

Body Composition and Gut Morphology of Migrating and Wintering Wilson's Snipe

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Abstract.—We analyzed carcass lipid, ash and protein dynamics of male and female Wilson's Snipe (*Gallinago gallinago delicata*) from arrival on wintering areas in coastal Texas until departure for spring migration. In addition, we analyzed seasonal variation in mass and length of digestive organs to document changes that may increase gut capacity and digestive efficiency of migrating and wintering Wilson's Snipe. Lipid reserves of female snipe remained relatively stable from fall to winter, whereas body protein increased by 3% during this time. Females catabolized lipids and protein prior to spring migration. Conversely, lipid reserves of male snipe increased by 44% from fall to winter and were at least maintained from winter to spring. Furthermore, we observed a trend ($P = 0.021$) for increasing lipid content in males during spring. Because male snipe accumulate fat reserves prior to spring departure, it appears they employ a "time-selected" strategy for spring migration. In contrast, female snipe migrate later in spring when food may be more available. Thus, females apparently rely more on dietary nutrients acquired at migration stopover sites to and likely employ an "energy-selected" strategy for spring migration. Gut morphology of male snipe remained unchanged throughout the non-breeding period whereas length of small intestine, caeca, and large intestine decreased by 6%, 8% and 8%, respectively from fall to winter in females. Small intestine length increased by 6% in females from winter to spring. Received 4 March 2008, accepted 5 July 2008.

Key words.—body composition, *Gallinago gallinago delicata*, gut morphology, nutritional ecology, Texas Gulf Coast, Wilson's Snipe.

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Digestive tract morphology and body composition can be dynamic throughout the avian life cycle and may change in response to nutrient requirements for reproduction (Ankney 1977; Drobney 1984; Brown and Fredrickson 1987), migration (Piersma and Jukema 1990; Summers *et al.* 1992; Piersma *et al.* 1996; Piersma and Gill 1998), and molt (Thompson and Drobney 1996). More specifically, gastrointestinal (GI) organs respond to changes in diet quality and quantity in a number of avian species (Leopold 1953; Ankney 1977; Moss 1983; Walsberg and Thompson 1990), including migrant shorebirds (Piersma *et al.* 1993; Piersma *et al.* 1999). Such changes in GI morphology allow many birds to efficiently obtain and store nutrients needed for basal metabolic requirements, thermoregulation, reproduction, growth, migration and molt. Knowledge of gut morphology relative to diet composition and nutritional requirements is one way to identify important avian habitats and critical

periods when food is limited (Piersma *et al.* 1993; Biebach 1996).

Wilson's Snipe (*Gallinago gallinago delicata*; hereafter referred to as snipe) is a highly migratory species, breeding primarily in boreal peatlands north of 37°N latitude and wintering south of this latitude into northern South America (Tuck 1972; Arnold 1994). Tuck (1972) suggested that fat storage in snipe provided most of the energy required for fall and spring migration with as much as 50% additional fat being accumulated prior to migration. Presumably, snipe lose considerable body mass through lipid catabolism during fall migration and gradually rebuild nutrient reserves on wintering areas prior to departure in spring. Both Whitehead (1965) and Tuck (1972) found that snipe increased their body mass by as much as 10% in April prior to spring migration. However, their data were based on live body mass, which may be biased by mass of ingesta. In addition, estimating body compo-

sition from body mass has limitations such as inter-observer bias and low power of predicting fat and lean mass (Krementz and Pendleton 1990; Rogers 1991).

The Gulf Coast of Texas, particularly the upper and middle coast, contains the highest concentration of wetlands in the state (Moulton *et al.* 1997), which serve as important wintering habitat for snipe (Arnold 1994; Mueller 1999). We investigated nutrient reserve dynamics of snipe wintering along the central Gulf Coast of Texas and determined the extent of premigratory nutrient storage. We hypothesized that snipe would arrive on wintering areas with minimal lipid reserves and that these reserves would reach their maximum just prior to spring migration. In addition, we evaluated variation in gut morphology of snipe throughout winter to help determine when changes in diet or nutrient requirements occurred. If snipe store somatic nutrients after arrival on wintering areas and prior to spring migration, we would expect digestive tract organs to be largest soon after fall migration and during the period shortly preceding spring migration.

METHODS

Study Site

We conducted this study in the rice prairies and coastal marshes along the central Gulf Coast of Texas from October 1997 through April 1998. Collection sites comprised 5 habitat types including harvested rice fields, mud flats (i.e. recently plowed rice fields), fallow rice fields (i.e. idle rice fields containing vegetation), drained impoundments and coastal marshes. Our study area experienced average to wet conditions throughout winter. October-April rainfall was 24% above the 30-year average during our study and monthly Palmer Drought Severity Indices suggest normal to very moist conditions (NOAA 2008a; NOAA 2008b). Additional information about vegetation composition and land use practices associated with the study area can be found in McCloskey and Thompson (2000).

Specimen Collection

We collected snipe ($N = 372$) by shooting and systematically alternated between habitat types throughout the non-breeding period (Texas Parks and Wildlife Department permit #SPR-0597-888, U.S. Fish and Wildlife Service permit #PRT-834726, Texas A&M University-Kingsville IACUC approval #1997-11-27A). We typically collected four birds/day distributed throughout the diurnal period to allocate sampling across the non-breed-

ing period. We separated the non-breeding period into three seasons based on molt intensity of collected individuals (McCloskey 1999). A fall molting period was delineated as 6 October-13 November 1997, a non-molting winter period as 14 November 1997-4 February 1998 and a spring molting period as 5 February-10 April 1998.

Necropsy Procedure

To correct nutrient reserve values for variation in body size, we measured lengths of the culmen, skull, tarsus, middle toe and keel using digital calipers (nearest 0.01 mm). The central culmen was measured from intersection of skin and premaxilla to distal tip of the bill. Skull length was measured from external occipital protuberance to distal tip of the bill. Tarsus length was measured from proximal to lateral condyles of the tarsometatarsus. Middle toe length was measured from base of nail to junction with tarsometatarsus. Keel length was measured from the anterior to posterior tip of the cranial process on the crest of the sternum after removing the left breast muscle.

The digestive tract was dissected into the upper digestive tract (esophagus and proventriculus), gizzard, small intestine, liver, caeca and large intestine. Using a meter stick, we measured lengths of the unstretched upper digestive tract, large and small intestine and caeca (nearest 1 mm). Measurements were made before the removal of ingesta to reduce variation associated with the elasticity of these organs. Gizzard length was measured (nearest 0.01 mm) from its junction with the proventriculus to the most anterior point using digital calipers. Combined lengths of the upper digestive tract, gizzard, small intestine, large intestine and caeca comprised total digestive tract length. Contents of organs as well as adhering fat were removed and organs washed, towel-dried and weighed (nearest 0.01 g). Combined mass of the emptied upper digestive tract, gizzard, small intestine, large intestine and caeca comprised the total digestive tract mass.

To evaluate changes in specific proteinaceous tissues, we removed the left breast muscle (i.e. pectoralis and supra-coracoideus) and heart. The breast and heart were stripped of adhering fat, washed, towel-dried and weighed (nearest 0.01 g). We doubled the mass of the left breast to represent total tissue mass of pectoral musculature.

Carcass Analysis

Following necropsies, all excised organs and adhering fat were returned to the body cavity and all specimens were frozen. Thawed specimens were plucked, oven dried to constant mass at 80°C and ground in a coffee grinder. We placed 10-g samples of ground homogenate into cellulose thimbles (also dried to constant mass) and washed them with petroleum ether in a modified Soxhlet® apparatus to extract lipids (Dobush *et al.* 1985). We placed the lean thimble contents from each specimen into porcelain crucibles and burned them at 550°C in a muffle furnace for approximately 10 hours to derive ash and ash-free lean (i.e. protein) content of each carcass.

Statistical Analysis

We performed all analyses using SAS statistical software (Version 8, SAS Institute Inc. 1999). Intraspecific

variation in nutrient reserves can result from variation in individual body size (Alisauskas and Ankney 1987; Thompson and Drobney 1996). To determine if nutrient reserves were related to body size, we performed a principal components analysis for each sex using the correlation matrix (PROC PRINCOMP) derived from the five skeletal variables measured on each bird. Eigenvalues were 2.73 for females and 2.76 for males and explained 55% of the original variation in our data for each sex. We then regressed lipid, ash, and protein content for male and female snipe on PC_1 . Carcass lipid mass was not related to structural size ($P > 0.05$) for males or females. However body ash and protein mass for male and female snipe were related to structural size and were subsequently corrected for structural size (y_i) using the following equation:

$$y_i = y_{obs} - [a + b(PC_1)] + Y_{obs}$$

where y_{obs} is the unadjusted ash or protein mass for an individual snipe and Y_{obs} is the mean unadjusted ash or protein mass for male and female snipe (Alisauskas and Ankney 1987). Corrected values for ash and protein were used in subsequent analysis.

We tested each data set for normality (PROC UNIVARIATE) and homogeneity of variance (PROC ANOVA) within seasons. We investigated effects of season on gut morphology and nutrient reserve dynamics using analysis of variance (PROC GLM) and used Tukey's Multiple Comparisons procedure to test for significant ($P < 0.05$) differences. To determine daily rates of accumulation or loss of nutrient reserves during each season, we regressed lipid, ash, and protein content against Julian date (PROC REG).

RESULTS

Nutrient Reserve Dynamics

Ingesta-free body mass of female snipe remained stable across the non-breeding period (Table 1). Body mass of male snipe increased by 5% ($P = 0.014$) from fall to winter, but then remained unchanged from winter to spring. Female snipe maintained lipid levels from fall to winter, then catabolized lipids from winter to spring as fat reserves declined ($P < 0.001$) by 20%. However, we detected no trends within seasons for lipid mass of females during fall ($r^2 = 0.035$, $P = 0.264$, $N = 38$), winter ($r^2 = 0.03$, $P = 0.103$, $N = 90$), or spring ($r^2 = 0.025$, $P = 0.152$, $N = 83$). Males increased ($P = 0.001$) lipid reserves by 44% from fall to winter, then maintained these reserves through spring. However, we detected no within-season trends in lipid reserves for males during fall ($r^2 = 0.067$, $P = 0.192$, $N = 27$) or winter ($r^2 = 0.01$, $P = 0.453$, $N = 61$), but found that males accumulated lipid re-

serves at a rate of 0.05 g day^{-1} throughout spring ($r^2 = 0.096$, $P = 0.021$, $N = 55$). Percent fat (fat/lean body mass, \pm SE) of males and females was greatest in winter (females: 30.6% [± 1.03], males: 34.9% [± 1.83]) compared fall (females: 27.5% [± 1.62], males: 24.9% [± 2.24]) and spring (females: 23.8% [± 1.17], males: 30.4% [± 1.73]).

Protein content (females: $r^2 = 0.261$, $P < 0.001$; males: $r^2 = 0.334$, $P < 0.001$) and ash content (females: $r^2 = 0.135$, $P < 0.001$; males: $r^2 = 0.242$, $P < 0.001$) were related to body size in both male and female snipe. Protein mass increased from fall to winter in both male (5%, $P < 0.001$) and female (3%, $P = 0.022$) snipe (Table 1). There was no change ($P = 0.573$) in protein mass in males from winter to spring. Protein content decreased for male snipe at a rate of 0.01 g day^{-1} ($r^2 = 0.094$, $P = 0.030$, $N = 50$) during spring, but remained unchanged during fall ($r^2 = 0.04$, $P = 0.346$, $N = 27$) and winter ($r^2 = 0.02$, $P = 0.277$, $N = 58$). Protein mass of female snipe declined by 3% ($P = 0.004$) from winter to spring, a trend that was also evident in our within-season analysis that indicated that protein mass declined at a rate of 0.02 g day^{-1} during spring ($r^2 = 0.145$, $P < 0.001$, $N = 78$). There were no within-season trends for protein mass of female snipe during fall ($r^2 = 0.001$, $P = 0.845$, $N = 33$) or winter ($r^2 = 0.002$, $P = 0.677$, $N = 81$).

Changes in pectoral muscle mass appeared to be the main influence in the changes in carcass protein of male and female snipe. Pectoral muscle mass in females mimicked patterns in overall protein stores, with a 9% increase ($P < 0.001$) from fall to winter and a 5% decrease ($P < 0.001$) from winter to spring. Heart mass of females exhibited similar seasonal changes, increasing 9% from fall to winter ($P < 0.001$) and decreasing 4% from winter to spring ($P = 0.030$) (Table 1). Pectoral muscle and heart mass in males increased by 13% and 11%, respectively ($P < 0.001$) from fall to winter.

Mineral content of male snipe remained unchanged across seasons. We detected a marginally significant ($P = 0.049$) seasonal difference for females (Table 1) suggesting that ash content was 5% greater ($P = 0.040$)

Table 1. Ingesta-free body mass, nutrient reserve and proteinaceous tissue (mean ± SE) dynamics of female and male Wilson's Snipe throughout the non-breeding period (Oct 1997-Apr 1998) along the Texas Gulf Coast.

Variable	F (df)	P ^a	Fall	P ^b	Winter	P ^b	Spring
Females							
Body mass	0.72 (2, 206)	0.490	107.49 (± 1.31, N = 39)		107.71 (± 0.72, N = 89)		106.44 (± 0.75, N = 81)
Lipid	8.89 (2, 208)	<0.001	6.75 (± 0.40, N = 38)	0.070	7.81 (± 0.26, N = 90)	<0.001	6.24 (± 0.28, N = 83)
Ash	3.06 (2, 193)	0.049	3.74 (± 0.09, N = 34)	0.040	3.92 (± 0.04, N = 82)	0.708	3.87 (± 0.03, N = 80)
Protein	5.12 (2, 189)	0.007	19.60 (± 0.22, N = 33)	0.022	20.21 (± 0.11, N = 81)	0.004	19.64 (± 0.13, N = 78)
Breast	16.27 (2, 215)	<0.001	27.77 (± 0.40, N = 39)	<0.001	30.28 (± 0.24, N = 93)	<0.001	28.62 (± 0.31, N = 86)
Heart	9.01 (2, 216)	<0.001	0.96 (± 0.02, N = 39)	<0.001	1.05 (± 0.01, N = 94)	0.030	1.01 (± 0.01, N = 86)
Males							
Body mass	4.11 (2, 144)	0.018	99.12 (± 1.80, N = 29)	0.014	103.96 (± 0.96, N = 63)	0.310	101.9 (± 0.84, N = 55)
Lipid	6.95 (2, 140)	0.001	5.99 (± 0.52, N = 27)	0.001	8.60 (± 0.45, N = 61)	0.065	7.28 (± 0.39, N = 55)
Ash	2.11 (2, 139)	0.125	3.55 (± 0.06, N = 28)		3.67 (± 0.03, N = 60)		3.60 (± 0.04, N = 54)
Protein	8.11 (2, 132)	<0.001	18.21 (± 0.21, N = 27)	<0.001	19.03 (± 0.13, N = 58)	0.573	18.85 (± 0.08, N = 50)
Breast	19.89 (2, 149)	<0.001	25.24 (± 0.48, N = 30)	<0.001	28.62 (± 0.31, N = 64)	0.007	27.25 (± 0.30, N = 58)
Heart	12.43 (2, 149)	<0.001	0.93 (± 0.02, N = 30)	<0.001	1.03 (± 0.01, N = 64)	0.800	1.02 (± 0.01, N = 58)

^aP-value from ANOVA testing the effects of season on each variable.

^bP-value from Tukey's Multiple Comparisons test showing differences between fall and winter or between winter and spring.

in winter than in fall. However, regression analyses indicated that daily mineral content of female snipe did not significantly change during fall ($r^2 = 0.05$, $P = 0.188$, $N = 34$), winter ($r^2 = 0.01$, $P = 0.345$, $N = 82$) or spring ($r^2 = 0.003$, $P = 0.621$, $N = 80$). Likewise, we detected no significant change in mineral mass of male snipe during fall ($r^2 = 0.05$, $P = 0.251$, $N = 28$), winter ($r^2 = 0.006$, $P = 0.545$, $N = 60$) or spring ($r^2 = 0.04$, $P = 0.154$, $N = 54$).

Gut Morphology

Mass of digestive tract organs of female snipe remained unchanged among seasons (Table 2). However, pancreas mass of female snipe increased 50% ($P < 0.001$) from fall to winter, but remained stable ($P = 0.691$) from winter to spring.

Mass of digestive tract components in male snipe was dynamic from fall to winter. Gizzard mass declined 11% ($P = 0.034$), small intestine increased 20% ($P = 0.030$) and liver mass increased 14% ($P = 0.027$). Mass of digestive tract components in male snipe remained unchanged between winter and spring (Table 3).

Overall digestive tract length of female snipe decreased 5% ($P = 0.004$) from fall to winter and increased 4% ($P = 0.005$) from winter to spring (Table 2). The reduction in digestive tract length from fall to winter was evident across several digestive tract components including small intestine, caeca and large intestine ($P \leq 0.032$). An increase in length of small intestine of females from winter to spring drove the increase in total digestive tract length, as length of all other digestive tract components remained unchanged (Table 2). Length of the total digestive tract and its components remained unchanged ($P \geq 0.081$) in male snipe across seasons (Table 3).

DISCUSSION

Male and female snipe appeared to undergo a period of mid-winter lipogenesis, exhibiting a winter fat index of 31-35% fat. Fall migrants arrived on wintering areas apparently in a somewhat energy-depleted state as

they increased both fat and protein reserves from fall to winter. Winters along the Texas Gulf Coast are relatively mild and availability of prey items (i.e. invertebrates) is probably not limited during this period (Pienkowski 1983). However, highly variable habitat conditions such as drought, flooding and short periods of freezing can occur and may decrease the predictability of food resources. Unpredictable environments may necessitate storage of energy to meet nutrient demands during periodic food shortages (Lima 1986; Rogers 1987; McNamara and Houston 1990; Rogers and Smith 1993; Biebach 1996).

Female snipe exhibited decreases in absolute lipid content and percent fat from winter to spring. Even in extreme conditions, most birds limit fat accumulation to reduce costs associated with large fat reserves. For example, there is an increase in energy demand for maintaining and transporting fat reserves as well as an increased risk of predation from reduced maneuverability and prolonged feeding bouts (for a review see Witter and Cuthill 1993). Catabolism of stored fat prior to migration may indicate that energy intake is inadequate to maintain body mass of female snipe, or more likely, that spring food supply along the Texas Coast, as well as along migration routes, is highly predictable. Regardless of why it occurs, this pattern of somatic lipid dynamics stresses the energetic reliance of female snipe on their diet at stopover sites during spring migration.

Alerstam and Lindstrom (1990) suggested birds employ three different migration strategies that allow maximum reproductive success: (1) migrate as fast as possible (time-selected), (2) minimize total energy expenditure (energy-selected), or (3) minimize predation. The "time-selected" strategy implies that the decision to stop and duration of stay at a particular staging area depends on how much fat an individual has and how much it can accumulate at future stopovers (Lyons and Haig 1997). The "energy-selected" strategy implies the departure fat loads are independent of expected fat deposition rates at future stopover sites (Lyons and

Table 2. Changes in mass and length (mean ± SE) of the digestive tract, liver and pancreas of female Wilson's Snipe throughout the non-breeding period (Oct 1997-Apr 1998) along the Texas Gulf Coast.

Variable	F (df = 2, 215)	P ^a	Fall (N = 39)	P ^b	Winter (N = 93)	P ^b	Spring (N = 86)
Mass (g):							
Total digestive tract	0.65	0.524	4.30 (± 0.13)		4.18 (± 0.08)		4.14 (± 0.08)
Upper digestive tract	1.45	0.238	0.89 (± 0.02)		0.86 (± 0.01)		0.90 (± 0.02)
Gizzard	2.45	0.088	1.82 (± 0.06)		1.70 (± 0.03)		1.67 (± 0.04)
Small intestine	0.44	0.6476	1.43 (± 0.09)		1.44 (± 0.05)		1.38 (± 0.05)
Caeca	0.12	0.889	0.06 (± 0.004)		0.06 (± 0.002)		0.06 (± 0.002)
Large intestine	2.80	0.063	0.11 (± 0.005)		0.12 (± 0.004)		0.12 (± 0.004)
Liver	1.70	0.186	2.24 (± 0.08)		2.20 (± 0.04)		2.33 (± 0.05)
Pancreas	7.74	<0.001	0.20 (± 0.02)	<0.001	0.30 (± 0.01)	0.691	0.28 (± 0.01)
Length (mm):							
Total digestive tract	7.41	<0.001	623 (± 11)	0.004	589 (± 5)	0.005	615 (± 6)
Upper digestive tract	3.62	0.028	100 (± 1)	0.857	100 (± 1)	0.024	98 (± <1)
Gizzard	2.62	0.075	21 (± <1)		20 (± <1)		20 (± <1)
Small intestine	7.56	<0.001	386 (± 8)	0.011	361 (± 4)	0.002	384 (± 5)
Caeca	4.22	0.016	66 (± 2)	0.032	61 (± 1)	0.062	64 (± 1)
Large intestine	3.82	0.023	51 (± 2)	0.017	47 (± 1)	0.431	48 (± 1)

^aP-value from ANOVA testing the effects of season on each variable.

^bP-value from Tukey's Multiple Comparisons test showing differences between fall and winter or between winter and spring.

Table 3. Changes in mass and length (mean \pm SE) of the digestive tract, liver and pancreas of male Wilson's Snipe throughout the non-breeding period (Oct 1997-Apr 1998) along the Texas Gulf Coast.

Variable	F (df = 2, 149)	P ^a	Fall (N = 30)	P ^b	Winter (N = 64)	P ^b	Spring (N = 58)
Mass (g):							
Total digestive tract	0.33	0.722	3.76 (\pm 0.14)		3.86 (\pm 0.08)		3.89 (\pm 0.09)
Upper digestive tract	2.92	0.057	0.76 (\pm 0.02)		0.83 (\pm 0.01)		0.83 (\pm 0.02)
Gizzard	3.19	0.044	1.75 (\pm 0.07)	0.034	1.56 (\pm 0.04)	0.582	1.62 (\pm 0.04)
Small intestine	3.58	0.030	1.09 (\pm 0.08)	0.030	1.31 (\pm 0.05)	0.954	1.29 (\pm 0.05)
Caeca	0.53	0.591	0.05 (\pm 0.005)		0.05 (\pm 0.003)		0.06 (\pm 0.003)
Large intestine	0.46	0.630	0.10 (\pm 0.001)		0.11 (\pm 0.009)		0.10 (\pm 0.004)
Liver	7.71	<0.001	1.89 (\pm 0.07)	0.027	2.16 (\pm 0.06)	0.215	2.30 (\pm 0.06)
Pancreas	7.97	<0.001	0.16 (\pm 0.02)	-0.071	0.23 (\pm 0.02)	0.074	0.29 (\pm 0.02)
Length (mm):							
Total digestive tract	0.88	0.417	602 (\pm 12)		586 (\pm 6)		594 (\pm 7)
Upper digestive tract	2.55	0.081	98 (\pm 1)		98 (\pm 1)		96 (\pm 1)
Gizzard	0.75	0.474	20 (\pm <1)		20 (\pm <1)		20 (\pm <1)
Small intestine	0.77	0.464	371 (\pm 9)		362 (\pm 5)		371 (\pm 6)
Caeca	1.59	0.208	65 (\pm 2)		61 (\pm 1)		63 (\pm 1)
Large intestine	1.51	0.224	48 (\pm 2)		45 (\pm 1)		46 (\pm 1)

^aP-value from ANOVA testing the effects of season on each variable.

^bP-value from Tukey's Multiple Comparisons test showing differences between fall and winter or between winter and spring

Haig 1997). The "predation-minimization" strategy suggests that fuel loads at departure from stopover sites are influenced by predation risk, as heavier birds are more vulnerable to predation than lighter birds (Biebach 1996).

Male snipe begin spring migration at least ten days before female snipe (Whitehead 1965; Tuck 1972; McCloskey and Thompson 2000). Similar to male American Woodcock (*Scolopax minor*) (Owens and Krohn 1973), spring migration, territory establishment, and courtship displays can be energetically demanding activities for male snipe and can occur when snow and ice make food less available. In our study, male snipe gained a significant amount of fat in preparation for spring migration and maintained a relatively high fat index. In contrast, females did not store fat during spring and had a lower fat index. Thus, it appears that male snipe use a "time-selected" strategy during spring migration and accumulate considerable fat reserves prior to departure from wintering grounds. This is consistent with their need to arrive on breeding areas early to establish territories in the best possible locations. In contrast, female snipe likely employ a more energy-selected strategy, as they migrate later in spring when resources are more available, and thus probability of reaching another stopover site with adequate food availability is higher. Sandpipers increased speed of spring migration as the season progressed, suggesting that later migrating birds (i.e. females) require shorter stopovers because energy acquisition rate was higher due to increased prey availability and birds did not need to accumulate fat reserves because of a greater likelihood of accumulating fat at future stopover sites (Lyons and Haig 1997).

Some shorebird species increase body protein in conjunction with accumulation of fat reserves (Piersma 1990; Piersma and Jekuma 1990; Biebach 1996). Snipe increased breast muscle and heart mass from fall to winter, which likely provided extra power needed to fly as they accrued somatic lipids (Driedzic *et al.* 1993). The increase in heart mass may be necessary to provide additional

oxygen and fuel required to support flight in heavier birds (Driedzic *et al.* 1993). The increase in body protein from fall to winter may also represent a return to a pre-migration state after protein depletion during fall migration and molt.

Digestive tract morphology of males remained similar across all three seasons, possibly because snipe consumed easily digestible animal foods throughout the non-breeding period (McCloskey 1999). With easily digestible foods that are readily available, snipe may not need to increase size of their digestive tract organs to enhance digestive efficiency (Piersma *et al.* 1993; Karasov 1996) and may benefit through reduced costs associated with maintaining the smallest effective digestive organ size (Witter and Cuthill 1993; Biebach 1996). Furthermore, when food quality is high, digestive efficiency is limited by physiological processes such as enzyme activity and nutrient absorption rates, rather than by physical limitations such as gut capacity (Robbins 1993).

Little information exists on the dynamics and function of the avian pancreas during the non-breeding season. Studies have shown the pancreas to change in size in relation to feeding/ fasting in some avian species (Ankey 1977, Lee *et al.* 2002), but the response is usually accompanied by similar responses from other digestive organs and is grouped together with general digestive functions. Fat is digested by lipase from the pancreas and bile salts from the liver (Robbins 1993). Furthermore, pancreatic hormones may play a role in avian pre-migratory fat loading (Totzke *et al.* 1997). The increase in pancreas and liver mass of male snipe from fall to winter in this study may relate to the increase in lipid mass. For females, only the pancreas increased with increasing lipids, but they had less absolute amounts of fat than males despite their larger size, which may have reduced the need for increased mass in these organs.

Only female snipe exhibited a change in length of the small intestine, caeca and large intestine. The volume of the GI structure of birds can influence food retention time and nutrient absorption rates, which in turn can

influence digestion rates and rates of growth, nutrient storage, and reproduction (Karasov 1996). Many shorebirds are "income" breeders (Drent and Daan 1980), relying on exogenous nutrients obtained on the breeding grounds to meet protein and lipid requirements for egg production (Klaassen *et al.* 2001). Female snipe in this study did not store a significant amount of lipids prior to spring migration, so the increased gut capacity may allow females to consume more food at stopover sites or breeding areas in preparation for egg production.

Snipe wintering along the Texas Gulf Coast do not appear to be limited by nutrients as foods consumed were of relatively high quality (McCloskey 1999). Additionally, lipid storage early during spring migration may not be as crucial for snipe as once thought, especially for females which are later spring migrants. Although migration may be energetically costly for snipe, other factors such as food predictability may influence changes in body composition observed in this study and may be more important for snipe at certain times in their annual cycle.

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