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Research Article

Carcass Composition and Digestive-Tract Dynamics of Northern Pintails Wintering Along the Lower Texas Coast

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Abstract

We collected 341 northern pintails (Anas acuta) along the lower Texas coast, USA, to investigate dynamics of carcass and digestive tract components during winter to help assess the ability of this region to support wintering pintail populations. Pintails relied more on endogenous lipid and protein reserves during winter of a dry year than a normal to wet year. Carcass fat remained relatively stable during the wet winter; however, pintails catabolized approximately 65% of their lipid reserves between arrival in October and departure at the end of February during the dry winter. Somatic protein mass also declined over both winters as pintails catabolized up to 20% of their muscle mass. Gizzard atrophy explained most of the changes in somatic protein during the wet winter, whereas catabolism of breast muscle also contributed to changes in protein mass during the dry winter. Ingesta-free digestive tract mass was greatest in early December, and then declined abruptly through February during both winters. Pintails departed the lower Texas coast in late February approximately 20% lighter in body mass than when they arrived in autumn. Mid-continent pintails may frequently opt to winter in southerly latitudes where they can maintain minimal endogenous reserves due to the moderate climate, limited human disturbance, and relatively dependable, but often lower-quality food resources. However, potential consequences of pintails initiating spring migration with reduced energy reserves include greater reliance on spring staging and breeding areas to meet their nutrient requirements for migration and reproduction, later arrival on breeding grounds, and reduced survival and reproductive success. Nutrient reserve dynamics of wintering, mid-continent pintails support the need for enhanced conservation of productive spring staging and breeding habitats for this population. It also provides additional concern over the loss of productive wintering sites along the western Gulf Coast. (JOURNAL OF WILDLIFE MANAGEMENT 70(5):1316–1324; 2006)

Key words

Anas acuta, carcass composition, digestive tract, Laguna Madre, lipids, northern pintail, protein, Texas, winter.

Body mass decline in birds during winter has been explained by 2 competing hypotheses. The *energy-deficit hypothesis* suggests that mass loss is a result of environmental factors, such as limited food availability or decreasing temperatures, which require the use of endogenous reserves to compensate for reductions in energy acquisition or increased energy demands (Owen and Cook 1977, Peterson and Ellarson 1979, Kaminsky and Ryan 1981, Miller 1986). Conversely, the *endogenous-rhythm hypothesis* infers that an endogenous mechanism regulates the size of stored reserves to optimize energy expenditure and survival (Reinecke et al. 1982, Williams and Kendeigh 1982, King and Murphy 1985). Support for endogenous control of body mass in wintering waterfowl has frequently come from studies of captive birds that underwent predictable fluctuations in body mass despite readily available access to high-quality foods (Perry et al. 1986, Loesch et al. 1992). However, the magnitude of change in body mass or deviation from the typical pattern is likely the result of proximate environmental factors such as winter habitat quality (King and Farner 1966). For instance, annual variation in body condition of wintering waterfowl is often correlated with winter habitat conditions, particularly food availability and quality in relation to the amount of

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precipitation (Miller 1986, Whyte et al. 1986, Heitmeyer 1988, Smith and Sheeley 1993). The extent of body mass loss or the inability to build nutrient reserves during critical periods may have immediate or cross-seasonal impacts on an individual. In fact, Raveling and Heitmeyer (1989) found that pintail production declined following dry winters with reduced food availability in California, USA. Stored lipids provide insulation and energy reserves to wintering birds and can influence the probability of surviving during extremely low temperatures or periods of negative energy balance (King 1972, Raveling 1979). Additionally, females periodically use lipid reserves acquired during winter and spring migration to compensate for their inability to meet daily nutrient requirements for reproduction on the breeding grounds (Krapu 1981, Esler and Grand 1994, Hobson et al. 2005). Furthermore, male ducks may rely on stored lipid reserves to provide energy necessary to defend their mates (Krapu 1981).

Somatic lipid and protein catabolism during winter may delay initiation of certain annual cycle events, such as prebasic molt (Richardson and Kaminski 1992), which in turn may influence timing of subsequent events. Delayed clutch formation by females in poor body condition can result in reduced egg mass, smaller clutch sizes, and lower reproductive success (Krapu 1981, Eldridge and Krapu 1988). Therefore, winter body condition of waterfowl may

have immediate or cross-seasonal influence on waterfowl fitness (Heitmeyer and Fredrickson 1981, Krapu 1981, Haramis et al. 1986, Hepp et al. 1986, Nichols and Hines 1987, Raveling and Heitmeyer 1989, Hobson et al. 2005).

The Texas coast, USA, winters up to 78% of northern pintails (*Anas acuta*) in the Central Flyway (U.S. Fish and Wildlife Service 1999) with most birds wintering in rice-producing areas (Texas Parks and Wildlife Department, unpublished data). Rice agriculture provides readily available and abundant, high-energy foods to waterfowl (Fredrickson and Taylor 1982, Miller 1987) and rice fields provide important habitat to pintails in several major wintering areas (Miller 1986, Cox and Afton 1997). However, large declines in rice acreage in Texas, as well as predicted future declines (Alston et al. 2000), compounded with considerable loss of freshwater wetlands adjacent to the coast (Moulton et al. 1997) may be reducing the capacity of western Gulf Coast wintering areas to support historical numbers of pintails. Because adjacent wintering areas (e.g., coastal La., USA) have also experienced considerable wetland loss (Dahl and Johnson 1991), options for pioneering new wintering areas may be limited. Based on availability and proximity to the rice prairies, pintails may use coastal estuaries and lagoons to a greater degree with conversion of the remaining rice prairies to other land uses. However, forced emigration of pintails to coastal habitats where birds consume foods that have poor nutritional characteristics (Ballard et al. 2004) may have unforeseen effects on survival and fecundity. Similarly, if coastal habitats do not provide the quality or quantity of foods necessary to maintain wintering pintails in optimal body condition, birds wintering in Texas may experience lower survival or greater reductions in fecundity, which will further contribute to continental population declines in this species.

The objective of this study was to investigate body mass, carcass composition, and digestive tract dynamics of northern pintails wintering along the lower coast of Texas to help assess the ability of this region to meet nutrient requirements of this species during winter.

Study Area

We evaluated nutrient reserve dynamics of northern pintails in the Laguna Madre along the lower Texas coast. The Laguna Madre is a shallow (generally <1-m-deep) coastal lagoon that extends approximately 208 km from Corpus Christi Bay to Port Isabel. It ranges from 5–8 km wide. Freshwater inflow from mainland drainages is limited and evaporation typically exceeds precipitation, often resulting in hyper-saline conditions. Salinities are generally >35 parts per thousand (ppt), but vary seasonally and can reach >50 ppt (McMahan 1968). The Laguna Madre has vast meadows of sea grasses, with shoalgrass (*Halodule wrightii*) dominating in most areas (Onuf 1996). Freshwater wetlands adjacent to the Laguna Madre are important sources of dietary freshwater for waterfowl foraging in the lagoon (Adair et al. 1996); however, during dry winters freshwater can be limited and spatially concentrated.

The climate of the region is semi-arid to subtropical with mild autumn and winter temperatures, averaging 14.2°C with lowest temperatures typically occurring in late December to early January (National Oceanic and Atmospheric Administration [NOAA] 1999). Mild temperatures compounded with strong coastal winds promote high evaporation rates throughout most of the year and influence seasonal availability of wetlands. Annual rainfall averages about 67 cm (Brown et al. 1977), with most precipitation occurring in April and September. However, tropical storms and hurricanes can have large impacts on precipitation patterns and wetland habitat conditions. Precipitation was markedly different between the 2 winters of this study. In 1997–1998, rainfall was 133% of normal along the lower Texas Coast (30-yr average; NOAA 1997, 1998, 1999). The 5 climate stations along the coast ranged from 20–58% above average precipitation during April 1997–March 1998. April–March of 1998–1999 had average to dry conditions as precipitation averaged 83% of normal, with 9 months during the period experiencing below-normal rainfall. Based on rainfall patterns, we refer to 1997–1998 as the wet winter and 1998–1999 as the dry winter.

Methods

We conducted fieldwork under protocol certified by Texas A&M University–Kingsville Institutional Animal Care and Use Committee (approval no. 1-97-41) and under federal (no. MB810027) and state (no. SPR-0697-888) scientific collection permits. We collected pintails from October through February 1997–1998 and 1998–1999 throughout the Laguna Madre by shooting at estuarine feeding sites or along traditional flight corridors to avoid potential biases associated with collecting birds over decoys (Greenwood et al. 1986). Although pair status may explain some of the variability in body condition of wintering waterfowl, we were unable to determine pair status for a large proportion of the birds sampled because of collection methods. Given the open, expansive mudflats throughout the Laguna Madre, we collected 84% of the birds by pass shooting because of the inability to approach foraging birds in most areas.

We weighed each specimen immediately after collection to determine fresh body mass (1 g) and we took a series of external structural measurements to correct carcass components for body size (Ankney and Afton 1988, Ankney and Alisauskas 1991). Measurements (0.01 mm) included bill width at widest point of the premaxilla, central culmen from intersection of skin and premaxilla to the tip of bill nail, diagonal culmen from proximal tip of the posterior lateral lobe of the premaxilla to bill nail, skull length from external occipital protuberance to tip of bill nail, wing chord (1 mm) from wrist on bent wing to tip of the most distal primary, tarsus length from proximal to lateral condyles of the metatarsus, and middle toe length from base of nail to junction with metatarsus. We measured keel length from tip of cranial process to end of medial caudal process following removal of half of the pectoralis muscle during the final necropsy.

We examined each specimen for contour plumage molt in

9 major plumage regions comprised of 34 feather tracts modified from Billard and Humphrey (1972). We assessed molt intensity using a grab-sample technique to expose each feather sheath to determine the proportion of new feather growth (Titman et al. 1990). We identified growing feathers as those with blood present in the calamus, or those in which only the emerging feather sheath was present. We calculated molt intensity for each feather tract as the percentage of incoming feathers from each grab-sample. We determined molt intensity for each plumage region by averaging across all feather tracts comprising a region and calculated total molt scores as the average intensity of the 9 plumage regions.

We necropsied pintails to evaluate digestive-organ and other muscle-mass dynamics. We determined age (i.e., hatch-year vs. after-hatch-year) and sex of each pintail by plumage characteristics (Carney 1992) and corroborated with characteristics of the bursa and gonads. We excised and weighed (0.01 g) the left breast muscles (pectoralis and supra-coracoideus), left leg muscles (muscles attached to the tibiotarsus and metatarsus), and heart to examine somatic protein dynamics. We removed and dissected the digestive tract into the upper digestive tract (UDT; esophagus and proventriculus), gizzard, small intestine, caeca, and large intestine. We determined lengths (1 mm) of the UDT, small intestine, caeca, and large intestine on unstretched digestive tract components before removal of ingesta to reduce variation in measurements associated with elasticity of these organs. We measured mass (0.01 g) of each digestive tract organ with its contents after removing any adhering fat, then emptied, washed, and patted dry each organ with a paper towel before reweighing. We removed the liver and pancreas from the carcass and weighed them separately (0.01 g). Following necropsies, we returned all excised organs and fat to the body cavity and froze them for later carcass composition analyses.

Subsequently, we thawed and plucked pintails. We weighed and chopped the plucked carcass into approximately 2-cm-cube pieces and oven-dried to constant mass at approximately 80°C (Kerr et al. 1982). We weighed and then ground the dried carcass to powder in an electric coffee grinder and mixed by hand to ensure homogeneity. We defined carcass water as fresh body mass (excluding wet feather mass and gastrointestinal contents) minus carcass dry mass. We determined carcass composition by lipid extraction with petroleum ether in a modified Soxhlet apparatus (Dobush et al. 1985), followed by ashing in a muffle furnace to determine protein and mineral content (Ankney and Afton 1988).

Statistical Analysis

Carcass components can show significant intraspecific variation in response to structural size (Alisauskas and Ankney 1987, Ankney and Afton 1988, Ankney and Alisauskas 1991). To explain additional variation in somatic nutrient reserves, we used principal component analysis (PROC PRINCOMP; SAS Institute 1999) on the 8 morphological measurements to correct nutrient-reserve values for structural size. The first principal component

Table 1. Sex and age (after hatch year [AHY] or hatch year [HY]) distribution of northern pintails collected from the southern Texas Coast, USA, during Oct–Feb 1997–1998 and 1998–1999.

Year	Sex	Age	Oct	Nov	Dec	Jan	Feb	Total
1997–1998	F	AHY	4	10	7	10	3	34
		HY	0	5	9	6	1	21
	M	AHY	7	15	19	12	7	60
		HY	2	7	7	11	3	30
1998–1999	F	AHY	2	20	20	21	10	73
		HY	0	4	8	2	5	19
	M	AHY	5	21	26	21	20	93
		HY	1	2	1	2	5	11

score (PC_1) of the correlation matrix can be interpreted as a measure of body size with positive scores indicating above-average body size and negative scores indicating below-average body size (Pimental 1979, Alisauskas and Ankney 1987). To determine if a relationship existed between carcass composition variables and body size, we individually regressed lipid, protein, and ash content (PROC REG; SAS Institute 1999) on PC_1. A carcass component is influenced by body size if a significant relationship ($P < 0.05$) is found between the variable and PC_1. For carcass components influenced by body size, we used residuals from the regression equations to derive a new value adjusted for structural size. We generated values corrected for structural size using methodology described by Ankney and Alisauskas (1991). Body, carcass, ash, and protein masses were related to body size and required use of corrected values in subsequent analyses. Carcass fat was marginally related to structural size of males during the wet winter ($P = 0.047$). However, correcting somatic lipid reserves for structural size may be an over-correction because the absolute mass of a bird's somatic lipids represents its usable lipid reserve, which may not have a relationship with body size (see Sedinger et al. 1997). Thus, we used uncorrected values of carcass fat in subsequent analyses.

We assessed scatter plots of all carcass and digestive-tract components across julian date for linear and nonlinear trends. Subsequently, we investigated trends in carcass and digestive tract parameters by sex and year using regression analysis (PROC REG; SAS Institute 1999).

Results

Body Mass and Composition

We collected 260 after-hatch-year (AHY) and 81 hatch-year (HY) pintails from the Laguna Madre during 1997–1998 and 1998–1999 (Table 1). Because 45% of the monthly sample sizes of HY birds were ≤ 2, we omitted all HY individuals from our analyses; thus, all results refer to AHY birds (ad). Furthermore, there was no relationship ($r^2 < 0.09$, $P > 0.217$) between carcass fat or protein and molt scores of adult male or adult female pintails during any month by year combination.

Body mass.—Ingesta-free body mass of male and female pintails varied by month ($F \geq 9.21$, $P < 0.001$) and exhibited similar patterns between years ($F \leq 1.36$, $P \geq$
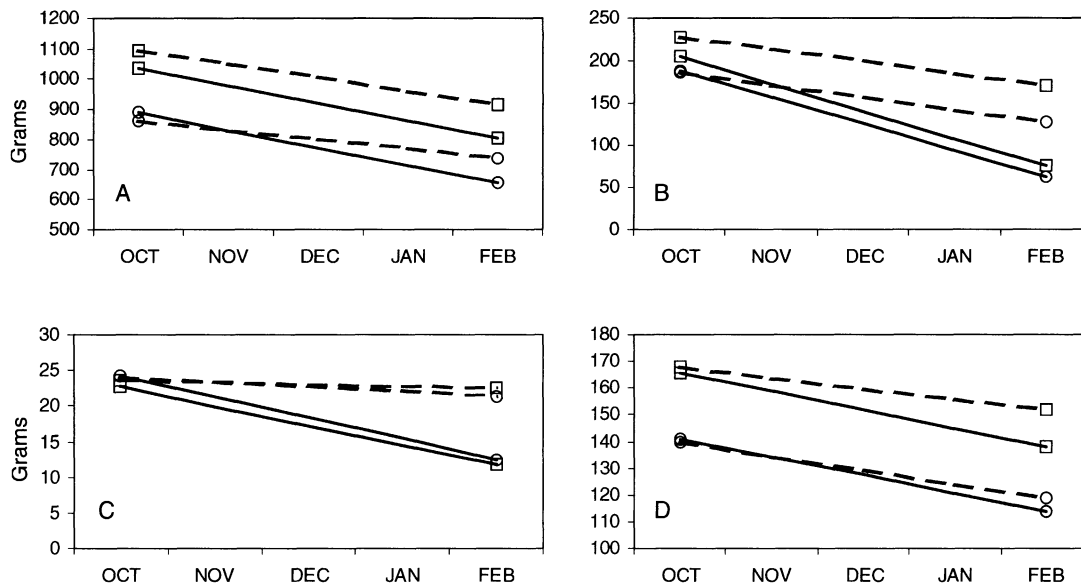
Figure 1. Trend in ingesta-free body mass (A), somatic fat (B), percent fat (C), and somatic protein (D) of adult male (□) and female (○) northern pintails collected along the lower coast of Texas, USA, during wet (1997–1998: – – – – –) and dry (1998–1999: ———) winters.

0.283). Pintails were heaviest during arrival in October and body mass declined throughout winter (Fig. 1A). During the wet winter, average body mass was 12% (104.7 g) lighter for females and 15% (138.3 g) lighter for males in February than in October ($r^2 \geq 0.13$, $P \leq 0.040$). During the dry winter, body mass declined at a higher rate than during the wet winter as male (216.5 g) and female (168.8 g) pintails departed the lower Texas coast about 20% lighter than their average arrival body mass ($r^2 \geq 0.44$, $P < 0.001$). On average, females were 58 g lighter and males were 89 g lighter by the end of February in the dry winter than in the wet winter. Males were approximately 22% heavier than females in October each year and 19% heavier in February.

Somatic fat.—Average lipid content differed by 18% between years for females (wet winter = 164.4 g; dry winter = 135.0 g; $P = 0.042$), and by 28% for males (wet winter = 204.4 g; dry winter = 147.2 g; $P < 0.001$), but there were no year by month interactions ($F \leq 2.33$, $P \geq 0.060$). We detected no trends in somatic fat for adult males or females during the wet winter ($r^2 \leq 0.08$, $P \geq 0.109$; Fig. 1B), although there was a single female with extremely low fat reserves in late October of the wet winter that had a large effect on this result. When this individual was removed from the analysis, there was a significant decline in lipid reserves of female pintails even during the wet winter ($r^2 = 0.18$; $P = 0.013$). In the dry winter, pintails catabolized $\geq 63\%$ of their lipids by the end of February as somatic fat declined for males ($r^2 = 0.34$, $n = 93$, $P < 0.001$) and females ($r^2 = 0.27$, $n = 73$, $P < 0.001$). Percent body fat remained relatively stable during the wet winter for each sex, averaging approximately 24% of carcass mass in October and dropping to about 21% by the end of February (Fig. 1C). During the dry winter, % fat declined from about 23% of carcass mass at arrival to $\leq 13\%$ by the end of February ($r^2 \leq 0.27$, $P < 0.001$). In both years, females generally maintained a greater percentage of body fat than males throughout winter.

Somatic mineral.—Carcass ash remained stable during the wet winter for adult females ($r^2 = 0.04$, $n = 34$, $P = 0.282$), however, there was a moderate declining trend in the dry winter ($r^2 = 0.07$, $n = 73$, $P = 0.027$). Carcass ash did not display any trends for males either year ($P \geq 0.248$). On average, adult males contained 22% more carcass ash than adult females.

Somatic protein.—Both males and females catabolized protein throughout winter each year (Fig. 1D). Adult females exhibited similar trends in carcass protein dynamics each year, catabolizing 15% (wet winter: $r^2 = 0.24$, $n = 34$, $P = 0.003$) and 19% (dry winter: $r^2 = 0.40$, $n = 73$, $P < 0.001$) of their protein between October and the end of February. Adult males also catabolized carcass protein throughout winter in both years (Fig. 1D). However, adult males retained greater lean mass throughout the wet winter, catabolizing only 9% of their protein mass, whereas during the dry winter they catabolized 17% (Fig. 1D). On average, adult males carried 20% more ash-free lean mass than females.

Changes in mass of breast and leg muscles, gizzard, and heart explained $\geq 69\%$ of the change in somatic protein of pintails. Gizzard mass had the largest influence on changes in protein mass for both males and females during the wet winter (i.e., had the most significant coefficient for the 4-variable model), whereas, atrophy of breast muscle had the largest influence during the dry winter. During both years, each of these muscle groups displayed significant coefficients for carcass protein.

During the wet winter, breast and heart mass remained stable across winter for males and females ($r^2 \leq 0.05$, $P \geq 0.082$). However, mass of breast muscles decreased ($r^2 \geq 0.31$, $P < 0.001$) by approximately 18% in both males and females by the end of February in the dry winter (Fig. 2A). Similarly, heart mass declined by 21% for females ($r^2 = 0.11$, $n = 73$, $P = 0.004$) and by 10% for males ($r^2 = 0.05$, $n = 93$, P
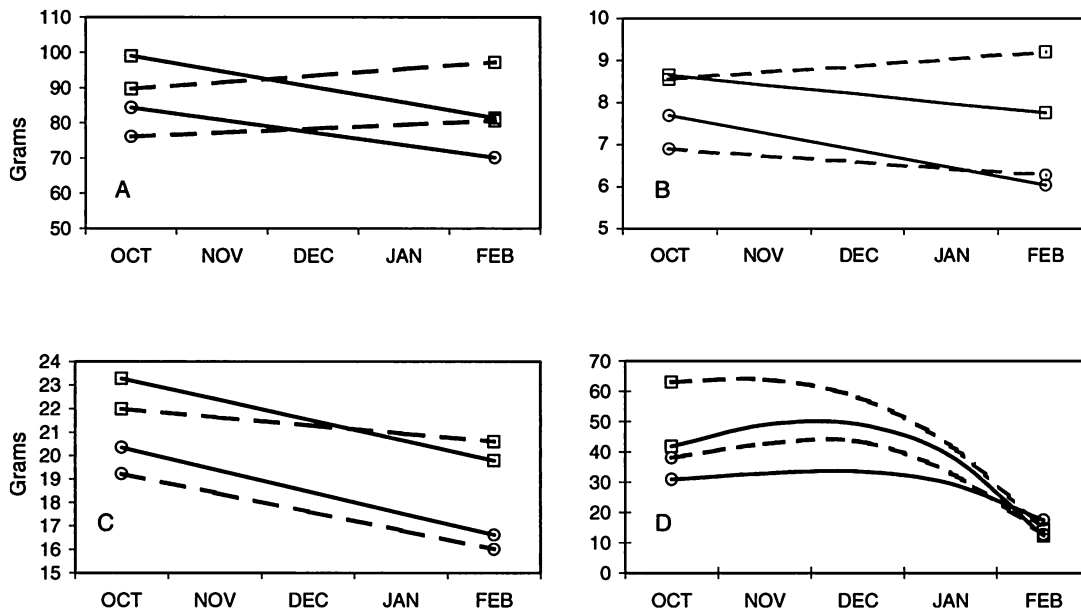
Figure 2. Trend in mass (g) of breast muscle (A), heart (B), leg muscle (C), and gizzard (D) of adult male (□) and female (○) northern pintails collected along the lower coast of Texas, USA, during wet (1997–1998: – – – – –) and dry (1998–1999: ————) winters.

= 0.027) between October and the end of February during the dry winter (Fig. 2B).

Leg muscle mass did not exhibit a trend for males in the wet winter ($r^2 = 0.02$, $n = 60$, $P = 0.279$), but decreased from 19.2 g to 16.4 g (15%; $r^2 = 0.17$, $n = 34$, $P = 0.015$) for females (Fig. 2C). During the dry winter, leg muscle mass reduced by 21% in females ($r^2 = 0.17$, $n = 73$, $P < 0.001$) and by 15% in males ($r^2 = 0.18$, $n = 93$, $P < 0.001$).

A quadratic function best described gizzard mass (Fig. 2D). Increases in gizzard mass from October to early December occurred for both sexes, followed by a significant decline through February. Males showed strong declines in gizzard mass both years ($r^2 \geq 0.43$, $P \leq 0.001$). Gizzard mass in females was relatively stable in the wet winter ($r^2 = 0.15$, $n = 34$, $P = 0.078$) and declined in the dry winter ($r^2 = 0.13$, $n = 73$, $P = 0.008$).

Gut Morphology

Morphology of the digestive tract varied moderately throughout winter for females, and more notably for males (Tables 2 and 3). Females displayed little variation in gut morphology during the wet winter. Mass of the total digestive tract exhibited a quadratic trend for females during the dry winter and for males during both winters. Changes in gizzard mass appeared to have the greatest influence in the decline in mass of the total digestive tract for females, however, reductions in caeca and large intestine mass also contributed to the decline (Table 2). Length of the female digestive tract increased during early winter, and then decreased through February during the dry winter. Changes in length of the gizzard and caeca were primarily responsible for this quadratic trend. The pancreas and liver exhibited no trends in mass either year for females.

Table 2. Relationship between digestive tract organs and Julian date for female northern pintails throughout winter along the lower coast of Texas, USA, during 1997–1998 (wet year) and 1998–1999 (dry year).

	Wet year (1997–1998; n = 34)			Dry year (1998–1999; n = 73)		
	Regression line	r^2	**P-value**	**Regression line**	r^2	**P-value**
Mass (g)						
Total digestive tract	66.7 − 0.09x	0.057	0.167	48.9 + 1.18x − 0.002x²	0.119	0.013
Upper digestive tract	5.4 + 0.07x − 0.001x²	0.169	0.057	4.8 + 0.02x − 0.001x²	0.054	0.143
Small intestine	13.4 − 0.02x	0.078	0.109	11.6 − 0.01x	0.013	0.350
Caeca	1.2 + 0.0002x	0.001	0.909	0.9 + 0.01x − 0.0001x²	0.120	0.012
Large intestine	1.5 − 0.002x	0.032	0.308	1.3 − 0.002x	0.080	0.016
Pancreas	2.3 + 0.004x	0.064	0.148	2.3 + 0.002x	0.045	0.072
Liver	17.5 − 0.01x	0.039	0.265	17.6 + 0.01x	0.005	0.551
Length (mm)						
Total digestive tract	1,882 + 1.61x	0.015	0.491	1,886 + 7.20x − 0.054x²	0.006	0.531
Upper digestive tract	263 − 0.25x	0.238	0.003	267 − 0.06x	0.028	0.157
Small intestine	1,324 + 0.71x	0.007	0.644	1,267 + 5.37x − 0.039x²	0.074	0.071
Caeca	272 + 0.10x	0.013	0.522	231 + 1.52x − 0.011x²	0.146	0.004
Large intestine	77.1 + 0.04x	0.019	0.443	75.7 − 0.03x	0.012	0.365
Gizzard	61.2 − 0.04x	0.064	0.148	55.9 − 0.05x	0.087	0.012

Table 3. Relationship between digestive-tract organs and Julian date for male northern pintails throughout winter along the lower coast of Texas, USA, during 1997–1998 and 1998–1999.

	Wet year (1997–1998; $n = 60$)			Dry year (1998–1999; $n = 93$)		
	Regression line	r^2	P-value	Regression line	r^2	P-value
Mass (g)						
Total digestive tract	$89.9 + 0.17x - 0.004x^2$	0.493	<0.001	$64.4 + 0.51x - 0.005x^2$	0.411	<0.001
Upper digestive tract	$8.5 + 0.04x - 0.001x^2$	0.350	<0.001	$6.2 + 0.04x - 0.0003x^2$	0.107	0.006
Small intestine	$16.1 - 0.04x$	0.172	0.001	$14.4 - 0.02x$	0.076	0.007
Caeca	$1.6 - 0.003x$	0.100	0.015	$1.4 - 0.0003x$	0.001	0.712
Large intestine	$2.0 - 0.005x$	0.166	0.001	$1.7 - 0.003x$	0.125	0.001
Pancreas	$2.9 - 0.001x$	0.003	0.683	$2.9 - 0.002x$	0.013	0.283
Liver	$25.5 - 0.07x$	0.280	<0.001	$21.5 + 0.005x$	0.002	0.643
Length (mm)						
Total digestive tract	$2,234 - 0.72x$	0.004	0.636	$2,196 + 1.47x$	0.079	0.007
Upper digestive tract	$292 - 0.08x$	0.021	0.279	$310 - 0.10x$	0.061	0.017
Small intestine	$1,482 - 0.36x$	0.001	0.782	$1,454 + 1.36x$	0.090	0.004
Caeca	$309 - 0.28x$	0.018	0.306	$287 + 0.28x$	0.065	0.014
Large intestine	$80.8 + 0.07x$	0.013	0.399	$78.1 + 0.02x$	0.006	0.482
Gizzard	$68.3 + 0.07x - 0.002x^2$	0.464	<0.001	$60.4 + 0.22x - 0.002x^2$	0.424	<0.001

Males displayed greater changes in gut morphology over winter than females during both years. Total digestive tract mass was greatest during late autumn and declined abruptly from early December through February during both years. All digestive tract organs were lighter by the end of February, except caeca in the dry winter (Table 3). Mass of the upper digestive tract and gizzard followed a similar quadratic trend present in the total digestive tract each year. Small intestine, caeca (wet winter only), and large intestine of males exhibited linear reductions in mass throughout winter (Table 3). Mass of the pancreas remained stable throughout winter during both years. Liver mass declined considerably from October to the end of February in the wet winter, but remained stable during the dry winter. Total digestive tract length did not change during the wet winter, but increased in length throughout the dry winter. The increase in length was attributable to increases in small intestine and caeca lengths. The upper digestive-tract length exhibited a declining trend during the dry winter, and the gizzard displayed a quadratic trend, peaking in length during mid-winter and declining considerably through February.

Discussion

Pintails catabolized lipid and protein across winter and departed the lower Texas coast with reduced nutrient reserves. Declining somatic nutrient reserves over winter is apparently a consistent pattern of nutrient-reserve dynamics for pintails throughout the mid-continent region (Thompson and Baldassarre 1990, Smith and Sheeley 1993), but is inconsistent with pintails wintering in the Central Valley of California (Miller 1986). Pintails wintering in the Central Valley exhibited a pattern of mid-winter declines in body mass followed by building of endogenous reserves prior to departure in spring. Thus, pintails depart coastal Texas wintering areas weighing approximately 20% (~200 g) less than pintails departing wintering areas in California (Miller 1986). Endogenous nutrients, particularly lipids, were reduced at a time when birds increased them in preparation

for spring migration in California (Miller 1986, Heitmeyer 1988).

Whether body condition of pintails wintering along the lower Texas coast was diminished enough to influence survival or reproductive remains uncertain. Female pintails rely on endogenous reserves accumulated during winter and spring migration to meet nutrient requirements for reproduction (Krapu 1981, Esler and Grand 1994). Therefore, departing wintering grounds with reduced nutrient reserves may influence their ensuing reproductive success if reliance on spring habitats is high and conditions of these habitats are poor. Additionally, prolonged migration that results in later arrival on breeding areas and delayed nest initiation may influence breeding propensity and, for birds that opt to nest, it likely reduces reproductive success. It is well established that later nest initiations negatively impact reproductive success in northern pintails through progressively smaller clutch sizes (Flint and Grand 1996, Guyn and Clark 2000), lower nest success (Flint and Grand 1996), reduced brood survival (Guyn and Clark 1999), and a reduced propensity to renest (Grand and Flint 1996). Most pintails departed the lower coast of Texas by early March, apparently earlier than pintails leaving California (Miller 1986), the Southern High Plains (Smith and Sheeley 1993), and the Rice Prairie region immediately north of the lower coast of Texas (B. Ballard, unpublished data). Deficient endogenous reserves and the reduction of flight range capabilities may stimulate earlier migratory movements and require a more protracted migration to include more frequent stops to rebuild somatic reserves. Most pintails wintering in Texas probably do not experience major ecological barriers (e.g., mountain ranges) during spring migration and also have the opportunity to exploit numerous stopover habitats before arrival on breeding areas (Pederson et al. 1989). Therefore, assuming that these birds can arrive on breeding areas in a timely manner and with sufficient endogenous stores, there may be no advantage to build and maintain large nutrient reserves prior to migra-

tion. The difference in winter fat accumulation for pintails in California may be due to different migration strategies (e.g., possibly longer, nonstop flights across portions of the Pacific Ocean or mountainous terrain in route to breeding areas in Alas., USA, or western Canada). Additionally, climatic conditions along the more northerly migration routes in western North America are likely less predictable, making foraging opportunities less certain. Therefore, larger nutrient reserves are necessary to provide energy at times when migratory stopover sites may be limited or widely dispersed or less likely to provide adequate foraging conditions. However, because carrying large reserves will increase the transport cost, birds that have the opportunity to stop frequently can reduce the energetic cost of migration because they are able to cover shorter segments with smaller reserves (Alerstam et al. 2003).

Pintails in California (Miller 1986) and the Southern High Plains (Smith and Sheeley 1993) did not catabolize protein and relied extensively on stored fat during winter. In contrast, pintails along the Texas Coast catabolized significant amounts of protein during both wet and dry winters. Protein catabolism may be a response to ameliorate energy balance or to provide necessary amino acids when protein intake is inadequate (Kendall et al. 1973). However, based on protein content of the winter diet of pintails in this region (Ballard et al. 2004) and the amount of protein needed to meet daily maintenance requirements (2.03–2.88 g based on equations from Robbins 1993), pintails along the lower Texas Coast would only be required to consume 12.3–33.6 g of food to meet daily maintenance requirements. Thus, protein catabolism was probably not in response to amino acid deficiencies, but appeared to be in response to the negative energy balance. Further, pintails catabolized somatic fat and protein at relatively constant rates throughout winter resulting in percent fat remaining stable. Reducing lean body mass concurrent with fat stores may be a strategy to maintain the effectiveness of the fat reserve (Reinecke et al. 1982). Advantages of reducing body mass include reduced energy demands from lower basal metabolic costs, lower activity energy expenditure to carry the smaller body mass, and potentially reduced risk of predation because of less time spent foraging to meet their energy needs (Biebach 1993). Further, reduced body mass may be a strategy for some avian species to achieve greater maneuverability (relative to carrying heavy fuel loads) in order to decrease susceptibility to predators (Lima 1986).

The gizzard explained much of the reduction in protein during the wet winter; however, diet quality did not change, again supporting the notion that pintails were using this protein store to meet energy demands (Korschgen 1977). Breast muscle had the largest influence on reductions in protein during the dry winter, even though gizzard mass declined more than in the wet winter. Greater reductions in breast, leg, gizzard, and heart masses during the dry winter suggest that pintails were distributing protein catabolism across muscles and organs, possibly emphasizing the degree of negative energy balance. Increases in flight-muscle mass

prior to migratory movements occur in preparation for long-distance movements or in response to deposition of premigratory fat (Evans and Smith 1975, Gaunt et al. 1990). The reduction in breast-muscle mass during the dry winter prior to departure further suggests that pintails probably did not make large-scale movements after departing the lower Texas coast. Pintails departing wintering areas along the lower Texas coast may rely on rice prairie habitats immediately north along the central Texas coast to accumulate energy prior to further migratory movements.

Although the lower coast of Texas appears to provide a low-energy diet for wintering pintails (Ballard et al. 2004), it has other characteristics that would seem attractive to wintering waterfowl, which may compensate for its relatively energy-poor foods. For instance, the considerable size (200 km long and 5–13 km wide; Cornelius 1977) and shallow depths of the Laguna Madre provide abundant foraging and roosting habitat. Additionally, the primary food of pintails in this region (shoalgrass) remains stable and predictable from year to year relative to foods in highly dynamic freshwater systems. Further, the moderate winter climate reduces the probability of cold stress and possibly eliminates the need for maintaining larger lipid stores that are typical of birds wintering in more unpredictable environments (Evans and Smith 1975). Disturbance and hunting pressure are also relatively light along the lower coast of Texas compared to adjacent regions (Texas Parks and Wildlife Department, unpublished data), primarily because of large private land holdings that limit access. Therefore, pintails along the lower Texas coast may employ a strategy to sustain themselves in a highly predictable environment throughout winter without accumulating heavy fuel loads, thereby reducing their energy demands and risk of depredation.

Most of the variation in the digestive tract relates to a decrease in mass from early winter to the end of February. Atrophy of the gizzard explained much of the decrease in digestive tract mass, particularly for females. The proportion of seeds in the diet can influence gizzard mass because increased grinding action is required to breakdown hard seed coats (Thompson and Drobney 1996). However, seed consumption did not decrease between winter and spring for either sex; thus, it cannot explain changes in digestive tract mass. Hypertrophy of the digestive tract can improve protein assimilation of the diet (Reinecke et al. 1982, Austin and Fredrickson 1987, Thompson and Drobney 1996), but digestive-tract mass decreased at a time when we expected birds to improve digestive efficiency.

Diet quality declined from winter to spring (Ballard et al. 2004), which was opposite of the expected trend during the dry winter if diet quality alone was influencing changes in gut morphology. Changes in diet quality (i.e., digestibility) or volume of foods consumed can influence digestive-tract morphology (Moss 1974, Ankney 1977, Kehoe and Ankney 1985, Ankney and Scott 1988). In general, diet quality has an inverse relationship to gut length and mass, whereas quantity of food consumed has a direct relationship.

Therefore, it appears that diet quality did not play a major role in decreases in gut mass from December through February.

The increase in gut length of males concurrent with reductions in digestive tract mass during the dry winter is puzzling and must have been the result of longer, thinner-walled digestive tracts. The increase in length corresponds to considerable reductions in diet quality and may have been a combination of reducing mass while attempting to increase digestive efficiency. Because smaller organs reduce energy expenditure, it is adaptive for birds to maintain the smallest functional organ size possible (Moss 1974). Mass of upper digestive-tract contents increased considerably in male pintails from winter to spring during the dry winter; thus, corresponding increases in total digestive-tract length was probably due to increased food consumption. However, nutrient reserves continued to decline through the end of February, and potential increases in food consumption did not appear to influence these trends. Diet quality was likely so poor in late winter (Ballard et al. 2004) that increased food consumption was not enough to result in a positive energy balance.

Management Implications

Regardless of whether the endogenous-rhythm hypothesis or the energy-deficit hypothesis explains body condition

dynamics of pintails in southern Texas, protection and management of freshwater wetlands along the Texas coast would benefit this species. Providing a better-quality diet in areas where diet quality is relatively poor or providing energy during late winter when reductions in somatic fat and protein occur will enable pintails to rebuild endogenous reserves to provide energy and nutrients for migration and reproductive activities. Protection and management of these areas is particularly important if they are critical for pintails wintering along the lower Texas coast to acquire nutrients prior to making more extensive movements to northern staging and breeding areas. Further, the availability of quality habitat on wintering grounds may also partially mitigate for loss of habitat or drought on migratory routes.

Acknowledgments

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