

SEASONAL CARCASS COMPOSITION AND ENERGY BALANCE OF FEMALE BLACK DUCKS IN MAINE

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ABSTRACT.—Female Black Ducks (*Anas rubripes*) collected in Maine during the summer, fall, and winter of 1974–1976 showed significant seasonal variation in body weight, nonfat dry weight, gizzard and pectoral muscle weight, and fat, moisture, and protein content. Variation of body weight within and among seasons was correlated more strongly with carcass protein content, and with fat content during seasons of heavy lipid deposition, than with three structural size variables (culmen, tarsus, and sternum). Regression equations including fat and protein as independent variables accounted for 80–90% of the annual and seasonal variation in body weight; structural size variables alone accounted for less than 30%.

Immature females averaged 54 and 99 g lighter, and carried 54 and 59 g less fat than adults during the fall and winter. Ducks of both age classes lost weight in December and January. Adult and immature females metabolized 59 and 64 g of fat and 17 and 25 g of protein in winter compared with 46 g of fat during the nesting season. Nutrient reserves are thus equally as important for the winter survival of these birds as for successful reproduction. Seasonal changes in carcass composition suggest that (1) fat deposited in late fall provides an energy reserve during winter, (2) a reduction in lean weight during winter may lower daily energy requirements and increase the effective amount of energy reserves, and (3) declining body weights during late winter may be an endogenous rhythm that reflects a shift in the expected benefits of an energy reserve compared to the costs of carrying additional weight.

The composition of the carcass in birds was first analyzed in migratory passerines (e.g., Connell et al. 1960). These studies indicated that lean body weight in healthy birds was relatively constant, and that seasonal variations in weight depended on fat stores (Odum et al. 1964). Lipid deposition was attributed primarily to either the energy demands of long-range migratory flight (Odum et al. 1961) or overnight survival during cold weather (Ken-deigh and Blem 1974); the contribution of stored nutrients during reproduction received less attention (e.g., Ricklefs 1974:261–265).

More recently, however, field studies of Snow Geese (*Anser caerulescens*; Ankney and MacInnes 1978), Common Eiders (*Somateria mollissima*; Korschgen 1977), Maccoa Ducks (*Oxyura maccoa*; Siegfried et al. 1976), Wood Ducks (*Aix sponsa*; Drobney 1980), and Canada Geese (*Branta canadensis*; Raveling 1979) have demonstrated the seasonal variability of lean body weight and the importance of energy reserves during reproduction in waterfowl. We chose the Black Duck (*Anas rubripes*) for our work because no comparable data were available for the dabbling ducks, and because the species is present in Maine throughout the year.

The study was restricted to females because of their high nutrient requirements during the breeding season (King 1973). Our objectives were to (1) detect seasonal changes in female body weight and composition, (2) identify the carcass components associated with weight changes, and (3) relate changes in female energy balance to the energy requirements of winter weather and reproduction.

STUDY AREA AND METHODS

Nesting females were collected between April and August 1974–1976 from beaver (*Castor canadensis*) ponds and meadow streams within 55 km of Orono, Maine. These inland wetlands are classified by Golet and Larson (1974) as deep and shallow marshes associated with seasonal flats, shrub swamps, and bogs. The fall sample was obtained from cooperating hunters during October, November, and early December 1974–1975; these birds came from the freshwater sites described above and from intertidal habitats (see Hartman 1963) in Penobscot and Frenchmans bays, Maine. The winter collection was made during banding operations at Frenchmans Bay in late January and early February 1976. The winter sample

was random with respect to age, but not entirely random with respect to weight. A few birds weighing less than 800 g or more than 1,100 g were included in the sample to determine carcass composition at the extremes of body weight.

In the laboratory, females collected during the nesting season were classified as prelaying, laying, or postlaying (Reinecke and Owen 1980). All birds described as molting were flightless when collected. We used the presence of a cloacal bursa to identify immature birds (less than one year old) in the fall and winter samples. Each bird was weighed to the nearest gram, and then dissected to obtain weights for the flight muscles (*Mm. pectoralis*, *supracoracoideus*, *coracobrachialis*), gizzard, and gonads. In the fall of 1975 we began measuring tarsus, culmen, and sternum lengths to the nearest 0.1 mm. Prior to chemical analysis, each bird was plucked, re-weighed, and frozen. The frozen carcasses were sectioned with a meat saw and homogenized. Duplicate 100-g subsamples were taken to the Maine Agricultural Experiment Station for analyses of protein and lipid content. A second set of duplicate 100-g subsamples was dried for 48 h at 50–55°C to determine moisture content. The residual dry matter was ground in a Wiley mill or mortar and pestle, and a 3-g subsample from each was ashed in a muffle furnace.

We could not obtain complete data for each specimen. Sample sizes are, therefore, variable, and are indicated where appropriate in the text and tables. The complete set of data on carcass composition is included as an Appendix for further reference.

RESULTS AND DISCUSSION

SEASONAL CHANGES IN BODY WEIGHT AND COMPOSITION

Body weights of female Black Ducks varied significantly during the year (1-way ANOVA, $P < 0.001$), but the seasonal means overlapped considerably (Fig. 1). The annual weight curve was approximately bimodal and similar to that of the Mallard (*Anas platyrhynchos*; Folk et al. 1966). The minimum mean weight during the annual cycle was 85% of the maximum mean compared with 86% for the Mallard (Folk et al. 1966). Seasonal weight losses of 40–50% have been reported for female Snow Geese (Ankney and MacInnes 1978) and Common Eiders (Milne 1976, Korschgen 1977), but are apparently not typical of healthy dabbling ducks. Seasonal changes in nonfat dry weight were also significant ($P < 0.05$), and paralleled changes in body weight (Fig. 1). Thus, weight variation in the Black Duck cannot be attributed solely to fluctuating lipid stores.

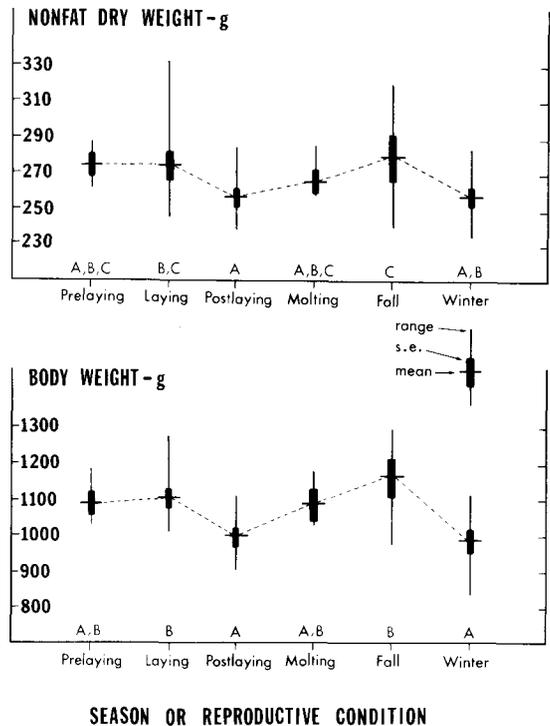


FIGURE 1. Seasonal variation of body weight and nonfat dry weight in adult female Black Ducks. Letters designate sets of means not significantly different from each other (1-way ANOVA and Duncan's Test, $P < 0.05$).

Gizzards weighed the least during laying and postlaying, and flight muscles least during wing molt and winter (Fig. 2). Similar relationships have been noted in field studies of other waterfowl species. Keith (1961) and Korschgen (1977) described gizzard atrophy in nesting ducks. Flight muscles lose weight during wing molt in the Common Eider (Milne 1976, Korschgen 1977), Canada Goose (Raveling 1979), and Snow Goose (Ankney 1979). Gizzard and flight muscle weight losses have been attributed to active protein mobilization (Korschgen 1977) and to atrophy (Ankney 1977), but neither hypothesis has been adequately tested. Recent studies of the Red-billed Quelea (*Quelea quelea*; Kendall et al. 1973, Jones and Ward 1976), suggest that at least some of the gizzard and pectoral muscle weight losses in waterfowl are due to the redistribution of amino acids for egg and feather production, or muscle development.

Figure 3 illustrates annual variation in the carcass composition of female Black Ducks. Seasonal changes in ash content were not significant ($P > 0.10$). Body water was strongly and positively related to protein content, but independent of body fat. For example, when the data for all seasons were pooled, the product-moment correlation (r) of protein and water

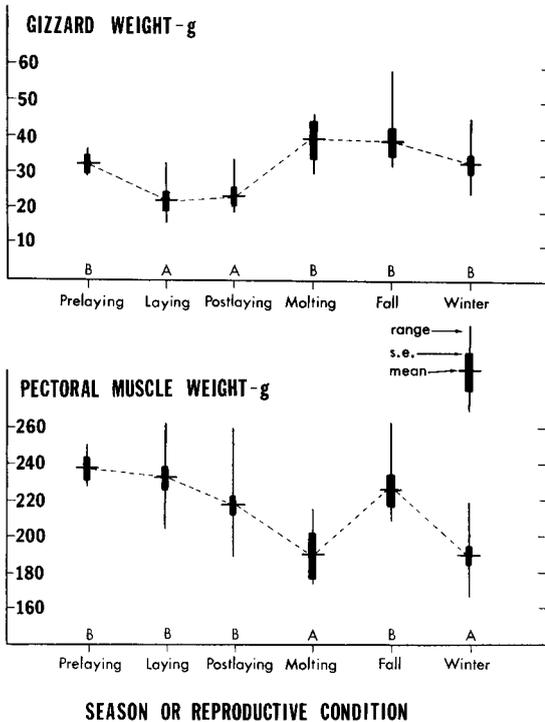


FIGURE 2. Seasonal variation of gizzard and pectoral muscle weight in adult female Black Ducks. Letters designate sets of means not significantly different from each other (1-way ANOVA and Duncan's Test, $P < 0.05$).

was 0.77 ($P < 0.001$); fat and water were, however, not related ($r = 0.22$; $P > 0.10$). When we considered seasonal samples separately, the relationships were similar, that is, protein and water highly correlated ($r = 0.73-0.91$; $P < 0.005$), and fat and water unrelated ($P > 0.25$). Body fat and water content are generally independent in birds, unlike mammals (Blem 1976).

Seasonal changes in the protein content of female Black Ducks did not exceed 12%, and were small compared to the 30+% reduction in body protein between laying and late incubation in the female Common Eider (Korschgen 1977). The protein content of laying females was slightly but not significantly higher than that of the prelaying and postlaying birds (Fig. 3). Any increases in protein content at this time were probably due to growth of the ovary and oviduct because gizzard weights decreased and the flight muscles were unchanged during the interval (Fig. 2).

Lipid reserves were highest during the fall (Fig. 3; $P < 0.05$) when adult females averaged 187 g of body fat (Appendix). Several individuals collected late in the fall carried as much as 250 g of fat. During the period of negative energy balance within the breeding season (prelaying vs. postlaying), approximately 46 g of fat were metabolized (Appen-

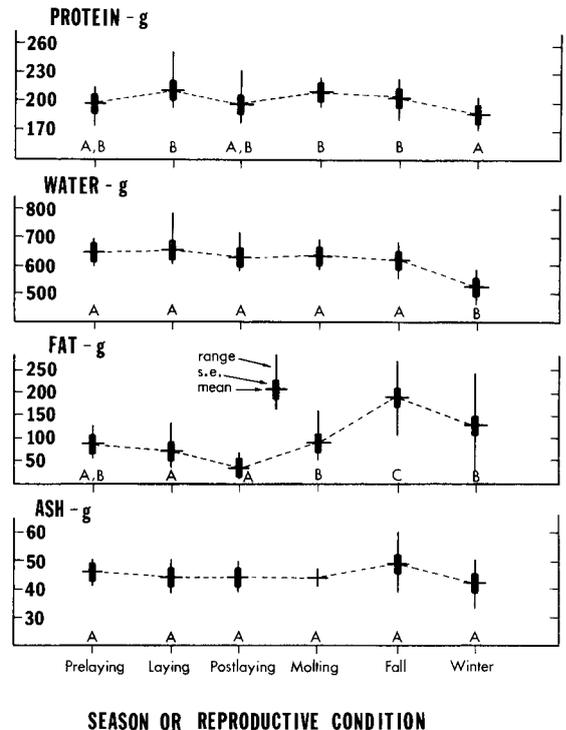


FIGURE 3. Seasonal variation in composition of the featherless carcass of adult female Black Ducks. Letters designate sets of means not significantly different from each other (1-way ANOVA and Duncan's Test, $P < 0.05$).

dix). This estimate of fat mobilization by breeding females is, however, based on a small sample of prelaying hens ($n = 4$), and does not separate yearling and adult birds (Krapu and Doty 1979). Drobney (1980) and Krapu (1981) have shown that Wood Duck and Mallard females metabolize about 100 g of body fat while nesting.

FACTORS AFFECTING WEIGHT VARIATION WITHIN AND AMONG SEASONS

The effect of structural size. We considered the possibility that the weight differences among the seasons (Fig. 1) were a function of structural size, because Palmer (1976) described north-south clinal variation of body size in the Black Duck. We assumed that the fall and winter collections would contain more northern birds (Geis et al. 1971), and we compared the culmen, tarsus, and sternum measurements of the fall and winter sample with those of birds from spring and summer. The differences between the mean sternum and culmen lengths were not significant ($P > 0.5$, $P > 0.2$, t -test), but a difference in tarsus length was detected ($P < 0.01$), suggesting that the fall and winter birds were smaller rather than larger. It is unlikely, therefore, that structural size differences were an important factor in the seasonal weight changes described.

TABLE 1. Correlation and regression statistics showing the relationship of carcass protein and fat content to seasonal weight changes.

| Source of sample | Sample size | Product-moment correlation coefficient (r) | | Regression coefficient of determination (r ²) |
|------------------|-------------|--|---------------------|---|
| | | Protein vs. body weight | Fat vs. body weight | |
| | | | | Protein and fat vs. body weight |
| All females | 85 | 0.83*** | 0.64*** | 0.87*** |
| Adult females | 51 | 0.74*** | 0.53*** | 0.79*** |
| Laying | 12 | 0.70** | 0.24 ^{ns} | 0.83*** |
| Postlaying | 16 | 0.81*** | 0.42 ^a | 0.85*** |
| Fall | 5 | 0.78 ^a | 0.70 ^a | 0.81 ^{ns} |
| Winter | 11 | 0.76** | 0.90*** | 0.80** |
| Immature females | 34 | 0.90*** | 0.82*** | 0.92*** |
| Fall | 14 | 0.85*** | 0.81*** | 0.88*** |
| Winter | 20 | 0.80*** | 0.78*** | 0.90*** |

^{ns} Not significant ($P > 0.10$).

^a $0.05 < P < 0.10$.

* $P < 0.05$.

** $P < 0.01$.

*** $P < 0.001$.

To determine the effect of structural size on body weight variation within seasons, we calculated product-moment correlations of the three structural size measurements with wet, lean, and lean dry body weights for samples of egg-laying ($n = 8$), winter adult ($n = 11$), and winter immature females ($n = 20$). Although 91% of the correlations (30 of 33) between size and weight were positive, only three were significant ($P < 0.05$). The highest coefficient of determination (r^2) was 0.29 for tarsus length versus lean dry weight. With larger sample sizes, structural measurements would be significantly correlated with body weight in the Black Duck, but probably could not explain more than 30–40% of the variation. Other waterfowl researchers have, however, accounted for a larger proportion of the variation in body weight and size by using measurements of wing length (Owen and Cook 1977), total length (Bailey 1979), or a combination of the two (Wishart 1979).

The effect of carcass composition. We used simple correlation and multiple linear regression analyses to relate changes of carcass composition to variation in body weight (Table 1). The multiple regression model initially included body weight as the dependent variable, and size measurements, carcass components, and their first-order interactions as independent variables. For the final analysis, however, we abandoned the complex model and restricted our attention to body fat and protein content because (1) body water was strongly related to protein (above), (2) ash was relatively constant (Fig. 3), (3) structural measurements were weakly correlated with body weight (above), and (4) the more complex

TABLE 2. The effect of age and season on female Black Duck body weight and composition (2-way ANOVA).

| Variable | Sample size | Treatment | |
|--------------------------------|-------------|--------------------|-----------------|
| | | Age | Season |
| | | Adult vs. immature | Fall vs. winter |
| Body weight | 63 | $P < 0.02$ | $P < 0.001$ |
| Nonfat dry weight ^a | 50 | $P < 0.05$ | $P < 0.001$ |
| Protein content ^a | 50 | $P < 0.05$ | $P < 0.001$ |
| Fat content ^a | 50 | $P < 0.005$ | $P < 0.002$ |
| Ash content ^a | 50 | ns ^b | $P < 0.001$ |
| Water content ^a | 50 | ns | $P < 0.001$ |
| Gizzard weight | 63 | ns | $P < 0.02$ |
| Pectoral muscle weight | 63 | ns | $P < 0.001$ |

^a Based on analysis of the unfeathered carcass.

^b Not significant ($P > 0.10$).

model explained little additional variation. As expected, most of the statistics were highly significant because the relationship investigated was that of parts to a whole. The multiple regressions of body weight on protein and fat content consistently accounted for 80–90% of the seasonal variation in body weight (Table 1). With the exception of winter adults, protein content was more strongly correlated with body weight than was fat. During the seasons of higher fat deposition, however, the correlation of fat content with body weight increased.

THE EFFECT OF WINTER WEATHER ON FEMALE BLACK DUCKS

We made a special effort to study the relationship of winter weather to female energy balance because the factors affecting natural mortality in waterfowl are not well understood (Stout and Cornwell 1976). We tested the effect of age (adult vs. immature) and season (fall vs. winter) on body weight and composition with a 2-way ANOVA. Although both age and season had a significant effect on most variables (Table 2), none of the age-season interactions was significant ($P > 0.5$). Thus, we found no evidence that winter weather exerts a differential effect on juvenile and adult females.

Immature females averaged 54 and 99 g lighter, and carried 54 and 59 g less fat than adults during the fall and winter (Appendix). The significant age effect in the ANOVA indicates that Black Ducks are not fully mature in their first winter. In addition, it is consistent with the fact that the yearlings of some dabbling duck species weigh less and start nesting later in spring than the adults (Coulter and Miller 1968, Krapu and Doty 1979). The weight difference was a function of soft tissue and not structural size because (1) there were no age differences in carcass ash content (Table 2), (2) there were no age differences in tarsus, sternum, or culmen length ($P > 0.5$, $P > 0.5$, $P > 0.3$, t -test), and (3) skeletal growth in the

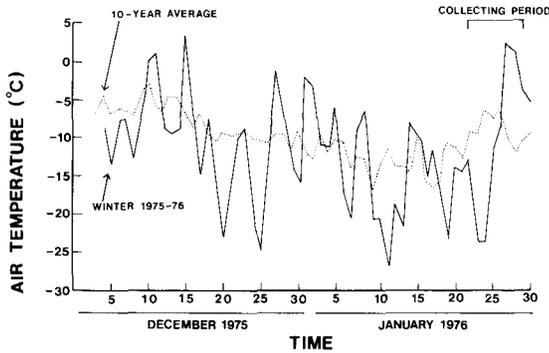


FIGURE 4. Daily temperature minima for Ellsworth, Maine (U.S. Dept. of Commerce, 1965–1976).

closely-related Mallard is known to cease at about eight weeks of age (Greenwood 1975).

The winter season had a significant effect on all carcass variables for both age classes (Table 2). Winter body weight as a percentage of fall body weight dropped 15 and 20% in the adult and immature birds. During this period of negative energy balance between fall and winter, adult and immature females mobilized 59 and 64 g of stored lipids, and 17 and 25 g of protein (Appendix). January is the coldest month of the year in Maine, and our collection of Black Ducks followed a period of below-normal temperatures (Fig. 4). The 60-, 30-, and 20-day periods before sampling were significantly colder ($P < 0.05$, $P < 0.10$, $P < 0.05$, paired t -test) than the mean for the preceding 10 years. Mortality of Black Ducks that we observed during January 1976 was probably related to air temperatures both directly via heat loss and indirectly through the limiting effect of ice conditions on foraging opportunities. Similar conditions caused considerable waterfowl mortality on the mid-Atlantic coast during the winter of 1976–1977 (Nelson 1978). If our samples are representative of conditions experienced by Black Ducks in Maine, then winter is the most stressful season of the year for these birds, whereas several other waterfowl species apparently experience peak stress late in incubation (Korschgen 1977, Ankney 1979, Raveling 1979, Krapu 1981). Although previous studies have stressed the relationship of lipid reserves to successful reproduction, our data indicate that body fat may be equally important to winter survival, at least for Black Ducks on the coast of Maine.

We calculated linear regressions of carcass fat, protein, ash, and water content on body weight for the winter birds ($n = 31$) in order to relate changes in carcass composition to declining weight (Fig. 5). The regressions were all significant ($P < 0.05$), and we found no evidence that the slope estimates for any of the carcass components differed between the age

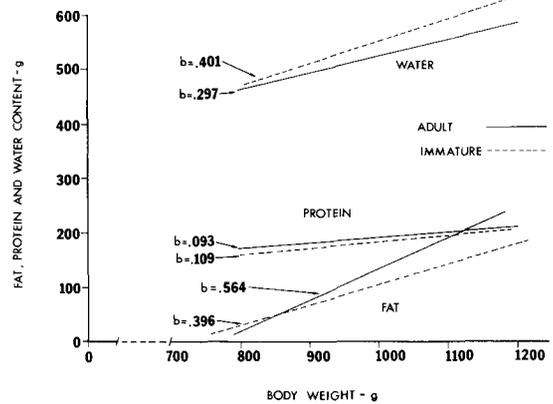


FIGURE 5. The relationship between body weight and carcass composition for female Black Ducks during winter.

classes ($P > 0.20$). We then pooled the data and calculated new estimates for fat ($b = 0.479$), protein ($b = 0.108$), water ($b = 0.323$), and ash ($b = 0.022$). These slope estimates can be interpreted as the weight in grams of each body component gained or lost per gram of body weight. The sum of the slopes (0.932) indicates that about 7% of the body weight was not accounted for in the analysis.

The regression analyses provided a convenient method for estimating energy and nitrogen balance from changes in body weight. For example, we know that well-nourished captive Mallards can tolerate three weeks of food deprivation, but cannot recover from weight losses higher than about 44% (Jordan 1953). If we assume that Black Duck mortality during winter also occurs with the loss of 44% of body weight, then an average female in fall at 1,166 g would survive to about 653 g body weight. Hagar (1950) reported a mean weight of 1.5 lbs (680 g) for a sample of 20 female Black Ducks that had starved to death during winter in Massachusetts. Based on our regression slope estimates and Hagar's terminal weight, starvation of an average winter adult at 989 g and an immature at 890 g (Appendix) would result in the loss of an additional 34 g of protein and the remaining body fat (≈ 120 g) in adults, and 23 g of protein and the remaining body fat (≈ 60 g) in juveniles. This would provide the adults with 1,000–1,100 kcal or eight to nine days survival time at ambient temperatures from -10 to -20°C (Wooley and Owen 1977: 364), and the immatures with 500–600 kcal and four to five days survival time.

CONCLUSIONS

Additional data are needed to determine whether the low body weights of juvenile Black Ducks during winter have an environmental or a genetic basis. The poor condition of young birds could be the result of a low feeding effi-

ciency because they have not achieved the foraging success that comes with age, as known in gulls (Searcy 1978) and other birds. The possibility that social interaction prevented feeding by juvenile Black Ducks is unlikely since Grandy (1972) observed little aggression in foraging flocks during the winter. Interestingly, Hopper et al. (1978) found no evidence of age-specific survival rates for Mallards wintering as far north as Colorado. We hope that the data presented here will stimulate further interest in the feeding ecology, social behavior, and survival rates of juvenile waterfowl in winter.

A second important area for future research is the physiological preparation for and response to winter conditions by waterfowl. Changes in body weight and carcass composition suggest the following interpretation for female Black Ducks wintering in the Northeast. First, we know that both the lean dry weight and the fat content of adult and immature birds decreased between fall and winter (Table 2 and Appendix). Second, even though the lean dry weight of both age classes reached a value less than or equal to the minimum seasonal mean for adults, the fat content remained at an elevated level (Appendix). Thus, it was apparently more valuable for the birds to retain some of the fat deposited during fall than to maintain the lean tissue with its potential for heat production. It seems likely, therefore, that (1) fat deposited during late fall provides an energy reserve and increased insulation at a relatively low maintenance cost (Kendeigh et al. 1977:138), (2) a reduction in lean tissue weight during winter may lower the daily energy requirement and increase the effective size of the lipid reserve, and (3) a decrease in energy reserves during winter, even under normal weather conditions or freely available food supplies (Raveling 1968), may be internally programmed to reflect a shift in the relative advantages of maintaining energy reserves and disadvantages of carrying extra weight.

The results of several recent studies provide additional support for this interpretation of the data. Peterson and Ellarson (1979) studied the carcass composition of Oldsquaws (*Clangula hyemalis*) wintering on Lake Michigan and showed that the lean dry weight and fat reserves of these birds declined together although the birds were exploiting an invertebrate food supply that could provide sufficient protein to maintain lean tissue weights. An example of how a reduction in body weight can represent "adaptation" rather than "stress" was reported by Freed (1981) who showed that female House Wrens (*Troglodytes aedon*) lose weight before the time when they work hardest to feed their

nestlings. The existence of an endogenous rhythm of decreasing body weights in wintering shorebirds was demonstrated by Dugan et al. (1981) who showed that severe weather only temporarily depressed body weights below an internally controlled level. The regulation of body weight and energy reserves described in these reports implies the existence of a mechanism for energy balance (Drent and Daan 1980), whereby individual birds continually assess both their energy (food) intake rates and reserves.

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APPENDIX. Female Black Duck body and component weights (\pm SE) by age, and season or reproductive condition.

| Variable | Adult | | | | | Immature | | |
|--------------------------------|------------------------------------|------------------------|----------------------|-----------------------|-----------------------|----------------------|------------------------|----------------------|
| | Prelying | Laying | Postlaying | Molting | Fall | Winter | Fall | Winter |
| Body weight | (4) ^a 1,094 \pm 32 | (12) 1,111 \pm 24 | (16) 999 \pm 13 | (3) 1,090 \pm 47 | (7) 1,166 \pm 51 | (11) 989 \pm 28 | (25) 1,112 \pm 22 | (20) 890 \pm 22 |
| Nonfat dry weight ^b | (4) 275 \pm 6 | (12) 275 \pm 7 | (16) 257 \pm 4 | (3) 267 \pm 5 | (5) 281 \pm 13 | (11) 259 \pm 4 | (14) 269 \pm 7 | (20) 243 \pm 5 |
| Protein ^b | (4) 199 \pm 8 | (12) 214 \pm 5 | (16) 199 \pm 3 | (3) 210 \pm 5 | (5) 206 \pm 8 | (11) 189 \pm 4 | (14) 202 \pm 4 | (20) 177 \pm 3 |
| Water ^b | (4) 651 \pm 14 | (12) 667 \pm 15 | (16) 625 \pm 9 | (3) 635 \pm 24 | (5) 619 \pm 23 | (11) 519 \pm 13 | (14) 633 \pm 15 | (20) 505 \pm 11 |
| Fat ^b | (4) 84 \pm 13 | (12) 74 \pm 10 | (16) 38 \pm 4 | (3) 94 \pm 33 | (5) 187 \pm 27 | (11) 128 \pm 18 | (14) 133 \pm 21 | (20) 69 \pm 11 |
| Ash ^b | (3) 46 \pm 3 | (12) 45 \pm 1 | (7) 43 \pm 1 | (2) 43-45 | (5) 49 \pm 3 | (11) 42 \pm 2 | (14) 46 \pm 1 | (20) 41 \pm 1 |
| Gizzard weight | (4) 33 \pm 1 | (12) 23 \pm 2 | (7) 24 \pm 2 | (3) 40 \pm 6 | (7) 40 \pm 3 | (11) 34 \pm 2 | (25) 36 \pm 2 | (20) 31 \pm 2 |
| Flight muscle weight | (4) 238 \pm 6 | (12) 235 \pm 6 | (16) 218 \pm 5 | (3) 190 \pm 12 | (7) 227 \pm 9 | (11) 191 \pm 5 | (25) 226 \pm 4 | (20) 179 \pm 6 |

^a Sample size.

^b Based on analysis of the unfeathered carcass.