



## ENERGY AND MACRONUTRIENT ASSIMILATION EFFICIENCIES OF SNOWY PLOVER (*CHARADRIUS ALEXANDRINUS*) FEEDING ON THE POLYCHAETE RAGWORM *NEREIS DIVERSICOLOR*

MACARENA CASTRO,<sup>1,4</sup> JOSE A. MASERO,<sup>2</sup> CESAR MEGINA,<sup>1</sup> JUAN A. AMAT,<sup>3</sup>  
AND ALEJANDRO PÉREZ-HURTADO<sup>1</sup>

<sup>1</sup>Departamento de Biología Animal, Facultad de Ciencias del Mar y Ambientales, Universidad de Cádiz, E-11510 Puerto Real, Spain;

<sup>2</sup>Grupo de Investigación en Conservación, Área de Zoología, Facultad de Ciencias, Universidad de Extremadura, Avenida de Elvas s/n, E-06071 Badajoz, Spain; and <sup>3</sup>Estación Biológica de Doñana, Consejo Superior de Investigaciones Científicas, Apdo 1056, E-41080 Sevilla, Spain

**ABSTRACT.**—Macronutrient (protein, lipids, and carbohydrates) assimilation efficiencies of wild birds have rarely been studied, but they may be particularly important for estimating the optimal diet. We assessed experimentally the energy and macronutrient assimilation efficiencies of captive Snowy Plover (*Charadrius alexandrinus*) feeding on the polychaete ragworm *Nereis diversicolor*, a major natural prey for migratory shorebirds (Charadrii) along intertidal habitats worldwide. Overall, Snowy Plover consumed  $8.64 \pm 1.54$  (SD) g of dry ragworms per day, and the apparent metabolizable energy was  $136.59 \pm 27.69$  kJ·day<sup>-1</sup> (3.5–4.0 times the basal metabolic rate). Assimilation efficiencies were  $80.04 \pm 2.04\%$ ,  $93.48 \pm 1.08\%$ ,  $84.75 \pm 2.01\%$ , and  $89.23 \pm 2.61\%$  for energy, proteins, lipids, and carbohydrates, respectively. Macronutrient assimilation efficiencies were similar during early winter and premigration and between male and female Snowy Plover. Relatively high protein assimilation by Snowy Plover may be associated with their specialized high-protein diet. Received 20 July 2006, accepted 14 July 2007.

Key words: assimilation efficiency, *Charadrius alexandrinus*, macronutrients, metabolizable energy, *Nereis diversicolor*, shorebirds, Snowy Plover.

### Eficiencia en la Asimilación de Energía y Macronutrientes en *Charadrius alexandrinus* al Alimentarse del Poliqueto *Nereis diversicolor*

**RESUMEN.**—La eficiencia de asimilación de macronutrientes (proteínas, lípidos y carbohidratos) por parte de las aves silvestres ha sido raramente estudiada, pero puede ser particularmente importante para estimar la dieta óptima. Evaluamos experimentalmente la asimilación de energía y macronutrientes por parte de individuos cautivos de la especie *Charadrius alexandrinus* alimentados con el poliqueto *Nereis diversicolor*, una de las presas naturales principales para las aves playeras migratorias (Charadrii) en ambientes intermareales a nivel mundial. En general, las aves consumieron  $8.64 \pm 1.54$  (DE) g de poliquetos secos por día, y la energía metabolizable aparente fue de  $136.59 \pm 27.69$  kJ·día<sup>-1</sup> (3.5–4.0 veces la tasa metabólica basal). Las eficiencias de asimilación fueron de  $80.04 \pm 2.04\%$ ,  $93.48 \pm 1.08\%$ ,  $84.75 \pm 2.01\%$  y  $89.23 \pm 2.61\%$  para energía, proteínas, lípidos y carbohidratos, respectivamente. Las eficiencias de asimilación de macronutrientes fueron similares durante el inicio del invierno y antes de la migración, y entre machos y hembras de *C. alexandrinus*. La asimilación de proteínas relativamente alta documentada para esta especie podría estar asociada con su dieta especializada de alto contenido proteico.

ESTIMATING FOOD REQUIREMENTS of individuals and populations requires accurately assessing the food (energy) acquisition rate and digestive efficiency of individuals (Castro et al. 1989, Karasov 1990). Digestive efficiency (i.e., the efficiency at which ingested food is converted to metabolizable energy) is, therefore, an

important measure for studies on the influence of individuals—and, hence, populations—on habitat energy flow. Ingested biomass (intake rate), the length of time food is in the gastrointestinal tract (retention time), and the ability of the intestinal tract to absorb nutrients (assimilation efficiency) are the major components

<sup>4</sup>Present address: Centro de Investigación en Ecosistemas de la Patagonia, Bilbao 449, Coyhaique, Chile. E-mail: [macarena.castro@ciep.cl](mailto:macarena.castro@ciep.cl)

of digestive efficiency (Karasov 1996). Inaccurate estimates of any of these components lead to errors in estimating food or energy requirements of individuals and, hence, to poor predictive models for assessing ecological energetics of populations and communities (Karasov 1986).

Energy assimilation efficiency depends on the nutrient composition of the prey consumed, as well as the ability of the intestines to absorb the nutrients (nutrient assimilation efficiency) and to transform them into energy through the various metabolic pathways (Murphy 1996). It has been suggested that nutrient assimilation efficiency influences dietary selection, in that individuals select prey on the basis of its nutritional composition and their ability to efficiently digest it (Witmer and Van Soest 1998). However, little information exists on macronutrient assimilation efficiencies for wild birds, except for some groups of nectarivorous and frugivorous birds for which assimilation of carbohydrates and lipids has been widely studied (Hainsworth 1974, López-Calleja et al. 1997, Levey and Martínez del Río 2001).

Polychaete worms are among the most common prey of migratory shorebirds (Charadrii) and other waterbirds in estuaries worldwide (Piersma 1996, Skagen and Oman 1996, Moreira 1997), but no empirical data on the energy or macronutrient assimilation efficiencies of polychaetes eaten by a shorebird have been reported. Zwarts and Blomert (1990) measured nutrient assimilation efficiencies of Whimbrels (*Numenius phaeopus*) fed Fiddler Crabs (*Uca tangeri*). Crabs and other hard-bodied prey are difficult to digest (Speakman 1987), so extrapolation of the results from Whimbrels to other bird species that feed on soft-body invertebrates such as polychaete worms would not be appropriate. Snowy Plover (*Charadrius alexandrinus*) are small migratory shorebirds that prey mainly on polychaete worms in intertidal areas (Skagen and Oman 1996, Pérez-Hurtado et al. 1997, Amat 2003), though they also eat some insects, seeds, crustaceans, and molluscs (Piersma 1996, Amat 2003). We assessed experimentally the energy and macronutrient assimilation efficiencies of Snowy Plover fed ragworms (*Nereis diversicolor*). In studies on seabirds (Hilton et al. 2000a, b) and birds of prey (Barton and Houston 1993), it was found that generalist species with a wide dietary spectrum had longer intestines and higher assimilation efficiencies than specialist species with a narrow dietary spectrum (Barton and Houston 1993; Hilton et al. 2000a, b). Accordingly, we predicted high energy and macronutrient assimilation efficiencies for Snowy Plover fed ragworms because of the species' generalist diet and the low inorganic content of ragworms.

Many models that estimate prey acquisition by declining shorebird populations feeding on polychaetes in estuaries use a theoretical value of 80% for energy assimilation efficiency (Zwarts and Blomert 1990, Moreira 1997, Stillman et al. 2000, Masero and Pérez-Hurtado 2001, Masero 2003, Goss-Custard et al. 2006). Therefore, our study provides the first published estimates of assimilation efficiency for a shorebird eating polychaetes, which will allow more accurate assessments of the number of prey necessary to sustain these populations.

## METHODS

**Capture and housing conditions.**—Twenty Snowy Plover were captured under license at Cádiz Bay in southern Spain (36°23'N, 6°8'W). (1) Five females and six males and (2) five females and

four males were captured and held in captivity during October–November 1998 (early winter) and February–March 1999 (pre-migratory period), respectively. All birds were adults and nonmolted. Most overwintering Snowy Plover leave the study area in late March (Masero et al. 2000), though there is a small resident population (Hortas 1997).

We detected no seasonal differences in body mass of Snowy Plover (early winter =  $38.81 \pm 2.87$  [SD] g; premigration =  $41.14 \pm 3.29$  g;  $t = -1.69$ ,  $df = 1$  and  $18$ ,  $P = 0.11$ ), and the birds maintained constant body mass during experiments. Thus, we assume that the captive birds were resident or were in a non-fattening state.

Birds were transported to Cádiz Marine Science Faculty, located 10 km from the sites of capture. Birds were acclimated to an aviary for one week and then housed individually in outdoor plastic-mesh cages (1 × 1 × 1 m). Each bird had *ad libitum* access to ragworms in plastic trays, with seawater and freshwater in a separate tray.

**Energy and macronutrient assimilation efficiencies.**—Prior to the experiment, we estimated that Snowy Plover ( $n = 4$ ) required 3.5–4.0 h to empty their digestive tract when fed ragworms (see methods in Dekinga and Piersma 1993). For each individual, we estimated the daily assimilation efficiencies during four consecutive days. Each trial began at 0900 hours (Greenwich Mean Time + 1 h), when the birds were fasted for 4 h and then weighed. We then replenished the water and supplied each bird with a known quantity of food. Total daily intake was the difference between dry food offered and dry food that remained. The remaining prey and excreta were removed daily after the fasting period. Total daily excreta of each individual was combined, homogenized, and stored frozen (−80°C).

Gross energy intake (GEI) per bird per day was estimated as the amount (g dry) of total protein ( $P_p$ ), lipids ( $L_p$ ), and carbohydrates ( $C_p$ ) ingested, multiplied by the energy density of these macronutrients ( $E_p$  was  $23.65 \text{ kJ g}^{-1}$  dry protein;  $E_l$  was  $39.55 \text{ kJ g}^{-1}$  dry lipid;  $E_c$  was  $17.16 \text{ kJ g}^{-1}$  dry carbohydrate; Crisp 1984). The gross energy output (GEO) per bird per day was estimated as the amount (g dry) of total protein ( $P_e$ ), lipids ( $L_e$ ), and carbohydrates ( $C_e$ ) excreted, multiplied by the energy density of these macronutrients plus the amount (g dry) of excreta composed of uric acid ( $A_e$ ) and urea ( $U_e$ ) times their energy density ( $E_a$  was  $11.5 \text{ kJ g}^{-1}$  dry uric acid;  $E_u$  was  $10.5 \text{ kJ g}^{-1}$  dry urea; Bell 1990).

Energy assimilation efficiency (AE) was calculated, following Castro et al. (1989), as

$$AE (\%) = 100 \times (GEI - GEO) / GEI$$

$$GEI = P_p \times E_p + L_p \times E_l + C_p \times E_c$$

$$GEO = P_e \times E_p + L_e \times E_l + C_e \times E_c + A_e \times E_a + U_e \times E_u$$

Assimilation efficiency for each macronutrient was calculated in the same way as the energy assimilation efficiency. Apparent metabolizable energy (AME;  $\text{kJ} \cdot \text{day}^{-1}$ ) was the difference between the total energy ingested and the energy excreted in a day (Miller and Reinecke 1984).

Protein content was determined by the Folin-phenol-reagent method, according to Lowry et al. (1951). Total lipid content was determined gravimetrically after extraction of a homogenized sample in chloroform and methanol (2:1, v/v) (Folch et al. 1957).

TABLE 1. Macronutrient composition (percentage  $\pm$  SD) of ragworms provided to captive Snowy Plover in 1998 (early winter) and 1999 (premigration). Number of ragworm composite samples analyzed per season is indicated in parentheses.

	Protein (%)	Lipids (%)	Carbohydrates (%)	Ash (%)
Early winter (10)	54.12 $\pm$ 4.26	14.31 $\pm$ 2.00	17.82 $\pm$ 0.76	13.76 $\pm$ 1.62
Premigration (10)	54.94 $\pm$ 4.65	13.83 $\pm$ 4.53	17.78 $\pm$ 0.88	13.45 $\pm$ 1.79
$t_{18}$	1.85	1.85	1.86	1.37
$P$	0.08	0.09	0.08	0.18

Carbohydrate content was determined by a colorimetric method using the phenol-sulphuric acid reagent (Dubois et al. 1956). Ash content was measured gravimetrically after total combustion in a furnace at 550°C.

Total N in the excreta was determined using a Carlo Erba 1106 elemental analyzer (SerCon, Crewe, United Kingdom). We assumed that 75% of excreted N was uric acid and 25% was urea (Karasov 1990).

**Temperature.**—Temperatures were recorded every hour. An estimation of the time the ambient temperature remained below the thermoneutral zone of the species was calculated by using the index

$$\sum_{i=0}^{i=24} |T_{hi} - T_{lc}|$$

where  $T_{hi}$  is the temperature at hour  $i$  (from 0 to 24) and  $T_{lc}$  is the lower critical temperature (LCT; 24.6°C, following the equation of Kendeigh et al. [1977] and assuming a mean body mass for Snowy Plover of 36.26  $\pm$  2.69 g;  $n = 20$ ).

The duration of daylight hours was similar in both periods (early winter: 11.18  $\pm$  0.50 h of light; premigratory period: 11.01  $\pm$  0.74 h of light;  $t = -0.71$ ,  $df = 1$  and 23,  $P = 0.48$ ).

**Statistical analyses.**—The data were inspected for normality and homoscedasticity and normalized using arcsine transformation if needed.  $P$  values were adjusted with the Bonferroni test to control for type-I errors when needed (Rice 1989). An analysis of variance (ANOVA) for repeated measures, using mean air temperature as covariate (Klaassen et al. 1990), was used to test the effect of season and sex on energy and macronutrient assimilation efficiencies. The effect of season and sex on assimilation variables was analyzed because seasonal variation in nutrient assimilation efficiencies has been shown (Lepczyk et al. 2000), and a requirement for energy or nutrients or both could exist, associated with gender but independent of fattening state (Piersma and Morrison 1994, Egeler and Williams 2000). Mean daily values for each of the four-day trials were used for calculations, except for the correlation between gross ingested food and body mass, in which the value of food ingested every day and body mass of the corresponding day were used. Unless stated otherwise, results are presented as means  $\pm$  SD.

## RESULTS

**Prey composition.**—Energy density of ragworms was 21.48  $\pm$  2.73 kJ g<sup>-1</sup> of ash-free dry mass (AFDM) ( $n = 20$ ). Protein, lipid, carbohydrate, and ash contents of ragworms were 54.58  $\pm$  4.38%, 13.96  $\pm$  3.43%, 17.79  $\pm$  1.99%, and 13.65  $\pm$  1.65%, respectively.

Macronutrient composition of ragworms was similar between seasons (Table 1).

**Assimilation efficiencies.**—The birds ( $n = 20$ ) consumed 8.64  $\pm$  1.54 g dry ragworms per day (dry mass/wet mass = 0.18  $\pm$  0.07 g; wet mass/AFDM = 5.42  $\pm$  0.21 g;  $n = 20$ ) or 169.13  $\pm$  29.99 kJ day<sup>-1</sup>. No correlation was found between daily food intake and body mass of birds ( $r = 0.26$ ,  $P = 0.25$ ,  $n = 80$ ). The birds excreted 32.4  $\pm$  6.9 kJ day<sup>-1</sup>, which yields an AME of 136.59  $\pm$  27.69 kJ day<sup>-1</sup> and a mean assimilation efficiency of 80.04  $\pm$  2.04% for energy, 93.48  $\pm$  1.08% for proteins, 84.75  $\pm$  2.01% for lipids, and 89.23  $\pm$  2.61% for carbohydrates. Energy and macronutrient assimilation efficiencies were similar during early winter and premigration, and between males and females (Tables 2 and 3).

**Temperature.**—Daily temperature during the experiments varied between 6.75°C and 23.88°C. Mean temperature was significantly different between the two seasons (October–November: 17.99  $\pm$  3.28°C; February–March: 14.87  $\pm$  1.88°C;  $t = 2.95$ ,  $df = 1$  and 23,  $P < 0.007$ ). There was also a significant difference between seasons in the number of days colder than the LCT of Snowy Plover: in early winter, the mean difference between mean hourly temperature and LCT was 10.38  $\pm$  3.21°C, and in premigration it was 6.6  $\pm$  3.28°C ( $t = -2.97$ ,  $df = 1$  and 23,  $P < 0.006$ ). The temperature coefficient for a Snowy Plover of 36.26 g is 0.024 (Watts °C<sup>-1</sup>) according to the allometric relation of Aschoff (1981). This means that estimated thermoregulation costs for Snowy Plover in the present study were significantly higher in early winter (22.11  $\pm$  6.75 kJ day<sup>-1</sup>;  $n = 9$ ) than during premigration (14.26  $\pm$  6.69 kJ day<sup>-1</sup>;  $t = 2.95$ ,  $df = 1$  and 18,  $P < 0.018$ ,  $n = 11$ ).

## DISCUSSION

Snowy Plover feeding on ragworms showed high values of energy and macronutrient assimilation efficiencies, as expected for a generalist feeder eating soft-bodied prey. Research on shorebirds feeding on soft-bodied invertebrates yielded values of energy assimilation between 72% and 84% (Hockey and Underhill 1984, Kersten and Visser 1996), depending on the non-organic-matter content of the prey. We fed ragworms to Snowy Plover in seawater so that the birds could remove sediment adhering to the ragworms. Thus, our estimate of energy assimilation efficiency is likely similar to what would be found for Snowy Plover feeding on ragworms in the wild.

Temperature differed, on average, 3°C between seasons, which yielded a difference of  $\sim$ 8 kJ day<sup>-1</sup> in energy expenditure for temperature maintenance. We did not measure the daily activity of Snowy Plover in the cages, but this cost should be balanced by the heat increment of feeding and the heat generated

TABLE 2. Mean ( $\pm$  SD) daily body mass, food ingested, excreta produced, and energy assimilation efficiency of captive Snowy Plover (sample size in parentheses; AFDM = ash-free dry mass).

	Body mass (g)	Gross ingested food (g AFDM)	Excreta (g AFDM)	Net ingested food (g AFDM)	Gross ingested energy (kJ day <sup>-1</sup> )	Energy in excreta (kJ day <sup>-1</sup> )	Apparent metabolizable energy (kJ day <sup>-1</sup> )	Energy assimilation efficiency (%)								
<b>Early winter</b>																
Males (6)	35.89 $\pm$ 2.51	8.60 $\pm$ 0.73	2.29 $\pm$ 0.43	6.31 $\pm$ 0.85	169.72 $\pm$ 14.90	30.60 $\pm$ 5.13	137.36 $\pm$ 25.57	83.37 $\pm$ 2.05								
Females (5)	35.69 $\pm$ 2.32	9.44 $\pm$ 1.37	2.57 $\pm$ 0.19	6.87 $\pm$ 1.24	184.68 $\pm$ 26.04	34.52 $\pm$ 2.27	142.03 $\pm$ 27.20	82.79 $\pm$ 1.04								
<b>Premigration</b>																
Males (4)	37.76 $\pm$ 3.54	8.34 $\pm$ 0.62	2.61 $\pm$ 0.38	5.73 $\pm$ 0.81	162.60 $\pm$ 12.15	34.48 $\pm$ 4.59	134.58 $\pm$ 24.84	82.38 $\pm$ 1.03								
Females (5)	35.65 $\pm$ 1.58	8.38 $\pm$ 0.91	2.45 $\pm$ 0.23	5.92 $\pm$ 0.90	163.30 $\pm$ 17.89	32.17 $\pm$ 2.48	125.37 $\pm$ 26.13	81.28 $\pm$ 2.03								
Statistical effects																
Season																
<i>F</i> <sup>a</sup> <i>P</i>	1.34	0.26	1.12	0.30	0.02	0.96	0.55	0.47	0.59	0.45	1.11	0.31	0.83	0.30	0.04	0.88
Season $\times$ sex																
<i>F</i> <sup>b</sup> <i>P</i>	1.26	0.28	0.21	0.66	0.01	0.99	0.20	0.66	0.09	0.76	0.02	0.88	0.24	0.63	0.41	0.53

<sup>a</sup>df = 1 and 17.<sup>b</sup>df = 1 and 15.

through activity, given that we did not record an increase in the ingested food or assimilation efficiency.

We found that Snowy Plover assimilated at least 80% of proteins, lipids, and carbohydrates, which suggests little digestive (enzymatic) limitation. It is noteworthy that Snowy Plover processed proteins more efficiently than lipids and carbohydrates. Protein is costly to digest compared with fat or carbohydrate digestion, so a protein-rich diet requires more energy for digestion than a lipid or carbohydrate-rich diet (Crisp 1984, Murphy 1996). In birds, nitrogen resulting from deamination is excreted mainly as uric acid and urea. The energetic costs of forming and disposing of these nitrogenous waste products (11.5 kJ g<sup>-1</sup> dry mass in uric acid and 10.5 kJ g<sup>-1</sup> dry mass in urea) reduce the value of protein as a substrate for energy metabolism (Murphy 1996).

A nutrient-based digestive specialization has been proposed among passerines. Cedar Waxwings (*Bombycilla cedrorum*) and thrushes (*Turdus migratorius*, *Hylocichla mustelina*, *Catharus minimus*, and *C. guttatus*) showed digestive specialization for efficient utilization of sugars and lipids, respectively, which corresponded with the more common macronutrients in their diets (Witmer and Van Soest 1998). Snowy Plover and other small shorebird species that feed on polychaete worms may show a nutrient-based digestive specialization, in that their assimilation efficiency of protein is higher than that of other macronutrients and they commonly feed on a high-protein diet.

The AME of Snowy Plover was 3.5–4.0 times the basal metabolic rate (BMR). This value is generally accepted as the maximum sustained energy-expenditure for birds (Drent and Daan

TABLE 3. Mean ( $\pm$  SD) daily ingested and excreted protein, lipids, carbohydrates, and assimilation efficiency of these macronutrients of captive Snowy Plover (sample size in parentheses; AFDM = ash-free dry mass).

	Gross ingested protein (g AFDM)	Protein in excreta (g AFDM)	Protein efficiency (%)	Gross ingested lipids (g AFDM)	Lipids in excreta (g AFDM)	Lipid assimilation efficiency (%)	Gross ingested carbohydrates (g AFDM)	Carbohydrates in excreta (g AFDM)	Carbohydrate assimilation efficiency (%)									
<b>Early winter</b>																		
Males (6)	4.52 $\pm$ 0.38	0.27 $\pm$ 0.05	94.01 $\pm$ 1.07	1.08 $\pm$ 0.09	0.12 $\pm$ 0.02	89.73 $\pm$ 2.04	1.17 $\pm$ 0.16	0.14 $\pm$ 0.03	90.21 $\pm$ 2.49									
Females (5)	4.95 $\pm$ 0.71	0.33 $\pm$ 0.01	93.47 $\pm$ 1.03	1.17 $\pm$ 0.01	0.13 $\pm$ 0.01	89.42 $\pm$ 1.01	1.25 $\pm$ 0.16	0.16 $\pm$ 0.02	90.24 $\pm$ 1.61									
<b>Premigration</b>																		
Males (4)	4.37 $\pm$ 0.32	0.31 $\pm$ 0.05	93.22 $\pm$ 0.89	1.03 $\pm$ 0.08	0.13 $\pm$ 0.02	88.67 $\pm$ 1.58	1.09 $\pm$ 0.08	0.19 $\pm$ 0.04	86.69 $\pm$ 2.98									
Females (5)	4.38 $\pm$ 0.48	0.28 $\pm$ 0.05	93.64 $\pm$ 1.37	1.03 $\pm$ 0.11	0.12 $\pm$ 0.01	89.06 $\pm$ 1.91	1.09 $\pm$ 0.12	0.17 $\pm$ 0.01	88.50 $\pm$ 1.43									
Statistical effects																		
Season																		
<i>F</i> <sup>a</sup> <i>P</i>	0.13	0.72	2.37	0.14	0.55	0.47	1.12	0.31	0.57	0.46	0.01	0.91	1.12	0.31	0.06	0.81	0.01	0.94
Season $\times$ sex																		
<i>F</i> <sup>b</sup> <i>P</i>	2.50	0.14	0.13	0.72	0.46	0.51	0.21	0.66	0.14	0.71	0.02	0.88	0.21	0.66	0.21	0.65	0.32	0.58

<sup>a</sup>df = 1 and 17.<sup>b</sup>df = 1 and 15.

1980, Piersma 2002) but is not expected for a captive bird with constant body mass, no tissue synthesis, and low thermoregulation costs ( $<1 \times$  BMR). Nonetheless, a study on migrating shorebirds found that Red Knot (*Calidris canutus*), Ruff (*Philomachus pugnax*), European Golden-Plover (*Pluvialis apricaria*), Common Greenshank (*Tringa nebularia*), and Common Sandpiper (*Actitis hypoleucos*) can sustain a maximum energy expenditure  $\geq 7 \times$  BMR (Kvist and Lindström 2003).

Some migratory shorebird populations are globally endangered (Stroud et al. 2002, Thomas et al. 2006). Inaccurate estimates of energy assimilation efficiency can lead to erroneous estimates of food consumption and, hence, to erroneous assessments of how many prey are necessary to maintain declining shorebird populations. Our results empirically confirm what modelers of ecological energetics have long assumed: shorebirds that eat soft-bodied prey assimilate, on average, 80% of dietary energy. However, more studies such as ours are needed to determine whether assimilation efficiency varies among bird species that eat different types of prey.

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