Nutrient reserves of wintering American Black Ducks in the St. Lawrence estuary, Quebec

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Abstract

Recent studies in Maine have suggested that winter is energetically stressful for American Black Ducks *Anas rubripes* (hereafter called black ducks). In this study, we examined the dynamics of nutrient reserves in black ducks wintering in the St. Lawrence estuary, Quebec, which is a very harsh environment. Black ducks collected in October, December, and March were subjected to fat and protein analyses. Fat reserves increased from October to December and decreased from December to March. Protein reserves remained stable from October to December but decreased from December to March. Fat and protein reserves were similar in both sexes. Fat reserves of immatures were similar to those of adults, but protein reserves of immatures were smaller than those of adults. These comparisons were not confounded by differences in structural size, because we corrected for size using total body length as a covariable. Variations in nutrient reserves of black ducks in the St. Lawrence estuary were similar to those documented in captive black ducks and in several other species of waterfowl wintering in milder environments. Body weights of adult black ducks wintering in the St. Lawrence estuary were similar to those of captive black ducks. Our data are consistent with the hypothesis that energy reserves of wintering black ducks are regulated by an endogenous cycle rather than by environmental conditions.

Introduction

Winter has traditionally been viewed as a period of stress for birds in temperate regions. In waterfowl, decreases in body weight and fat reserves during winter have been taken as evidence that birds were metabolizing endogenous reserves to survive periods of stress (Hanson 1962; Peterson and Ellarson 1979; Kaminsky and Ryan 1981; Albright et al. 1983). Reduced food availability, short day length, and cold weather were commonly seen as stressful. Recent studies linking body weight to winter survival in waterfowl lent some support to this hypothesis (e.g., Haramis et al. 1986; Conroy et al. 1989).

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However, an alternative hypothesis is that winter decline in body weight and fat reserves is part of an endogenous cycle. Captive American Black Ducks *Anas rubripes* (hereafter referred to as black ducks), Mallards *Anas platyrhynchos*, and Canvasbacks *Aythya valisineria* fed *ad libitum* increased their body weight in fall, reached maximum weight in December, and lost weight in late winter (Hepp 1986; Perry et al. 1986; Pattenden and Boag 1989). This pattern is not unique to captive birds and has now been reported in several species of wild waterfowl (Reinecke et al. 1982; Whyte and Bolen 1984; Baldassarre et al. 1986; Miller 1986).

Among North American dabbling ducks, black ducks winter at the most northerly latitudes (Bellrose 1980). It is thus of interest to examine the dynamics of energy reserves in relation to habitat condition in this species. In the St. Lawrence estuary, Quebec, there is a wintering population of black ducks that has to cope with cold temperature (average minimum temperature in January is -20°C), extensive ice cover (>90% ice cover from mid-December to late March), short day length (<9 h), and limited natural food resources (mostly *Gammarus* spp. and *Littorina*) (Savard 1990; see also Jorde and Owen 1988). The objective of this study is to examine the dynamics of energy reserves (fat and protein) of black ducks wintering in the harsh environment of the St. Lawrence estuary.

Methods

Study area

Black ducks were collected from a population of 2000–4000 birds wintering on the St. Lawrence estuary at the mouth of the Saguenay River, Quebec (Reed and Bourget 1977; Lehoux et al. 1985; Savard 1990). Tidal currents and the flow of the Saguenay maintain patches of ice-free water and mudflats along the north shore of the St. Lawrence estuary throughout winter. In October and December, ducks were collected 7 km upriver from the mouth of the Saguenay near Baie-Ste-Catherine; in March, after the ducks had moved downriver, they were collected near Grandes-Bergeronnes, 20 km from the confluence of the Saguenay.

Collection of birds and carcass analyses

Black ducks were collected on 14–17 October (fall sample), on 12–14 December (early winter sample), and on 8 March (late winter sample). Birds were shot and frozen within a few hours. Birds were weighed to the nearest gram upon thawing. Culmen, tarsus length, mid-toe length (excluding toenail), sternal length, and bill width (at the posterior end of the nare) were measured with a caliper to the nearest 0.1 mm. Total body length

(from the tip of the bill to the tip of the longest tail feather) and wing length were measured to the nearest millimetre with a ruler. Inspection of the cloaca was used to sex and age the birds. Presence of the bursa of Fabricius was used as the criterion to classify birds as immatures (< 1 year old). All other birds were classified as adults.

Feathers were sheared and discarded, and the following organs were excised: the skin with adhering subcutaneous fat, the abdominal fat mass, the right breast muscles, the right leg muscles (including all muscles originating from either the femur or the tibiotarsus), and the gizzard. The remains of the bird after removal of these organs is referred to as the carcass. The digestive tract was emptied and the weight of its contents subtracted from fresh body weight to obtain ingesta-free body weight (hereafter referred to as body weight).

Abdominal fat was assumed to be 100% fat and was not subjected to further analysis. Muscles were chopped. The skin and carcass were ground and homogenized in a Hobart meat grinder while still frozen (to minimize fat losses). All tissues were freeze-dried to constant weight. The carcass and skin homogenates were subsampled by taking 100- and 75-g aliquots, respectively, for freeze-drying. Fat content of the dried tissues was determined by ether extraction using a Rafatec apparatus (Gauthier et al. 1984). Duplicate 1-g samples of each tissue were subjected to a 30-min extraction (except for skin, 1 h) with petroleum ether. A third extraction was performed if the first two differed by more than 3%. Total body fat was defined as the summation of the fat content in the skin (subcutaneous fat), breast and leg muscles, gizzard, carcass, and the abdominal fat mass.

Extractions were performed on only half of the ducks collected. Ducks were randomly selected, although we added a few very lean and very fat individuals to ensure that predictive equations would cover the range of values encountered. For the remaining birds, fat was estimated from water content using the regression equation between fat and water content established for each organ in specimens that were analyzed. These equations are presented in Table 1. The r^2 values show that the predictive equations did not estimate the fat content of the breast and gizzard as well as that of other organs. However, the bias in total body fat is slight, because these two organs accounted for less than 5% of total body fat.

The lean (i.e., fat-free) dry weight of the skin, breast and leg muscles, and gizzard was assumed to be 100% protein (Drobney 1982). Because the carcass included bones, mineral content was determined by ashing a 5-g dried sample. The lean dry weight (LDW) of the carcass minus the ash content was assumed to be 100% protein. Total body protein was defined as the summation of the LDW of the skin, breast and leg muscles, gizzard, and carcass, minus the ash content.

Analysis of covariance (ANCOVA) was used to analyze the variations in body fat and protein using total body length as a covariable (Blem 1984). Condition indices were tested using multiple regression analysis. Statistical analyses were performed using SAS (SAS Institute Inc.

1983) and Statgraphics (Statistical Graphics Corporation 1988).

Results
Correction for structural size
Structural size is often an important source of variation in energy reserves of birds, especially protein reserves (Johnson et al. 1985; Alisauskas and Ankney 1987). To identify a morphometric measurement that could account for as much variance as possible in structural size (Johnson et al. 1985; Moser and Rusch 1988), we correlated seven morphometric measurements with LDW of birds (note that LDW includes the mineral content of the bones, an important component of structural size). The strongest correlations were found with wing length and total body length, both variables explaining about 54% of the variance in LDW (Table 2). We chose to retain total body length as our index of structural size for the remaining analyses.

Variations in energy reserves
Variations in body weight, fat, and protein according to season, sex, and age were examined with ANCOVA using total body length as a covariable (Blem 1984). Values presented in Figures 1 and 2 are standardized for structural size by ANCOVA; original data are presented in Appendix 1, along with sample sizes. In all ANCOVA models, interactions among season, sex, and age were nonsignificant ($P > 0.05$, except in one case $P = 0.047$). Thus, main effects can be considered separately.

Table 1
Regression equations of fat content (%) on water content (%) in different organs of black ducks (N = 25)

Organ	r^2	Intercept	Slope	SE[a]	P
Skin	0.977	94.19	−1.344	2.728	<0.001
Breast muscles	0.688	47.12	−0.628	0.453	<0.001
Leg muscles	0.833	77.21	−1.013	1.055	<0.001
Gizzard	0.521	57.22	−0.758	1.142	<0.001
Carcass	0.828	70.53	−0.970	1.209	<0.001

[a] Standard error of estimate.

Table 2
Correlation between seven morphometric measurements and lean dry weight of black ducks (N = 51)

Measurement	r^2	P
Total body length	0.534	<0.001
Culmen	0.252	<0.001
Bill width	0.464	<0.001
Tarsus length	0.026	0.082
Mid-toe length	0.130	0.002
Sternal length	0.419	<0.001
Wing length	0.542	<0.001

Figure 1
Body weight, total body fat, subcutaneous fat, and abdominal fat of black ducks according to season, sex, and age. Mean weights are standardized for structural size using total body length as a covariable in the ANCOVA. Means with the same letter did not differ significantly at the 0.05 level (mean ± least square difference).
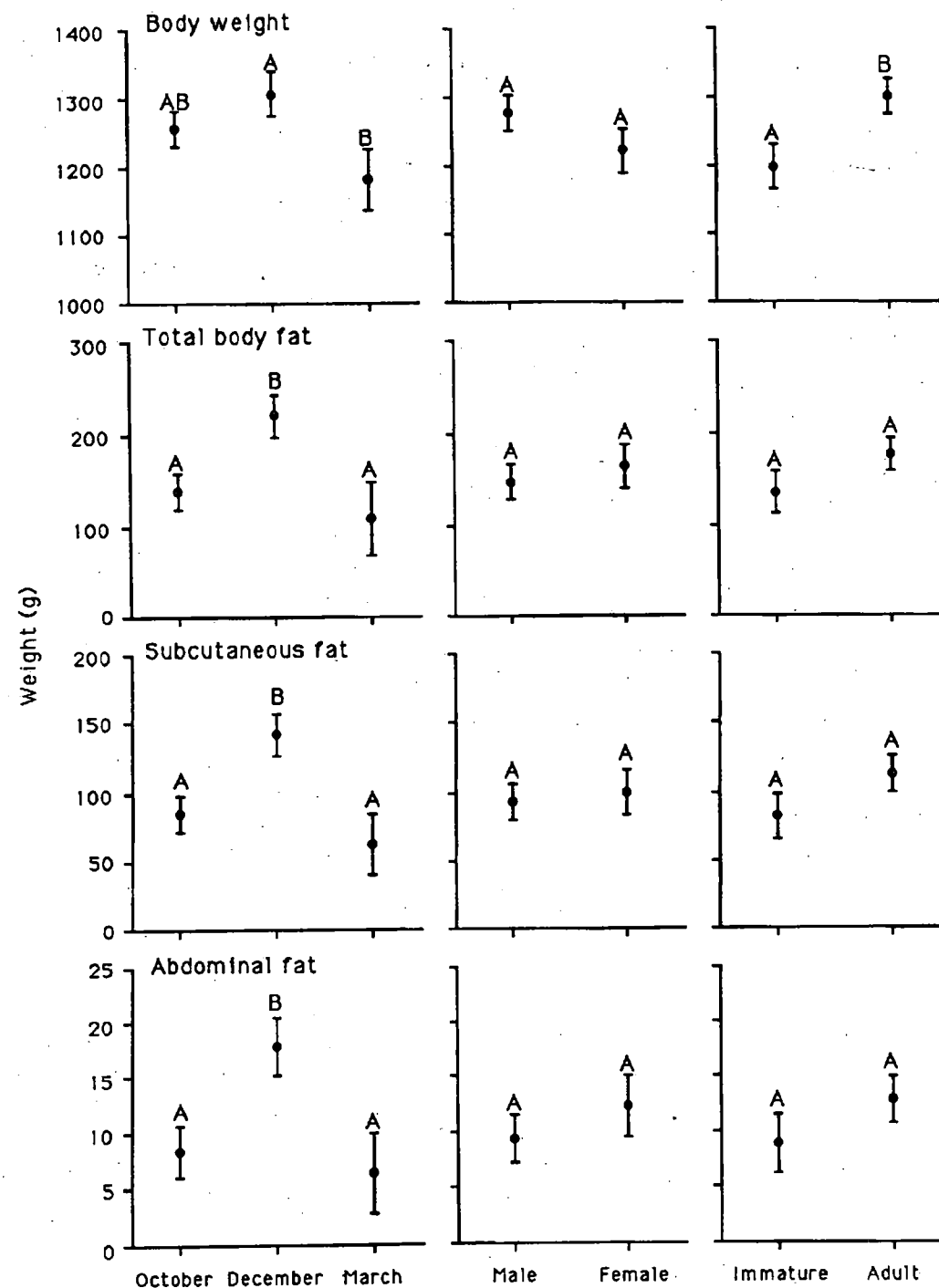
Figure 2
Total body protein, breast protein, leg protein, and gizzard protein of black ducks according to season, sex, and age. Mean weights are standardized for structural size using total body length as a covariable in the ANCOVA. Means with the same letter did not differ significantly at the 0.05 level (mean ± least square difference).
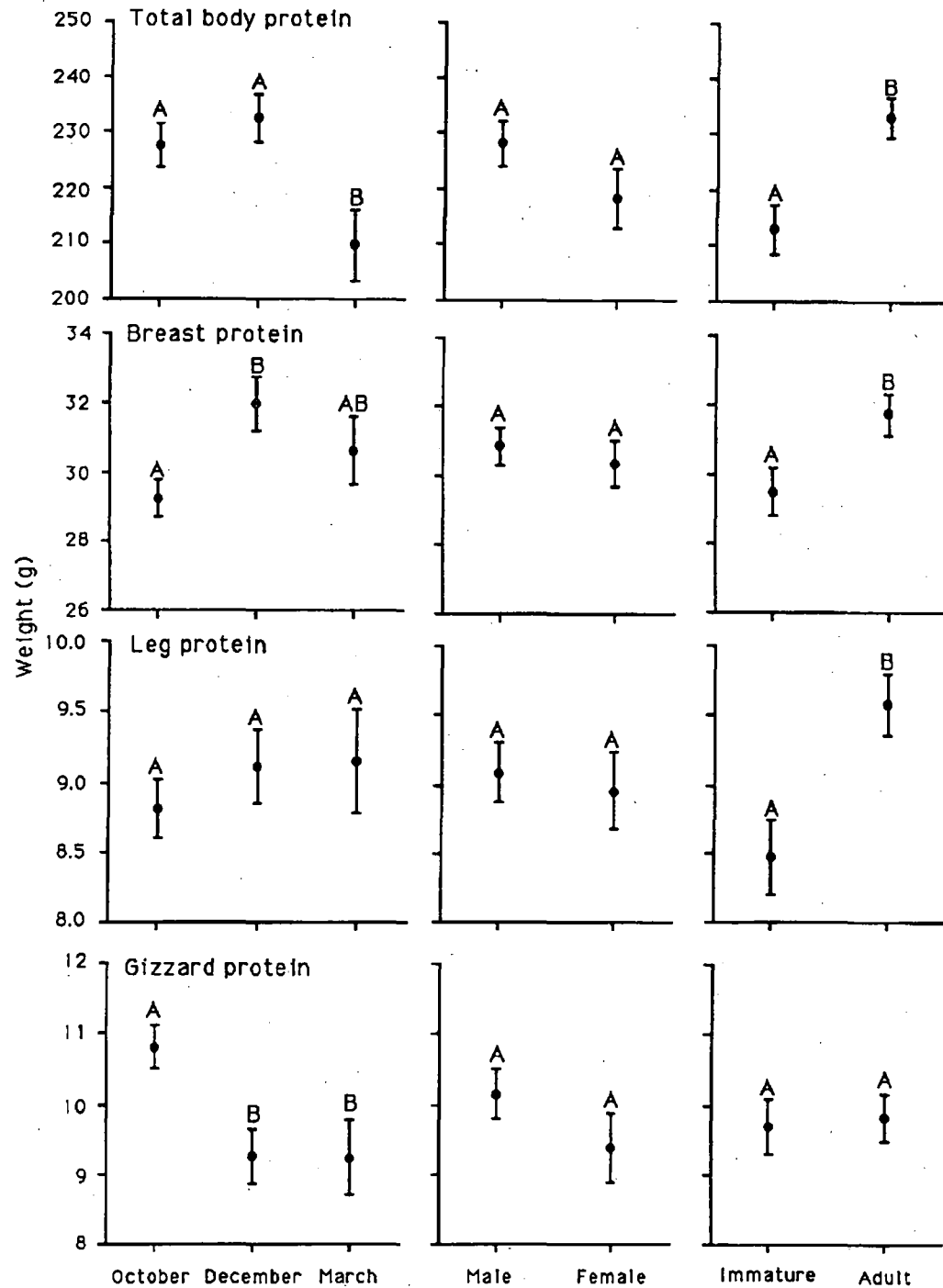

Table 3
Analysis of covariance of body weight, total body fat, subcutaneous fat, and abdominal fat according to season, sex, and age for wintering black ducks, using total body length as a covariable

Variable	Source of variation[a]	F	P	df
Body weight	Full model	9.48	<0.001	12
	Season	2.72	0.079	2
	Sex	1.60	0.214	1
	Age	6.01	0.019	1
	Body length	15.21	<0.001	1
Total body fat	Full model	5.70	<0.001	12
	Season	5.49	0.008	2
	Sex	0.30	0.585	1
	Age	1.85	0.181	1
	Body length	6.97	0.012	1
Subcutaneous fat	Full model	5.74	<0.001	12
	Season	5.57	0.008	2
	Sex	0.11	0.740	1
	Age	2.63	0.156	1
	Body length	4.93	0.035	1
Abdominal fat	Full model	3.76	<0.001	12
	Season	4.82	0.014	2
	Sex	0.65	0.426	1
	Age	1.33	0.256	1
	Body length	4.11	0.050	1

[a] All interactions (season × sex, season × age, sex × age, season × sex × age) were nonsignificant (P > 0.05), except season × sex for subcutaneous fat (P = 0.047).

Table 4
Analysis of covariance of total body protein, breast protein, leg protein, and gizzard protein according to season, sex, and age for wintering black ducks, using total body length as a covariable

Variable	Source of variation[a]	F	P	df
Total body protein	Full model	10.25	<0.001	12
	Season	4.38	0.020	2
	Sex	2.40	0.129	1
	Age	11.00	0.002	1
	Body length	13.62	<0.001	1
Breast protein	Full model	10.39	<0.001	12
	Season	3.88	0.029	2
	Sex	0.26	0.611	1
	Age	5.45	0.025	1
	Body length	12.37	0.001	1
Leg protein	Full model	5.73	<0.001	12
	Season	0.48	0.620	2
	Sex	0.11	0.740	1
	Age	9.80	0.003	1
	Body length	2.33	0.135	1
Gizzard protein	Full model	2.43	0.019	12
	Season	5.43	0.008	2
	Sex	1.91	0.175	1
	Age	0.08	0.778	1
	Body length	3.21	0.081	1

[a] All interactions (season × sex, season × age, sex × age, season × sex × age) were nonsignificant (P > 0.05).

Body weight. Black ducks were significantly heavier in December than in March (Fig. 1). However, the overall effect of season on body weight was not significant in the ANCOVA (P = 0.08) (Table 3). Body weight did not differ between sexes but differed among age classes (Table 3), immatures being significantly lighter than adult birds (Fig. 1).

Fat reserves. Black ducks collected in December were significantly fatter than those collected in October or March (Table 3, Fig. 1). Body fat declined by 51% between December and March. Fat levels of ducks in October were similar to those of ducks in March. There were no significant differences in total body fat, subcutaneous fat, or abdominal fat between sexes or between immatures and adults (Table 3, Fig. 1).

Protein reserves. Body protein of ducks was significantly lower in March than in October or December (Table 4, Fig. 2). Ducks collected in March had 10% less protein than those collected in December. Seasonal variation in protein of the breast, leg, and gizzard differed from the pattern observed for total body protein. Breast protein increased significantly between October and December and tended to decrease between December and March, although the difference was not significant (Fig. 2). Leg protein did not vary significantly among seasons (Table 4), although it tended to increase between October and December. Gizzard protein decreased significantly between October and December (Table 4, Fig. 2) but remained constant between December and March.

Protein did not differ between sexes for any of the muscles (Table 4). Total and gizzard protein tended to be higher in males but not significantly so (Fig. 2). Protein level differed significantly between age classes for all muscles except gizzard (Table 4), being higher in adult birds than in immatures (Fig. 2).

Condition indices
We attempted to predict body fat and total protein using external body measurements. Body weight and morphometric measurements that correlated significantly with LDW (i.e., all measurements except tarsus length; Table 2) were entered as independent variables in the multiple regressions. Males and females were analyzed

Table 5
Multiple regression of total body fat (g) and protein (g) on body measurements (mm) of black ducks[a,b]

Dependent variable	R^2	SE	Predictive equation
Male			
Total fat	0.692	62.3	Y = 0.6381(BW) − 673.38
Total fat/LDW	0.566	0.238	Y = 0.00186(BW) − 1.8392
Total fat/TL	0.714	0.103	Y = 0.00117(BW) − 0.00210(TL)
Total protein	0.895	7.30	Y = 0.1039(BW) + 8.6601(BIW) + 0.1692(TL) − 191.50
Total protein/TL	0.866	0.0125	Y = 0.000177(BW) − 0.000430(TL) + 0.01523(BIW)
Female			
Total fat	0.819	37.1	Y = 0.5507(BW) − 488.39
Total fat/LDW	0.719	0.166	Y = 0.00186(BW) − 1.5474
Total fat/TL	0.779	0.070	Y = 0.000924(BW) − 0.8009
Total protein	0.903	6.54	Y = 0.1301(BW) + 1.6565(CU)
Total protein/TL	0.735	0.0136	Y = 0.000219(BW) − 0.000491(TL) + 0.3985

[a] Only significant variables (P < 0.05) are included, and they are presented in decreasing order of significance in the predictive equations.
[b] BW = body weight, TL = total body length, LDW = lean dry weight, BIW = bill width, CU = culmen.

separately, because the parameters and the explanatory power of the predictive equations differed between sexes (Table 5).

Fat reserves. For both sexes, body weight was the only variable entered in the model to significantly predict total fat (Table 5). None of the morphometric measurements significantly improved the model. Body weight alone explained 82% of the variation in total fat in females but only 69% in males.

Johnson et al. (1985) and Moser and Rusch (1988) suggested the use of condition indices scaled for structural size instead of total fat in predictive equations based on external measurements. We derived two indices: total fat/LDW (the lipid index of Johnson et al. 1985) and total fat/total body length (TL), the variable we retained as our index of structural size in the previous analysis. For both sexes, body weight was again the best predictor of total fat/LDW (Table 5). However, the percentage of variation explained by the model was lower for total fat/LDW than for total fat. For total fat/TL, body weight alone was also the best predictor in females. In males, however, the model entered total length in addition to body weight in the predictive equation. In females, the predictive equation explained slightly less variance in total fat/TL than in total fat, whereas the opposite was true in males.

In several species of waterfowl, abdominal fat is frequently used as a predictor of body fat in dead birds (Wishart 1979; Gauthier and Bédard 1985; Hohman and Taylor 1986). To test its usefulness as a predictor of body fat in black ducks, we substituted abdominal fat for body weight in the multiple regression analysis. For both sexes, abdominal fat was a good predictor of total fat and total fat/TL (Table 6). In the predictive equation of total fat/TL

for females, culmen was also found to be significant and was included in the model. As we found for body weight, more variation in total fat was explained by abdominal fat in females (93%) than in males (74%).

Protein reserves. For males, body weight, total length, and bill width were entered by the model in the predictive equation of total protein, whereas body weight and culmen were the variables entered for females (Table 5). For total protein/TL, the same variables were entered in the model for males, but total length was entered in the model instead of culmen for females. For males, the predictive equations of total protein and total protein/TL both explained over 86% of the variation. For females, however, the equations explained 90% of the variation in total protein but only 74% in total protein/TL.

Discussion

Our sample sizes are small, which reflects the difficulties involved in collecting ducks in the St. Lawrence estuary in winter. Despite the small samples, changes in energy reserves were consistent for both sexes and age classes during winter. For instance, the increase in fat reserves from October to December and the decrease from December to March were observed in both sexes and age classes (Appendix 1). This was also reflected by the lack of significant interactions in the ANCOVA (Tables 3 and 4). We thus feel confident that the patterns we observed are real.

Table 6
Multiple regression of total body fat (g) on abdominal fat (g) of black ducks[a,b]

Dependent variable	R^2	SE	Predictive equation
Male			
Total fat	0.736	57.1	Y = 8.469(AF) + 88.50
Total fat/TL	0.735	0.098	Y = 0.0145(AF) + 0.1534
Female			
Total fat	0.925	25.46	Y = 8.960(AF) + 57.62
Total fat/TL	0.935	0.043	Y = 0.0159(AF) − 0.0091(CU) + 0.5796

[a] Only significant variables (P < 0.05) are included, and they are presented in decreasing order of significance in the predictive equations.
[b] AF = abdominal fat, CU = culmen, TL = total body length.

Correction for structural size

We attempted to eliminate variation associated with structural size from the analysis. The goal was to find an external measurement highly correlated to structural size that could be used to correct for size differences. Moser and Rusch (1988) argued that skeletal volume was the best measure of "size" in birds. LDW has also been used as an index of structural size (Bailey 1979; Johnson et al. 1985). Because skeletal volume is difficult to obtain, we used LDW.

There are at least two sources of variation in LDW: variation in muscle and bone mass due to structural size, and variation in muscle mass due to change in protein reserves. The unexplained variance in correlations between morphometry and LDW is presumably associated with variation in protein reserves. We found that wing length and total body length explained similar amounts of variance in LDW. For Mallards wintering in the United States, Ringelman and Szymczak (1985) reported that wing length was the best index of structural size. However, we chose total body length to correct for size differences because it is a good index of structural size in several other species of ducks (Bailey 1979; Wishart 1979; Chappell and Titman 1983). Moser and Rusch (1988) also found that total body length was highly correlated with skeletal volume in Canada Geese *Branta canadensis*.

The absolute weights of fat and protein in an individual are commonly referred to as fat and protein reserves. However, we prefer to define "reserves" as the standardized weights of fat and protein obtained from the ANCOVA after correcting for structural size. The importance of the size correction can be illustrated by performing an analysis of variance on the fat and protein data without using total body length as a covariable. When this was done, adults carried significantly more fat than immatures and males significantly more protein than females. These differences, however, disappeared in the ANCOVA (Tables 3 and 4), indicating that fat reserves did

not differ among ages and protein reserves did not differ among sexes after we corrected for structural size.

Condition indices

Body weight is a good predictor of body fat in some species (Chappell and Titman 1983) but not in others (Wishart 1979; Gauthier and Bédard 1985; Hohman and Taylor 1986). In wintering Mallards, body weight accounted for only 46% of the variation in body fat (Ringelman and Szymczak 1985). In black ducks, body weight was a good estimator of fat reserves, explaining 69% of the variance in males and 82% in females (Table 5). The correlation between body weight and fat was probably slightly inflated, because changes in body protein paralleled changes in fat (Figs. 1 and 2). Poorer correlations would be expected if protein levels were stable or changed in a direction opposite to fat levels. Thus, one should be cautious in applying predictive equations of fat during periods of the annual cycle when such situations are suspected to occur.

All predictive equations for protein reserves combined body weight with one or two morphometric measurements (Table 5). This is not surprising, given the influence of structural size on protein mass (see above). The equations for protein reserves generally performed better than did those for fat reserves.

Johnson et al. (1985) suggested that it is better to derive predictive equations for condition indices (i.e., ratios that account for structural size) rather than for absolute weight when comparing energy reserves among individuals. We derived such equations using LDW and total body length (Tables 5 and 6). These equations, however, often had less predictive power than those derived for absolute weight. As an alternative, we recommend the use of predictive equations to estimate absolute weight of fat or protein in individual birds, but using ANCOVA, correcting for structural size with total body length as a covariable, to compare among individuals (see also Blem 1984).

Dynamics of energy reserves

Seasonal variations in body weight and nutrient reserves of black ducks wintering in the St. Lawrence estuary conformed to the general pattern reported by Hepp (1986) for captive black ducks. Body weight tended to increase from October to December and decrease from December to March. Variations in body weight resulted from variations in both fat and protein reserves (Figs. 1 and 2).

Total protein reserves of adults were 20 g higher than those of immatures (Fig. 2). Twenty grams of protein is equivalent to 81.6 g of fresh muscle mass, assuming a water content of 75.5% for fat-free muscles (derived from equations in Table 1). Thus, 80% of the 102-g difference in body weight between adults and immatures (Fig. 1) was due to difference in muscle mass. This difference may have resulted from incomplete growth of immatures in their first winter.

If wintering in northern latitudes is energetically stressful for black ducks, as suggested by Albright et al.

(1983), black ducks from the St. Lawrence estuary should have lower body weights than captive ducks maintained under less stressful conditions. The mean body weight of adult black ducks from the St. Lawrence estuary was intermediate between mean body weights of captive adults fed a restricted diet and those fed *ad libitum* during corresponding time periods (data from Hepp 1986). In March, adult males from the St. Lawrence tended to be heavier than captive adults fed *ad libitum*. Data were too limited for a meaningful comparison among immatures. Apparently, adult black ducks wintering in the St. Lawrence were not energetically stressed by their environment.

Variations in body weights that we observed (fall increase and winter decline) are similar to those reported in captive Mallards and Canvasbacks (Perry et al. 1986; Pattenden and Boag 1989) and in wild Mallards, Green-winged Teals *Anas crecca*, and Northern Pintails *Anas acuta* (Whyte and Bolen 1984; Baldassarre et al. 1986; Miller 1986). Yet these species winter under a variety of environmental conditions, ranging from mild to very harsh winters. This similarity suggests that the dynamics of energy reserves in wintering waterfowl are primarily regulated by an endogenous cycle rather than by environmental conditions (Hepp 1986; Perry et al. 1986).

Several factors could account for such an energy cycle during winter. First, loss of body mass could be adaptive (e.g., by reducing flight cost) and could result from voluntary anorexia (King and Murphy 1985). Second, behavioural or physiological processes occurring in winter may be more important than previously thought in shaping the dynamics of body reserves. Courtship and pair maintenance activities may impose feeding constraints on wintering ducks (Hepp and Hair 1984). In Northern Pintails, Miller (1986) found that the winter decline in body weight was associated with increased courtship activity. Prebasic moult, a phenomenon recently examined by Heitmeyer (1987) in Mallards but still largely unknown in other ducks, is another potentially important constraint for wintering ducks.

All this evidence suggests that winter may not always be energetically stressful for ducks, even when they are wintering under harsh conditions. King and Murphy (1985) warned about concluding that an animal is nutritionally stressed without a detailed knowledge of the nutrient demand. Biological processes taking place during the winter period may be more important in determining the dynamics of energy reserves of waterfowl than environmental conditions, as is the case during the breeding season.

References
Albright, J.J.; Owen, Jr., R.B.; Corr, P.O. 1983. The effects of winter weather on the behavior and energy reserves of black ducks in Maine. Trans. Northeast Fish Wildl. Conf. 40:118–128.

Alisauskas, R.T.; Ankney, C.D. 1987. Age-related variation in the nutrient reserves of American coott (*Fulica americana*). Can. J. Zool. 65:2417–2420.

Bailey, R.O. 1979. Methods of estimating total lipid content in the redhead duck (*Aythya americana*) and an evaluation of condition indices. Can. J. Zool. 57:1830–1833.

Baldassarre, G.A.; Whyte, R.J.; Bolen, E.G. 1986. Body weight and carcass composition of nonbreeding green-winged teal on the southern high plains of Texas. J. Wildl. Manage. 50:420–426.

Bellrose, F.C. 1980. Ducks, geese and swans of North America. Stackpole Press, Harrisburg, Pa.

Blem, C.R. 1984. Ratios in avian physiology. Auk 101:153–155.

Chappell, W.A.; Titman, R.D. 1983. Estimating reserve lipids in greater scaup (*Aythya marila*) and lesser scaup (*Aythya affinis*). Can. J. Zool. 61:35–38.

Conroy, M.J.; Costanzo, G.R.; Moser, E.B. 1989. Winter survival of female black ducks on the Atlantic coast. J. Wildl. Manage. 53:99–109.

Drobney, R.D. 1982. Body weight and composition changes and adaptations for breeding in wood ducks. Condor 84:300–305.

Gauthier, G.; Bédard, J. 1985. Fat reserves and condition indices in greater snow geese. Can. J. Zool. 63:331–333.

Gauthier, G.; Bédard, J.; Huot, J.; Bédard, Y. 1984. Spring accumulation of fat by greater snow geese in two staging habitats. Condor 86:192–199.

Hanson, H.C. 1962. The dynamics of condition factors in Canada geese and their relation to seasonal stresses. Arct. Inst. North Am. Tech. Pap. No. 12.

Haramis, G.M.; Nichols, J.D.; Pollock, K.N.; Hines, J.E. 1986. The relationship between body mass and survival of wintering canvasback. Auk 103:506–514.

Heitmeyer, M.E. 1987. The prebasic molt and basic plumage of female mallards (*Anas platyrhynchos*). Can. J. Zool. 65:2248–2261.

Hepp, G.R. 1986. Effects of body weight and age on the time of pairing of American black ducks. Auk 103:477–484.

Hepp, G.R.; Hair, J.D. 1984. Dominance in wintering waterfowl (Anatini): effects on distribution of sexes. Condor 86:251–257.

Hohman, W.L.; Taylor, T.S. 1986. Indices of fat and protein for ring-necked ducks. J. Wildl. Manage. 50:209–211.

Johnson, D.H.; Krapu, G.L.; Reinecke, K.J.; Jorde, D.G. 1985. An evaluation of condition indices for birds. J. Wildl. Manage. 49:569–575.

Jorde, D.G.; Owen, Jr., R.B. 1988. Efficiency of nutrient use by American black ducks wintering in Maine. J. Wildl. Manage. 52:209–214.

Kaminsky, S.; Ryan, R.A. 1981. Weight changes in redheads and canvasbacks during the winter. N.Y. Fish Game J. 28:215–222.

King, J.R.; Murphy, M.E. 1985. Periods of nutritional stress in the annual cycles of endotherms: fact or fiction? Am. Zool. 25:955–964.

Lehoux, D.; Bourget, A.; Dupuis, P.; Rosa, J. 1985. La sauvagine dans le système du St-Laurent. Unpubl. report, Can. Wildl. Serv., Quebec Region, Québec.

Miller, M.R. 1986. Northern pintail body condition during wet and dry winters in the Sacramento valley, California. J. Wildl. Manage. 50:189–198.

Moser, T.J.; Rusch, D.H. 1988. Indices of structural size and condition of Canada geese. J. Wildl. Manage. 52:202–208.

Pattenden, R.K.; Boag, D.A. 1989. Effects of body mass on courtship, pairing, and reproduction in captive mallards. Can. J. Zool. 67:495–501.

Perry, M.C.; Kuenzel, W.J.; Williams, B.K.; Serafin, J.A. 1986. Influence of nutrients on feed intake and condition of captive canvasback in winter. J. Wildl. Manage. 50:427–434.

Peterson, S.R.; Ellarson, R.S. 1979. Changes in oldsquaw carcass weight. Wilson Bull. 91:288–300.

Reed, A.; Bourget, A. 1977. Distribution and abundance of waterfowl wintering in southern Québec. Can. Field-Nat. 91:1–7.

Reinecke, K.J.; Stone, T.L.; Owen, Jr., R.B. 1982. Seasonal carcass composition and energy balance of female black ducks in Maine. Condor 84:420–426.

Ringelman, J.K.; Szymczak, M.R. 1985. A physiological condition index for wintering mallards. J. Wildl. Manage. 49:564–568.

SAS Institute Inc. 1983. SAS user's guide: statistics. Cary, N.C.

Savard, J.-P.L. 1990. Population de sauvagine hivernant dans l'estuaire du Saint-Laurent: écologie, distribution et abondance. Can. Wildl. Serv. Tech. Rep. No. 89, Quebec Region, Québec.

Statistical Graphics Corporation. 1988. Statgraphics. Rockville, Md.

Whyte, R.J.; Bolen, E.G. 1984. Variation in winter fat depots and condition indices of mallards. J. Wildl. Manage. 48:1370–1373.

Wishart, R.A. 1979. Indices of structural size and condition of American wigeon (*Anas americana*). Can. J. Zool. 57:2369–2374.

Appendix 1
Body weight (g), fat (g), and protein (g) of black ducks wintering in the St. Lawrence estuary according to sex, age, and month of collection (mean ± SE)

	N	Body weight[a]	Total body fat	Subcu- taneous fat	Abdominal fat	Total body protein	Breast protein	Leg protein	Gizzard protein
Mid-October									
Male									
Immature	7	1292±25	130±23	77±15	5.5±2.4	232±2	30.3±0.5	8.67±0.22	11.16±0.64
Adult	2	1315±133	99±65	60±46	5.7±4.7	243±13	29.8±1.4	9.14±0.32	12.51±2.01
Female									
Immature	9	1118±40	129±20	82±13	7.3±2.0	204±5	26.4±0.8	8.25±0.18	9.36±0.53
Adult	3	1164±80	133±48	82±35	9.2±5.7	211±9	37.6±2.7	8.74±0.14	9.43±0.06
Mid-December									
Male									
Immature	4	1326±29	232±27	150±18	19.5±4.5	229±4	31.7±1.1	8.68±0.28	8.71±0.29
Adult	11	1504±42	306±31	203±21	22.6±3.2	258±6	34.7±0.9	9.99±0.30	10.11±0.44
Female									
Immature	1	1170	127	68	10.4	224	31.5	8.75	9.34
Adult	5	1301±53	254±32	165±20	21.4±4.1	227±9	31.3±1.1	9.26±0.32	9.27±0.28
Early March									
Male									
Immature	1	1073	67	38	1.7	188	26.6	7.50	8.67
Adult	6	1351±42	150±27	84±17	9.6±3.4	245±7	36.2±0.8	11.21±0.51	8.71±0.29
Female									
Immature	1	1022	43	23	0.8	177	26.5	8.37	8.67
Adult	1	1288	179	109	13.5	230	33.3	9.55	8.77

[a] Fresh (field) body weight less weight of ingesta.