AGE-SPECIFIC CHANGES IN THE MAJOR BODY COMPONENTS AND CALORIC VALUES OF GROWING WOOD DUCKS

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ABSTRACT.—Analyses of the major body components of pen-raised Wood Ducks (*Aix sponsa*) revealed that body-fat indices (g fat/g lean dry weight) decreased rapidly during the first week of life from a value of approximately 0.30 at hatching. Low values of about 0.10 were then maintained until an age of 2 weeks, after which a gradual increase in the fat index occurred until a value of 0.39 was reached at about 6 weeks. A slight decrease in body fat then occurred as asymptotic weight was approached. Body-water indices (g water/g lean dry weight) were low at hatching and increased rapidly to a maximum value of about 3.14 at 1 week, declining gradually thereafter throughout the remainder of the growing period. Ash indices (g ash/g lean dry weight) and the caloric values of lean dry and ash-free lean dry biomass did not change significantly throughout the growing period. Live-weight caloric values, however, varied in a pattern similar to that of the fat index. The abrupt increases in body water and decreases in body fat during the first week of life seem to typify growing waterfowl and clearly differentiate them from other precocial species of birds such as Japanese Quail. Whole-body counting of potassium-40 was not successful in accurately predicting the total body fat of growing Wood Ducks. *Received 25 September 1978, accepted 1 December 1978.*

STUDIES of avian energetics often require values for caloric equivalents and the major body components of growing birds. Although such information is currently available for a number of avian species, most of this work has dealt with smaller passerines (e.g. Odum et al. 1965; Ricklefs 1967; Myrcha and Pinowski 1969, 1970; Diehl et al. 1972; Blem 1975, 1978). Only a few such studies have been conducted on waterfowl, and none of these has been conducted in such a way as to make its results directly comparable to those obtained from studies of other species. Marcstrom (1966) reported the changes in the major body components of Mallard (*Anas platyrhynchos*) ducklings during the first week of life, and Sugden and Harris (1972) reported the caloric values and major body components of growing Lesser Scaup (*Aythya affinis*). Cain (1976) reported caloric values of growing Black-bellied Whistling-Ducks (*Dendrocygna autumnalis*). Our study was designed to determine similar values for growing Wood Ducks (*Aix sponsa*) and to present this information in such a way as to make the results directly comparable to those obtained from studies of other avian species. In order to do this, the standardized procedure of Brisbin and Tally (1973) was used, in which changes in major body components and caloric values are expressed as functions of increasing age, with age being expressed as a percentage of the total growing period.

Information concerning the patterns of storage and utilization of body fat is particularly important for an understanding of the energetic adaptations of growing birds to environmental stress (e.g. Allen 1976, Blem 1976). Such information would be of even greater value if it could be collected without sacrificing the birds being studied. The current method of measuring body fat, however, requires destructive sampling followed by a lengthy series of solvent extractions of the carcass (e.g. Rogers and Odum 1964, Child 1969). Total body fat has been successfully estimated

in large, live mammals by the use of whole-body gamma-radiation-counting procedures to determine natural body ^{40}K (Lohman et al. 1966, Lohman et al. 1968, Roessler and Dunavant 1967). This technique has not been tried with birds. A second objective of this study was, therefore, to evaluate the ability of the ^{40}K gamma-counting technique to estimate total body fat in living birds.

<div align="center">MATERIALS AND METHODS</div>

Wood Ducks were hatched from eggs collected from a wild population inhabiting a river swamp ecosystem of the upper southeastern coastal plain near Aiken, South Carolina. Eggs were hatched in a commercial turning incubator, and ducklings were raised in captivity using techniques described by Fendley and Brisbin (1977). Briefly, ducklings were removed from the incubator approximately 24 h after hatching and were housed in outdoor rearing pens equipped with heated shelter boxes and a small swimming pool. A commercial game bird feed (Purina Game Bird Startena) was provided *ad libitum* throughout the growing period. According to the manufacturer's specifications, this feed contained a minimum of 30% crude protein, a minimum of 2.5% crude fat, and a maximum of 6.5% crude fiber. A total of 102 ducklings were sacrificed and frozen for biomass analysis as follows: 7 on day 1, 8 on day 7, 7 on day 14, 10 on day 21, 7 on day 28, 10 on day 35, 9 on day 42, 10 on day 49, 10 on day 56, 10 on day 63, 8 on day 70, and 6 on day 77.

Frozen birds were partially thawed and subjected to whole-body gamma-counting procedures for 100 min to determine total body ^{40}K. Gamma-ray spectra were obtained with a whole-body counter using four NaI(Tl) detectors in conjunction with a 1,024-channel analyzer. The design, construction, and performance of the spectrometer system are described elsewhere (Levy et al. 1976). Intercomparisons both for the calculation of ^{40}K body burdens from the same data and for absolute values from independent measurements on reference specimens have been made with similar counting equipment in use at other laboratories, as described by Levy et al. (1976).

After the gamma-counting procedures, all birds were refrozen, homogenized in a meat grinder, and the total body homogenate subsampled according to the procedure of Brisbin (1968). Homogenized subsamples were then dried to a constant weight in a freeze drier, and using the analytical procedures of Rogers and Odum (1964) and as later modified by Child (1969), lipids were then extracted in a commercial blender using 95% ethanol. Subsequent extractions with boiling petroleum ether were then made.

The remaining lean dry residues of four randomly-selected birds from each age group were then ground in a Wiley Mill, and caloric values of 0.6–1.0-g aliquots were determined using a Parr adiabatic oxygen bomb calorimeter. Additional 0.6–1.0-g aliquots of the lean dry component were also burned in a muffle furnace at 500°C for 4 h to determine the percentage of ash. Live-weight caloric values were calculated for each individual for which a lean dry caloric value had been determined. Calculations were made on the assumption of a constant caloric value of 9.0 kcal/g extracted fat (Odum et al. 1965, Barrett 1969). Ash-free caloric values were also calculated for the lean dry biomass.

Biomass data were analyzed following the design of Brisbin and Tally (1973), with changes in body composition and caloric value being expressed as functions of increasing age. Age was expressed as percent of the total growing period (defined as the amount of time required to attain 99% of asymptotic weight). The Wood Ducks used in this study were obtained from a population in which the average times required for hens and drakes to attain 99% of asymptotic weight were 63 and 65 days, respectively (Fendley and Brisbin 1977). No attempt was made to identify or analyze for differences due to sex, and a median age of 64 days was therefore chosen to represent the average growing period for the birds used in this study.

A correlation analysis was used to determine the relationship between the whole-body ^{40}K determinations and the carcass composition of total body water, fat, and lean dry weight. Emphasis was placed upon the determination of predictive relationships for estimating the amount of total body fat in live birds from ^{40}K whole-body counts alone. All statistical analyses were based upon computer programs using the Statistical Analysis System (Service 1972).

<div align="center">RESULTS</div>

Analyses of variance for lack of fit indicated that both fat indices (g fat/g lean dry weight) and water indices (g water/g lean dry weight) varied significantly between
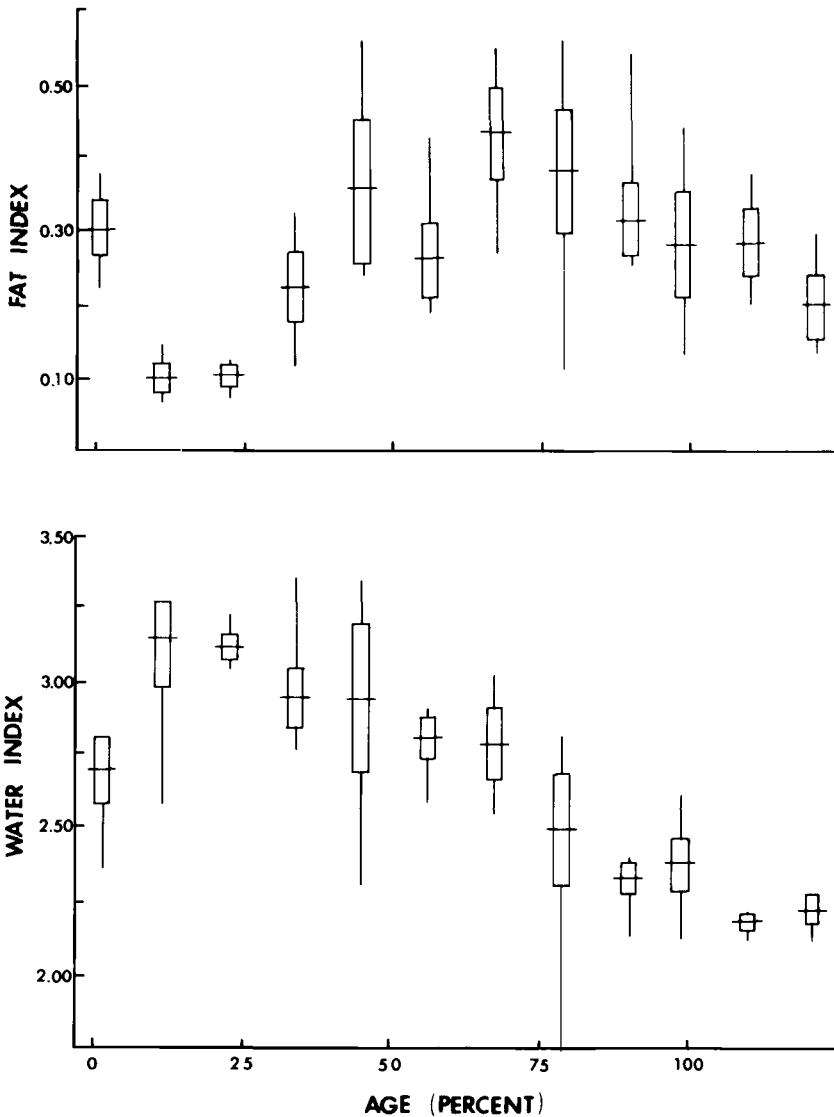
Fig. 1.   Changes in fat indices (g fat/g lean dry weight) and water indices (g water/g lean dry weight) of growing, pen-raised Wood Ducks. Age is expressed in terms of percent of a total growing period of 64 days (see text). Horizontal lines represent means, rectangles represent ±two standard errors of the mean, and vertical lines represent the range. Sample sizes range between seven and 10 birds for each age period, and are given in the text.

age groups of the Wood Ducks studied ($F = 13.52$; df $= 9, 78$; $P \leq 0.01$, and $F = 19.59$; df $= 9, 78$; $P \leq 0.01$ for the fat index and water index, respectively). Mean values for fat indices of the various age groups (Fig. 1) varied from 0.10 to 0.39, with maximum average values occurring at 65% of the total growing period (49 days). Minimum fat content was shown by ducklings between the second and third weeks of life, following a rapid decrease in total body fat during the first week after hatching. A gradual decrease in fat also occurred as asymptotic weight was approached, at ages greater than 65% of the total growing period (Fig. 1).

TABLE 1. Ash indices and caloric values of lean dry and ash-free lean dry weight of growing, pen-raised Wood Ducks.

	N	Mean[a]	Stan-dard error	Maximum	Minimum
Ash index[b]	29	0.17	0.01	0.22 (11)[c]	0.12 (2)
Caloric value of lean dry weight[d]	42	4.63	0.04	5.21 (88)	3.67 (88)
Caloric value of ash-free lean dry weight[d]	42	5.55	0.05	6.24 (88)	4.39 (88)

[a] Means are based on values from all birds studied, as none of these parameters varied significantly between age groups.
[b] g ash/g lean dry weight.
[c] Values in parentheses represent ages, expressed as percent of the total growing period, at which the maximum and minimum values occurred.
[d] kcal/g.

Water indices showed a sharp increase during the ducklings' first week of life, declining gradually thereafter throughout the remainder of the growing period (Fig. 1). Maximum average values for the water index (3.14) occurred at 1 week (25% of the total growing period), and minimum average water content occurred shortly after the attainment of 99% of asymptotic weight.

Neither ash indices (g ash/g lean dry weight) nor lean dry caloric values varied significantly between the age groups studied ($F = 1.72$; df = 9, 19; $P > 0.05$, and $F = 1.15$; df = 9, 32; $P > 0.05$ for ash index and lean dry caloric value, respectively). Caloric values of ash-free lean dry weight similarly did not vary significantly with age ($F = 1.10$; df = 9, 32; $P > 0.05$). Average values for ash indices, lean dry caloric values, and ash-free lean dry caloric values are presented in Table 1. Lean dry caloric values of the various age groups of ducks are also presented in Fig. 2.

Live-weight caloric values, however, did vary significantly between age groups ($F = 13.24$; df = 9, 32; $P \leq 0.01$). As indicated in Fig. 2, changes in live-weight
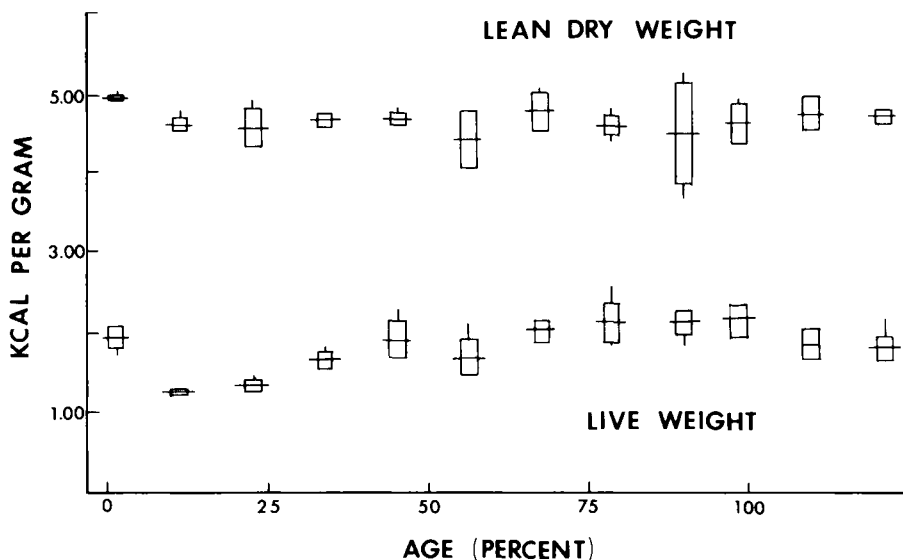

Fig. 2. Changes in caloric values of lean dry and live-weight biomass of growing, pen-raised Wood Ducks. Age is expressed in terms of percent of a total growing period of 64 days (see text). Symbols are as explained in Fig. 1. Sample sizes are four birds each for all age periods.

TABLE 2. Partial correlation coefficients for major body components and ^{40}K content of growing wood ducks.

	Fat index	Water index	g fat/g live-weight	g fat/g dry weight	^{40}K
Fat index[a]	—	0.37[d]	0.79	0.57	−0.08
Water index[b]	**[c]	—	0.21	0.17	0.09
g fat/g live-weight	**	NS	—	0.22	0.06
g fat/g dry weight	**	NS	*	—	−0.27
^{40}K[c]	NS	NS	NS	*	—

[a] g fat/g lean dry weight.
[b] g water/g lean dry weight.
[c] Measured as pCi/g live weight.
[d] Entries above the diagonal represent correlation coefficients (r).
[e] Entries below the diagonal represent levels of significance: single and double asterisks represent significant correlations at the ≤0.05 and ≤0.01 levels of probability, respectively. NS indicates no significant correlation. The correlation matrix was calculated with 76 df.

caloric values showed the same general pattern with increasing age as did fat indices, indicating a close relationship between the two. A minimum value of 1.26 kcal/g live-weight occurred at 11% and a maximum of 2.13 kcal/g live-weight at 77% of the total growing period. Changes in live-weight caloric values with increasing age showed a significant lack of fit to a linear model ($F = 6.58$; df $= 8, 32$; $P ≤ 0.01$). Both quadratic and cubic models were similarly unable to explain a significant amount of the variability in live-weight caloric value.

The results of the correlation analysis among values for major body components, caloric values, and ^{40}K whole-body gamma-counts are summarized in Table 2. Whole-body ^{40}K counts were correlated (negatively) only with g fat/g dry weight. Positive correlations were shown between fat index and water index, g fat/g live-weight, and g fat/g dry weight. Grams fat/g live-weight and g fat/g dry weight were also positively correlated.

DISCUSSION

One of the values of expressing changes in major body components and caloric values of growing birds as functions of percentage of the total growing period is that it allows direct comparisons to be made to similar studies of other species at comparable stages of growth and physiological maturation. The results of the present study on Wood Ducks, for example, may now be directly compared to those reported earlier by Brisbin and Tally (1973) for another precocial species, the Japanese Quail (*Coturnix coturnix japonica*). A comparison between the Wood Duck and the Japanese Quail, both of which were studied under *ad libitum* feeding regimes using the same commercial game bird feed, reveals some striking and as yet unexplained differences in the patterns of change in total body water and fat throughout the growing period.

The continual increase in the fat index shown by Japanese Quail during the first 25–30% of their growing period (Brisbin and Tally 1973) is in sharp contrast to the pattern shown by the Wood Ducks. Wood Ducks show a rapid decrease in body fat during the first week of life, followed by the maintenance of low fat index levels of approximately 0.10 throughout the first 25% of their growing period. The increase in body fat of Wood Ducks between 25 and 65% of the growing period serves to bring their fat indices close to comparable levels shown by the Japanese Quail at the same relative age. During the latter 35% of the growing period, however, fat indices of the growing quail continue to increase to values averaging near 0.90, with

maximum values near 1.40. Wood Ducks, on the other hand, show a gradual decline in body fat content during this same period, with fat indices averaging less than 0.30 and with maximum values of less than 0.45 at the attainment of 99% of asymptotic weight. The latter third of the Wood Duck's growth period is a time of extremely rapid body- and wing-feather growth, and the energy demands of these processes might well represent significant drains on energy reserves of body fat. As feather growth continues, body fat indices continue to decline well after the attainment of asymptotic weight in this species (Fig. 1). Bellrose (1976) indicates that young wild Wood Ducks switch from a diet rich in animal matter to a mainly vegetarian diet during this same period. Dietary shifts, however, could not account for the decline in body fat reserves which was observed in this study.

The rapidly declining and continuing low levels of body fat during the first 3 weeks of the Wood Duck's life are even more surprising when it is recalled that the birds studied had access to *ad libitum* high quality feed throughout this period. Apparently the declining fat reserves shown during this period are related to intrinsic processes of physiological maturation of body tissues, as described by Ricklefs (1967, 1974), rather than being strictly a result of nutritional status. Such a pattern, if observed in free-living wild ducklings, could easily be misinterpreted. The period of early decline in fat content of the Wood Ducks corresponds with the period of transition from yolk absorption through the time when the ducklings must first begin to find their own food. Marcstrom (1960, 1966) has shown that Capercaillie (*Tetrao urogallus*) chicks and Mallard ducklings will use up fat reserves from the yolk and die in an average of 5 and 7.5 days, respectively, if unfed. Other precocial birds also have been shown to have high levels of fat content at hatching, as revealed by studies of growing Lesser Scaup (Sugden and Harris 1972) and Double-crested Cormorants (*Phalacrocorax auritus*) (Dunn 1975). The pattern of change in the fat index of the cormorants during the early part of their growing period is particularly similar to that of the Wood Ducks. Calculated as g fat/g live-weight, however, the fat content of the newly hatched Wood Ducks (24.6%) was over twice as great as that of newly hatched Lesser Scaup. It has been suggested that high fat reserves in both the yolk sacs and bodies of such newly hatched birds may provide insulation from chilling and provide stored energy reserves for use during the first critical days of life. The low levels of fat in newly hatched Japanese Quail seem to be the exception to the rule for precocial species studied thus far and resemble more closely the patterns of gradual fat increase during early life that are shown by various altricial species of birds and mammals (Ricklefs 1967; Brisbin 1969, 1970).

Captive-raised waterfowl such as Lesser Scaup (Sugden and Harris 1972) and particularly Wood Ducks, as reported in this study, seem to show lipid indices that are considerably higher than those of wild-collected adult galliforms (West and Meng 1968, Szwykowska 1969). The fat indices of the Wood Ducks were comparable, however, to those reported for growing nestlings of passerine species (Ricklefs 1967) and adult nonmigrant adult passerines (Kale 1965, Odum et al. 1965). Growing doves (Brisbin 1969) and gulls (Brisbin 1965) have fat indices that seem to be, respectively, slightly lower and slightly higher than those reported here for the growing Wood Ducks.

Age-specific changes in the water indices of the growing Wood Ducks also show striking differences from those of Japanese Quail (Brisbin and Tally 1973). The greatest differences between these species occur during the first 15–20% of the growing period. While Japanese Quail, like most other species of birds studied to date

(Marcstrom 1960, Ricklefs 1967, Brisbin 1969, Myrcha and Pinowski 1969, Diehl et al. 1972, Blem 1975, Dunn 1975), show sharp decreases in water content during the period of early growth, the Wood Ducks actually increase their body water content significantly during this same period. Sugden and Harris (1972) also report relatively low body water contents of Lesser Scaup ducklings at the time of hatching. This divergence from the usual pattern of continuing body dehydration with growth may be a phenomenon unique to waterfowl. Mallard ducklings, unlike Lesser Scaup and Wood Ducks, do not seem to show significant body hydration during early growth (Marcstrom 1966), although data presented by Marcstrom do not include liver and yolk sac in calculations of body weight. Further studies are indicated to document more precisely this unusual phenomenon of post-hatching body hydration and to determine its significance with respect to the early development and maturation of duckling body tissues during the early days of life.

By the time that about 20% of the growing period has been attained, both Japanese Quail and Wood Ducks have attained essentially equivalent body water indices of between 3.00 and 3.25, Wood Ducks having increased and quail having decreased their water indices to these levels from the time of hatching. The decline in water content during the remaining part of the growing period actually seems to be more rapid in the Wood Duck than in the Japanese Quail. By the time asymptotic weight has been attained, however, the water indices of the Wood Ducks seem to be a bit lower than those shown by most other species of birds (e.g. doves, passerines, and quail), which generally exhibit water indices of between 2.5 and 3.0 at the end of the growing period (Brisbin 1969; Ricklefs 1967; Blem 1975, 1976; Brisbin and Tally 1973). Ash indices of the Wood Ducks (Table 1) are generally higher than those reported by Ricklefs (1967) for growing passerines, a condition probably attributable to the relatively lighter bone structure of the latter.

The tendency for both lean dry weight and ash-free lean dry weight to retain a constant caloric value throughout the growing period (Table 1) is similar to the situation with many of the other species of birds that have been studied (e.g. Ricklefs 1967, Brisbin 1969, Dunn 1975). Again, the pattern shown by growing Japanese Quail seems to be atypical, as caloric values of lean dry weight show a significant decrease with age throughout the growing period of this species (Brisbin and Tally 1973, Blem 1978). Average lean dry caloric values shown by the Wood Ducks throughout the growing period (Table 1) were very similar to those values reported for other species of birds, values ranging from 4.4 to about 5.0 kcal/g lean dry weight (Odum et al. 1965, Brisbin 1969, Brisbin and Tally 1973, Blem 1975, Dunn 1975). Ash-free lean dry caloric values of the Wood Ducks and other species reported in the literature are even closer, with average values often differing by less than 0.1 kcal/g.

Age-specific variations in the caloric values of live-weight biomass have been reported for nearly every species of bird that has been studied. In most cases, live-weight caloric values have increased with age due to simultaneous decreases in total body water content and increases, in most cases, in body fat content. The same trend was generally shown by the Wood Ducks, although the changes in live-weight caloric value across time were slightly more complex, undoubtedly due to the unusual pattern of changes in body fat content. As in the present case, other workers (e.g. Myrcha and Pinowski 1969, Diehl et al. 1972, Brisbin and Tally 1973, Blem 1975) have found close similarities between the pattern of variation in body fat content and changes in live-weight caloric value. The inability of linear, quadratic,

and cubic functions to predict adequately live-weight caloric values as functions of increasing age is undoubtedly due to the abrupt changes of these values during the first 3 weeks of life (Fig. 2). As summarized by Ricklefs (1974), the live-weight caloric values of many species of birds may be expressed adequately as linear functions of age, expressed as the attainment of an increasing percentage of the adult weight. Correlation coefficients of those regressions presented by Ricklefs (1974) ranged from 0.99 to 0.69. A similar coefficient, when calculated for the live-weight caloric values of the Wood Ducks, showed a value of 0.66 but, nonetheless, showed a significant lack of fit to a linear model. This suggests that some of the growth-related changes in live-weight caloric values that have been reported for other avian species may also not be best described by a linear model. Such a determination can only be made, however, when the test for lack of fit is employed, and this can only be done when replicate sampling is performed within given age categories.

Until further studies have been conducted, it would appear that the best procedure for estimating live-weight caloric values of growing Wood Ducks would be to use average or interpolated values for ducklings between hatching and 40% of the growing period, as indicated in Fig. 2. For older birds between 40 and 100% of the total growing period (4–9 weeks, a constant caloric value of 2 kcal/g live-weight may be assumed.

Although the whole-body gamma counting of total body ^{40}K has proven to be a useful tool in predicting the total body fat of large domestic mammals, the present study did not show any useful predictive relationships between whole-body ^{40}K content and any indicator of body fat content of the growing Wood Ducks (Table 2). The only significant correlation demonstrated was between ^{40}K content and g fat/g dry weight, and the predictability of that relationship was less than 10%. While previous studies have used the ^{40}K method to determine total body fat in adult organisms, the present study dealt with a series of growing birds of varying ages. Moreover, the ^{40}K method of estimating total body fat is based on the assumption that total body water remains relatively constant in the subjects under study. As indicated by Fig. 1, however, body water was far from constant in the growing Wood Ducks, and this fact alone could have caused significant deviations in total body counts of ^{40}K/g live body weight, independent of any changes in body fat. Although better predictions could perhaps be obtained by correcting total ^{40}K live counts for individual differences in body water through some covariate procedure, such a process would not be of use in studies involving live birds. It is possible, however, that the ^{40}K technique may still prove useful in predicting changes in total body fat of live adult migrant birds, whose body water often tends to remain quite constant during changes in the amount of total body fat (Odum et al. 1964).

In conclusion, it should be noted that the patterns of change in major body components and caloric values of growing precocial waterfowl such as the Wood Duck do not seem to conform to the patterns that have been generally established for other precocial species such as the Japanese Quail (Brisbin and Tally 1973). As more information becomes available for an increasing number of species, however, it is becoming increasingly apparent that it is not always possible to generalize either growth-related patterns of change or absolute values for body composition and caloric value. Such a situation would suggest that further studies should be conducted on additional species in order to understand better the ecological and evolutionary factors responsible for the patterns being observed. Studies of additional waterfowl and gallinaceous species would be particularly important in terms of explaining the

strikingly different behavior of both body water and fat content during the growth of Wood Ducks and Japanese Quail.

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