The aim of this paper is to examine the relationship between the progress of postjuvenal molt in the European Tree Sparrow (*Passer m. montanus*) and the accompanying changes in weight and body composition: water, dry weight, fat, lean dry weight, ash, and caloric value. Most papers using this approach deal with migratory birds and are usually limited to the study of body weight and fat variations; only rarely do they consider lean weights (Odum and Perkinson 1951; King and Farner 1959, 1966; Blyumental 1961, 1967; King 1963; King et al. 1965; Zimmerman 1965; Blyumental et al. 1966; Dolnik 1967a, b, c, and others). There have been fewer studies of resident species (Williamson 1956; Dolnik 1967a, b, d), and there are only a few papers analyzing the body composition of populations living in the wild (Turček 1960; Odum et al. 1964; King et al. 1965; Helms et al. 1967; Szwykowski, in press). Only Newton (1968) using Bullfinches (*Pyrrhula pyrrhula*) has so far analyzed in detail the variations in water, fat, and lean dry weight in relation to the stage of molt.

European Tree Sparrows are resident in central Poland and only a small per cent of juveniles disperse within a radius of 6-8 km (Pinowski 1965a). During the molt period they are found in flocks on fields where they feed almost exclusively on weed seeds (Pinowski and Wojcik 1968, 1969). The molt is closely followed by a period of intensive autumn sexual behavior (Pielowski and Pinowski 1962; Pinowski 1965b, 1967).

Birds for analysis were anesthetized with chloroform soon after capture, weighed to the nearest 0.01 g, their molt described, their gullet and stomach contents removed, and then weighed again. The gullet and stomach contents, after the removal of grit, were dried to constant weight and weighed to the nearest 0.0001 g. After removal of gullet and stomach contents, bodies were dried to constant weight in a vacuum desiccator at 40-50°C. Water content of the bodies of the sparrows was calculated from the difference in body weights before and after drying. The data thus obtained enabled us to calculate the caloric value of 1 g dry weight, the caloric value of 1 g ash-free dry weight, and of 1 g live weight.

The ash content in the bodies of the birds investigated was calculated from the difference in sample weights before and after burning them in the calorimeter. The amount of fat in the bodies of sparrows was determined with the method known variously as "Puzanov's," or "Besson and Hamon's," or "Besson's" (Krauze et al. 1966). It entails a double extraction of the material which is placed in glass vessels with porous glass bottoms, first with a steam of petroleum ether with 10 per cent ethyl alcohol added, and then with condensate solvent. The time of extraction was fixed at 3 hr, after it had been found that further drying and extracting resulted in no change in the weight of the sample analyzed.

In 1966, 38 Tree Sparrows were captured and their plumage removed. After drying to constant weight, it was weighed to the nearest 0.0001 g. The caloric value of plumage was investigated for different stages of molt.

THE MOLT

Both juvenile and adult European Tree Sparrows have a complete molt. The molting season of the population as a whole lasts from the end of July to mid-October (Deckert 1962; Dolnik 1967a; Pinowski 1968), but juveniles from the first broods start earlier and molt more slowly than do those from later broods (Deckert 1962; Pinowski 1968).

The following scores (after Newton 1966) were used in recording the state of molt of individual feathers: old feather, 0; feather missing or in small pin stage, 1; feather in large pin or brush stage, 2; feather brush to half-grown,
3; feather half to three-quarters grown, 4; and feather three-quarters to full length, 5.

For purposes of analysis, the molt was later divided into 18 steps according to the molt in the primaries, and apportioned to the following five phases (see figs. 2, 4, and 5).

Phase 1: from the juvenal plumage to the shedding of primaries 1 (innermost), 2, and 3, and growth to stage 4 of primary 3; greater wing-coverts also in molt.

Phase 2: from the end of phase 1 to the growth of the primary 5 to stage 4; besides primaries and wing-coverts, the secondaries, medium and lesser coverts, scapulars, and feathers of the dorsal and ventral tracts also in molt, but the new feathers only at stage 2.

Phase 3: from the end of phase 2 to the growth of the primary 7 to stage 4; this is the period when the body feathers grow most intensively and the rectrices are replaced, from the middle to the extremes.

Phase 4: from the end of phase 3 to the growth of the last primary to stage 4; this is the period when most feathers are in stages 3–5, and the intensity of their growth decreases as they reach full length (Newton 1967).

Phase 5: birds fully molted.

The sequence of molt in European Tree Sparrows is similar, as a rule, to the molt of the House Sparrow, *Passer domesticus* (Zeidler 1966). A comparison of the molt of 42 European Tree Sparrows and of 313 House Sparrows in 1968 showed that the former first replace their middle rectrices and only later

FIGURE 1. Carcass composition of European Tree Sparrows at different phases of postjuvenal molt.

WEIGHTS DURING MOLT

European Tree Sparrows maintained body weight in the period of the most intensive shedding of feathers in phase 2 of molt (fig. 1, table 1). The loss of feathers was offset, to a considerable degree, by an increase in fat deposition (figs. 1 and 2). The weight increase in the ensuing periods was apparently due to an increase in water content (phase 3), and to the growth of new feathers (figs. 1, 2, and table 1). Other authors have also found a small rise in weight during molt in passerines and a slight loss towards the end (Baldwin and Kendeigh 1938; Putzig 1939; Newton 1966, 1968; and others). King and Farner (1966) recorded, however, a considerable increase in the body weight of male White-crowned Sparrows (*Zonotrichia leucophrys gambelii*) near the end of molt, but this was associated with the deposition of migratory fat.

WATER CONTENT

The water content of European Tree Sparrows was highest during the period of the most intensive growth of the body feathers, but fell again during the growth of the barbs (fig. 1, table 1). Similarly, although there is no change in the proportion of water in the carcasses (minus feathers) of Bullfinches during molt, the water content in the feathers alone increases considerably and can amount to 7 per cent of the total water content of the bird (Newton 1968).

Lillie (1940) pointed out that the weight of
TABLE 1. Carcass composition (mean g ± 95% confidence interval) of European Tree Sparrows at different phases of postjuvenal molt (percentages in parentheses).

<table>
<thead>
<tr>
<th>Molt phase</th>
<th>No. of birds</th>
<th>Weight of birds</th>
<th>Water content</th>
<th>Dry weight</th>
<th>Fat content</th>
<th>Lean dry weight</th>
<th>Ash content</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>7</td>
<td>22.56 ± 1.7</td>
<td>(66.5)</td>
<td>7.31 ± 0.33</td>
<td>1.422 ± 0.232</td>
<td>5.850 ± 0.280</td>
<td>0.767 ± 0.095</td>
</tr>
<tr>
<td>2</td>
<td>15</td>
<td>22.53 ± 0.90</td>
<td>(65.9)</td>
<td>7.50 ± 0.39</td>
<td>1.703 ± 0.965</td>
<td>5.870 ± 0.540</td>
<td>0.795 ± 0.060</td>
</tr>
<tr>
<td>3</td>
<td>11</td>
<td>23.74 ± 0.74</td>
<td>(66.2)</td>
<td>7.83 ± 0.42</td>
<td>1.540 ± 0.229</td>
<td>6.213 ± 0.370</td>
<td>0.815 ± 0.115</td>
</tr>
<tr>
<td>4</td>
<td>8</td>
<td>23.38 ± 1.45</td>
<td>(64.0)</td>
<td>8.16 ± 0.35</td>
<td>1.367 ± 0.173</td>
<td>6.680 ± 1.560</td>
<td>0.818 ± 0.195</td>
</tr>
<tr>
<td>5</td>
<td>19</td>
<td>23.34 ± 0.79</td>
<td>(62.4)</td>
<td>8.37 ± 0.32</td>
<td>1.425 ± 0.211</td>
<td>6.998 ± 0.700</td>
<td>0.916 ± 0.154</td>
</tr>
</tbody>
</table>

Growing feathers in domestic hens exceeds three times the weight of the plumage after molt, and that the weight of feather pulp (93 per cent water) can reach 25 per cent of the total body weight. Dolnik (1967a) stated that molt is characterized by a considerable retention of water, as compared with the other periods of life. Our data, however, show that changes in the total water content of European Tree Sparrows during molt were small. The water content in the feathers of 10 fully molted European Tree Sparrows caught on 27-28 October amounted to 12-15 per cent.

**FAT CONTENT**

The fat content increased just before the most intensive stage of molt, when the primaries and body plumage are replaced (phase 2), and fell after this period. Fat level was lowest near the end of molt and started rising thereafter (fig. 1, table 1).

The fat content in the annual cycle is smallest during molt both in migratory and resident birds (Odum and Perkinson 1951; King and Farner 1959; Zimmerman 1965; Dolnik and Blyumental 1967; Dolnik 1967a; and others). Williamson (1956) could not detect any relationship between fat content and the molt of the Anna Hummingbird (*Calypte anna*).

Newton (1968) provided evidence for variations in the fat content of juvenile Bullfinches during molt analogous to those we recorded in European Tree Sparrows (fig. 3). On the other hand, during the molt of adult Bullfinches, there was a continual increase in the fat content. Mainly protein and carbohydrate metabolism was recorded during molt (Dolnik 1967a), but, according to our data, there was a deposition of fat just before the period of the most intensive metabolism, during which the fat is rapidly used up. This would have been very difficult to record in a less detailed study. Dolnik (1967a) described the annual cycle of the fat content of European Tree Sparrows, and, as in other species, the fat was low during molt compared with other times of year.

**LEAN DRY MATERIAL**

The lean dry content increased during molt, particularly in phases 3 and 4 (fig. 1, table 1), during the growth of the new feathers (fig. 2). Newton (1968) recorded in the plumage-free body of juvenile Bullfinches the

![Figure 3](image-url)
reverse trend in the lean dry weight, which increased in the first phases of molt and declined during the intensive growth of feathers, only to increase again after the end of molt. It follows from the comparison of our data for European Tree Sparrows (with feathers) with those of Bullfinches (without feathers) that the increase in the lean dry content occurs first in the bird's body, and its further increase is due to the growth of feathers (figs. 1, 2). This initial increase in the lean dry material of the body is offset by the intensive shedding of feathers in this period (fig. 2).

ASH CONTENT

The ash content increased during molt (fig. 1, table 1). As feathers are almost entirely composed of keratin, they leave almost no mineral parts, and when burnt in a macrobomb, the ash content is very small indeed. The increase in the ash during molt, therefore, was presumably due to the mineralization of juveniles' skeletons. The ash content (mean g ± 95% confidence interval) in juvenile European Tree Sparrows, 14 days old and just before leaving the nest, amounts to 0.483 ± 0.115 (Myrcha and Pinowski 1969), while in adult males it amounts to 0.923 ± 0.119. In spite of a similar stage of molt the juveniles caught might have differed in age, and consequently there were no significant variations in the ash content. The long period of time between the captures of 5 September and 23–26 October, when the birds were fully molted (phase 5), contributed to the increase in the ash content between different phases of molt. These data indicate that the deciding factor here is the mineralization of bones progressing with age, and not stage of molt. In chicks, the most intensive phase of mineralization occurs in their first month of life, but even at 90 days the young do not have their bones fully mineralized (Anorova 1965; Bauman 1968). The growth of the House Sparrow's skull takes more than 200 days (Ruprecht 1968), while the ossification of the House Sparrow's skull (Nero 1951) and that of the European Tree Sparrow (Danilov 1964) takes at least as long.

DRY WEIGHT

The dry weight of European Tree Sparrows increased steadily during molt (figs. 1, 4, and table 1), due mainly to the increase in lean dry weight. An initial increase in the fat content compensated for the loss of lean dry material caused by the shedding of the old feathers. The juvenal plumage before molt weighed only 0.77 g, 51 per cent of the weight (1.5 g) of the dry plumage after the end of molt on 26–28 October (see fig. 2). Similar figures on plumage weights were given by Korelus (1947): adult birds in spring, 1.56 g; juveniles just after leaving the nest, 0.94 g. Thus the plumage weighs 61 per cent as much in juveniles as in adults. Juvenile body feathers differ from those of the adult in being weaker, looser in texture, and having fewer barbs and barbules (Korelus, 1947; Van Tyne and Berger 1959:96; Newton 1968).

CALORIC VALUE

The caloric value of 1 g of homogenized fresh tissue from European Tree Sparrows increased

<table>
<thead>
<tr>
<th>Molt phase</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
</tr>
<tr>
<td>No. of birds</td>
</tr>
<tr>
<td>Biomass</td>
</tr>
<tr>
<td>Dry mass</td>
</tr>
<tr>
<td>Ash-free dry mass</td>
</tr>
</tbody>
</table>
steadily during molt, particularly from phase 3. At the same time there was a decrease in the caloric value of 1 g of the ash-free dry material (table 2). The decrease in the value of this latter index was due to the utilization of fat. A simultaneous and quite considerable increase in the caloric value of the new tissues was caused by a decrease in the relative water content in the body during the last phases of molt due to the completion of the growth of feathers. This is in agreement with the reports of other authors who state that the caloric value of the tissue, not only of birds but also of mammals, depends primarily on the water content, and secondarily on the fat content (Górecki 1965; Myrcha 1968, 1969; Szywykowska, in press). Szywykowska (in press) recorded a considerable slowing in the rate of increase in the caloric value of partridges (Perdix perdix) during molt (June–September), connected with a drop in the fat content of the body. At the same time the proportion of protein in their bodies increased considerably due to the growth of feathers.

The caloric value of the dry mass of the sparrows studied here approximates the value given by Odum et al. (1965) and Szywykowska (in press) for other non-migratory birds, but is somewhat lower than the values recorded by Kale (1965) for the Long-billed Marsh Wren (Telmatodytes palustris griseus).

The caloric value of 1 g of dry European Tree Sparrow plumage did not vary during molt. This index (mean cal ± 95% confidence interval), however, was characterized by considerable individual variation (4543 ± 1003). The caloric value of the primaries and rectrices of fully molted birds was somewhat higher (5622 ± 227) than the caloric value of the feathers of the dorsal and ventral tracts (5291 ± 356).

MOLT IN RELATION TO ANNUAL CYCLE

After molt, European Tree Sparrows start their autumn sexual behavior, when they pair, copulate, occupy nest-holes, and build their nests which will thereafter be used as a roosting place in winter, and as a breeding site in the spring (Pinowski 1965b, 1966, 1967, 1968; Pielowski and Pinowski 1962). The earlier they end their molt (and hence are sexually active) the better chance they stand of occupying a better tree-hole and pairing off. Although the young from later broods molt more rapidly than those from the earlier broods (see Pinowski 1965b, 1967, 1968; Blyumental 1967; Dolnik 1967a, c), they still finish molting and become sexually active 4–6 weeks later, and so stand less chance of gaining a good site. On the basis of data from Kendeigh (1934) and Davis (1955), King and Farner (1961) calculated that the metabolism of the House Sparrow increases during molt by only 7.6 per cent. During molt, European Tree Sparrows feed on weed seeds which are then plentiful and easily accessible. Nevertheless the amount of food in the gullet and stomach of roosting birds varies and decreases as the molt progresses (fig. 5). The cause is still unclear, as birds feed together in a flock and, as a rule, within the same field, so that they have available the same supply of food for the same time. There is no relationship between the total body weight and the amount of food in the gullet and stomach (Pinowski and Wójcik, in prep.). However, it seems possible that the rate of molt is set, not by the total amount of food eaten, but by the quantity in the diet of certain limiting components required for feather synthesis, which might be insufficiently

![Figure 5. Dry weight of food in the gullet and stomach of European Tree Sparrows at different phases of the postjuvenal molt.](attachment:image.png)
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LITERATURE CITED


OUDM, E. P., AND J. D. PERKINSON, JR. 1951. Relation of lipid metabolism to migration in birds.


PINOWSKI, J. 1965b. Overcrowding as one of the causes of dispersal of young Tree Sparrows. Bird Study 12:27-33.


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