

Dehydration of seabird prey during transport to the colony: effects on wet weight energy densities¹

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We present evidence to indicate that dehydration of prey transported by seabirds from capture sites at sea to chicks at colonies inflates estimates of wet weight energy densities. These findings and a comparison of wet and dry weight energy densities reported in the literature emphasize the importance of (i) accurate measurement of the fresh weight and water content of prey, (ii) use of dry weight energy densities in comparisons among species, seasons, and regions, and (iii) cautious interpretation and extrapolation of existing data sets.

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La déshydratation des proies transportées par les oiseaux marins des sites de captures en mer jusqu'aux petits dans les colonies entraîne une surestimation des densités énergétiques reliées aux masses fraîches. Nos résultats et des comparaisons des densités énergétiques reliées aux masses fraîche et sèche telles que rapportées dans la littérature montrent l'importance (i) de mesurer avec précision la masse fraîche et le contenu hydrique des proies, (ii) d'utiliser les densités énergétiques reliées à la masse sèche pour faire des comparaisons entre les espèces, les régions et les saisons, et (iii) d'interpréter et d'extrapoler avec réserve les données existantes de la littérature.

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Introduction

Seabird energetics and the impact of seabird populations on fish stocks have received considerable attention in recent years (e.g., Whittow and Rahn 1984; Furness and Monaghan 1987). While estimates of seabird energy requirements have become more elaborate, little attention has been paid to prey characteristics that might influence energetics calculations (Croxall *et al.* 1985).

The lipid and water composition of fish eaten by seabirds vary widely among seasons and locations (Percy and Fife 1981; Montevecchi and Piatt 1984). Furthermore, estimates of energy contents are influenced by analytical method (Hopkins *et al.* 1984; Dobush *et al.* 1985; McClintock 1986) and by food sampling procedure (e.g., whether prey were collected from predators or directly from the ocean; Clarke and Prince 1980; Harris and Wanless 1985).

Standardized, replicable measurements of energy and organic contents are needed for comparisons of research results (e.g., biomass consumption, growth rates), to prevent inappropriate inferences from obscuring interpretation of findings. This problem has recently caused concern for many researchers (Birkhead and Nettleship 1984; Threlfall and Mahoney 1984; Coulson 1985; Harris and Wanless 1985; McClintock 1986).

To quantify a previously unidentified factor that can influence fresh energy density estimates of prey, we simulated foraging flights of different distances and measured the dehydration of capelin (*Mallotus villosus*), the major food of seabirds in the Newfoundland and Labrador region (Brown and Nettleship 1984). Findings are applicable to marine birds that carry fish dangling crosswise from the bill (e.g., puffins, Razorbills (*Alca torda*), terns) and are relevant to energetics models and ecological considerations involving these species.

Methods

On 14 July 1985, 15 male and 15 gravid female capelin were taken from a beach trap at Cape Broyle (47°06' N, 53°03' W), Newfoundland, within the foraging range of the largest Atlantic Puffin (*Fratercula arctica*) colonies in North America, and were stored in seawater until the start of the experiment ~100 min later. These capelin were slightly heavier and longer than those delivered to Common Murre (*Uria aalge*) chicks and considerably larger than those fed to Atlantic Puffin and Razorbill chicks in Newfoundland and Labrador (Piatt 1987). The mean (\pm SE) fresh weights of the male and female capelin were 34.3 ± 2.1 and 19.2 ± 1.8 g, respectively. The capelin were weighed (Pesola 50-g balance) and measured (millimetres, total length), then placed on an elevated, shaded drying rack in the back of a pickup truck. The weather was sunny with an air temperature of ~20°C, which is typical of weather during the breeding season. The truck was driven at 60 km/h (i.e., approximate alcid flight speed; Harris and Hislop 1978), and fish were weighed to the nearest 0.5 g every 15 min for 1 h, when fish lengths were remeasured. Fish weights were analyzed using linear regressions of weight on time, and a repeated measures design ANOVA was used to calculate the variances in weight due to sex, length, and time, after variance due to other factors was removed (partial sums of squares analysis). Coefficients of variation ($CV = SD/\bar{x} \times 100$) were used to compare the variability of wet and dry weight energy density estimates. The organic compositions of male and gravid female capelin collected at the same site (Montevecchi and Piatt 1984) were used to estimate the energy densities of the capelin used in the present study.

Results

Dehydration of the transported capelin is revealed by their progressive weight loss as a function of travel time ($F = 531.8$, $df = 4,25$, $p < 0.0001$; Fig. 1). Males and females exhibited different rates of dehydration (males: weight = -0.049 (time) + 34.1; females: weight = -0.037 (time) + 19.1), because males were larger, i.e., had a greater surface area. When weight loss due to fish length was partialled out in a repeated measures design ANOVA, sex was not a significant source of dehydration ($F = 3.64$, $df = 1,28$, $p > 0.05$), whereas initial fish length was

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TABLE 1. Energy content of selected fish determined on wet and dry weight bases

	Date	Location	% water	kJ/g		Source of fish*	Basis of energy estimate†
				Wet	Dry		
Capelin							
Male	June	Newfoundland	80.2	3.8	19.2	S	C
	July	Newfoundland	78.3‡	4.1	19.2		
	Oct.	Newfoundland	67.2	9.5	29.0	S	C
Female							
Gravid	June	Newfoundland	76.5	4.6	19.6	S	C
	July	Newfoundland	73.5‡	5.3	19.6		
Spent	June	Newfoundland	80.0	3.9	19.5	S	C
Post-spawn	Oct.	Newfoundland	67.1	9.5	28.9	S	C
Mixed	June	Newfoundland	81.0	3.9	20.5	S	C
	Aug.	Newfoundland	76.0	5.8	24.2	S	C
	Aug.-Sept.	Labrador	75.9	6.0	24.9	M	B
Sand lance	June	Scotland	72.6	6.5	22.2	M	B
	July	Quebec	63.5	7.3	20.0	M	C
	Aug.-Sept.	Labrador	69.9	7.0	23.3	M	B
Sprat							
Large	June	Scotland	64.3	10.9	25.6	M	B
Small	June	Scotland	72.4	6.7	21.4	M	B
Whiting	June	Scotland	81.7	4.1	22.1	S	B

NOTE: Data from Newfoundland (Montevecchi and Piatt 1984), Labrador (Bradstreet 1983), Quebec (Montevecchi *et al.* 1984), and Scotland (Harris and Hislop 1978).

*M, meal collected from birds; S, fish collected from the sea.

†C, composition analysis; B, bomb calorimetry.

‡This study. Wet weight estimates calculated from quantities (g) of protein and lipid estimated in freshly caught fish (Montevecchi and Piatt 1984) assuming all weight loss due to dehydration. Dry weight estimates as reported in Montevecchi and Piatt (1984).

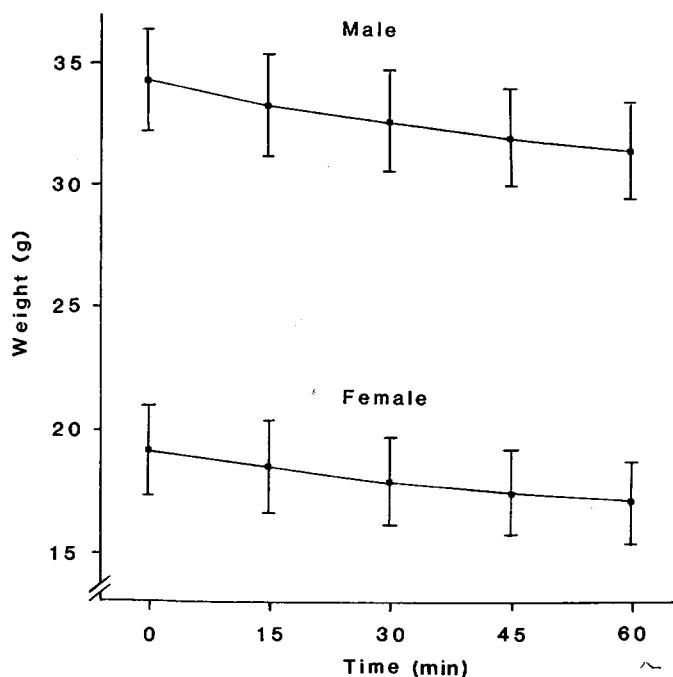


FIG. 1. Mean (\pm SE) wet weights of male and gravid female capelin exposed to a 60 km/h wind stream measured at 15-min intervals for 1 h.

($F = 44.8$, $df = 7,223$, $p < 0.0001$). On average, males lost 8.7% and females 11.5% of their body weight to dehydration during the 1-h test. This sex difference is a consequence of the greater relative surface area of females. For each sex the highest percentage of water loss occurred during the first 15 min. Body

lengths were not significantly affected by the experimental treatment; the mean total lengths of the capelin at the start (male = 176.2 ± 3.3 mm, female = 146.7 ± 4.3 mm) and at the end of the experiment (male = 175.3 ± 3.1 mm, female = 145.3 ± 4.2 mm) were not significantly different.

Discussion

Because of dehydration during transport from feeding sites to colonies, analysis of prey collected in colonies can result in wet energy densities that are higher than those of fish freshly removed from water. Consequently, energy density estimates may vary among colonies as a function of the average foraging range. In our experiment, for example, dehydration from wind flow resulted in increases of 7.9 and 15.2% in the fresh energy densities of male and female capelin, respectively (see Table 1).

Table 1 shows that slight changes in percent water result in much larger changes in the wet weight energy densities. Overall the wet weight energy densities of the seabird prey listed in Table 1 are 2.5 \times more variable (CV = 36.12) than the dry weight estimates (CV = 14.61). The wet weight energy densities of male, female (gravid and spent), and mixed capelin of different sexes, age-classes, and reproductive condition collected in June and July are about 5 \times more variable (CV = 12.72) than dry weight estimates (CV = 2.44, Table 1). Capelin collected from August to October had much higher wet and dry weight energy densities than fish collected in June and July. This variation represents a real seasonal change in fish composition due to lipid storage (Montevecchi and Piatt 1984). Throughout the year, lipid and water content are inversely related (Henderson *et al.* 1984; see also Harris and Hislop 1978). Thus, wet and dry weight energy density estimates are

influenced by physiological variations in lipid levels, whereas only the wet estimates are biased by dehydration effects.

During the breeding season alcids may forage at various distances from colonies (e.g., 10–60 km; Harris and Hislop 1978; Furness and Barrett 1985; Harris and Wanless 1985; Cairns *et al.* 1987), and puffins often spend considerable time circling in colony vicinities, especially when *Larus* gulls impose intense kleptoparasitic pressures, before delivering fish to chicks (personal observation). Our findings suggest that wet weight energy densities would be inflated from fresh levels if prey collected at breeding sites were subjected to wind- or sun-induced dehydration after prey capture and before bomb calorimetric or organic analyses. Similar arguments apply to water loss from samples, which occurs during the interval from collection until analysis (e.g., Ricklefs 1982).

The presentation of energy density in terms of dry weight circumvents problems associated with prey dehydration, and these data are undoubtedly the best to use for comparative purposes. Wet weight data are, however, biologically important. Analyses of fresh prey are needed to assess (i) transport costs associated with parental food delivery (an important energetics consideration in itself; see Ricklefs 1983), (ii) amount of moisture available to developing chicks which obtain their water solely from parental meals, and (iii) food consumption of chicks in the field, which is based on the wet weights of meals.

Taken together, these observations indicate a need for caution in interpreting data and comparisons. For example, Montevecchi *et al.* (1984) reported the organic composition and wet energy values of sand lance with low water contents. Compared with sand lance collected elsewhere, these fish had the highest wet weight energy densities, even though they had the lowest dry weight energy densities (Table 1). Harris and Hislop (1978) suggested that sprats and sand lance were selectively fed to puffin chicks because of their much higher energy densities (wet weight). However, the data in their Table VII suggested that, on a dry weight basis, most prey were energetically equivalent except for possibly sprat. Most of the fish they examined were from chick meal collections and exhibited low water contents (as low as 64% in sprat). The highest water content (82%) found in their study was from whiting collected by trawling. Coulson (1985) and Harris and Wanless (1985) estimated the energy consumption of murre chicks based on number of meals delivered and capelin energy densities calculated from fishery-collected specimens without distinguishing the sex of capelin consumed. It is clearly necessary to (i) measure the water content of prey delivered to chicks before extrapolating results and (ii) compare dry weight energy densities across studies.

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