Phenotypic Flexibility of Body Composition in Relation to Migratory State, Age, and Sex in the Western Sandpiper (Calidris mauri)

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ABSTRACT

We investigated the flexibility of body composition in relation
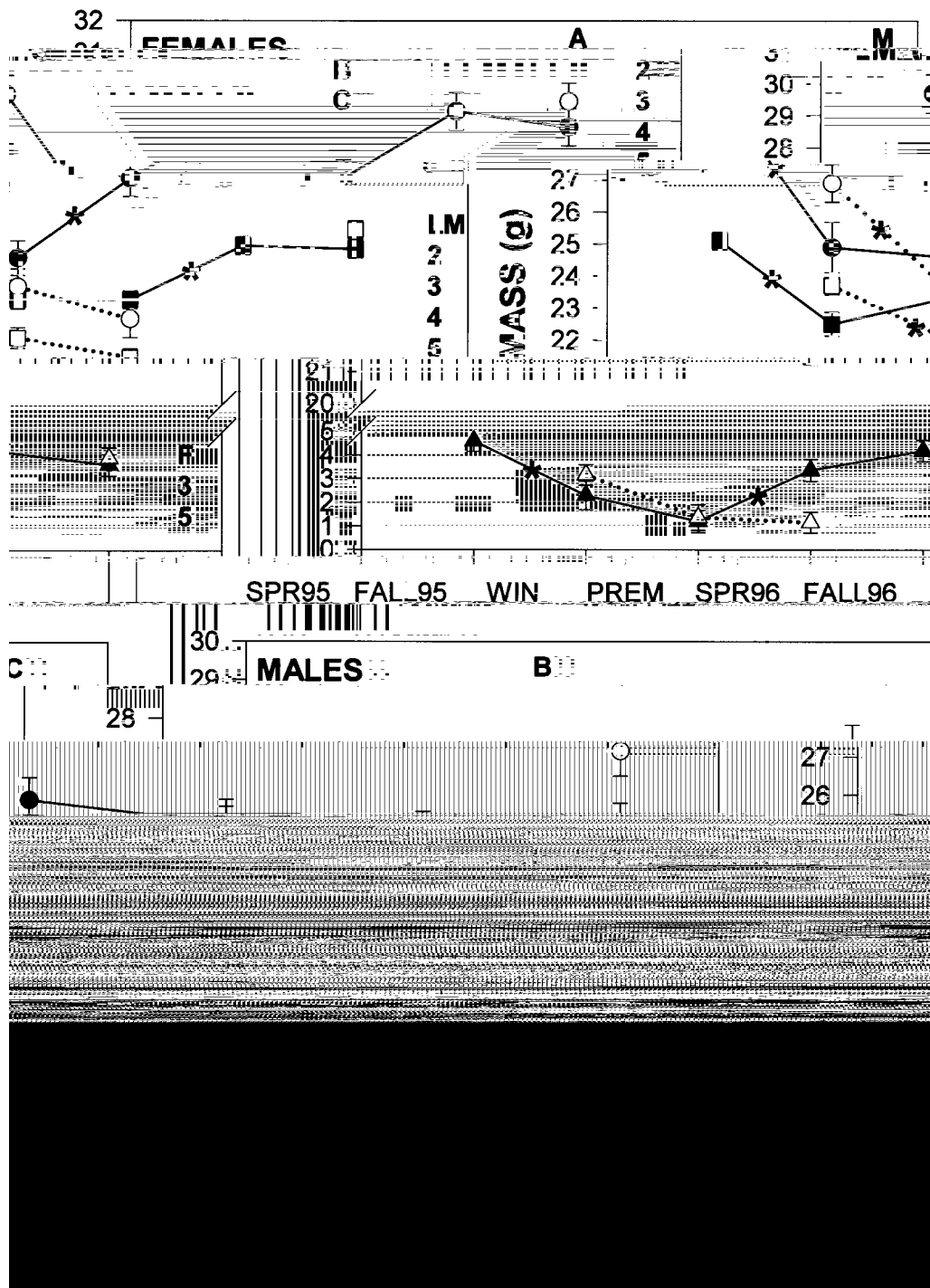
Figure 1. Female and male body mass (*circles*), wet lean mass (*squares*), and fat mass (*triangles*) of adult (*filled symbols*) and juvenile (*open symbols*) western sandpipers. Values are least squares means (±SE) controlling for body size (PC1) during spring (*Spr*), fall (*Fall*), winter (*Win*), and premigration (*Prem*). Asterisks indicate Bonferroni-corrected significance between adjacent stages. Letters along the top margin indicate significant age differences at that stage for body mass (*A*), wet lean mass (*B*), and fat mass (*C*). Numerals along the right margin indicate the following significant differences for mass (*M*), lean mass (*LM*), and fat (*F*): 1995 spring adult versus 1996 spring adult (*1*); 1995 fall adult versus 1996 fall adult (*2*); 1996 fall adult versus winter adult (*3*); 1995 fall juvenile versus 1996 fall juvenile (*4*); 1996 fall juvenile versus winter juvenile (*5*).

ages and stages (Fig. 1; mass: $F_{9,134} = 19.7$, $P = 0.0001$; lean dry mass: $F_{9,119} = 15.4$, $P = 0.0001$; fat: $F_{9,120} = 7.4$, $P = 0.0001$). Body mass, lean mass, and fat mass were lowest during winter and increased during migration. The small sample of adult females ($n = 8$) from fall 1995 were most similar to wintering birds. During premigration, adults increased body mass by the deposition of fat only. This was followed by an increase in lean mass between premigration and spring stopover. Total body mass tended to increase during this transition as well ($P = 0.01$). Hence, 40% of the mass gain from winter to spring stopover consisted of lean body components. In Panama, adults maintained greater lean mass than juveniles during premigration and tended to do so in winter ($P = 0.006$). Female juveniles had greater fresh and lean mass in fall 1996 than in fall 1995.

Body mass did not vary significantly among samples of male migrant sandpipers ($F_{5,91} = 1.5$, $P = 0.19$), but lean and fat mass differed in some cases (dry lean mass: $F_{5,88} = 4.5$, $P = 0.001$; fat: $F_{5,90} = 2.9$, $P = 0.018$; Fig. 1). In fall 1996, juveniles were fatter than adults and, like juvenile females, had greater lean mass than juvenile males in fall 1995.

Female Body Composition

Controlling for body structural size (PC1), we found that female body composition changed dramatically through the year in relation to migration, and there were several age differences

Figure 2. Organ and muscle sizes in adult (*filled circles*) and juvenile (*open squares*) female western sandpipers during spring (*S*), fall (*F*), winter (*W*), and premigration (*P*). Values are least squares means ($\pm$ SE) controlling for body size (PC1). Asterisks indicate Bonferroni-corrected significance between adjacent stages. The letter *A* at the top margin indicates a significant age difference at that stage. Numerals along the right margin indicate significant differences: 1995 spring adult versus 1996 spring adult (*1*); 1995 fall adult versus 1996 fall adult (*2*); 1996 fall adult versus winter adult (*3*); 1995 fall juvenile versus 1996 fall juvenile (*4*); 1996 fall juvenile versus winter juvenile (*5*).
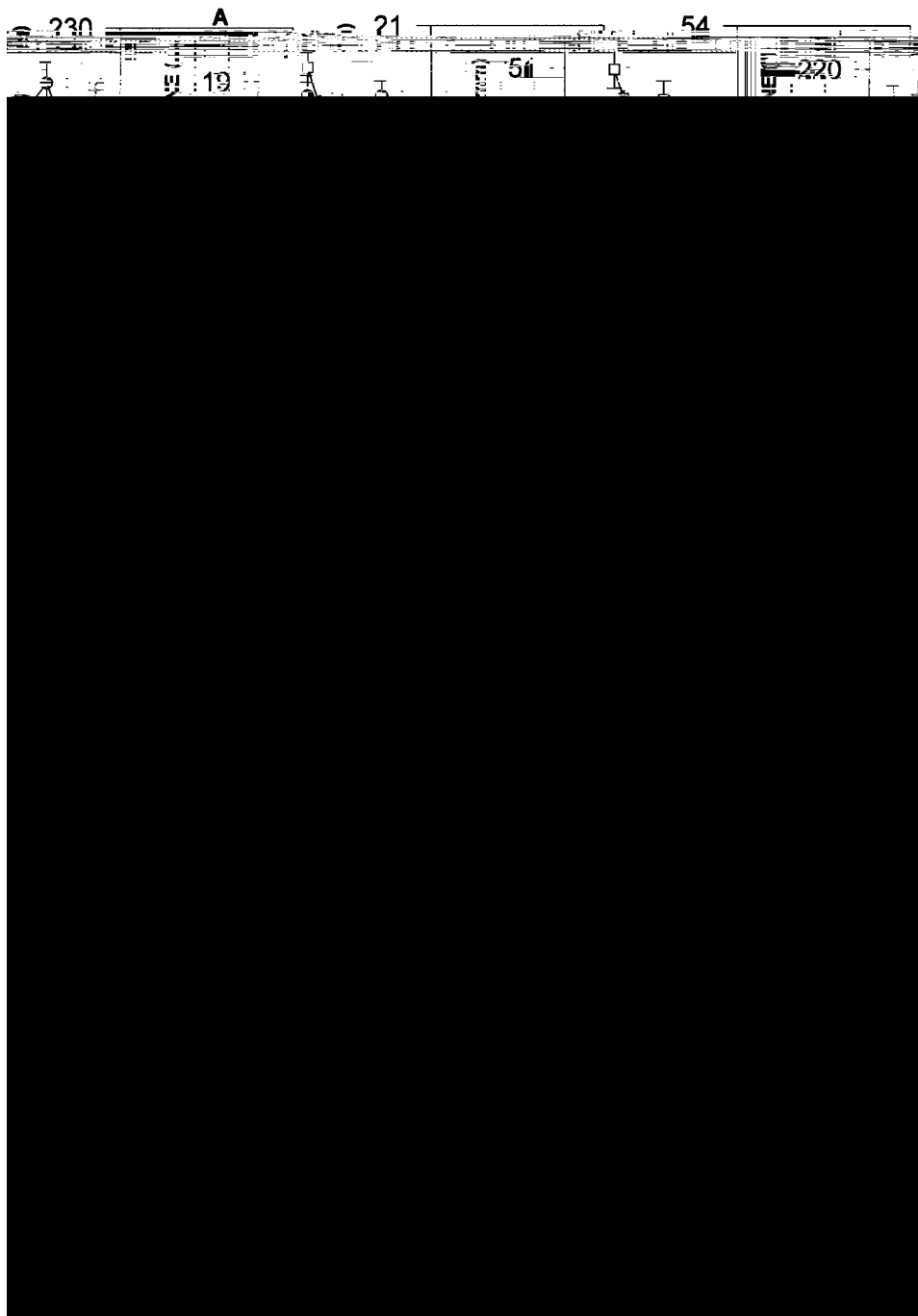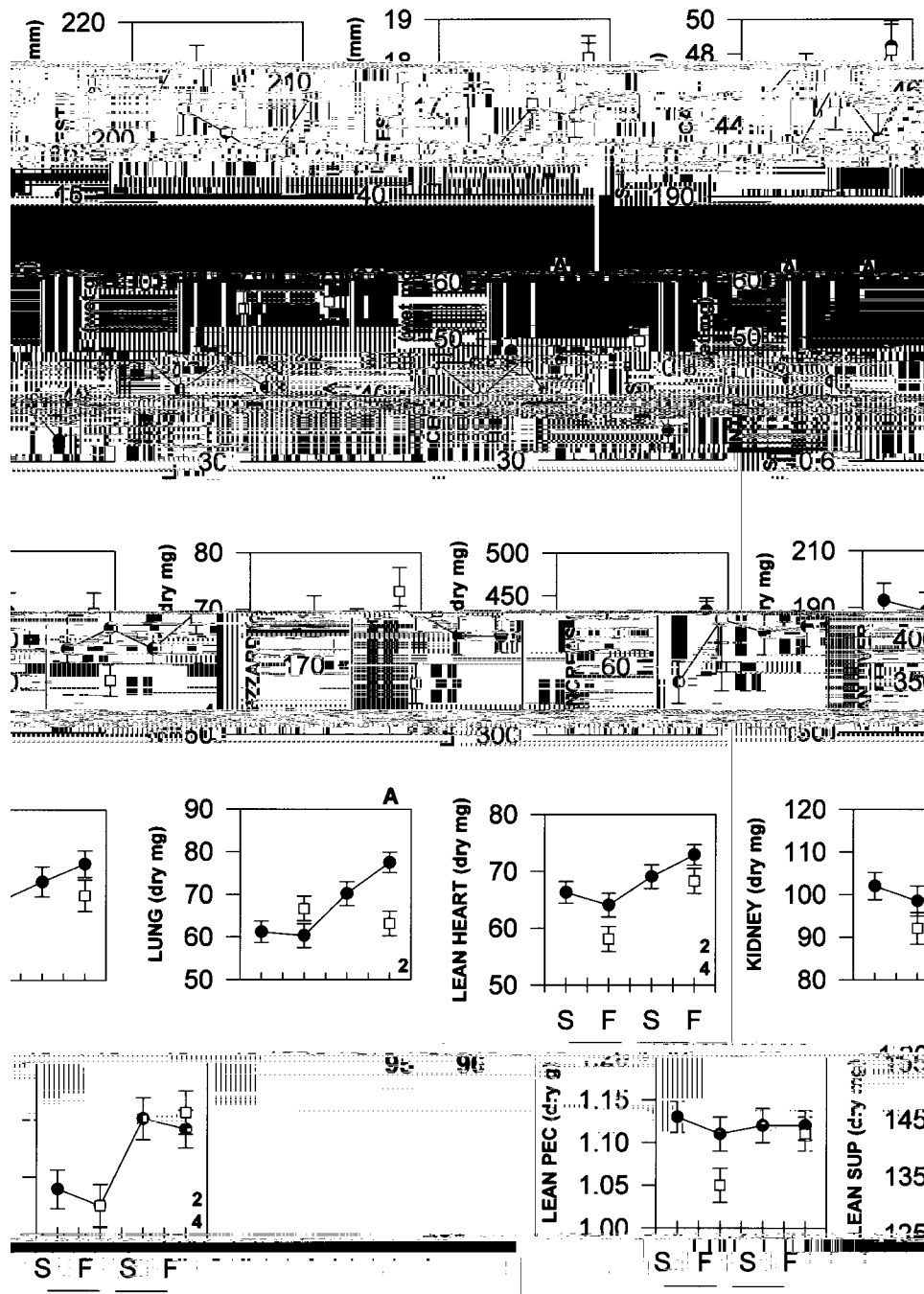
Figure 3. Organ and muscle sizes in adult (*filled circles*) and juvenile (*open squares*) male western sandpipers during spring (*S*) and fall (*F*). Values are least squares means ($\pm$ SE) controlling for body size (PC1). Asterisks indicate Bonferroni-corrected significance between adjacent stages. The letter *A* at the top margin indicates a significant age difference at that stage. Numerals along the right margin indicate significant differences: 1995 fall adult versus 1996 fall adult (*2*); 1995 fall juvenile versus 1996 fall juvenile (*4*).

gizzards than adults; (3) adult lung mass was greater in spring 1996 than spring 1995; and (4) pectoralis was smaller in fall-migrating juveniles than in fall-migrating adults in both years of study.

Sex Differences

Controlling for body size (PC1) and log(body mass − component mass), there were no sex differences in the masses

Table 2: Allometric ($\log_{10}-\log_{10}$) ordinary least squares (OLS) and reduced major axis (RMA) regressions of body component lengths and wet masses versus body mass (g) for male and female western sandpipers ($n = 240$)

		OLS			RMA		
	(b_I)	r^2	Slope (b)	Intercept (a)	r^2	Slope (b_R)	Intercept (a)
Length (mm):							
Small intestine	.34[a]	.14	.30 ± .05	1.89 ± .07	.14	.80 (.71–.89)	1.18 ± .06
Large intestine	.34[a]	.04	.20 ± .07*	.95 ± .10	.04	1.06 (.93–1.20)	−.26 ± .10
Combined ceca	.34[a]	.04	.20 ± .07*	1.38 ± .09	.04	1.01 (.88–1.13)	.24 ± .10
Mass (g):							
Whole gut	1.00[b]	.30	1.02 ± .10	−1.27 ± .14	.30	1.86 (1.68–2.09)	−2.45 ± .15
Gizzard	1.00						

lean mass change in premigratory adult females and found none ($F_{1,11} = 1.7$, $P = 0.22$).

Intraspecific Scaling and Multivariate Analysis

All body components scaled significantly with fresh body mass (Table 2). Except for the whole gut and its major components (gizzard and small intestine), OLS regression slopes (*b*; or scaling exponents) generally differed from those found in interspecific studies that have also used OLS regression. As would be expected, RMA regression slopes were much higher than OLS regression slopes. In particular, RMA regression indicated that, except for pectoralis and supracoracoideus muscles, body components became disproportionately large with increasing mass, and this was especially true for digestive organs. Across the entire sample of males and females, only the wet masses of pectoralis, supracoracoideus, and lung were strongly positively related to body size as measured by PC1 (pectoralis: $r^2 = 0.27$, $P = 0.001$; supracoracoideus: $r^2 = 0.28$, $P = 0.001$; lung: $r^2 = 0.13$, $P = 0.001$).

The first three principal component axes explained 62% of the variation in body component masses (PC1: 35%; PC2: 16%; PC3: 11%; Table 3). All variables loaded positively on the first principal component axis, which reflected absolute component mass. The second principal component axis mainly reflected differences in residual variation related to the digestive system, including liver (loading negatively) and components related to exercise performance (loading positively). The kidneys were not clearly segregated into either the digestive or exercise category, possibly reflecting their important role in both aspects of metabolism. The third principal component axis was difficult to interpret, but residual variation in lipid masses all loaded strongly negatively, indicating that low PC3 scores may be associated with being fat.

We used a modification of the biplot technique (Gabriel 1971; Piersma et al. 1996, 1999*b*) to visualize relationships among body components. Gabriel (1971) developed the method with a two-dimensional plane but encouraged the extension to three-dimensional representations, provided they could be accurately produced. For this analysis, the eigenvectors for the first three principal components of variable were plotted, and vectors from the origin (0, 0, 0) were drawn to each point. The length and proximity of these vectors in space is an indication of the strength of the relationships among variables and were examined by graphical rotation of the plots (Fig. 4*a*, 4*b*). Along the PC2 axis, segregation between "exercise" and "digestive" components (positive and negative PC2 values, respectively) is readily apparent (Fig. 4*a*). Adding PC3 indicated that large intestine and ceca were most closely related to each other, as were (1) liver and pancreas, (2) heart and lung, (3) gizzard and small intestine, and (4) pectoralis, supracoracoideus, and the remaining carcass.

Table 3: Eigenvectors of the first three principal components of log-transformed masses of body components of male and female western sandpipers ($n = 226$)

Body Component	PC1	PC2	PC3
Gizzard	.319	−.088	−.014
Small intestine	.285	−.389	.046
Large intestine	.195	−.296	.520
Combined ceca	.226	−.188	.551
Pancreas	.325	−.286	−.252
Liver	.353	−.205	−.232
Kidney	.367	−.004	−.110
Heart	.268	.219	−.082
Lung	.227	.288	−.115
Pectoralis muscle	.290	.393	.099
Supracoracoideus muscle	.182	.386	.157
Remaining carcass	.207	.396	.319
Total lipid	.283	.056	−.372

Note. Small intestine, large intestine, and ceca were entered as wet mass. Liver, heart, pectoralis, supracoracoideus, and carcass were entered as lean dry mass. Other components were entered as dry mass.

Discussion

Body composition of female western sandpipers changed markedly in response to migration. As expected, migrants were much fatter than wintering birds, yet 40% of the total mass increase of migrants was lean tissue. Lean mass deposition rates of 20%–40% of total mass have been reported previously in premigratory birds as well as during real and simulated stopover (Lindström and Piersma 1993; Klaassen and Biebach 1994; Klaassen et al. 1997; Karasov and Pinshow 1998). We could have overestimated seasonal lean mass deposition if the typical bird captured at the Fraser estuary was relatively fat depleted from flight or if refueling sandpipers tend to deposit lean mass before fat (McLandress and Raveling 1981; Carpenter et al. 1993; Klaassen et al. 1997). Some migrant birds, such as the blackcap (*Sylvia atricapilla*), appear to catabolize and deposit fat and lean mass simultaneously (Karasov and Pinshow 1998).

All organs and muscles were enlarged during migration, but the relative increases were greater for digestive organs than for exercise components. Within the digestive organs, the liver and pancreas showed the greatest relative increase from winter to migration, and the large intestine and ceca the smallest. The ingestion of hard-shelled prey can alter shorebird stomach mass (Piersma et al. 1999*a*), but it is unlikely that this can explain the seasonal changes in digestive organs we measured. Western sandpipers eat mostly soft-bodied worms and small crustaceans, and mollusks and other hard-shelled animals were rarely noted in gizzard contents of our sample at any time of the year (C. G. Guglielmo, personal observation). Moreover, the two organs
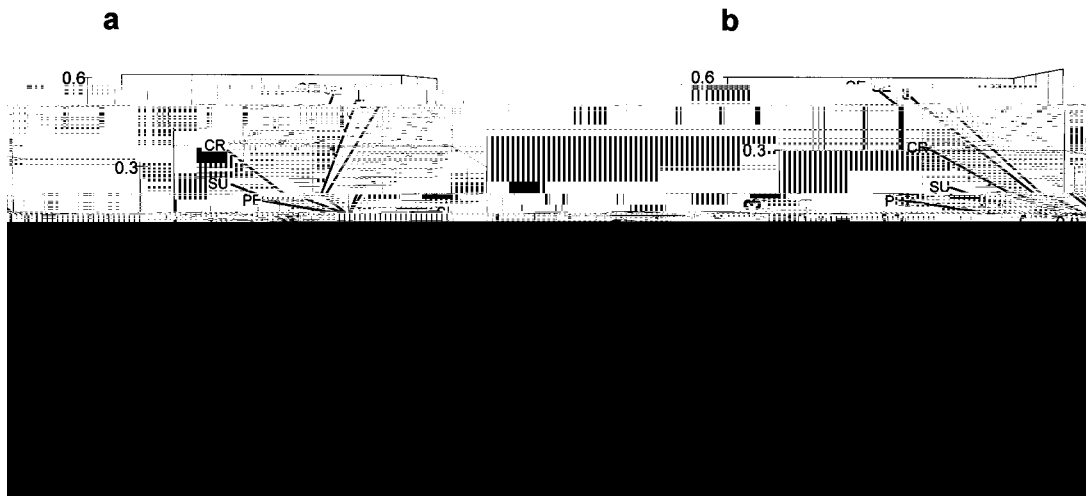
a   b

Figure 4. Three-dimensional projections of eigenvectors for body components on the first three principal component axes. Vectors are drawn from the origin (0, 0, 0) to points defined by the three eigenvectors and are viewed coming toward the viewer (*a*) and after 90° rotation (*b*). The length and proximity in space of these vectors to each other indicate the strength of the relationships among them. Abbreviations are liver (*LV*), pancreas (*P*), ceca (*CE*), large intestine (*LI*), small intestine (*SI*), gizzard (*G*), kidney (*K*), heart (*H*), lung (*LU*), pectoralis (*PE*), supracoracoideus (*SU*), lean carcass (*CR*), and total body fat (*F*).

that changed most dramatically are associated with digestive enzyme secretion (pancreas), bile production, and postabsorptive nutrient processing (liver) rather than bulk processing of ingesta. This suggests that variation in nutrient load, not prey type, was the primary factor driving digestive system change.
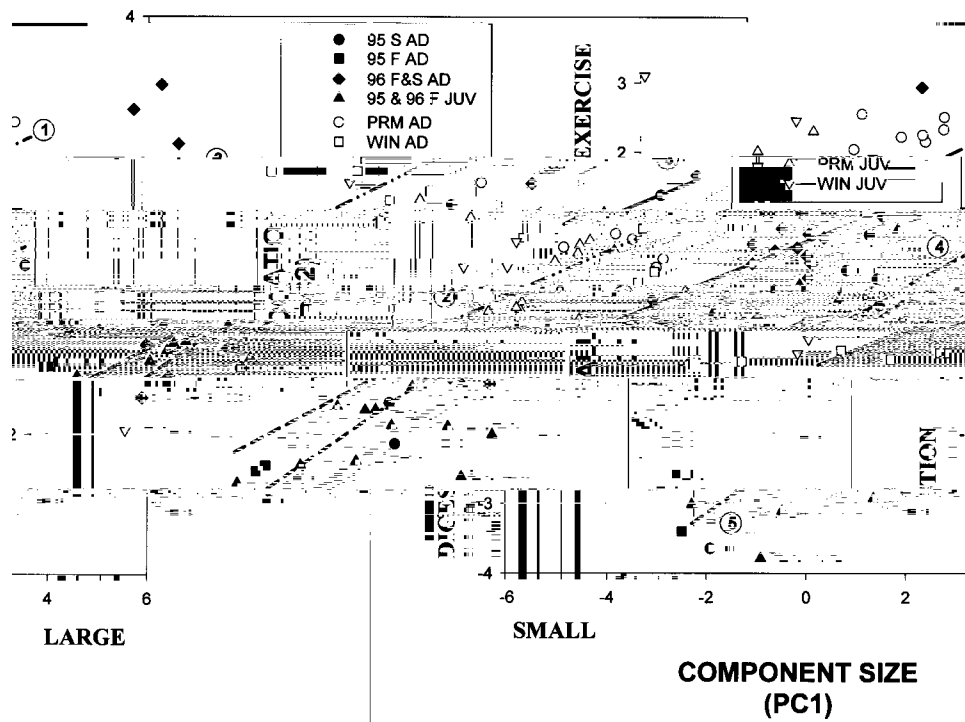
Figure 5. Principal component scores for female western sandpipers on the first two axes from a principal components analysis of body composition. Open and filled symbols represent birds collected in Panama and birds collected during migratory stopover at the Fraser estuary, respectively. PC1 reflected overall component masses, and PC2 reflected exercise (positive loadings) versus digestive components (negative loadings). Migrants had higher PC1 scores than birds in Panama (F = 121.5, P). Regression lines used in ANCOVA are shown

specific scaling exponents for pectoralis from OLS regression

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