail and Mallard data respectively: Wheat (*Triticum aestivum*) agg% DM = 1.1 and 3.6; Ammannia (*Ammannia coccinea*) agg% DM = <0.1 and 1.7; Arrowhead (*Sagitaria* spp.) agg% DM = 0 and 2.2; Johnsongrass (*Sorghum halepense*) agg% DM = 3.7 and 0.2; Lambsquarters (*Chenopodium album*) agg% DM = 0.1 and 1.8; Pickleweed (*Salicornia virginica*) agg% DM = 4.0 and <0.1; Ryegrass (*Lolium* spp.) agg% DM = 0.2 and 1.6; Swamp Timothy (*Crypsis schoenoides*) agg% DM = 4.0 and 0; midge larvae (Chironomidae) agg% DM = 0.4 and 2.9.

Only three mallards consumed wheat in Year 2 (32.9, 43.5, and 64.7 agg% DM of their diets, respectively). One Mallard and one Pintail actively feeding at the CRP obtained some rice seed, probably from nearby fields (<0.3 agg% DM).

Non-feeding Ducks

Suisun Marsh—Non-feeding Pintails and Mallards collected from Suisun consumed Alkali Bulrush, Sea Purslane, and Wild Millet most frequently, and these items dominated the diets (Table 4). Only about 5% of non-feeding Pintails and 3% of non-feeding Mallards contained midge larvae in Suisun, the most-frequently used invertebrate, and none of these ducks had consumed agricultural grains.

The Delta—Non-feeding Pintails in the Delta consumed Smartweed seeds most frequently (75% of all birds), which formed half of the diet, followed by tomato seeds, which formed one-quarter of the diet (Table 5). A small amount of wheat had been consumed by one non-feeding Pintail (4.3 agg% DM).

Table 4. Foods of 178 non-feeding Northern Pintails (35 pass-shot; 143 hunter-donated) and 270 Mallards (48 pass-shot; 222 hunter-donated) in Suisun Marsh, California, during combined 1997-98 and 1998-99 (only foods >5.0 agg% dry mass [agg% DM] in at least 1 duck species included in table).

	% осст	urrence	agg%	% DM
Foods	Pintails	Mallards	Pintails	Mallards
Marsh seeds				
Alkali Bulrush (Schoenoplectus maritimus)	58.5	67.1	37.1	33.0
Sea Purslane (Sesuvium verrucosum)	50.5	51.1	23.6	17.5
Swamp Timothy (Crypsis schoenoides)	22.0	20.0	8.4	6.3
Wild Millet (Echinochloa crusgalli)	24.9	47.1	12.6	22.7
Others ^a	9.1	13.0	15.7	17.1

"Items with <5.0 agg% DM (Pintail and Mallard data, respectively): Fat-hen (*Atriplex triangularis*) agg% DM = 3.1 and 4.5; Dock (*Rumex* spp.) agg% DM = 1.2 and 0.3; Pickleweed (*Salicornia virginica*) agg% DM = 4.7 and 2.2; Rabbitsfoot Grass (*Polypogon monspeliensis*) agg% DM = 1.1 and 1.9; Ryegrass (*Lolium* spp.) agg% DM = 0.1 and 1.1; Smartweed (*Polygonum* spp.) agg% DM = 2.3 and 3.8; corn (*Zea mays*) agg% DM = 1.8 and 0.3; Asters (*Aster* spp.) agg% DM = 1.0 and 0.5; Pondweed (*Potamogeton* spp.) agg% DM = 0.4 and 0.2; all other seeds <1.0 agg% DM in both species: agg% DM = 2.0 and 2.1; midge larvae (Chironomidae) % occ. = 4.9 and 3.0.

Table 5. Foods of 8 non-feeding Northern Pintails (2 pass-shot; 6 hunter-donated) and 19 Mallards (5 pass-shot; 14 hunter-donated) collected in the Sacramento-San Joaquin River Delta, California, during 1998-99 (only foods >5.0 agg% dry mass [agg% DM] in at least 1 duck species listed in table).

	% occ	urrence	agg	% DM
Foods	Pintails	Mallards	Pintails	Mallards
Commercial grains				
Corn (Zea mays)	12.5	42.1	12.5	35.4
Tomato (Lycopersicon esculentum)	25.0	21.1	24.9	11.9
Marsh and weed seeds				
Wild Millet (Echinochloa crusgalli)	0	15.8	0	11.8
Chickweed (Stellaria media)	12.5	5.2	< 0.1	5.2
Rabbitsfoot Grass (Polypogon monspeliensis)	12.5	10.5	11.7	< 0.1
Smartweeds (<i>Polygonum</i> spp.)	75.0	64.7	50.6	29.6
Others ^a				

^aItems <5 agg% DM, Pintail and Mallard data respectively: Flatsedges (*Cyperus* spp.) agg% DM = 0 and 2.6; midge larvae (Chironomidae) agg% DM = 0.2 and 0.1; segmented worms (Naiaidae, Lumbriculidae) agg% DM = 0 and <0.1; diving beetle larvae (Dytiscidae) agg% DM = <0.1 and 0.1.

Pintails consumed midge and diving beetle larvae, which formed <0.5% of the diet. Likewise, non-feeding Mallards in the Delta consumed Smartweeds most frequently, followed by corn, tomato seeds, and Wild Millet. Corn formed about 35 agg% DM of Mallard diets, followed by Smartweeds (about 30%), tomato seeds and Wild Millet (12% each). Less than 0.5% of the diet of non-feeding Mallards was formed of invertebrates.

Nutritional Value of Duck Foods

Nutritional content varied among the most-used foods in Suisun and the Delta (Ta-

ble 6). The heavily used Smartweeds in the Delta and Sea Purslane and Alkali Bulrush in Suisun had relatively the lowest ME values of the other foods. The commercial grains and tomato seeds all contained the highest ME values. Tomato seeds also had the highest CP and FAT content of any food consumed in both regions, followed by Sea Purslane. Wild Millet, which was important primarily in Suisun, but used in the Delta, had modest to high levels of ME.

The composite diet in Suisun consisted of $0.36~\rm kcal/g$ and $0.043~\rm g$ of CP from Sea Purslane, $0.43~\rm kcal/g$ and $0.022~\rm g$ of CP from Alkali Bulrush, $0.53~\rm kcal/g$ and $0.021~\rm g$ of CP from Wild Millet, and $0.15~\rm kcal/g$ and $0.008~\rm g$

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Table 6. Metabolizable Energy (ME), and percent Crude Protein (CP), Fat, Nitrogen-free Extract (NFE), and Crude Fiber (Fiber) content of important seeds consumed by Mallards and Northern Pintails in Suisun Marsh and the Sacramento-San Joaquin River Delta, California, during 1997-98 and 1998-99.

Food item	ME (kcal/g)	%CP	%Fat	%NFE	%Fiber
Suisun Marsh Sea Purslane (Sesuvium verrucosum)	1.5^{4}	17.9^k	8.2 ^k	38.2^{k}	31.9^{k}
Alkali Bulrush (Schoenoplectus maritimus)	$0.7-1.9^{\circ, n}$	8.3	3.2i	65.8	16.2^{j}
Wild Millet (Echinochloa crusgalli)	2.6-3.3°, d, m, s	$9.5 \text{-} 12.9^{ ext{d}, ext{f, m}}$	$2.2-5.1^{ m d,f,m}$	$67.1-69.1^{\mathrm{d,f,m}}$	$9.5 \text{-} 14.6^{ ext{d, f, m}}$
The Delta					
Smartweeds (Polygonum spp.)	$1.1-1.6^{c, d, s, t}$	$9.3-9.9^{d,j}$	$2.2-2.4^{d,j}$	$66.5-72.1^{d,j}$	$14.3 - 18.5^{d,j}$
Flatsedges (<i>Cyperus</i> spp.)	2.0^{r}	$8.9-9.0^{f, r}$	$4.0 - 4.8^{r, f}$	$59.4^{\rm f}$	19.5^{f}
Corn (Zea mays)	$3.6-4.0^{a, b, d, e}$	$7.8-8.8^{a, d, 1}$	$3.3-4.5^{d,1}$	$70.1-84.8^{d,1}$	$2.1-3.6^{d,1}$
Tomato seed (Lycopersicon esculentum)	3.2 ^{i, p}	$25.0-32.4^{\rm h,i}$	$20.0-26.3^{\text{h, i}}$	$16.0-16.8^{h, i}$	$21.4-35.1^{h,i}$
Wheat (Triticum aestivum)	$3.3-3.9^{a,b,c,g}$	$14.3 - 23.3^{a, d}$	$7.8^{\rm d}$	53.9^{d}	11.9^{d}

Bardwell et al. 1962, 'Swiderek et al. 1988, 'Loesch and Kaminski 1989, "Miller 1984, "Dugger et al. 2007, 'Ballard et al. 2004, Pnitrogen-corrected, Ppredicted from equations in Harris (1966) and Vohra (1972) = 2.9 kcal/g, then corrected for over-prediction of equations: 2.9 x 0.502, which is average percentage lower that predicted values are from actual Joyner at al. 1987, ^bReinecke at al. 1989, ^cCheckett at al. 2002, ^dPetrie at al. 1998, ^cMiller and Reinecke 1984, ^fMiller 1987, ^gSugden 1971, ^hYaseen at al. 1991, ^pPersia at al. 2003, ME estimated from feeding trials, 'Sherfy 1999, 'Sherfy et al. 2001, '= Hoffman and Bookhout 1985.

g of CP from Swamp Timothy, for a total of 1.47 kcal/g of ME and 0.99 g of protein. In the Delta, the composite diet consisted of 0.62 kcal/g and 0.043 g of CP from Smartweeds, 0.63 kcal/g and 0.014 g of CP from corn, 0.29 kcal/g and 0.026 g of CP from tomato seeds, 0.19 kcal/g and 0.007 g of CP from Wild Millet, 0.15 kcal/g and 0.022 g of CP from invertebrates, 0.10 kcal/g and 0.004 g of CP from Flatsedges, and 0.09 kcal/g and 0.004 g of CP from Rabbitsfoot Grass (no specific data available, so we used the Flatsedge value), for a total of 2.07 kcal/g ME and 0.123 g of CP in the composite diet. The Delta composite diet had 38.8% more ME and 24.2% more CP than the Suisun Diet.

DISCUSSION

Dietary Differences between Suisun Marsh and the Delta

Mallard and Pintail diets varied markedly between Suisun and the Delta, reflecting the patterns detected elsewhere between saline/brackish and freshwater habitats (Beter 1957; Tietje and Teer 1996; Ballard et al. 2004). In both California areas, seeds formed nearly the entire diets, a common feature in California wintering ducks (Miller 1987; Euliss and Harris 1987). Alkali Bulrush, Sea Purslane, and Wild Millet seeds dominated in Suisun, as shown by actively feeding and non-feeding ducks. In contrast, Smartweeds, corn, and tomato seeds predominated in the Delta, and invertebrates were relatively important compared to Suisun.

Routine foraging flights between Suisun and the Delta would affect the interpretation of our results if individual ducks obtained important quantities of foods in both areas. However, corn, wheat, and rice were found in only one Mallard and three Pintails donated by hunters in Suisun (Burns 2003), similar to findings of George *et al.* (1965), and no actively-feeding or pass-shot ducks in Suisun contained these grains. Likewise we detected no important quantity of dietary items from Delta ducks characteristic only of Suisun. For example, ducks consumed Wild Millet in Suisun, but it formed >10 agg% DM (11%)

in the Delta only for non-feeding Mallards. Also, ducks consumed large amounts of Smartweed seeds in the Delta, but this food always formed <4 agg% DM of the diet in Suisun. Alkali Bulrush and Pickleweed seeds, characteristic of Suisun, occurred only in trace amounts, and Sea Purslane not at all, in esophagi of Delta ducks. Finally, a posteriori analysis of direct band recoveries from ducks banded preseason during 1995-2004, showed that only 10.9% of recoveries of Mallards banded in Suisun were recovered in the Delta, and only 11.1% of recoveries of Mallards banded in the Delta were recovered in Suisun (R. Eddings, California Waterfowl Association, Sacramento, unpublished data). Overall, these data suggest the absence of routine inter-area movements, and body mass should reflect intra-regional dietary ef-

Diet and Body Mass in Suisun Marsh versus the Delta

Adequacy of body mass data—Contrary to expectations, Mallards and Pintails from the brackish habitats of Suisun tended to have larger or similar body mass compared to ducks from the freshwater environments of the Delta. We caution that our mixed-age samples, which we had to use because Suisun ducks had not been aged, could have biased body mass comparisons because AHY ducks usually have greater mass than HY ducks (Bellrose 1980; Haukos et al. 2001). However, body mass comparisons for our Delta Pintails showed no mass differences by age, and at baited sites in Suisun Marsh live-trapped HY Pintails had similar or greater mass than AHY females (M. R. Miller, unpublished data referenced in Austin and Miller 1995). Since Delta AHY Mallards tended to have greater mass than HY Mallard, any bias caused by unknown proportions of HY and AHY ducks from Suisun and Delta samples would be more important for Mallards than Pintails.

Diets and body mass—In Texas, greater body mass of ducks was associated with freshwater rather than coastal marine habitats because the former provided higher quality diets (explicit: Tietje and Teer 1988; implied:

Ballard et al. 2004). However, the larger body masses of ducks in Suisun, suggest that the brackish habitats of Suisun provided foods of greater nutritional quality compared to the freshwater Delta. Suisun ducks did consume seeds from a larger variety of plant species than did Delta ducks (30 species [Burns 2003] vs. 23 species), which is advantageous in achieving a balanced diet (Kaminski et al. 2003) and favorable to larger body mass. However, our composite diets consisting of the most important foods, clearly show that the Delta diet had markedly higher ME and CP contents than the Suisun diet, and corn, tomato seeds, and invertebrates in the Delta diet all had relatively higher ME, CP, or FAT, or all three, than all foods in Suisun. Unfortunately, direct ME and nutrient digestibility assays from feeding trials are unavailable for the majority of foods consumed in Suisun and the Delta, a pervasive problem generally for marsh seeds and other waterfowl foods (Dugger et al. 2007).

Consumption of corn by wintering waterfowl, although providing a good source of ME, results in poor condition of wintering ducks because of deficiencies in certain amino acids (Baldassarre et al. 1983; Jorde et al. 1983; Loesch and Kaminski 1989). However, protein contributed by even small amounts of protein-rich invertebrates (e.g., midge larvae 66% CP) (Krapu and Swanson 1975) or seeds improves high carbohydrate diets (Jorde et al. 1983). Invertebrates formed a measurable portion of the diet in the Delta, and even the low numbers consumed in Suisun might have been sufficient to help balance the diet in concert with Sea Purslane, which had a relatively high CP value. Dabbert et al. (1996) showed that corn and rice with protein levels well within the range or less than Suisun and Delta foods did not induce protein deficiency in HY game farm Mallards. Consumption of tomato seeds (28-32.5% CP) (Canella et al. 1979; Carlson et al. 1981; Yaseen et al. 1991) would have raised dietary protein of ducks feeding in the Delta.

We probably underestimated the consumption rates of wheat, tomatoes, and corn in ducks from the Delta, a critical consideration, because these foods had high ME con-

tent and would have contributed additional energy (kcal) to the composite diet. Landowners flooded harvested wheat fields in August and September, which was followed by intensive feeding by Pintails (Miller et al. 1993). As a result, these ducks likely removed most of the grain prior to our collections of actively-feeding ducks and prior to hunting season collections from hunt clubs. For example, four of six feeding ducks collected in wheat fields in September had wheat but none of six did so in October. A late start to field work in Year 1 (December) precluded collection of ducks in harvested grain fields immediately after landowners flooded the fields when seeds would have been most abundant. Also, the access limitation imposed on Staten Island in early October in Year 2 precluded collections in corn shortly after harvest. These circumstances likely reduced the quantity of grains in our samples of ducks.

The diet-body mass contradiction suggests that factors other than diet quality likely controlled comparative body mass between Suisun and the Delta. First, any nutritional advantage in Delta foods, as shown by the composite diet, could have been overwhelmed by regional differences in food abundance. Estimated waste corn density is 119-286 kg/ha in the Delta (Jones and Stokes Associates 1991), which is similar to or lower than estimates elsewhere (Baldassarre et al. 1983; Warner et al. 1985; Krapu et al. 2004). However, we did not find similar data for Smartweeds, wheat, tomatoes, or other seeds in the Delta, or for Sea Purslane, Wild Millet, Alkali Bulrush, or other marsh seeds in Suisun. Invertebrate density has been estimated in Suisun (Batzer and Resh 1992), where use by Mallards and Pintails was apparently low (Burns 2003; but see Batzer et al. 1993), but not in the Delta, where use was somewhat more important. Secondly, seasonal energy costs of ducks (Miller and Newton 1999) could be higher in the Delta. For instance, the average length of flights between diurnal roosts and nocturnal foraging areas in the Delta $(5.1 \pm 0.3 \text{ km})$ were double that in Suisun ($2.5 \pm 0.1 \text{ km}$) (Fleskes et al. 2005). Thirdly, Pintails are

known to move to the Delta in December from the San Joaquin (Fleskes et al. 2002) and Sacramento Valleys (M. R. Miller, unpublished telemetry data). The Sacramento Valley ducks had lower body mass at that time (Miller 1986) and could have reduced the average body mass we detected in the Delta compared to Suisun. Finally, the larger numbers of Mallards and Pintails, and other and grain-consuming waterfowl present in the Delta but not Suisun, such as Tundra Swans (Cygna columbianus), Sandhill Cranes (Grus canadensis), and Snow (Chen caerulescens), Ross' (C. rossii), and Greater White-fronted Geese (Anser albifrons) (Small 1994), could have increased competition and reduced food densities more rapidly in the Delta compared to Suisun.

Our working assumption that ME and CP content of composite diets is most important in controlling comparative duck body condition during winter in the two regions may need re-assessment. This will require estimates of duck population density (birds/ km²) and the density of their foods (kg/ha) in the managed wetlands of Suisun, and in the harvested grain and tomato fields in the Delta. Also needed are direct determinations of ME and nutrient composition of all critical foods from both regions. This research could directly document how waterfowl population size and density interact with food abundance, density, and nutritional quality to affect body mass of Mallards and Pintails in brackish and freshwater habitats.

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