D. C. THOMPSON AND D. A. BOAG

The molt in birds requires the expenditure of energy (Kendeigh 1949). The timing of the molt, relative to other activities, has been interpreted as an adaptation to minimize the energy drain on the bird (Payne 1972). The magnitude of the energy drain during molting appears to vary among species. Davis (1955) was unable to detect a significant increase in the level of metabolizable energy intake during the molt of *Passer domesticus*, whereas West (1962) reported a 27% increase in the intake of metabolizable energy by *Spizella arborea* for a period of one week during the molt.

Metabolic rate increases during molting. Autumnal molting in domestic fowl (Gallus gallus) has been shown to increase the standard metabolic rate by 30% over levels shown during the laying periods (Perek and Sulman 1945). Wallgren (1954) reported a 14% increase in standard metabolic rate during the post-nuptial molt of Emberiza citrinella and 26% in Emberiza hortulana. Payne (1972) stated that in most species of songbirds the metabolic rate increases from 5 to 30% above the rate of nonmolting birds. A major cause of the increased energy drain during molting results from loss of heat from highly vascularized feather papillae and increased surface area exposed to cool temperatures (Irving 1964, Payne 1972).

Blackmore (1969) suggested, however, that at low temperatures, House Sparrows (*Passer domesticus*) may save enough energy through increased insulative effectiveness, as the result of denser plumage, to balance that expended during the molt. Thus the molt would affect the overall energy balance only slightly.

The purpose of our study was to investigate energy consumption by caged Japanese Quail during molt at a low temperature. These data were collected from January to April 1973.

METHODS

Four male Japanese Quail (*Coturnix coturnix*) approximately 6 weeks of age, were placed in individual $8 \times 12 \times 12$ inch wire cages in a controlled environment chamber. They were induced to molt by lowering the ambient temperature of the chamber from approximately 22° C to $3.0 \pm 1.0^{\circ}$ C over the

period of one week. Subsequently the temperature was held constant at the lower value. The photoperiod was maintained at 12 hr light-12 hr dark throughout, with no attempt to imitate twilight.

The birds were provided with both high protein (26%) and low protein (16%) commercial ration. An outside feeding trough was divided in such a way that records of food consumption could be obtained for each bird. The amount of each type of ration consumed was determined to the nearest 0.1 g three times per week. Spillage was reduced by the addition of a lip on the inside of the trough and food that spilled was collected and weighed separately.

Droppings, deposited on waxed papers placed under each cage, were collected three times weekly, dried for 2 days at 50° C and weighed to the nearest 0.1 g.

Calorific determinations were made with a Parr Adiabatic Oxygen Bomb Calorimeter. Since the intestinal and cecal feees of gallinaceous birds differ in energy content (Pendergast and Boag 1971) all droppings collected during a given time period were ground together prior to analysis. Calorific content of droppings from each quail was measured for four time periods: at the beginning of the experiment, at the peak of molting, at a time randomly selected during the course of the experiment, and on the penultimate day of the experiment.

Metabolizable energy was calculated from the following equation:

M.E. = I - E

where M.E. = metabolizable energy; I = energy intake as food; E = energy lost in excreta. All energy values were averaged for weekly periods through the course of the experiment. In all cases the unit of energy used was the kilocalorie.

Metabolic rate, as reflected in oxygen consumption, was measured in an open circuit respirometer using a Beckman F-3 Paramagnetic Oxygen Analyser connected to a Mosely 680 strip chart recorder. Quail were housed in an animal chamber made from a one-gallon paint can. Ambient temperature was measured by a thermister probe (Yellow Springs Instrument Company) in the chamber. The chamber was housed in a controlled temperature cabinet. All oxygen consumption determinations were made at $-10.0 \pm 0.5^{\circ}$ C. Air supply to the quail was kept constant at 600 cc/min throughout the experiment. Water vapor and carbon dioxide were removed from outlet air by filtering through Drierite and Ascarite (Fisher Scientific Company).

All metabolic determinations were made over the period of 3 hr. For each determination the minimal oxygen consumption value, recorded over at least 10 continuous min, was used in the calculations. The methods of Depocas and Hart (1957) were used in calculations. All measurements were corrected to standard temperature and pressure.



FIGURE 1. Metabolized energy based on four Japanese Quail held at 3°C during molting. Mean, range, and two standard errors shown.

Each quail was tested for oxygen consumption at least once a week, at approximately the same time of day. Trials were conducted between 0900 and 1600 hr. The quail were not starved prior to testing.

The molt was dated from day 0, the first day of a period of sustained feather loss. All data were ordered with respect to day 0, negative days indicating days prior to the start of feather loss.

Student's t-test was used to compare the mean values obtained during the experiment. Significance was set at the 5% level.

RESULTS

The period of feather loss extended for approximately 28 days. The time interval between a change in environmental conditions at the beginning of the experiment and the initiation of feather loss varied from 31 to 43 days with a mean value of 39 days. Feather loss was greatest during the first 10 days and gradually declined until no feathers were lost on or after day 29. Rectrices, remiges, and virtually all body feathers were lost and replaced.

The calorific content of the food was determined to be 4.242 kcal/g (ration with 26% protein) and 3.832 kcal/g (ration with 16% protein). As no difference was found between calorific values of wastes of various individuals at different periods during the experiment a combined mean of 2.943 kcal/g for wastes was used in the calculation of metabolizable energy throughout the experiment.

Energy consumption, as indicated by metabolizable energy, increased during molting (fig. 1). To consider the significance of this change, the experiment was divided into three periods with respect to energy consumption: premolt (all days prior to day 0), peak molt (day 12 to 33) and postmolt (day 55 to the termination of the experiment).

During the premolt period, metabolizable energy averaged 54.6 kcal/bird/day (table 1). This amount increased to 68.2 kcal/bird/day during the peak molt period, then dropped to 50.5 kcal/bird/day in the postmolt period. The value recorded during peak molt was significantly greater than that recorded in either the premolt or postmolt periods, and the levels recorded during the premolt, although not significantly different from those recorded during the postmolt period, were, nevertheless, greater.

The intake of crude protein also changed during the experimental period (fig. 2). This involved a significant increase from 29.26 g of crude protein per week during the premolt period to 34.24 g per week during the peak molt period, an increase of 17%. The premolt and postmolt values were not significantly different.

TABLE 1. Changes in metabolized energy over the period of molt in Japanese Quail—based on 4 quail held at 3°C.

Stage of Molt		Metabolized energy (kcal/bird/day ± S.E.)
Premolt		54.6 ± 2.9
Molt	Day 1-7	56.7 ± 3.1
	8-14	51.8 ± 2.5
	15-21	57.9 ± 0.4
	22-28	68.2 ± 2.6 Mean molt 59.72
	29-35	67.2 ± 4.3
	36-42	63.2 ± 5.5
	43-49	56.7 ± 3.8
	50-56	55.5 ± 3.1
Postmolt		50.5 ± 3.9
Mean pre- and		
postmolt		52.55
Increase during molt		7.17
Total energy expended		
during molt		394.35 kcal/bird



FIGURE 2. Gross protein intake based on four Japanese Quail held at 3°C during molting. Mean, range, and two standard errors shown.

During the molting period the weekly body weights of individual quail varied more than during either the pre- or postmolt periods. There was, however, no net change in body weight during the experiment, the premolt mean $(128.8 \pm 3.6 \text{ g})$ was not significantly different from the postmolt mean $(130.3 \pm 3.2 \text{ g})$.

The total cost of the molt can be determined through summation of metabolizable energy values over and above the base lines established during the premolt and postmolting periods. This is approximated by the area under the curve of figure 1. The values for metabolizable energy during the pre- and postmolt periods were similar, averaging 52.55 kcal/bird/day. The total metabolizable energy during the molt averaged 59.72 kcal/ bird/day (Table 1). Thus, at 3°C an average of 7.17 kcal/bird/day (13.6%) was expended over and above the maintenance requirements. This resulted in a total of 394.35 kcal/bird expended over the 55 days of the molt (table 1).

Metabolic rate, as reflected in the oxygen consumption, also showed a marked change during molting (fig. 3). During the premolt period oxygen consumption tended to fall. This may reflect an acclimation to lowered temperature. The premolt values were about 2.10 cc O_2/g body weight/hr; however, because of their great variability, they were not compared with values for other periods. There was a rapid increase in oxygen consumption after molting began; all birds reached peak values within 14 days of initiation of feather loss. Oxygen consumption during the peak molt period averaged 3.48 cc O_2/g body weight/hr. The decline following this peak was relatively gradual; however, all birds reached their lowest value by day 55. The postmolt mean value of 2.11 cc O_2/g body weight/hr was significantly less than the peak molt mean of 3.48 cc O_2/g body



FIGURE 3. Oxygen consumption based on four Japanese Quail at -10° C during molting. Symbols represent individual birds.

weight/hr but probably not different from the premolt value.

DISCUSSION

Molting probably was initiated as the result of changed housing conditions, especially the decreased temperature regime. Fenna (1972) also has recorded molting in Japanese quail subjected to a decrease in temperature, independent of time of year.

Molting in quail apparently affects the energy balance of this species for a period of 55 days under the conditions described. Although feather loss occurred for only 28 days, the energy metabolized (fig. 1) and metabolic rate (fig. 3) remained above premolting levels until day 55, both reaching their final values within a day of each other. The 27 days following cessation of feather loss and prior to the stabilization of energy requirements likely represent the time required for full feather regrowth.

When compared with the premolt period the maximum increase in the metabolizable energy during the peak molt period was 24.9%. This value lies within the range of 5-30% suggested by Payne (1972) as representing the enery cost of molting in most species.

There appear to be two main routes leading to increased energy drain during the molt: the cost of production of the new plumage, and the heat lost from the greater exposure of the highly vascularized feather papillae.

Blackmore (1969) showed that, at 32° C, approximately 8.6% of the daily energy requirements of the House Sparrow are used in molting. At this temperature little, if any, energy would be lost to thermoregulation, and thus is a good estimate of the cost of plumage replacement. This value is slightly greater than the 7.6% calculated by King and Farner (1961) as the cost of replacing only the body

feathers. Among the Japanese Quail in this study the average daily increase in metabolizable energy during the molt was 7.17 kcal/ bird/day. If 8.6% of the mean daily energy requirements of molting birds (59.72 kcal) are lost to keratinization (5.14 kcal/bird/day) some 2.03 kcal/bird/day were lost to thermoregulation. Under the conditions reported here, one might expect the energy cost of feather replacement in Japanese Quail to be minimal as we could not be sure that every body feather was replaced. As for energy drain through loss of insulative efficiency during the molt, the presumed lower level of activity of caged birds would be expected to decrease energy loss below that of birds in the wild. On the other hand, the hirds were housed at a temperature well below that of thermoneutrality (Freeman 1967). This would be expected to increase the energy loss from the surface of the skin of molting birds. To what extent these various factors were compensatory is unknown. Thus energy costs of plumage replacements should be considered minimal and energy costs to thermoregulation as approximate.

Blackmore (1966) showed an increase in the rate of nitrogen metabolism during the molt in *Passer domesticus*. This would appear to be the result of increased protein requirements for the growth of feathers. The increase of 17% in crude protein intake noted in this experiment is probably a result of the elevated requirement for metabolizable energy rather than an expression of the true increase in protein requirements. The maximum increase in metabolizable energy was 24.9%, but the birds did not appear to be selecting for the higher protein pellets. Any increase in protein requirements was likely more than covered by the extra protein obtained through a concomitant increase in food consumption in response to the increase in energy requirements.

Blackmore (1969) suggested that, at low temperatures, *Passer domesticus* may save enough energy, through increased effectiveness of insulation combined with a brief molting period, to recover that expended during molting. Our data do not appear to support his conclusion as far as caged Japanese Quail are concerned. The energy requirements of quail before and after molting were not significantly different, although a larger sample size may have shown the lower postmolt energy requirements to have been real. Since no significant weight change was noted through the course of the experiment, the birds must have been feeding at approximately existence levels. Thus, without a change in pre- and postmolt energy requirements, any energy used during the molt would have been lost to the birds.

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Department of Zoology, University of Alberta, Edmonton, Alberta. Accepted for publication 28 August 1974.