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Author(s): Bart M. Ballard, Jonathan E. Thompson, Mark J. Petrie, Michael Chekett, David G. Hewitt

Source: *The Journal of Wildlife Management*, Vol. 68, No. 2 (Apr., 2004), pp. 371-382

Published by: Allen Press

Stable URL: <http://www.jstor.org/stable/3803313>

Accessed: 04/09/2009 15:07

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DIET AND NUTRITION OF NORTHERN PINTAILS WINTERING ALONG THE SOUTHERN COAST OF TEXAS

BART M. BALLARD,¹ Caesar Kleberg Wildlife Research Institute, MSC 218, Texas A&M University-Kingsville, 700 University Boulevard, Kingsville, TX 78363, USA

JONATHAN E. THOMPSON,² Caesar Kleberg Wildlife Research Institute, MSC 218, Texas A&M University-Kingsville, 700 University Boulevard, Kingsville, TX 78363, USA

MARK J. PETRIE, Ducks Unlimited, Inc., Pacific Northwest Office, 1101 SE Tech Center Drive, Suite 115, Vancouver, WA 98683, USA

MICHAEL CHEKETT,³ Department of Fisheries and Wildlife Sciences, School of Natural Resources, 302 Anheuser-Busch Natural Resources Building, University of Missouri, Columbia, MO 65211, USA

DAVID G. HEWITT, Caesar Kleberg Wildlife Research Institute, MSC 218, Texas A&M University-Kingsville, 700 University Boulevard, Kingsville, TX 78363, USA

Abstract: Most northern pintails (*Anas acuta*; hereafter pintails) in the Central Flyway winter within the Gulf Coast and adjacent rice prairies of Texas, USA. However, wintering habitat has declined in this region as a result of decreased rice production and changes in land use. Because pintails exhibit high winter site fidelity, more pintails are likely to rely on adjacent coastal habitats during winter as freshwater habitats along the Texas coast disappear. However, few studies have investigated the diet of pintails in estuarine environments. We estimated the composition and quality of the diet of pintails wintering along the lower Texas coast, and we compared our estimates to those for pintails in freshwater habitats. Proximate composition and true metabolizable energy (TME) were estimated for 4 foods in the diet of 253 pintails collected along the lower Texas coast during October–February 1997–1998 and 1998–1999. Shoalgrass (*Halodule wrightii*) rhizomes, wigeongrass (*Ruppia maritima*) seeds, dwarf surf clams (*Mulinia lateralis*), marine gastropods, and *Gammarus* amphipods comprised most of the pintail diet. Pintail diets in coastal habitats contained smaller proportions of protein and fat and a large proportion of ash compared to diets of pintails from freshwater habitats. As a result, the diet of pintails wintering along the lower Texas coast provided about half the TME of diets of pintails wintering in freshwater habitats. Because pintails rely on endogenous reserves acquired during winter and spring migration to support egg production, pintails wintering in Texas may experience greater reductions in recruitment and survival if displaced to coastal habitats.

JOURNAL OF WILDLIFE MANAGEMENT 68(2):371–382

Key words: *Anas acuta*, diet, dwarf surf clam, *Gammarus*, metabolizable energy, northern pintail, nutrition, salinity, shoalgrass, Texas coast, winter.

The Texas coast (inclusive of the Coastal Plain) is an important wintering area for many waterfowl species in the Central Flyway (Bellrose 1980). For example, an average of 78% of northern pintails tallied in the Central Flyway during midwinter surveys from 1993 to 2002 were on the Texas coast (Texas Parks and Wildlife Department, unpublished data). The continental pintail population currently is well below the long-term average, and much attention has been focused on the recovery of this species (Miller and Duncan 1999). Body condition in late winter and during spring migration influences recruitment in species such as pintails that nest early and rely heavily on stored reserves to support nutrient requirements for egg production (Krapu 1981,

Heitmeyer 1988, Mann and Sedinger 1993, Esler and Grand 1994). Wintering ground factors can therefore be important to recruitment. In fact, Raveling and Heitmeyer (1989) found that pintail production declined following dry winters when food availability was reduced.

Many areas of large winter concentrations of pintails (e.g., Central Valley of California, Louisiana, and the Texas coast) are strongly affiliated with rice production. Rice fields provide readily available and abundant, high-energy foods in areas where native wetlands have been lost to anthropogenic impacts. Rice fields produce more energy per unit area than native wetlands and can support more waterfowl (overwinter) per unit area than the declining native wetland base in Texas (Fredrickson and Taylor 1982, Miller 1987). However, rice acreage in Texas has declined by about 60% in the last 2 decades, and further declines are expected because of several problems experienced by the Texas rice industry (Alston et al. 2000). Reversion of rice fields back to native prairie marshes is unlikely given that land-use

¹ E-mail: bart.ballard@tamuk.edu

² Present address: Ducks Unlimited, Canada, #200, 10720-178 Street, Edmonton, AB T5S 1J3, Canada.

³ Present address: Arkansas Game and Fish Commission, 2 Natural Resources Drive, Little Rock, AR 72205, USA.

interests (Alston et al. 2000) and land-leveling practices used in rice production significantly alter natural hydrologic processes. Further, because of reduced agricultural price supports and urban encroachment, much acreage formerly planted in rice has been converted to dryland agriculture or developed. Compounding the loss of rice fields in Texas, coastal freshwater wetlands have declined by >100,000 ha since 1955 (Moulton et al. 1997).

As freshwater habitats along the Texas coast disappear, more pintails are likely to rely on adjacent estuarine habitats during winter. This is surmised because many pintails already winter in these habitats, and because of high winter site fidelity exhibited by pintails, particularly in coastal habitats (Hestbeck 1993). However, little is known about the quality and composition of pintail diets in estuarine environments because previous studies have suffered from small sample sizes (Koenig 1969, Thompson et al. 1992) or methodologies that may have biased results (Koenig 1969, McMahan 1970, Migoya and Baldassarre 1993). Thus, the nutritional consequences of a large component of the Central Flyway pintail population shifting their distribution from freshwater to saltwater environments are unclear. Saline wetlands provide less diversity (Serie and Swanson 1976, Euliss et al. 1991) and abundance of food (Tietje and Teer 1996) for dabbling ducks (*Anas* spp.) than freshwater wetlands, which may ultimately result in birds being in poorer body condition relative to birds wintering in freshwater habitats (Tietje and Teer 1988). Our objectives were to estimate the composition and nutritional quality of the diet of pintails wintering in the Laguna Madre of Texas. Additionally, we compared our findings to the composition and quality of pintail diets from rice fields and freshwater wetlands reported in literature to better understand the capability of coastal environments to provide wintering habitat for pintails.

STUDY AREA

We conducted our study in the Texas Laguna Madre, a long, relatively shallow (generally <1 m deep) coastal lagoon along southern Texas, USA, bordered by Padre Island (a barrier island) on the east and the mainland on the west. The Laguna Madre extends approximately 208 km from Corpus Christi Bay to Port Isabel and is from 5 to 8 km wide. It receives little freshwater inflow from mainland drainages, and evaporation typically exceeds precipitation, often resulting in hypersaline conditions. Salinities generally are >35 ppt but vary seasonally and can reach >50 ppt (McMahan 1968).

More than 79% of the seagrass along the Texas coast occurs in the Laguna Madre (Texas Parks and Wildlife Department 1999); shoalgrass and wigeongrass are the only species consumed by waterfowl in this region (Koenig 1969, McMahan 1970). Freshwater wetlands adjacent to the Laguna Madre are primarily seasonal, and density of basins averages 2.2 basins/km² throughout most of the region (McAdams 1987); however, freshwater can be limited and spatially concentrated during dry winters.

The climate of the region is semi-arid to subtropical, and annual rainfall averages 67 cm (Brown et al. 1977). April and September typically coincide with periods of greatest precipitation; however, tropical storms and hurricanes can impact precipitation patterns and wetland habitat conditions. Fall and winter temperatures are relatively mild (average 14.2 °C) with lowest temperatures typically occurring in late December to early January (National Oceanic and Atmospheric Administration 1999). Mild temperatures compounded with strong coastal winds promote high evaporation rates throughout most of the year and influence seasonal availability of wetlands.

The Laguna Madre region of Texas experienced markedly different rainfall during April–March between the first and second years of our study. In 1997–1998, rainfall averaged across 5 climate stations located adjacent to the Laguna Madre was 133% of normal (30-yr average; National Oceanic and Atmospheric Administration 1997, 1998, 1999). These stations ranged from 20 to 58% above average precipitation during April 1997–March 1998. April–March of 1998–1999 experienced average to dry conditions as precipitation averaged 83% of normal with 9 months experiencing below-normal rainfall. Northern portions of the Laguna Madre, where pintails appeared more abundant during our study, received considerably less precipitation than southern regions in 1998–1999. Climate stations in the upper Laguna Madre ranged from 10 to 40% below-normal rainfall, whereas stations in the lower Laguna Madre ranged from normal to 18% below normal during 1998–1999. Based on rainfall patterns, we refer to 1997–1998 as the wet year and 1998–1999 as the dry year.

METHODS

Diet Composition

Each week from October through February 1997–1998 and 1998–1999, we collected wintering pintails throughout the Laguna Madre of Texas.

We collected pintails by shooting along flight corridors and at feeding sites to avoid potential biases associated with collecting birds over decoys (Greenwood et al. 1986). All specimens were injected with 2–3 ml of 80% ethanol in their upper digestive tract (UDT) immediately following collection to prevent post-mortem digestion of food items. We excised the UDT (including esophagus and proventriculus) of each specimen from the mouth to the gizzard. All contents were extracted and stored in 80% ethanol. Foods were identified, sorted, and oven-dried to constant mass at 70–75 °C to quantify percent occurrence and aggregate percent dry mass of all foods consumed.

We defined the wintering period as the time pintails spent along the southern Texas coast (Oct–Feb in our study). Because of different physiological demands as a result of periods of molt, we delineated the wintering period into 3 seasons by determining the chronology of definitive female molts. We defined early winter as the period from when pintails arrived on the Laguna Madre (late Oct) to the period of light prealternate molt (<2% averaged across all feather tracts) to no molt by adult female pintails (i.e., 6 Dec in 1997 and 26 Dec in 1998). We determined midwinter by light pre-alternate molt or no molt by adult female pintails. Midwinter started on 7 December in 1997 and 27 December in 1998 and continued to 2 January in 1998 and 28 January in 1999 when pre-basic body molt had initiated in most adult females. Late winter extended from the end of the midwinter season to the time pintails departed the Laguna Madre (late Feb) and included increased intensity of the pre-basic body molt by adult female pintails. Males completed pre-alternate molt at approximately the same time as females; however, males do not begin the pre-basic molt until early to midsummer (Austin and Miller 1995) but remain in alternate plumage through spring. Despite sex-specific differences, we employed the same seasonal delineations for both sexes to maintain consistency for seasonal comparisons.

Nutrient Composition and Energy

We conducted feeding trials from early November through February on captive-reared, yearling, female pintails to determine TME for 4 major food items consumed by wild pintails during our study, following Sibbald (1986). When not in bioassays, pintails were housed in 2.44-m³ pens in an indoor facility with windows to provide a natural photoperiod. We maintained pintails on a commercial meat builder (crude protein

≥20%, crude fat ≥3.0%, and crude fiber ≤5.0%; Purina Mills, St. Louis, Missouri, USA). Pintails were provided grit throughout the study period. We collected shoalgrass rhizomes, shoalgrass foliage, dwarf surf clams, and *Gammarus* spp. (aquatic amphipods from the family Gammaridae) from pintail foraging sites in the Laguna Madre for use in our captive feeding trials. For each feeding trial, 7 female pintails were fed the test food and 3 female pintails served as controls to provide an estimate of endogenous contributions to excreta energy (Sibbald 1986).

Prior to each feeding trial, we fasted all pintails for 48 hr in individual metabolism cages (61 × 46 × 61 cm) where they had access to fresh water at all times. Pintails were precision-fed a known amount of each test food through a plastic tube (1.2 × 40 cm) inserted down the esophagus. On average (± SE), pintails received the following dry mass of each food: *Gammarus* spp. (2.65 ± 0.15 g), dwarf surf clam (3.99 ± 0.09 g), shoalgrass foliage (4.16 ± 0.12 g), and shoalgrass rhizomes (4.54 ± 0.18 g). Food was poured slowly into a funnel attached to the upper end of the tube and pushed down the tube with a wooden rod. Food that adhered to the funnel or tube was periodically washed into the bird's esophagus with distilled water. We fed experimental birds only once during a feeding trial; control birds were not fed. We returned experimental birds to individual metabolism cages immediately after being fed and placed pans beneath each cage that funneled fecal and urinary matter into a plastic bag. Pintails that regurgitated any portion of the test food were eliminated from the trial.

We collected excreta samples after 48 hr, and we froze samples for subsequent analysis. Samples were later thawed, and we removed feathers and grit that had passed through the digestive tract (Bilgili et al. 1982). Excreta samples were weighed to the nearest 0.01 g after being oven dried at 60 °C; 1-g subsamples were oven-dried to a constant mass at 80 °C to determine percent moisture. Gross energy of test foods (GE_f) and excreta from fed and fasted birds was determined on duplicate subsamples using a Parr adiabatic oxygen bomb calorimeter (30 atmospheres O₂). We calculated TME (kJ/g) according to Sibbald (1986), and we corrected TME to zero nitrogen balance (TME_N) following the procedures of Sibbald and Morse (1983). We also determined metabolizability (defined as TME_N/GE_f × 100%) for each food.

We determined the nutrient content of each of the 4 test foods by proximate analysis. We esti-

mated nitrogen content with a LECO FP-228 Nitrogen Determinator (LECO Corporation, St. Joseph, Michigan, USA) with 10% reruns by manual Kjeldahl with copper catalyst, and we multiplied percent nitrogen by 6.25 to estimate crude protein. We determined percent moisture by drying in a vacuum oven at 95–100 °C, crude fat by the indirect method, crude fiber by the asbestos-free method, and ash by heating in a cold furnace until 625 °C was reached after 15 hr (Association of Official Analytical Chemists 1984). For the remaining foods documented in pintail diets, we used published sources for proximate composition because we were unable to collect sufficient quantities for analysis.

Although our study provided TME_N values for major pintail food items in the Laguna Madre, assessing nutritional quality of pintail diets required TME_N estimates for all foods. We used the average values of TME_N of all known seeds in the diet of pintails to determine the nutritional composition of "other seeds." For *Cyperus* and *Scirpus* seeds, we used the regression equation from Petrie et al. (1998) to estimate TME_N , where TME_N is a function of percent crude fiber. The remaining 3 species of seeds (i.e., wigeongrass, *Eleocharis* spp., *Potamogeton* spp.) had percent crude fiber values well beyond the range of foods used by Petrie et al. (1998) to quantify the relationship between TME_N and fiber content. For these 3 seeds, we used the TME_N value estimated for *Cyperus*, which had the highest fiber content of any seed for which TME_N was determined directly through feeding trials or from percent crude fiber. Our method likely overestimated TME_N of these high-fiber foods given the negative relationship between TME_N and fiber (Petrie et al. 1998).

We calculated nutritional composition of pintail diets for each season and sex by multiplying the average percent dry mass of each food during each season by the proportional composition of each macronutrient (e.g., protein, fat, etc.). We then summed across food items for each macronutrient to determine the nutrient content of the seasonal diet. We also calculated TME_N for pintail diets by multiplying the TME_N value for each food by the proportional dry mass of that food and then summed all values to obtain an average TME_N value per gram of diet.

We investigated differences in aggregate percent dry mass of foods in pintail diets among seasons and between years for each sex using analysis of variance (ANOVA; PROC GLM; SAS Institute 1999). We considered differences significant if P

≤ 0.05 . We first used a 1-way model with all season*year combinations and tested for homogeneity of variances using Levine's test (SAS Institute 1999). Because of the robustness of ANOVA, we considered Levine's test significant if $P < 0.01$. If Levine's test was not significant, we ran a 2-way general linear model with year and season as main effects, and we tested for an interaction. When the season*year interaction was significant, we tested for seasonal effects within each year. If Levine's test failed, we used PROC MIXED (SAS Institute 1999) with the Kenward-Roger option, assuming unequal variances for the season-by-year combinations to test for seasonal differences.

RESULTS

Diet Composition

We examined UDTs from 351 pintails collected throughout the Laguna Madre of Texas. Two hundred and fifty-three of these pintails (137 males, 116 females) contained food in their UDT. We identified 11 plant taxa and 23 animal taxa in the diet; however, shoalgrass rhizomes and foliage, wigeongrass seeds, *Gammarus* spp., and dwarf surf clams were the only foods that were consumed by both sexes each season (Tables 1, 2). These 5 foods comprised >71% aggregate dry mass of the diet each season. Plant material was identified in 92% of all UDTs containing food, and pintail diets were dominated by plant material during all seasons except the late-winter diet of males in the dry year.

Consumption of plant material was consistent across seasons and years for females ($P \geq 0.233$; no season*year interactions $P = 0.435$). The proportion of plant material in the diet of males also remained similar ($P = 0.377$) across seasons during the wet year. During the dry year, however, plant material comprised a smaller proportion of the diet in late winter than in early winter ($P < 0.001$) and midwinter ($P = 0.008$; season*year interaction; $F = 5.9$; $df = 2, 131$; $P = 0.004$; Table 2).

Shoalgrass comprised over a third of the overall diet of both sexes and occurred in a greater percentage (72.3%) of pintails than any other food item. Pintails consumed primarily the underground rhizomes, and to a lesser extent the above-ground vegetative portion. Pintails seldom consumed vegetative parts of plant species other than shoalgrass. Wetland plant seeds comprised the remaining plant material in the diet of both sexes (Tables 1, 2). Wigeongrass seeds were the dominant species of seed consumed by both sexes, comprising 82% of seeds consumed. Pin-

Table 1. Frequency of occurrence (%) and aggregate percent dry mass of foods ingested by female northern pintails wintering along the lower Texas coast, USA, during October–February, 1997–1999.

Food item	Early winter		Midwinter		Late winter	
	Occurrence	Dry mass	Occurrence	Dry mass	Occurrence	Dry mass
1997–1998	<i>n</i> = 12		<i>n</i> = 12		<i>n</i> = 15	
Plant material	91.7	84.7	91.7	78.7	80.0	56.8
Shoalgrass rhizomes	50.0	27.9	83.3	57.3	40.0	17.8
Shoalgrass vegetation	25.0	2.2	16.7	4.3	13.3	tr
Wigeongrass seeds	66.7	46.3	41.7	16.9	40.0	33.3
Other seeds	8.3	8.3	8.3	tr	6.7	4.7
Animal material	33.3	15.3	33.3	21.3	66.7	43.2
Amphipoda	16.7	5.4	16.7	3.9	26.7	18.3
Isopoda	0.0	0.0	0.0	0.0	13.3	7.1
Gastropoda	16.7	3.9	0.0	0.0	33.3	8.9
Pelecypoda	8.3	6.0	25.0	17.4	26.7	8.9
1998–1999	<i>n</i> = 41		<i>n</i> = 27		<i>n</i> = 9	
Plant material	92.7	60.9	96.3	68.2	88.8	59.9
Shoalgrass rhizomes	68.3	25.2	70.4	36.2	44.4	29.9
Shoalgrass vegetation	43.9	9.4	25.2	3.3	22.2	tr
Wigeongrass seeds	48.8	15.1	51.9	23.4	55.5	30.0
Other seeds	22.0	11.2	11.1	5.3	0.0	0.0
Animal material	61.0	39.1	59.3	31.8	66.6	40.1
Amphipoda	29.3	6.0	11.1	2.9	22.2	tr
Isopoda	9.8	3.2	3.7	tr	11.1	tr
Phoronida	7.3	2.2	0.0	0.0	11.1	4.8
Gastropoda	12.2	5.9	25.9	11.8	22.2	2.5
Pelecypoda	41.5	17.4	37.0	10.4	55.5	18.3
Shell fragments	19.5	4.4	14.8	6.3	33.3	12.9

Table 2. Frequency of occurrence (%) and aggregate percent dry mass of foods ingested by male northern pintails wintering along the lower Texas coast, USA, during October–February, 1997–1999.

Food item	Early winter		Midwinter		Late winter	
	Occurrence	Dry mass	Occurrence	Dry mass	Occurrence	Dry mass
1997–1998	<i>n</i> = 19		<i>n</i> = 14		<i>n</i> = 19	
Plant material	89.5	83.2	100	68.2	100	72.9
Shoalgrass rhizomes	58.0	41.7	64.3	46.1	57.9	34.0
Shoalgrass vegetation	21.1	2.5	7.1	tr	10.5	5.4
Wigeongrass seeds	58.0	33.7	57.1	20.9	42.1	26.8
Other seeds	5.3	5.3	7.1	1.2	10.5	6.7
Animal material	47.4	16.8	64.3	31.8	47.4	27.1
Amphipoda	21.1	4.7	35.7	3.5	21.1	5.6
Isopoda	10.5	2.7	0.0	0.0	15.8	tr
Gastropoda	15.8	6.4	42.9	10.2	21.1	7.6
Pelecypoda	15.8	3.0	28.6	15.7	31.6	12.3
Shell fragments	0.0	0.0	14.3	2.4	0.0	0.0
1998–1999	<i>n</i> = 41		<i>n</i> = 23		<i>n</i> = 21	
Plant material	97.6	75.3	91.3	58.0	76.2	21.3
Shoalgrass rhizomes	75.6	35.3	78.3	46.6	61.9	11.4
Shoalgrass vegetation	31.7	7.3	39.1	10.9	14.3	tr
Wigeongrass seeds	53.7	22.3	13.0	tr	28.6	8.6
Other seeds	24.4	10.4	4.3	tr	4.8	1.3
Animal material	48.8	24.7	65.2	42.0	90.5	78.7
Amphipoda	19.5	2.8	4.3	tr	9.5	tr
Isopoda	2.4	tr	13.0	1.1	14.3	tr
Phoronida	7.3	tr	4.3	1.1	42.9	6.3
Gastropoda	7.3	3.6	26.1	11.9	23.8	10.9
Pelecypoda	39.0	11.1	61.0	20.6	81.0	57.0
Shell fragments	9.8	5.5	21.7	6.5	19.0	3.8

Table 3. Nutrient composition (% dry mass basis), gross energy (GE; kJ/g), and true metabolizable energy corrected to zero nitrogen balance (TME_N ; kJ/g) of foods consumed by northern pintails along the lower Texas coast, USA, during winter 1997–1998 and 1998–1999.

Food item	Aggregate % dry mass					GE	TME_N	
	Protein	Fat	Fiber	Ash	NFE ^a		kJ/g	SE
Plant								
Shoalgrass rhizomes ^b	7.7	0.6	11.5	29.1	51.1	12.09	3.77	0.04
Shoalgrass foliage ^b	18.8	0.6	15.6	15.6	49.4	15.36	3.43	0.13
Wigeongrass seeds ^c	7.8	2.9	35.2	3.1	51.0	^d	5.94 ^e	^d
<i>Cyperus</i> spp. ^f	8.9	2.8	19.9	7.2	61.1	22.18 ^g	5.94 ^h	^d
<i>Eleocharis</i> spp. ^f	6.8	2.1	38.9	11.9	40.2	^d	5.94 ^e	^d
<i>Polygonum</i> spp. ^f	9.5	2.2	18.3	3.5	66.5	19.29 ^g	6.65 ⁱ	0.38
<i>Scirpus</i> spp. ^f	8.3	3.2	16.2	6.4	65.8	20.55 ^g	8.08 ^h	^d
<i>Potamogeton</i> spp. ^j	10.5	6.6	41.1	8.4	33.4	^d	5.94 ^e	^d
Animal								
<i>Gammarus</i> spp. ^b	47.0	3.6	9.7	29.7	10.0	16.66	9.88	0.25
Dwarf surf clams ^{bk}	4.0	0.2	1.2	94.3	0.3	0.92	0.00	1.00
Gastropoda ^l	9.4	0.6	2.2	87.8	0	17.41	2.51 ^m	^d

^a Nitrogen-free extract (NFE) = 100% – (crude protein + crude fat + crude fiber + ash).

^b Analyzed in this study.

^c Nutrient composition of wigeongrass seeds from Swiderek et al. (1988)

^d Information not available.

^e Used TME_N value of *Cyperus* because it had highest fiber value in regression equation.

^f Nutrient composition from Bardwell et al. (1962).

^g Gross energy values from Hoffman and Bookhout (1985)

^h TME_N values estimated by regression on percent fiber content of 7 species of seeds from Petrie et al. (1998).

ⁱ TME_N of *Polygonum* from Petrie et al. (1998).

^j Nutrient composition of *Potamogeton* seed is average of values presented in Anderson and Low (1976).

^k Contents of dwarf surf clams included shell and tissue.

^l Nutrient composition values from Jorde and Owen (1988).

^m TME_N values estimated by regression on percent ash content of 5 invertebrate species from Jorde and Owen (1988) and this study.

tails also consumed seeds from *Cyperus*, *Eleocharis*, *Polygonum*, *Potamogeton*, and *Scirpus*; however, consumption of these genera was infrequent (no genera occurred in >4% of UDTs), particularly in the dry year. Seed consumption by females did not vary across seasons ($P = 0.370$) or between years ($P = 0.221$). Males consumed proportionally more seeds in early winter ($\bar{x} = 35\%$, $SE = 5.2$) than in midwinter ($\bar{x} = 9\%$, $SE = 4.1$; $t = 3.13$, $df = 38.8$, $P = 0.009$).

Overall, bivalves (pelecypods) formed the largest animal component of the pintail diet (Tables 1, 2). Dwarf surf clam was the dominant animal food in the diet and represented 84% of bivalves consumed by pintails in the Laguna Madre. The family Mytillidae (almost exclusively *Amygdalum* spp.) represented the remaining bivalves consumed. Mytillidae were observed in 9% of UDTs and constituted <5% of the diet during any season.

Gastropods made up <12% of the pintail diet each season and primarily were represented by the genus *Bittium*. *Bittium* was present in the pintail diet during each season except in the midwinter diet of females during the dry year, when gastropods were absent from the diet altogether (Table 1).

Amphipods of the genus *Gammarus* predominated the crustacean component of the pintail diet and were the second most frequently consumed invertebrate. During the wet year, females consumed more crustaceans in late winter than in early or midwinter ($P = 0.019$; Table 1). Although frequently ingested by females during late winter of the wet year, crustaceans comprised only a trace during late winter of the dry year.

Nutrient Composition and Energy

Crude protein varied from 6.8 to 10.5% for all plant material consumed by pintails, except shoalgrass vegetation, which contained the greatest proportion of crude protein of all plant material (18.8%; Table 3). Animal material exhibited more variability in protein content ranging from 4% in dwarf surf clams to 47% in *Gammarus*. Crude fat was <3.7% for all foods except *Potamogeton* seeds (6.6%). Ash comprised a large component of animal species (30–94%) and a larger proportion of shoalgrass rhizomes (29%) than other plant material (<16%). Nitrogen-free extract (NFE) ranged from 33 to 67% of the dry mass for plant material and was ≤10% for invertebrates (Table 3).

Despite comprising a large proportion of the diet in most seasons, shoalgrass rhizomes contained relatively little protein and fat compared to most other foods, and pintails metabolized little energy from shoalgrass rhizomes relative to most seeds and invertebrates (Table 3). Most seeds consumed by pintails were similar in nutrient composition; however, *Potomegeton* and *Eleocharis* seeds contained a greater proportion of fiber and were presumably less digestible. The ability of pintails to extract energy from seeds was related to the fiber content of the seed as percent fiber explained 94% ($r^2 = 0.941$, $F = 79.4$, $n = 7$, $P < 0.001$) of the variability in TME_N .

Gammarus had the most favorable nutrient and energy content of all foods consumed. Protein content was 2.5–11.8 times greater in *Gammarus* than in any other food consumed by pintails in our study (Table 3). *Gammarus* also had a relatively large proportion of fat; only *Potomegeton* seeds had proportionally more fat. Fat was 15.5 times greater in *Gammarus* than in the frequently consumed dwarf surf clam. Additionally, *Gammarus* provided ≥ 1.5 times more TME_N than any other animal material. Based on percent dry mass, mollusks appeared to be important to pintails during mid- and late winter, though they contained low proportions of protein, fat, and TME_N relative to other food items. Mollusks were comprised of a large portion of shell (85% of the dry mass for dwarf surf clams) resulting in a large proportion of ash and low TME_N (Table 3). Percent ash averaged 8.1 times greater in mollusk species than in plant species, and 94% ($r^2 = 0.936$, $F = 58.05$, $n = 6$, $P = 0.002$) of the variability in TME_N for invertebrates was explained by percent ash based on regression analysis. Consequently, dwarf surf clams and gastropods, which contained the greatest proportion of shell mass, had the least amount of TME_N . Shells of the bivalve *Amygdalum* spp. were much thinner than the shells of dwarf surf clam or gastropods, and TME_N values were presumably greater.

Metabolizability varied considerably among foods, and pintails metabolized proportionally more energy from *Gammarus* (59.3%) than other foods. Plant material was intermediate in metabolizability (range = 22.3–39.3%), with shoalgrass rhizomes being intermediate in metabolizability among plant material (31.1%). However, shoalgrass rhizomes were metabolized at a higher efficiency than shoalgrass foliage (22.3%). Mollusks generally were least metabolizable, although variable (range = 0–30.8%).

Table 4. Proximate composition (% dry matter) and true metabolizable energy corrected to zero nitrogen balance (TME_N ; kJ/g) of the diet of northern pintails collected along the lower Texas coast, USA, during October–March 1997–1998 and 1998–1999.

	Protein	Fat	Fiber	Ash	NFE ^a	TME_N
Wet winter (1997–1998)						
Females						
Early winter	9.88	1.90	23.75	21.59	42.88	5.02
Midwinter	9.41	1.07	13.95	35.04	40.53	3.47
Late winter	17.78	2.19	17.63	30.39	32.09	5.78
Males						
Early winter	11.08	1.90	20.13	24.65	42.24	4.90
Midwinter	8.84	1.21	13.96	41.01	34.98	3.85
Late winter	11.07	1.53	16.49	32.28	38.63	4.60
Dry winter (1998–1999)						
Females						
Early winter	12.24	1.45	13.51	39.91	32.89	4.27
Midwinter	8.79	1.36	15.28	39.66	34.91	3.56
Late winter	7.49	1.23	14.70	45.56	31.02	3.10
Males						
Early winter	9.70	1.53	16.82	33.46	38.49	4.23
Midwinter	9.16	0.59	7.89	52.94	29.42	2.93
Late winter	7.03	0.77	6.23	74.84	11.13	1.84

^a Nitrogen-free extract (NFE) = 100% – (protein + fat + fiber + ash).

In the wet year, protein and fat comprised a smaller component and ash a larger component of the pintail diet during midwinter than early winter or late winter (Table 4). Consequently, pintails extracted the least amount of TME_N from an average gram of diet during midwinter. Females generally doubled their consumption of protein and fat from midwinter to late winter during the wet year, primarily through increased ingestion of crustaceans. Females increased the metabolizable energy content of their diet by 66% from midwinter to late winter, while males increased TME_N by 19%.

Diet quality gradually declined from early winter to late winter of the dry year for both sexes (Table 4). In fact, pintail diets provided less TME_N during each season of the dry year compared to the wet year, except for the midwinter diet for females, which contained more TME_N during the dry year. The large dietary component of mollusks during late winter of the dry year resulted in poor diet quality as protein and fat content were low and ash content was high. Pintails extracted less energy per gram of diet during late winter of the dry year than in early or midwinter, or in any season during the wet year (Table 4).

DISCUSSION

Pintails wintering in the Laguna Madre primarily fed on foods that typically are abundant and available (Cornelius 1984). Availability of food

items is a primary factor influencing food choice by wintering waterfowl in many areas (Euliss and Harris 1987, Miller 1987, Euliss et al. 1991, Thompson et al. 1992). Euliss et al. (1991) observed pintails responding to food availability by feeding on wigeongrass seeds that had become wind-rowed as a result of foraging activities of red-heads (*Aythya americana*) and American wigeon (*Anas americana*). We found a similar response in our study as we often observed pintails foraging intensely through shoalgrass that had become wind-rowed along the shoreline. Invertebrates often are found in high densities and become more available to dabbling ducks when wind-rowed in seagrasses or detritus (Bousfield 1973, Serie and Swanson 1976). Similarly, *Gammarus* amphipods often were observed in relatively high densities in wind-rowed shoalgrass where they were easily accessible to foraging pintails.

Pintails typically feed on plant seeds during winter in California (Euliss and Harris 1987, Miller 1987) and Louisiana (Glasgow and Bardwell 1962). Although seeds made up a notable proportion of the diet, shoalgrass (primarily rhizomes) comprised >50% of the plant material consumed by pintails in the Laguna Madre of Texas and was the predominant food during most seasons. Because shoalgrass rhizomes and foliage provided less TME_N than any of the species of seeds, the large dietary component may have been related to its great abundance and availability in the Laguna Madre.

Gammarus was the most digestible food consumed by pintails along the southern Texas coast and provided the greatest energy per gram of dry mass. The TME_N for *Gammarus* (9.88 kJ/g) fed to pintails during our study was similar to values obtained when *Gammarus* was fed to black ducks (*Anas rubripes*; 9.71 kJ/g; Jorde and Owen 1988). Soft-bodied invertebrates such as *Gammarus* provide more TME_N because of their greater digestibility than mollusks. Further, dabbling ducks can consume larger amounts of soft-bodied invertebrates and maintain a high rate of energy acquisition (Jorde and Owen 1988), which may be important during periods of rapid formation of endogenous reserves (i.e., premigratory period).

The variability in consumption of *Gammarus* across seasons and years may have been related to its availability. The smaller contribution of *Gammarus* to the midwinter diet of pintails in both years corresponds to the period when many species of *Gammarus* migrate to deeper water (Bousfield 1973), reducing their availability to pintails

foraging in shallow water along the shore. Additionally, some species of *Gammarus* have little tolerance for extreme salinities (Bousfield 1973). Because salinity in the Laguna Madre can be influenced by precipitation, this may explain the absence of *Gammarus* from the pintail diet during late winter of the dry year. Dwarf surf clams become more abundant when salinities are 30–45 ppt and decline when salinities are reduced from freshwater inflows (Cornelius 1984). This may explain the greater contribution of dwarf surf clams to the pintail diet during the dry year when salinities were presumably greater. Dwarf surf clams are among the most abundant invertebrates in the Laguna Madre (Cornelius 1984), and because of their sessile nature, probably are readily available throughout winter. During feeding trials, pintails lost more body mass when fed dwarf surf clams than any of the other test foods. This is consistent with findings for free-ranging black ducks that also lost body mass when restricted to diets comprised primarily of mollusks during winter (Albright et al. 1983). Additionally, digestive efficiencies decline as ingestion rate of mollusks increases (Jorde and Owen 1988). Therefore, TME_N values would be even lower for dwarf surf clams under more intense foraging situations.

Similarity of diets between sexes of pintails (Miller 1987) and gadwalls (*Anas strepera*; Paulus 1980) have been found during winter, and dietary differences among male and female pintails become more apparent after they leave wintering areas (Krapu 1974). Pintails (particularly hens) shift their diet from plant to animal material in late winter (Euliss and Harris 1987, Miller 1987, Euliss et al. 1991) to meet the increased demand for protein during egg production. Accordingly, female pintails in the Laguna Madre consumed a higher-quality diet than males during late winter. For instance, 59% of animal material consumed by females during late winter of the wet year was crustaceans, whereas animal material consumed by males was $\geq 72\%$ mollusks.

The diet of pintails wintering in the Laguna Madre was of poor quality compared to that of pintails wintering in freshwater habitats (Table 5). In general, dietary protein and fat were less than that reported for diets of pintails wintering in freshwater habitats. However, dietary crude fiber appeared similar between diets of pintails wintering in fresh and saline habitats (Table 5). The greatest disparity in diets between habitats was in the ash component. Pintails wintering in freshwater habitats consumed diets relatively low in

Table 5. Nutrient composition (% dry mass) and true metabolizable energy corrected to zero nitrogen balance (TME_N; kJ/g) content of the diet of northern pintails feeding in freshwater habitats (presented from other studies) and in saltwater habitats (from our study in the lower Texas coast, USA, winters of 1997–1998 and 1998–1999).

Location / habitat	Protein	Fat	Fiber	Ash	NFE	TME _N
California—rice fields ^a						
Fall (Aug–Sep)	7.0	1.5	9.3	5.4	76.8	11.5
Winter (Oct–Jan)	11.9	2.2	19.6	10.1	56.2	7.5
Spring (Feb–Mar)	28.9	2.7	13.1	16.9	38.4	10.0
California—seasonal freshwater marshes (Oct–Feb) ^b	25.8	3.4	8.6	7.4	54.8	11.7
California—Evaporation ponds (Sep–Mar) ^c	37.7	4.6	16.5	7.7	33.5	9.6
Texas—Playa wetlands (winter) ^d	15.4	2.9	12.0	12.1	57.6	10.0
Louisiana—Prairie Marshes (Nov–Jan) ^e	15.8	2.5	14.5	9.8	52.2	f
Mexico—Fresh/brackish marshes and agriculture (Nov–Feb) ^g	13.2	3.7	14.4	7.3	61.4	8.8
Laguna Madre (this study) ^h						
Early winter (Oct–Dec)	9.7–12.2	1.5–1.9	13.5–23.8	21.6–39.9	32.9–42.9	4.2–5.0
Midwinter (Dec–Jan)	8.8–9.4	0.6–1.4	7.9–15.3	35.0–52.9	29.4–40.5	2.9–3.9
Late winter (Jan–Feb)	7.0–17.8	0.8–2.2	6.2–17.6	30.4–74.8	11.1–38.6	1.8–5.8

^a Calculated from data presented in Miller (1987).

^b Calculated from data presented in Euliss and Harris (1987). Percent volume was used instead of % dry mass. Proximate composition for *Ammania*, sprangle top, and "other seeds" was assumed to be averages of all seeds presented in Miller (1987).

^c Calculated from Euliss et al. (1991). Proximate composition of brine flies and other animals was considered the average of non-gastropod invertebrates presented in Miller (1987).

^d Aggregate percent dry mass presented in Sheeley and Smith (1989).

^e Values presented by Bardwell et al. (1962) as the average proximate composition of individual pintails sampled.

^f Data insufficient to estimate TME_N of diet.

^g Aggregate percent drymass presented in Migoya and Baldassarre (1993).

^h Range of nutrient composition and TME_N from our study.

ash (5–17%), primarily because mollusks rarely comprised a large proportion of the diet. In general, chironomid midge larvae and other soft-bodied invertebrates dominated the animal component of pintail diets in freshwater habitats (Euliss and Harris 1987, Miller 1987, Migoya and Baldassarre 1993). Conversely, the animal component of the diet of pintails wintering in the Laguna Madre typically comprised >70% mollusks, resulting in ash ranging from 22 to 75% of the diet. The high ash content most likely influenced the energy available to wintering pintails in Texas because percent ash explained most of the variability in TME_N provided by invertebrates.

In general, pintail diets from estuarine habitats along the Texas coast provided less than half the TME_N supplied by rice fields and other freshwater habitats during winter (Tables 4, 5). The consequences of the low energy diet from the Laguna Madre is that birds need to increase food intake to meet daily energy expenditure (DEE), and/or rely on endogenous reserves, or emigrate from the area to find sites with higher quality foods. We estimated DEE for pintails wintering along the lower Texas coast to range from 851 to 1,151 kJ/day based on basal metabolic rate × 3 (Prince 1979).

During the wet year, pintails were required to ingest 156–288 g dry mass of food each day to maintain body mass. During the dry year, intake needed to meet DEE ranged from 226 to 527 g dry mass with greatest intake needed during late winter because of the poor quality diet.

Daily energy expenditure for pintails wintering in rice fields is estimated to range between 611 and 1,063 kJ/day (Austin and Miller 1995) with daily intake required to meet DEE ranging from 83 to 148 g/day. Similarly, intake requirements for pintails in the southern High Plains of Texas were <94 g dry mass/day based on our calculations from reported estimates of body mass and diet composition of collected pintails (Sheeley and Smith 1989, Smith and Sheeley 1993). Therefore, to meet DEE, pintails wintering along the southern coast of Texas must consume approximately 2 times more food during wet years than birds wintering in freshwater habitats, and potentially up to 3.5 times more when conditions are dry. However, because of decreased digestive efficiency as rate of food intake increases (Jorde and Owen 1988), TME_N also would be expected to decrease, potentially compounding the problem of lower energy availability for pintails in the

Laguna Madre. Further, our estimate of TME_N for pintail diets in the Laguna Madre may be biased high because we used the energy value for *Cyperus* to estimate TME_N for other seeds in the diet that had greater fiber content. However, these foods were only a minor component of the pintail diet, so any error associated with these foods should not affect our overall conclusions.

For some waterfowl species, quantity and quality of food on wintering areas influences the physiological condition of individuals returning to breeding areas (Heitmeyer and Fredrickson 1981). Pintails rely on endogenous lipid and protein reserves obtained on wintering and migration areas to support egg production, maintenance, and incubation (Krapu 1974, Mann and Sedinger 1993, Esler and Grand 1994). Pintail production declines following dry winters when food availability on wintering areas is reduced (Raveling and Heitmeyer 1989). Pintails in the Laguna Madre likely relied on endogenous reserves during winter given the low amount of energy extracted from their diet. This hypothesis is supported by recent findings that pintails in the Laguna Madre lost approximately 20% of their body mass over winter (Ballard 2001).

MANAGEMENT IMPLICATIONS

Anderson et al. (2000) observed the greatest densities and largest proportion of pintails along the Texas coast in rice fields. Although rice fields have replaced many of the historical freshwater prairie marshes associated with the Texas coastal plain, they have retained many of the ecological services (e.g., foraging sites for waterfowl and other water birds, roost sites, etc.) that typically are lost when wetlands are replaced by other agricultural land uses. Rice provides more energy than most native seeds and more energy per ha than native wetlands (Fredrickson and Taylor 1982, Miller 1987). Rice fields therefore probably have moderated the effects of native wetland loss to waterfowl populations wintering along the Texas coast due to their ability to support large numbers of waterfowl in relatively concentrated areas. However, reversion of rice fields back to native prairie marshes is unlikely given land-use interests (Alston et al. 2000) as well as land-leveling practices used in rice production that significantly alters natural hydrologic processes. Current and future reductions in rice acreage and freshwater wetlands adjacent to the Texas coast may adversely impact pintail populations in the Central Flyway if pintails increase their reliance

on saline habitats during winter. If coastal habitats do not provide sufficient foods to maintain wintering pintails in optimal body condition, pintails wintering in Texas may suffer disproportionately high reductions in survival or fecundity, which will further contribute to population declines in this species.

ACKNOWLEDGMENTS

We are very appreciative of the King Ranch, Inc., and Kenedy Ranch for allowing access to their properties. We thank P. Deorfler, R. Heilbrun, J. McCloskey, S. Perez, and D. Thompson for laboratory assistance. Fieldwork was conducted under protocol certified by Texas A&M University-Kingsville Institutional Animal Care and Use Committee (approval #1-97-41) and under federal (#MB810027) and state (#SPR-0697-888) scientific collection permits. This is manuscript 03-110 of the Caesar Kleberg Wildlife Research Institute.

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Received 10 December 2002.

Accepted 17 December 2003.

Associate Editor: Sheaffer.