

BIOENERGETICS OF THE BREEDING CYCLE OF THE RING DOVE

I. LEHR BRISBIN, JR.

ALTHOUGH birds have been a frequent subject of bioenergetic studies, few of these studies have dealt with the breeding cycle. Estimations of energy requirements during the major phases of the breeding cycle have been based, for the most part, on indirect measurements. Direct measurements of energy intake and utilization have been difficult to obtain because of the reluctance of most birds to nest and raise young under captive conditions that would permit frequent weighings of adults and young and quantification of food intake.

The Ring Dove (*Streptopelia risoria*) has long been known for the ease with which it may be bred in captivity, being highly tolerant of disturbance during the breeding cycle. In addition the Ring Dove is capable of existing and raising young on a uniform diet of commercial pigeon food, thus greatly simplifying the quantification of caloric intake. Because of its adaptability to laboratory conditions, the Ring Dove has been a favorite subject for many studies, especially in the fields of behavior (Lehrman, 1955, 1964), physiology (Riddle, 1928; Riddle et al., 1930; Riddle et al., 1933), and endocrinology (Riddle, 1947). Thus a great deal of background information exists on many aspects of its breeding cycle. All these factors combine to make the Ring Dove an ideal subject for a study of energy flow during a bird's breeding cycle.

Two approaches were used in this study. In the first, carcasses of both the breeding adult birds and their growing nestlings were separated into the three major body components, namely, water, fat, and lean dry weight. From these data the caloric values of biomass changes in the young and adult birds were estimated and related to other aspects of the energy budget. A similar approach has been commonly used in studying the bioenergetics of premigratory lipid deposition in small passerines (see for example Odum and Perkinson, 1951; Gifford and Odum, 1965) and has also been used by King et al. (1965) in a field study of breeding White-crowned Sparrows.

The second approach is a direct experimental measurement of the caloric intake of the adult birds and the associated weight changes of the adult birds and growing nestlings. The information gained in this manner was combined with the data obtained from the carcass analyses to provide a more complete picture of the bioenergetics of the breeding birds.

The effect of brood size was also evaluated by comparing the energy utilization of birds raising the normal two young per nest with those whose broods were experimentally reduced to one young per nest.

MATERIAL AND METHODS

Although the Ring Dove is known in the wild state (Peters, 1937: 92), the birds used in this study were from a stock with a long history of captive propagation and must be considered as representing a truly domestic strain.

Several races of the domestic Ring Dove have been described, characterized by different physiological responses to hormones such as prolactin or by different basal metabolic rates (Riddle, 1947). The doves used in this study were obtained from a breeder who raised his entire colony over a period of years from a single pair of birds. Therefore it is not likely that any of these birds differed from one another in racial background.

Birds were sexed according to the methods of Miller and Wagner (1955). Pairs of unknown age, but with prior breeding experience, were then placed in individual outdoor flight pens which were 8-10 feet in height and had floor areas of approximately 100 square feet. Each pen was furnished with a food shelf, several branches, and a nesting shelf and nest cup, similar to that described by Lehrman (1964). Food, water, and a commercial poultry grit were provided *ad libitum*.

Records were kept of the weight of food consumed daily by the breeding adult birds. The food used throughout this study was Purina Pigeon Chow Checkers containing a minimum of crude protein (15.0 per cent), a minimum of crude fat (2.5 per cent), a maximum of crude fiber (6.0 per cent), an average moisture content of 10.8 per cent, and supplemented with various amounts of minerals and required vitamins. The food was in the form of small pellets which the adult doves consumed intact. Nestling doves were also able to eat whole pellets by an age of 40 days.

Six 50-pound bags of food were used during the study. A random sample of food was taken from the first, third, and fifth bags for caloric analysis. Caloric determinations were made with a Parr adiabatic oxygen bomb calorimeter, using fresh food directly from the bag without previous drying. A total of 15, 9, and 5 replications were tested of each of the three feed samples respectively. As there was no significant difference ($P \geq 0.05$) between the mean values for the three food samples, the average value of all 29 replications was used as a conversion factor. This value was 3.92 ± 0.02 (SE) Kcal/g fresh weight of food.

The birds were kept in outdoor pens where they bred during the warmer months of the year (late March through early November). This study was based on breeding cycles occurring during the months of April, May, June, September, and October.

Adult birds were weighed every third day, daily weights being estimated by interpolation, and nestlings were weighed daily. All birds were weighed on a triple beam balance to the nearest 0.1 g, and all weighings were made between 0800 and 1000 hours to minimize variation due to the diurnal weight cycle, as described by Baldwin and Kendeigh (1938: 424-430).

The nesting cycle of the Ring Dove is similar to that of the domestic pigeon except that the time intervals are shorter (Cuthbert, 1945). The cycle has been described in detail by several authors (Riddle and Braucher, 1933; Miller and Miller, 1958; Lehrman, 1964). The successive days of the breeding cycle are numbered here according to the following scheme: the day the second egg is laid is considered as day 0, and succeeding days are then numbered consecutively. On day 15 the eggs hatch and 28 days later (day 43) the young have achieved independence and are removed from their parents. The 10 days prior to day 0 are numbered -10 through -1 and represent the period of courting, nest-building, and egg-laying. The 10 days following day 42 are numbered +1 through +10. Our birds usually laid again 8-10 days after the young from the preceding cycle were removed from the pen. Thus days +1 through

+10 not only represent the 10 days following a given cycle, but also correspond to days -10 through -1 of the following cycle. In summary, the nesting cycle of the ring dove may be divided into three phases as follows: (1) courting phase (days -10 through -1 and days +1 through +10), (2) incubating phase (days 0 through 15), and (3) feeding nestlings (days 16 through 43).

Two pairs of breeding adult birds were sacrificed on each of the following days of the cycle for carcass analysis: -5, 0, 5, 10, 15, 23, 33, 43, and +5. Four nestlings were also sacrificed at each of the following ages: 1 day, 8 days, 18 days, 28 days, and 38 days. Individual carcass analyses of each of the nestlings and adult birds were made by the procedure routinely used in our laboratory for small passerines and described in detail by Rogers and Odum (1964). For the larger adult birds this procedure was modified by taking a 10 per cent random aliquot of the total homogenized biomass of the bird, following the method of Brisbin (1968), and then analyzing this random aliquot by the usual procedure. Briefly this procedure entails vacuum-drying the birds at 40°C to a constant weight and then extracting the dry residue with petroleum ether to remove the fat. Samples of the remaining lean dry residue were prepared for caloric analysis and burned in a Parr adiabatic oxygen bomb calorimeter, using the procedure described by Odum et al. (1965). Thus the carcass analysis of each individual indicated what proportion of the live weight of the bird was comprised by the three major body components of water, fat, and lean dry weight. By determining the caloric value of the lean dry weight and assuming 9.00 Kcal/g of extracted body fat, the caloric value of the live weight of each individual bird could then be determined using the procedure described by Odum et al. (1965).

Differences between mean values of all data were tested by a standard *t*-test procedure. A transformation of $100 - X$ was applied to all percentage data, before applying the *t*-test. Significant differences between means were accepted at the level $P \leq 0.05$ and highly significant differences at the level $P \leq 0.01$.

RESULTS

Body composition and weight of adult doves.—Each pair of breeding adult birds was considered to be a single functional unit, and no sex differences were considered. Riddle and Braucher (1933) have shown that both male and female Ring Doves show identical patterns of weight change throughout the breeding cycle.

Total weights of each pair of birds on day 0 averaged 302.5 ± 8.1 (SE) g for those birds raising one chick per nest and 305.3 ± 7.5 (SE) g for those raising two chicks per nest. Using the weight of each pair on day 0 as 100 per cent, the percentage weight changes through the succeeding days of the breeding cycle were calculated for each pair (Figure 1). At no time during the entire breeding cycle was there any significant difference between the weights of pairs raising two chicks per nest and those raising only one chick per nest.

Throughout the incubation period all pairs showed a highly significant increase in total body weight, reaching a peak on day 15 that represented a maximum increase of about 6–8 per cent over their pre-incubation weight. During the first 20 days of feeding nestlings there was a highly significant

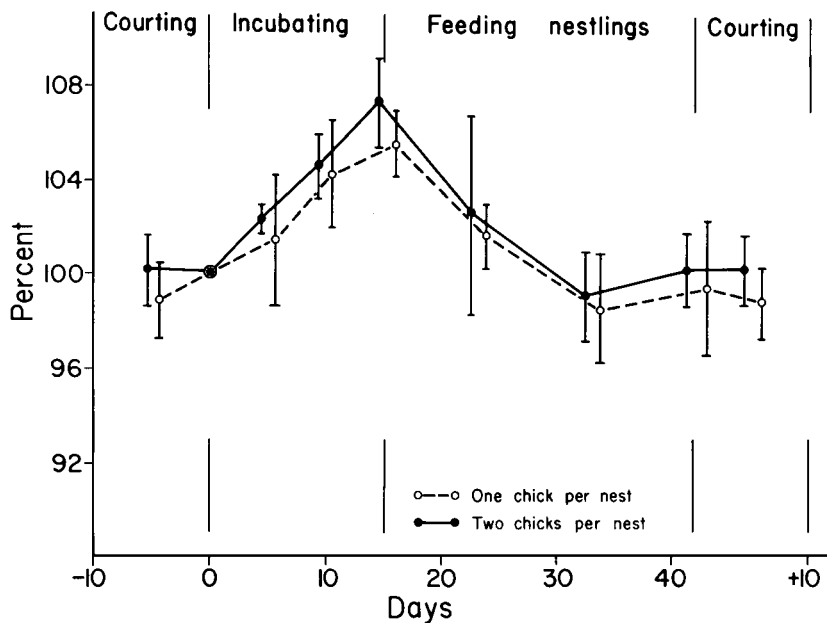


Figure 1. Variation of mean total body weight of breeding pairs of Ring Doves. Weight is expressed as percentage of the total weight of the pair on day 0. Each point represents the mean of four pairs of birds and vertical bars represent 2 standard errors above and below the mean.

decrease in total body weight, back to the original pre-incubation level. These findings are similar to those of Riddle and Braucher (1933) who found that incubating Ring Doves show a 7.5–8.5 per cent increase above their pre-incubation weight.

Changes in the fat indices (g fat/g lean dry weight) of the breeding adult doves are shown in Figure 2. Although the mean fat index is higher on day 15 than during the courting phase, the increase from day -5 through 15 is not statistically significant. Likewise neither is the slight decrease in mean fat index through the period of feeding nestlings significant. Fat index often showed a rather high variability between individual birds sacrificed on the same day, and no definite trends in this parameter could be detected throughout the breeding cycle. Mean values of fat indices ranged from 0.226 to 0.455 and were considerably lower than the fat indices of six nonbreeding doves sacrificed during the winter months. The winter birds had fat indices ranging from 0.479 to 0.720 ($\bar{X} = 0.604$).

Water indices (g water/g lean dry weight) of the adult birds were lowest during the courting phase and increased to a peak on day 15 (Figure 2). The increase from day -5 through 15 was highly significant as was the

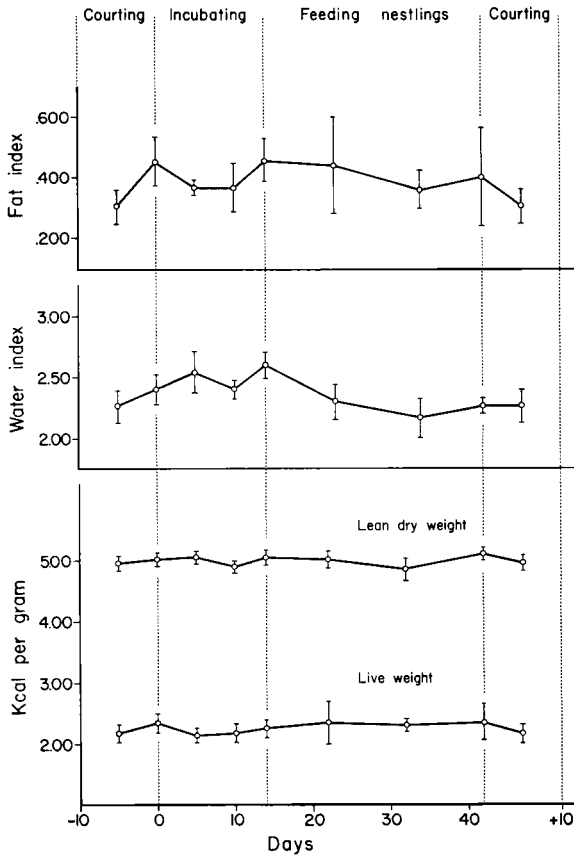


Figure 2. Variation of mean values of fat index, water index, and caloric density of live and lean dry weight of breeding adult Ring Doves. Each point represents the mean of four birds (two breeding pairs) and vertical bars represent 2 standard errors above and below the mean.

decrease from day 15 through +5. By day 33 when the nestlings were 18 days old, the water indices of the parent birds had declined to their pre-incubation low values.

No significant change occurred in the caloric value of either the lean dry weight or live weight of the adults throughout the breeding cycles (Figure 2). The mean values of these parameters for the entire cycle were 5.00 ± 0.02 (SE) Kcal/g lean dry weight and 2.26 ± 0.03 (SE) Kcal/g live weight.

A slight increase in the amount of body fat should be noted, concomitant with the increase in body water. While this increase in fat is not sufficient to be reflected in a significant increase in fat index, it is apparently suf-

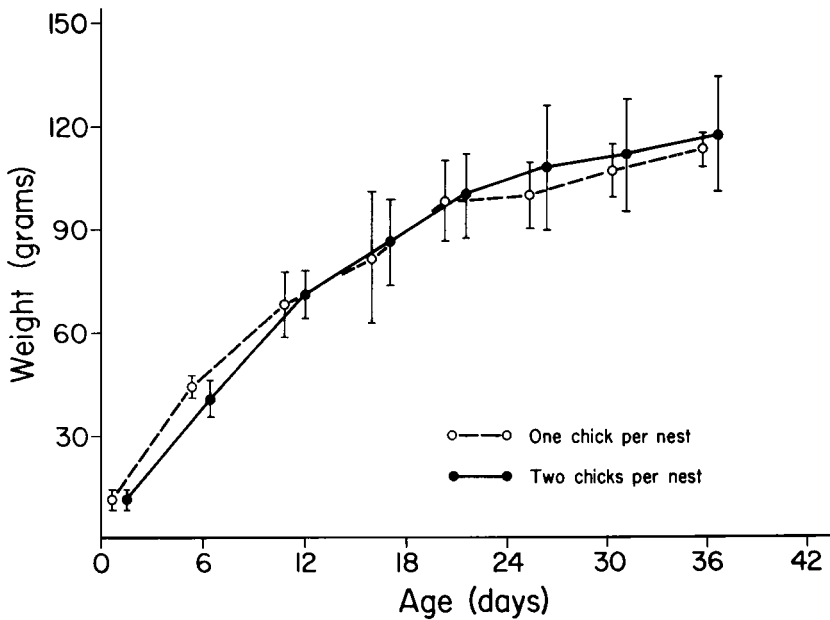


Figure 3. Mean growth in body weight of nestling Ring Doves. Each point represents the mean of four broods and vertical bars represent 2 standard errors above and below the mean.

ficient to maintain a homeostasis of live weight caloric density. Because of the high caloric value of fat, only 0.33 g of fat would have to be added for each gram of water added to maintain a constant caloric value of 2.26 Kcal/g live weight.

Body composition and weight of nestlings.—A comparison of the growth curves of nestlings raised one per nest with that of nestlings raised two per nest (Figure 3) is complicated by the fact that the same chicks are being weighed each time, and no independent readings are available for the age series. Davies (1947) has discussed this problem and indicated that *t*-tests may be used to compare means for any given day. Using this procedure no significant difference could be found between the mean weights of nestlings raised one per nest and those raised two per nest. These results differ from those of Riddle et al. (1932) who found that pigeon squabs raised two per nest were lighter in weight than squabs of the same age raised one per nest.

No correlation was found between fat index and age in the growing nestlings (Figure 4). Mean values ranged between 0.132 and 0.266 ($\bar{X} = 0.208$). On the other hand the mean water index showed a highly significant decrease with increasing age of the growing nestlings (Figure 4).

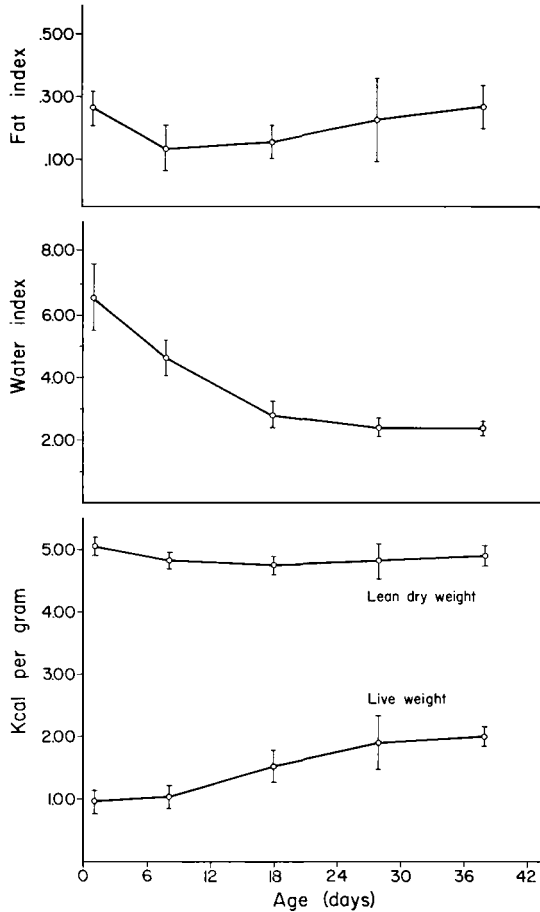


Figure 4. Variation of mean values of fat index, water index, and caloric density of live and lean dry weight of nestling Ring Doves. Each point represents the mean of four birds and vertical bars represent 2 standard errors above and below the mean.

The statistical analysis of the curvilinear decrease of water index was based on a log-transformation of the curve to a linear function. These results agree with those of Ricklefs (1967), who found a persistent tendency for the tissues of nestling Barn Swallows and Red-winged Blackbirds to desiccate with increasing age. The water indices of the 1-day-old dove chicks ranged from 5.57 to 8.62, and are among the highest ever reported in the literature for whole birds.

No significant increase or decrease could be found in the caloric value of the lean dry weight of the nestlings, which averaged 4.87 ± 0.04 (SE) Kcal/g throughout the growth period, but the caloric value of the live

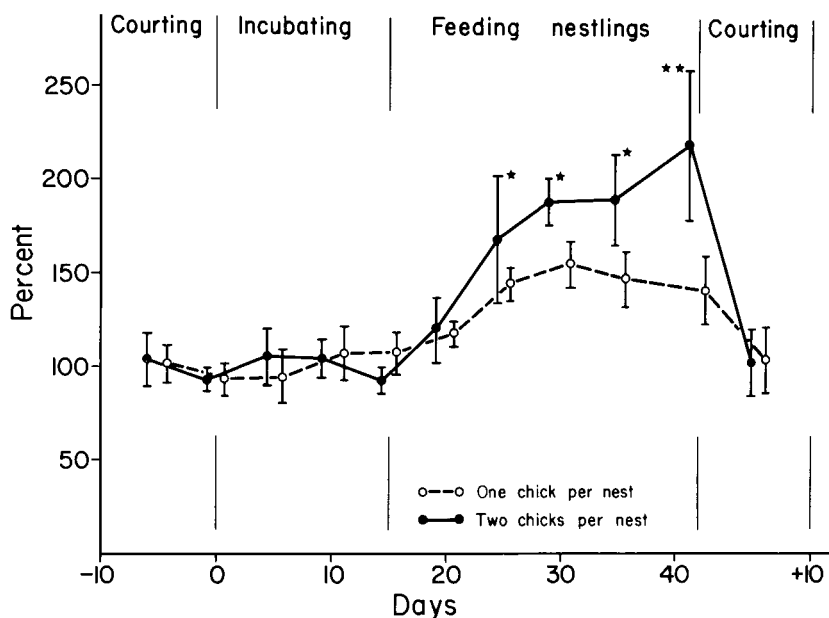


Figure 5. Variation in mean total daily caloric intake of breeding pairs of Ring Doves. Caloric intake is expressed as percentage of mean daily caloric intake of the pair during the courting and incubating periods. Each point represents the mean of four pairs of birds and vertical bars represent 2 standard errors above and below the mean. Single stars indicate a significant ($P \leq 0.05$) and double stars a highly significant ($P \leq 0.01$) difference between mean values for pairs feeding one young per nest and those feeding two young per nest.

weight increased as a highly significant linear function of age (Figure 4). This function is described by the equation:

$$C = 0.910 + 0.031t$$

where C = Kcal/g live weight, and t = age in days. Solving this equation for the mean caloric value of the live adult biomass (2.26 Kcal/g) showed that the live weight of the nestlings reached the caloric value of the adults at an age of 43 days, precisely the age when the nestlings attain adult body size and growth ceases (Figure 3). All energy calculations involving live dove biomass were based on the caloric conversion factors derived from the above equation through the age of 43 days. From that age on the conversion factor was assumed to be a constant 2.26 Kcal/g live weight.

Energy intake, productivity, and conversion efficiency.—As no significant difference was evident between the caloric intake of adult birds in the courting phase and the caloric intake of adult birds in the incubation phase, the caloric intakes for each pair of birds for each day during the

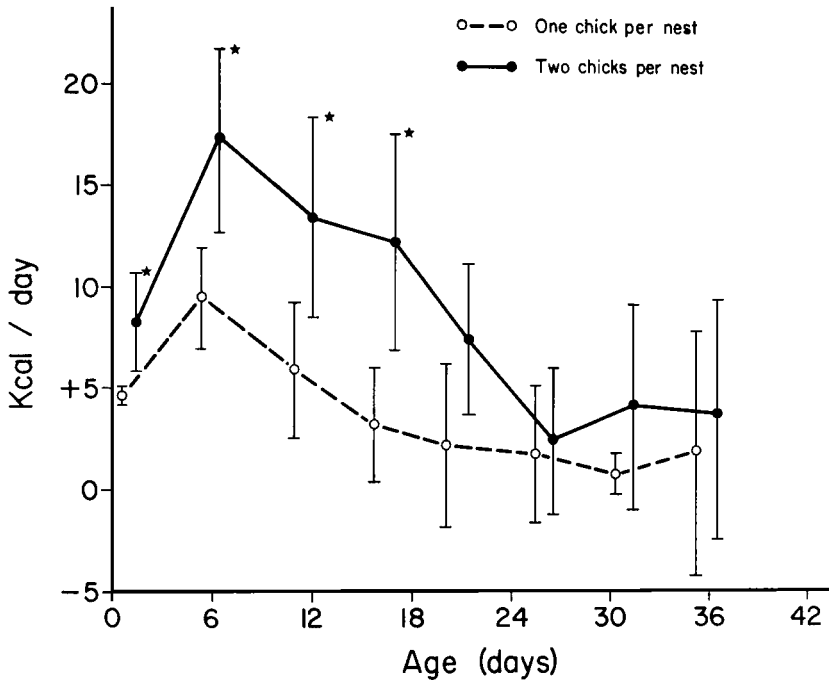


Figure 6. Variation in mean total nestling biomass productivity of breeding pairs of Ring Doves. Each point represents the mean of four nests and vertical bars represent 2 standard errors above and below the mean. Stars indicate a significant ($P \leq 0.05$) difference between nests containing one young and those containing two young.

courting and incubation phases were averaged together to give standard caloric intake values for the nonbreeding adults. These values averaged 102.8 ± 8.3 (SE) Kcal/day/pair for those birds raising one chick per nest and 108.4 ± 9.6 (SE) Kcal/day/pair for those raising two chicks per nest. Using these values as 100 per cent, the percentage changes for succeeding days throughout the breeding cycle were calculated for each pair of birds (Figure 5). There was no significant difference between the mean daily caloric intakes of pairs raising one chick per nest and those raising two chicks per nest until after the nestlings were 5 days old. Divergence between the 1- and 2-chick cycles began between the ages of 5 and 10 days, the caloric intakes of pairs raising two chicks per nest becoming significantly higher than those of pairs raising one chick per nest. From day 35 through day 43 the difference was highly significant.

The mean of all daily caloric intakes from day 25 through 43 was significantly higher than the mean for all values from day -5 through 25.

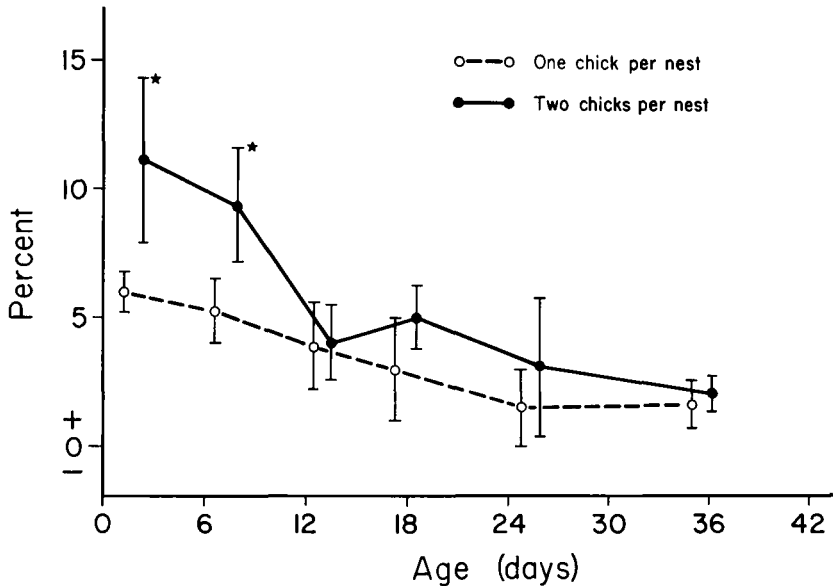


Figure 7. Variation in mean efficiencies of breeding pairs of Ring Doves in converting food energy into nestling biomass. Each point represents the mean of four pairs of birds and vertical bars represent 2 standard errors above and below the mean. Stars indicate a significant ($P \leq 0.05$) difference between pairs feeding one young per nest and those feeding two young per nest.

This was true regardless of whether there were one or two chicks per nest. The mean daily caloric intake increased 142 per cent from feeding one chick per nest and 182 per cent from feeding two chicks per nest, but there was no significant difference between the 1- and 2-chick cycles in the respective slopes of those increases in caloric intake between days 15 and 25. The total number of calories required to raise one chick from hatching to independence (at an age of 28 days), over and above the standard caloric intake for the nonbreeding adults, was 1134.9 and 922.5 Kcal for those chicks raised one and two per nest respectively. The difference between these latter values was statistically significant.

The daily productivity in terms of calories of weight gained per nest (Figure 6) was significantly greater for those nests containing two chicks than for those containing only one chick, until an age of 20 days, after which the 1- and 2-chick cycles showed no significant differences. The productivity increased sharply during the first 6 days following hatching, this increase being significant for the 2-chick cycles and highly significant for the 1-chick cycles. From an age of 6 through 16 days the productivity per nest was highly significantly greater than during the last 10 days of

TABLE 1
EFFICIENCY INDEX NUMBERS FOR BREEDING PAIRS OF RING DOVES

One chick per nest	Two chicks per nest
112.8	212.7
107.9	181.4
141.0	181.8
117.3	233.5
Mean = 119.7	Mean = 202.3
SE = 7.3	SE = 12.7

the growth period (age 26 through 36 days) in both the 1- and 2-chick cycles. The rates at which nestling productivity decreased from days 6 through 26 did not differ significantly between the 1- and 2-chick cycles.

The efficiency of energy conversion (Figure 7) is the ratio of Kcal of productivity of nestling biomass on a given day (Figure 6), divided by the Kcal of food energy consumed by the adult birds on that same day (Figure 5). This efficiency was significantly greater for the first 7 days after hatching for those pairs feeding two chicks per nest. From 7 days on no significant difference was evident between the energy-conversion efficiency of the 1- and 2-chick cycles, although the mean efficiency of feeding two chicks per nest was always slightly greater (Figure 7). The rate at which energy-conversion efficiency decreased with increasing age of the nestlings was highly significantly greater for the 2-chick than for the 1-chick cycles.

A modification of the procedure of Brisbin (1965) was used to calculate a single quantitative index of how efficiently each pair of birds converted food energy into nestling biomass throughout the entire growth period of the nestlings. The efficiency index number was calculated as the area under the efficiency-regression curve of each pair (Figure 7). The area under each curve was calculated by dividing it into a series of consecutive trapezoids and summing the areas of these trapezoids over the entire growth period of the nestlings. The efficiency index numbers for the eight pairs studied are given in Table 1.

The mean efficiency index number for the 2-chick cycles was 59.2 per cent greater than the mean for the 1-chick cycles, and this difference was highly significant. If the index number as calculated above is a valid indicator of how efficiently a given pair of birds can convert food energy into nestling biomass, it appears that feeding two chicks per nest instead of only one makes about 60 per cent more efficient utilization of the environmental food resources.

DISCUSSION

Body composition and weight of adult doves.—Most of the studies reported in the literature that have considered weight changes of breeding birds have dealt primarily with small passerines (Kendeigh, 1941, 1963; King et al., 1965; El-Wailly, 1966). These studies found that the body weight of the female undergoes drastic fluctuations, increasing to a maximum at the peak of ovogenesis, and declining sharply after laying. That the Ring Doves showed no such fluctuations was probably due to the fact that the total clutch weight of the Ring Dove is much smaller in relation to the body weight of the female than in the smaller passerines. The two eggs of the Ring Dove weigh about 10 g, or less than 7 per cent of the female's body weight. The 4-egg clutch of the Zebra Finch El-Wailly (1966) studied weighs about 4 g or 33–35 per cent of the female's body weight. Similarly the clutch weight of the House Wren (Kendeigh, 1963) represents over 70 per cent of the female's body weight.

The increase in total body weight shown by the incubating doves is another difference from the studies of smaller passerines, which show no tendency to increase in weight during incubation (see for example El-Wailly, 1966). While this weight increase during incubation may at first appear to be due to the hypertrophy of the crop in preparation for crop-milk production, only a part of this weight increase can be attributed directly to enlargement of the crop itself. Lehrman (1964) indicates that the crop of both male and female Ring Doves increases from a weight of 0.9 g at the time of laying to 3 g at the time of hatching. Thus the increase in crop weights for each pair is about 4 g or 1.34 per cent of the pair's total body weight. The observed weight increase during incubation of 6–8 per cent of total pair weight therefore must be due to other factors besides a simple hypertrophy of the crop alone. As discussed later, a general hydration of body tissues may account for this additional increase in body weight during incubation.

The loss in body weight of the adult doves after hatching seems, in many respects, to be simply a reversal of the processes causing an increase in body weight during incubation, the main factor apparently being a general dehydration of body tissues. In general the 6–8 per cent decrease in body weight of the doves feeding chicks is smaller than most values reported for weight loss of passerines feeding young. Some of these values include: Tree Sparrow, 10–20 per cent (Heydweiler, 1935), Song Sparrow, 9 per cent (Nice, 1937), and Bullfinch, 7–14 per cent (Newton, 1966). King et al (1965) also found a statistically significant decline in lean body weights of breeding White-crowned Sparrows during the feeding of young. Apparently the feeding of young is a more energy-demanding process in these wild passerines than in the captive Ring Doves, which

showed little or no change in lean body weight throughout the breeding cycle. The greater difficulty of obtaining sufficient food in the wild state may help explain this discrepancy.

Perhaps one of the more surprising aspects of this part of the study was that no trend in the fat indices of the adult birds was detectable throughout the breeding cycle. Birds are well known for their ability to mobilize and store fat for coming periods of high energy demands such as migration (see for example Odum and Perkinson, 1951), and adult birds preparing to feed young through an extended nestling period might be expected to store some fat prior to it. Ring Doves apparently store water and not fat prior to hatching for use during the period of feeding nestlings. A possible clue as to why this might be so lies in the composition of the crop-milk.

Patel (1936) describes crop-milk as a thick solution of masses of epithelial cells containing fat globules, sloughed from the wall of the crop. Murton et al. (1963) report the percentage composition of crop-milk as 13.3–18.8 per cent protein, 6.9–12.7 per cent fat, 1.5 per cent ash, and 65–81 per cent water. Since the body tissues of the adult doves average between 10–12 per cent fat and 60–65 per cent water, the loss of 1 g of adult body weight in the form of crop-milk would not cause any proportionately heavy drain on body fat stores, but would put a relatively heavy drain on body water reserves. It should also be remembered that the Ring Dove is native to the dry and semi-arid regions of the eastern Mediterranean (Peters, 1937), where water-availability could easily be a limiting factor to breeding birds that must produce large quantities of crop-milk with a proportionately high water content.

It should be noted that in this situation of fluctuating body water reserves, no constant ratio of water to nonfat materials exists such as has been reported in many migratory birds (Connell et al., 1960; Odum et al., 1964). Farrar (1966) reports this same varying ratio of water to nonfat body weight in captive juncos.

In light of the above findings it is of interest to consider the possible roles of several hormones during the breeding cycle. The role of prolactin in enhancing crop-milk production and crop enlargement during incubation is well documented (Riddle, 1947; Lehrman, 1964). General body weight increments following prolactin injections are also well-known (Miller and Riddle, 1943; Meier and Davis, 1967), and Meier and Farner (1964) found that prolactin-treated White-crowned Sparrows were heavier in all three major body components. Body fat of the sparrows increased 52 per cent after hormone injection, and lean dry weight and body water also increased by 12 and 22 per cent respectively. This 22 per cent increase in the body water of the prolactin-treated sparrows indicates that possibly the observed body-water increments of the incubating doves could

be under prolactin control. Unlike the prolactin-treated sparrows, however, the incubating doves showed no significant increase in the body fat component.

The caloric value of the lean-dry biomass of the adult doves seems to be somewhat higher than corresponding lean-dry caloric values for several species of passerines reported by Odum et al. (1965) and much closer to corresponding values found for lean-dry Mourning Dove biomass, which average 5.14 ± 0.02 (SE) Kcal/g (Brisbin, Ecology, in press). Similarly the live-weight caloric values of the adult Ring Doves also averaged slightly higher than corresponding live-weight caloric values for several species of passerines (summarized by Ricklefs, 1965), as did the live-weight caloric values of the Mourning Doves which averaged 2.61 ± 0.10 (SE) Kcal/g (Brisbin, Ecology, in press). Thus both live and lean dry columbid biomasses apparently tend to average slightly higher in caloric value than corresponding passerine biomass, other factors being equal.

Body composition and weight of nestlings.—The fact that the weights of chicks raised one per nest and those raised two per nest showed no significant difference at any age is in agreement with the findings of Royama (1966) who found no difference in the weights of nestling Great Tits raised in broods varying from three to eight per nest. However Murton et al. (1963) found nestlings from broods of one to be consistently heavier than those from broods of two in wild Wood Pigeons. Limited food resources in the wild probably prevented chicks raised two per nest from receiving enough food to express their maximum growth potential. In captivity where food is provided *ad libitum*, all chicks can apparently express their maximum growth potential whether they are raised one or two per nest. Further support for this hypothesis is provided by Murton et al. (1963) who report that the difference between the weights of 1- and 2-chick broods of Wood Pigeons is not obvious in the very young birds; the difference becomes significant only in the older nestlings. As will be shown later, the young birds are least dependent on environmental food resources for their energy intake early in the nestling period.

The lack of any trend in fat index with increasing age of the dove chicks is consistent with the findings of Ricklefs (1967) for nestling Red-winged Blackbirds and Barn Swallows. The fat indices found by Ricklefs are within the same general range as those for the dove chicks (0.2 to 0.4). Brenner (1964) found that the absolute amount of body fat increased with age in nestling Red-winged Blackbirds, but the amount of fat per gram of body weight showed no definite trend. This same situation exists in the nestling doves. Brenner (1964) goes on to suggest that body fat in nestling birds may serve as an energy reserve for periods when the food is scarce or unavailable to the population, but the consistently low values

of nestling fat indices (about one half those of the adult birds) found in this study and by Ricklefs (1967) do not support this conclusion.

The extremely high water indices of the very young dove chicks are similar in magnitude to the water indices Ricklefs (1967) reported for hatchling Red-winged Blackbirds and Barn Swallows, and are further supported by Riddle (1947) who found that the skeletons of Ring Dove chicks contain about 5 per cent more water than adult skeletons. Royama (1966) also showed a decrease of body water content with increasing age in nestling Bengalee Finches. The tendency of the younger dove chicks, with smaller body size, to have higher water indices is also in line with the findings of Farrar (1966) that in captive juncos birds of a lower lean-dry weight tended to have higher water indices. Variation of fat content had no effect on these trends in water balance, and here again there was no constant ratio between water and nonfat weight.

One of the technically important consequences of the high water content of the very young doves is that it lowers the live biomass caloric values. The calculation of caloric values for live animal biomass is of utmost importance for energy studies of living subjects, but very few such conversion factors are available in the literature. The most commonly cited conversion factor for nestling birds is 2.0 Kcal/g live weight (used for example by Brenner (1964) and by Dawson and Evans (1960)). The caloric values of the 1-day-old dove chicks ranged from 0.72 to 1.10 ($\bar{X} = 0.96$) Kcal/g live weight, and the live-weight caloric values found by Ricklefs (1967) ranged from less than 1.0 Kcal/g for the very young nestling blackbirds and swallows to nearly 2.0 Kcal/g for the older nestlings, thus closely approximating the live-weight caloric values found for the nestling doves in this study. These findings suggest that 1.0, rather than 2.0 Kcal/g live weight is a more accurate conversion factor to use with young nestling birds. There are, of course, dangers in referring the caloric conversion values from one species to another, and this study has further shown that even within a given species, caloric values of the live weight may vary more than twofold simply with increasing age.

Although no significant change in the lean-dry caloric values of the adult or nestling doves was noted throughout the course of the breeding cycle, the mean lean-dry caloric value for all of the adults, considered as a group, is higher than the mean lean-dry caloric value of all the nestlings, considered as a group, the difference between the two means being highly significant. Thus in future studies of birds of this type, lean-dry caloric determinations may possibly be made on a small selected group of individuals from any stage of the breeding cycle, and these values may then be safely applied to all birds sacrificed throughout the breeding cycle, thus greatly reducing the number of necessary caloric determinations that

must be made. These lean-dry caloric values are not interchangeable between adults and nestlings, and must be determined separately for each group.

Energy intake, productivity, and conversion efficiency.—Food-energy intake of the adult birds that were not feeding nestlings averaged 52.8 ± 3.01 (SE) Kcal/bird/day. This value is significantly lower than the mean daily energy intake of wild Mourning Doves, estimated by Schmid (1965) to be 71 Kcal/bird/day. The higher daily caloric intake of the wild Mourning Doves may represent the extra caloric cost of living in the wild state as opposed to captivity, other factors being equal.

The food-energy intake of the breeding doves exhibited no significant differences during the courting and incubating phases of the cycle, which is in general agreement with the findings of Riddle and Braucher (1933) who found that 14 out of 24 pairs of doves and pigeons showed a slight decrease in food consumption during incubation, while the other 10 pairs showed a slight increase. El-Wailly (1966) found that incubating Zebra Finches showed a significantly higher caloric intake during incubation.

The effect of prolactin in the incubating adult may again be considered here in that Miller and Riddle (1943) and Schooley et al. (1941) have shown that prolactin injections can cause an increase in the food consumption of hypophysectomized pigeons. The failure of the incubating doves to show such an increase is an indication of the difference of results obtained from hormone injections into hypophysectomized birds and those obtained from birds undergoing a normal breeding cycle. The presence or lack of synchrony with various required synergists (see Bates et al., 1962) may help explain this difference.

The caloric intake of the parents does not increase significantly until 5 to 10 days after the young hatch (Figure 5). During this period the weight of the parent birds declines significantly (Figure 1) and, energetically speaking, the nestlings may be considered as being cannibalistic, consuming energy stored in parental biomass. Thus the young make no additional impact on the environmental food resources until they are 5 to 10 days old, and the parent birds may be thought of as "energy buffers" imposed between the environmental food resources and the growing nestlings. The adaptive advantages of such a system are obvious: it assures a constant energy supply to the nestlings during the critical first few days of life and acts to lessen the harmful effects of any temporary failure of environmental food resources.

This study has shown that the total caloric cost of raising a chick from hatching to maturity is lower for two chicks per nest than for only one. Royama (1966) found this same phenomenon in nestling Great Tits, which had higher food-consumption rates per chick in small broods than in large

ones. Royama (1966) speculates that larger brood sizes provide a more favorable thermodynamic situation for each individual chick, thus reducing the caloric costs of maintaining body temperature. This same factor could easily apply to the dove chicks with the same results, and could further help explain how doves raising two chicks per nest were able to make 60 per cent more efficient use of environmental food calories than those raising only one per nest.

Lack (1956) and Murton et al. (1963) suggest that natural selection will favor the brood size best adjusted to the availability of environmental food energy. This study and that of Royama (1966) indicate that not only the availability of environmental food energy, but also the efficiency with which that energy is used are important factors in determining brood size.

Finally the energy budget of an incubating pair of Ring Doves may be calculated using the data presented here together with literature estimates of the several parameters not actually measured in this study. Riddle et al. (1930) found the basal metabolic rate of nonbreeding Ring Doves to be 4.5 Kcal/150 g body weight/4 hours (data rounded off to the nearest 0.5 Kcal), at temperatures comparable to those experienced by the doves in this study. Assuming 300 grams as the average weight of a pair of birds gives an average basal metabolic rate of 54/Kcal/pair/day.

Riddle et al. (1933) have shown that the basal metabolism of the female Ring Dove is the same during incubation as during the nonbreeding period (4.5 Kcal/150 g body weight/4 hours), but the basal metabolism of the male dove is depressed by 10 per cent during incubation to 4.0 Kcal/150 g body weight/4 hours. The basal metabolism of the incubating pair is, therefore, 4.5 + 4.0 Kcal/300 g body weight/4 hours, or about 51 Kcal/pair/day. The available productive energy of the incubating pair is the basal metabolism of the nonbreeding pair minus the basal metabolism of the incubating pair, or $54 - 51 = 3$ Kcal/pair/day. Thus a total of $15 \times 3 = 45$ Kcal of productive energy is available throughout the 15 days of incubation to each pair of birds. As shown above, the breeding pairs increase their total body weight by about 7 per cent during incubation, which means a total production of about 21 g of adult biomass (7 per cent of 300 g). Laboratory analyses have shown the caloric value of this biomass to be 2.26 Kcal/g (Figure 2), and thus the total biomass production of each incubating pair is $21 \text{ g} \times 2.26 \text{ Kcal/g} = 47$ Kcal. The close agreement of this figure with the 45 Kcal of available productive energy calculated from Riddle's data indicates that most if not all the available productive energy of the incubating pair is stored as biomass increment.

Riddle et al. (1933) attribute the reduction in basal metabolism of the

incubating male dove to his greater inactivity during this period. In light of the findings herein, this greater inactivity may be considered as an energy-conserving device, freeing about 45 Kcal of productive energy which is then stored in the form of a biomass increment in the parent birds. After the young hatch, this 45 Kcal of stored energy allows the parent birds to act as energy buffers, freeing the nestlings from any close dependency on environmental food resources for about the first week of life.

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SUMMARY

Changes in food intake, body weight, carcass composition, and caloric density were studied throughout the breeding cycle in both nestling and adult Ring Doves. Cycles raising one chick per nest were compared with those raising two.

During the incubation period adult birds showed a 6-7 per cent increase in total body weight associated with an increase in body water. A corresponding decrease of 6-7 per cent in total body weight was accompanied by a decrease in body water while the adults were feeding nestlings. Body fat and the caloric values of live and lean-dry adult biomass did not change throughout the cycle. Apparently an adequate water reserve during the breeding cycle is more critical than a reserve of stored fat for the Ring Dove, a native of dry and semi-arid areas.

At no time during the breeding cycle was any significant difference apparent in the weights of adults or nestlings attributable to raising one or two chicks per nest.

Fat indices (g fat/g lean-dry weight) of the nestlings were about half those of the adults and did not change with age. Water indices (g water/g lean-dry weight) were very high (5.57-8.62) in young nestlings and decreased curvilinearly with increasing age.

Lean-dry nestling biomass showed no change in caloric value, but the caloric value of live nestling biomass increased as a linear function of increasing age. The live-weight caloric value of the younger nestlings was closer to 1.0 Kcal/g than to the 2.0 Kcal/g usually cited in the literature.

The food intake of the adult birds showed no significant change until after the nestlings were 5 days old. Prior to this time food intake averaged 105.7 ± 6.0 (SE) Kcal/pair/day, there being no difference between the food intake of pairs raising one and two chicks per nest. The parent birds thus use their biomass reserves to free the nestlings from any direct dependency on environmental food resources during the first 5 days of life.

The total number of calories required to raise one chick from hatching to independence, over and above the standard caloric intake of the non-breeding adults, was 1134.9 and 922.5 Kcal for those chicks raised one and two per nest respectively.

Nestling productivity, in terms of Kcal of biomass gained per day, increased to a maximum at 6 days of age and then declined steadily throughout the remainder of the nestling period. The productivity was higher for nests containing two chicks until 20 days, after which no difference in productivity was evident between nests containing one and two chicks.

The efficiency of conversion of food energy into nestling biomass declined throughout the nestling period from an initial high of 10–15 per cent. Calculation of an efficiency index indicated that pairs raising two chicks per nest made about 60 per cent more efficient use of environmental food energy than those raising one per nest.

LITERATURE CITED

- BATES, R. W., R. A. MILLER, AND W. A. GOATES. 1962. Evidence in the hypophysectomized pigeon of a synergism among prolactin, growth hormone, thyroxine and prednisone upon weight of body, digestive tract, kidney and fat stores. *Endocrinology*, 71: 345–360.
- BALDWIN, S. P., AND S. C. KENDEIGH. 1938. Variations in the weight of birds. *Auk*, 55: 416–467.
- BRENNER, F. J. 1964. Growth, fat deposition and development of endothermy in nestling Red-winged Blackbirds. *J. Sci. Lab. Dennison Univ.*, 46: Art. 5.
- BRISBIN, I. L., JR. 1965. A quantitative analysis of ecological growth efficiency in the Herring Gull. Unpublished M. S. thesis, Athens, Univ. Georgia.
- BRISBIN, I. L., JR. 1968. A determination of the caloric density and major body components of large birds. *Ecology*, 49: 792–794.
- CONNELL, C. E., E. P. ODUM, AND H. W. KALE. 1960. Fat-free weights of birds. *Auk*, 77: 1–9.
- CUTBERT, N. L. 1945. The ovarian cycle in the Ring Dove (*Streptopelia risoria*). *J. Morphol.*, 77: 351–372.
- DAVIES, O. L. 1947. Statistical evaluation of growth curves. *Proc. Soc. Exp. Biol. Med.*, 66: 567–568.
- DAWSON, W. R., AND F. C. EVANS. 1960. Relation of growth and development to temperature regulation in nestling Vesper Sparrows. *Condor*, 62: 329–340.

- EL-WAILLY, A. J. 1966. Energy requirements for egg-laying and incubation in the Zebra Finch. *Condor*, 68: 582-594.
- FARRAR, R. B. 1966. Lean dry weight and water balance in Slate-colored Juncos. *Auk*, 83: 616-623.
- GIFFORD, C. E., AND E. P. ODUM. 1965. Bioenergetics of lipid deposition in the Bobolink, a transequatorial migrant. *Condor*, 67: 383-403.
- HEYDWEILER, A. M. 1935. A comparison of winter and summer territories and seasonal variations of the Tree Sparrow (*Spizella a. arborea*). *Bird-Banding*, 6: 1-11.
- KENDEIGH, S. C. 1941. Length of day and energy requirements for gonad development and egg-laying in birds. *Ecology*, 22: 237-246.
- KENDEIGH, S. C. 1963. Thermodynamics of incubation in the House Wren (*Troglodytes aedon*). *Proc. 13th Intern. Orn. Congr.*, 884-904.
- KING, J. R., D. S. FARNER, AND M. L. MORTON. 1965. The lipid reserves of White-crowned Sparrows on the breeding ground in central Alaska. *Auk*, 82: 236-252.
- LACK, D. 1956. Variations in the reproductive rates of birds. *Proc. Roy. Soc. London, Ser. B*, 145: 329-333.
- LEHRMAN, D. S. 1955. The physiological basis of parental feeding behavior in the Ring Dove. *Behavior*, 7: 241-286.
- LEHRMAN, D. S. 1964. The reproductive behavior of Ring Doves. *Sci. Amer.*, 211: 48-54.
- MEIER, A. H., AND K. B. DAVIS. 1967. Diurnal variations of the fattening response to prolactin in the White-throated Sparrow (*Zonotrichia albicollis*). *Gen. Comp. Endocrinol.*, 81: 110-114.
- MEIER, A. H., AND D. S. FARNER. 1964. A possible endocrine basis for premigratory fattening in the White-crowned Sparrow (*Zonotrichia leucophrys gambelli*). *Gen. Comp. Endocrinol.*, 4: 584-595.
- MILLER, R. A., AND O. RIDDLE. 1943. Ability of adrenal cortical hormones, prolactin and thyroxine to sustain weight of body and viscera of hypophysectomized pigeons. *Endocrinology*, 32: 463-474.
- MILLER, W. J., AND L. S. MILLER. 1958. Synopsis of behavior traits of the Ring Dove. *Anim. Behav.*, 6: 3-8.
- MILLER, W. J., AND F. H. WAGNER. 1955. Sexing mature Columbiformes by cloacal characteristics. *Auk*, 72: 279-285.
- MURTON, R. K., A. J. ISAACSON, AND N. J. WESTWOOD. 1963. The food and growth of nestling Wood Pigeons in relation to the breeding season. *Proc. Zool. Soc. London*, 141: 747-781.
- NEWTON, I. 1966. Fluctuations in the weights of Bullfinches. *Brit. Birds*, 59: 89-100.
- NICE, M. M. 1937. Studies in the life history of the Song Sparrow I. *Trans. Linn. Soc. New York*, 4: 1-247.
- ODUM, E. P., AND J. D. PERKINSON, JR. 1951. Relation of lipid metabolism to migration in birds: seasonal variation in body lipids of the migratory White-throated Sparrow. *Physiol. Zool.*, 24: 216-230.
- ODUM, E. P., S. G. MARSHALL, AND T. G. MARPLES. 1965. The caloric content of migrating birds. *Ecology*, 46: 901-904.
- ODUM, E. P., D. T. ROGERS, AND D. L. HICKS. 1964. Homeostasis of the nonfat components of migrating birds. *Science*, 143: 1037-1039.
- PATEL, M. D. 1936. The physiology of the formation of "pigeon's milk." *Physiol. Zool.*, 9: 129-152.

- PETERS, J. L. 1937. Check-list of birds of the world, vol. 3. Cambridge, Massachusetts, Harvard Univ. Press.
- RICKLEFS, R. E. 1967. Relative growth, body constituents, and energy content of nestling Barn Swallows and Red-winged Blackbirds. *Auk*, 84: 560-570.
- RIDDLE, O. 1928. Studies on the physiology of reproduction in birds XXIII. Growth of gonads and bursa fabricii in doves and pigeons, with data for body growth and age at maturity. *Amer. J. Physiol.*, 86: 248-265.
- RIDDLE, O. 1947. Endocrines and constitution in doves and pigeons. Carnegie Inst. Washington, Publ. 572.
- RIDDLE, O., AND P. F. BRAUCHER. 1933. Studies on the physiology of reproduction in birds XXXIII. Body size changes in doves and pigeons incident to stages of the reproductive cycle. *Amer. J. Physiol.*, 107: 343-347.
- RIDDLE, O., G. CHRISTMAN, AND F. G. BENEDICT. 1930. Differential response of male and female Ring Doves to metabolism measurement at higher and lower temperatures. *Amer. J. Physiol.*, 95: 111-120.
- RIDDLE, O., T. C. NUSSMAN, AND F. G. BENEDICT. 1932. Metabolism during growth in a common pigeon. *Amer. J. Physiol.*, 101: 251-259.
- RIDDLE, O., G. C. SMITH, AND F. G. BENEDICT. 1933. Studies on the physiology of reproduction in birds XXXII. Basal metabolism and the temperature factor in brooding Ring Doves. *Amer. J. Physiol.*, 105: 428-433.
- ROGERS, D. T., AND E. P. ODUM. 1964. Effect of age, sex and level of fat deposition on major body components in some wood warblers. *Auk*, 81: 505-513.
- ROYAMA, T. 1966. Factors governing feeding rate, food requirement and brood size of nestling Great Tits, *Parus major*. *Ibis*, 108: 313-347.
- SCHOOLEY, R. K., O. RIDDLE, AND R. W. BATES. 1941. Replacement therapy in hypophysectomized juvenal pigeons. *Amer. J. Anat.*, 69: 123-154.
- SCHMID, W. D. 1965. Energy intake of the Mourning Dove, *Zenaidura macroura marginella*. *Science*, 150: 1171-1172.

Institute of Ecology, University of Georgia, Athens, Georgia. Mailing address: Savannah River Ecology Laboratory, Bldg. 772-G, U. S. Atomic Energy Commission, Savannah River Operations Office, Aiken, South Carolina 29801.