ECOLOGICAL ASPECTS OF MIGRATION, AND PRE-MIGRATORY FAT DEPOSITION IN THE LESSER REDPOLL, *CARDUELIS FLAMMEA CABARET*

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This paper is a sequel to an earlier paper on the Lesser Redpoll (Evans 1966a), in which I discussed the timing of its annual (post-nuptial) molt in relation to the timing of breeding and autumn migration and described variations in the total weights of birds during late summer and autumn. This paper extends two facets of the previous work: (1) movements of Redpolls in relation to food, particularly the seed crop of birch (*Betula*), and (2) weight changes, which are re-assessed in the light of analyses of body composition and fat content during molt, prior to and during migration, and on the wintering grounds. Unless otherwise stated, all references to Redpolls refer to the small British race *Carduelis flammea cabaret*, which breeds chiefly in northern Britain and winters usually in southern Britain, the Low Countries of Europe, and parts of western Germany (Evans 1966a; Erard 1966; Mohr 1967).[1]

The Redpoll is of both ecological and physiological interest in that during most of the year it is able to live almost exclusively on the seeds of birch trees, and that only when birch is unobtainable does it turn to the seeds of other (herbaceous) plant species. In late summer and autumn the most important alternative foods are seeds of meadowsweet (*Filipendula ulmaria*), rosebay (*Chamaenerion angustifolium*), and greater willow-herb (*Epilobium hirsutum*). The sizes of the seed crops of these three plants (as of most herbaceous plants) vary much less from year to year than do those of trees such as birch, which often show an approximately biennial pattern of heavy fruiting (table 2). The Redpoll's preference for, and dependence on, birch seed as its main food in Scandinavia has been stressed by Svärdson (1957), Peiponen (1957, 1962) and Evans et al. (1967), and in Britain by Evans (1966a) and Newton (1967a). The first half of the present paper describes the effects of variations in food availability on the habits of Redpolls during the parts of their annual cycle from the end of breeding until the following spring, and is based on fieldwork carried out in three areas: Roughtinglinn (near Ford) and Craster, both in Northumberland (fig. 1) in northern England (55½°N), and Wytham, Berkshire, about three miles from Oxford in southern England (51½°N). Roughtinglinn is an area of damp birch woodland, surrounded by young conifer plantations, in the foothills of the Cheviot Hills. Under the birches there is a good growth of meadowsweet and in clearings, dense stands of rosebay. The study area at Craster lies just inland from the coastal village, and is an area of rough and often wet ground (formerly partly cultivated) on both sides of a stream. Tall willows (*Salix*) border the stream, and the damp ground is covered by meadowsweet and greater willow-herb, while the areas formerly cultivated are largely overgrown with rosebay. The woodland at Wytham contains predominately mature oak (*Quercus robur*), but the area in which Redpolls occur (Marley Wood) also has scattered clumps of birches on the edge of some treeless areas, whose ground vegetation contains meadowsweet and willow-herbs. Thus all three areas contain the same important food plants, except that Craster has no birch trees.

Other areas in north Northumberland at about 55½°N (e.g., inland in birch woods near Wooler and Chatton, and on the coast near Bamburgh, Seahouses, Newton, and Howick, fig. 1) were visited regularly, but although they held one or more of the preferred food plants, Redpolls were rarely found there. It is not clear why the areas at Roughtinglinn and Craster were particularly favored by the birds, except that they provide food in a sheltered position, fresh water, extensive cover close to the feeding areas, and roosting places nearby.

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[1] Editor's note: In the A. O. U. Check-lists (1957, Fifth ed.) and in other North American literature this species is referred to as the Common Redpoll, *Acanthis flammea*.

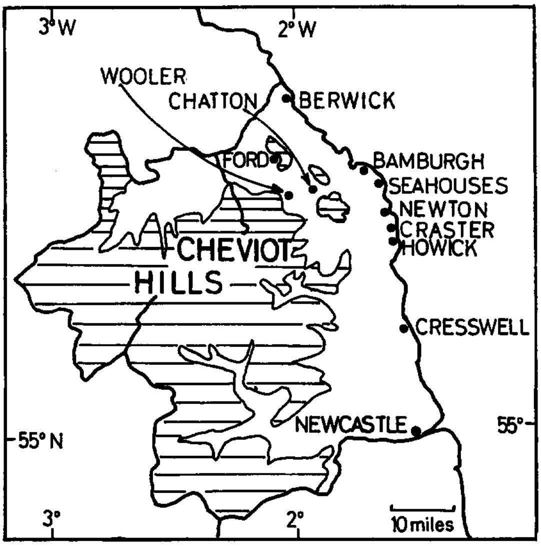

FIGURE 1. Northumberland, England, with localities mentioned in the text. (The county of Roxburghshire, Scotland, is also shown, to the northwest of Northumberland.) Land over 500 ft is shaded.

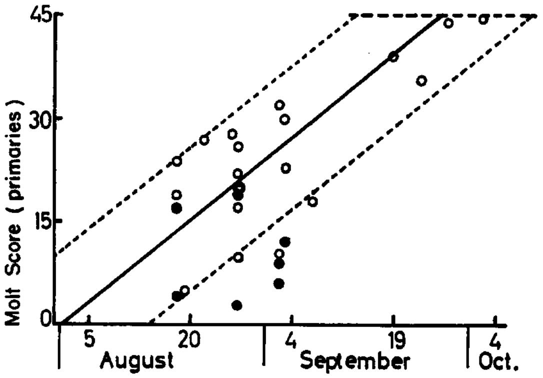

FIGURE 2. Molt scores of Redpolls caught in Northumberland in 1965. Open circles = males; filled circles = females. The regression line and 95 per cent limits for the molt scores in 1964 are also shown. It will be noted that several 1965 scores are much lower than those on the corresponding date in 1964, i.e., molt started later in 1965.

TERMINATION OF BREEDING

In northern England, Redpolls may be found breeding between May and late July, which, if the first nesting is successful, allows them to rear a second brood. Most adults begin their 6–8 week molt as their last young reach independence. Thus the end of their breeding season in any one year may be measured with reasonable accuracy by establishing (by methods outlined in my earlier paper) the average date on which their molt starts. This varies slightly from year to year. For example, in Northumberland, molt began, on the average, on 11 August in 1963, but 10 days earlier in 1964 (Evans 1966a); in 1965 the limited data (fig. 2) suggest a later start than in 1964. The birch seed crops in the Cheviots in these three years (assessed roughly by the proportion of trees bearing seed and the amount of seed carried per tree) were moderate, poor, and good, respectively. Thus molt began earlier and the breeding season was slightly curtailed in the year in which there was a poor birch crop. This might have been expected, for, when available, birch seeds may form an important part of the diet of nestling Redpolls in England (Newton 1967a), while in Finmark nestling Mealy Redpolls (*C. f. flammea*) are fed almost entirely on seeds of dwarf birch (*Betula nana*) until these cease to be available (Peiponen 1962).

The variation in timing of the end of the Redpoll's breeding season is, however, slight compared with that of the Bullfinch (*Pyrrhula pyrrhula*) which in southern England may extend its breeding and delay molt by more than two months if conditions are particularly favorable (Newton 1966). However, the Bullfinch is a sedentary species in Britain, while the Redpoll migrates at much the same date each autumn, and since adult Redpolls complete their molt between breeding and migration, their breeding season cannot be extended appreciably if the date of departure is fixed. Although there is insufficient information to show conclusively that adult Redpolls molt slightly more rapidly in autumns with good than poor crops of birch seed, the data for 1963 and 1964 fit such a hypothesis (as would be expected if breeding continues slightly later in good birch years).

MOVEMENTS JUST BEFORE AND DURING MOLT

It is necessary to consider separately the movements of adults and of juveniles during this period, since the latter move more. They can do this because they replace only body (not wing and tail) feathers in August and September, so their flight efficiency is not impeded, whereas that of the adults may be.

Inland at Roughtinglinn, flocks of juvenile Redpolls build up steadily during late summer, but the size of these flocks and their length of stay are dependent on the amount of birch seed available. In 1965 when the

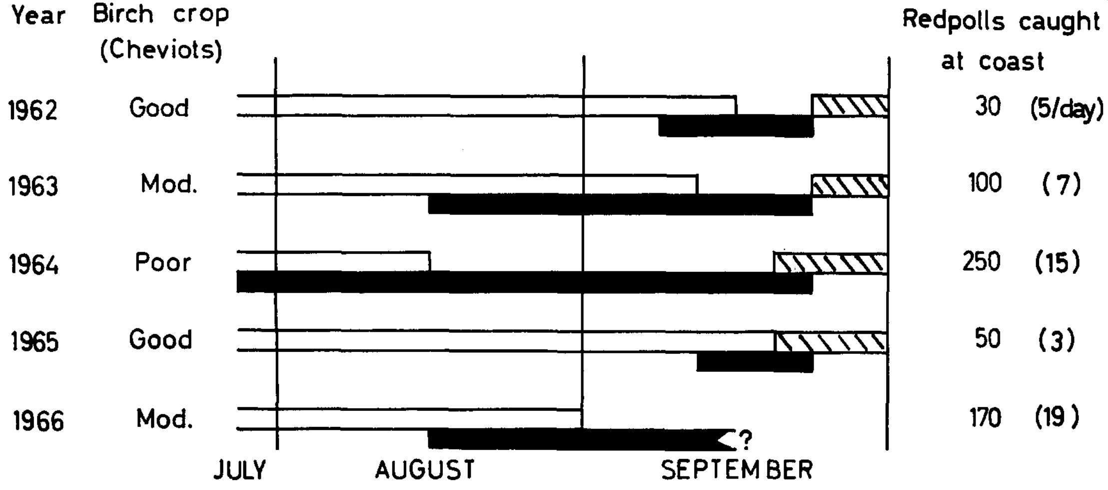

FIGURE 3. Birch crops and the movements of Redpolls within Northumberland in different years. Open bar = Redpolls present at Roughtinglinn (inland); filled bar = Redpolls present at Craster (coast); shaded bar = movements south along the coast. Numerals at the right of the figure are the numbers of birds caught, and the numbers trapped per day, between late July and the end of September (trapping ceased in mid-September in 1966).

birch crop was good, large flocks stayed until late September; the highest numbers (about 400) were recorded in the middle of that month. They fed exclusively on birch seed on the trees, ignoring the heavy crops of ripening meadowsweet seeds below, and descending only to drink. In 1964 when the birch crop failed, most juveniles left Roughtinglinn by late July, and the few which stayed fed on meadowsweet seeds which were ignored in years with good birch crops. The meadowsweet crop lasted in 1964 only until late August, after which most of the remaining juvenile Redpolls left the area. A very few stayed, as did the adults which were molting there, and these turned to a diet of rosebay and/or greater willow-herb seeds, which ripen slightly later than meadowsweet. In other years both the birch crops and the dates to which the juveniles stayed at Roughtinglinn were intermediate between those in 1964 and 1965, and are summarized diagrammatically in figure 3. This figure also shows the dates of the main arrival of juvenile Redpolls each year at the coastal study area at Craster (about 20 mi. SE of Roughtinglinn), and, as may be seen, birds arrived early in years when they left Roughtinglinn early (years when the Cheviot birch crop was poor) and vice versa.

At Craster many (if not all) of the adult Redpolls which began their molt there in early August stayed until it was completed in late September, as shown by birds retrapped several times during this period; none was retrapped elsewhere. In most autumns the number of adults caught at Craster considerably exceeded the estimated size of the local breeding population, so some adults had evidently moved in just before they began molt. One recovery supports this: a female ringed at Cresswell (17 mi. S) on 28 May (during the breeding season) was recaught at Craster on 25 August, while molting. (The reasons for the autumn concentrations of molting birds at Craster were considered in my earlier paper.) In contrast to the behavior of the adults, the arrivals and subsequent movements of juveniles were closely dependent on local changes in availability of certain foods. As there is no birch, all the birds at Craster took meadowsweet seeds as their preferred food while the crop lasted. When all of this was eaten, the adults stayed but changed to a diet of willow-herb seeds (as at Roughtinglinn), while most of the juveniles departed, at least some to another large area of uneaten meadowsweet, two miles south at Howick.

In September 1965 juveniles were netted from flocks feeding at Roughtinglinn and Craster and transported to Seahouses (14 mi. ESE and 9 mi. NNW respectively) to see if on release they would return to these two important feeding areas. On 12 September, 24 and then 17 birds from Roughtinglinn were released at the coast at Seahouses. Immediately on release each flock flew west towards Roughtinglinn but broke up a few seconds afterwards. Thereafter, single birds or small groups flew in many directions (except seawards), but none of the birds was recaptured later among a further 30 birds caught at Roughtinglinn or 210 birds caught elsewhere that autumn. Similarly three birds taken from Craster on 23 September were not recaught among a further 95 birds netted there that autumn, though one was recovered 2 mi. N of Seahouses a few days after release. Thus juvenile Redpolls either have no strong attachment to particular feeding area or cannot home to it. Since some juveniles return to Craster in later years, after migration, the former explanation is probably correct.

As mentioned above, in the five autumns studied, large numbers of Redpolls, chiefly juveniles, arrived at Craster at some time in August or September, though their main arrival date varied from year to year, depending on the size of the birch crop in the Cheviot Hills nearby. Some local movements of juveniles occurred when the meadowsweet crop was exhausted. Nevertheless, in all five years the main departure on southward migration of all the Redpolls from Craster took place in the last week of September, irrespective of the availability of the preferred foods. In confirmation, the main passage of Redpolls further south on the east coast of England at Spurn, Yorkshire, and the first arrivals at Wytham in southern England, occurred in late September in these five years (Yorkshire Naturalists' Union Ornithological Reports 1962–66; I. Newton, pers. comm.).

AUTUMN MIGRATION

MIGRATION PATTERN

In autumn, many, if not most, of the Redpolls breeding in northern Britain move south through England, and some cross the English Channel into Holland, Belgium, and parts of France and Germany. The numbers of birds migrating to the European continent vary from year to year, at least in part in relation to the abundance of birch seed in England, as will be shown later. In most years some Redpolls of the race *cabaret* winter as far east as the Rhine-Main-Nahe area (8–9°E). Although these might include birds which had bred in the Alps (where the Redpolls are morphologically very similar to *C. f. cabaret*), recoveries of birds ringed in Germany in winter (Mohr 1967) indicate that most of them reach Germany through Belgium in autumn, and so probably come from Britain. (In confirmation, a bird recovered near Frankfurt/Main in February 1966 had been ringed in Northumberland in September 1965.) Redpolls of the race *cabaret* also occur regularly in winter in the forests of the extreme north and northeast of France (Erard 1966), but are seen further south only occasionally. The most southerly recoveries to date of Redpolls ringed in Britain were in the Rhone Valley, at 45°N in November 1959 and at 44½°N and 43½°N in February and March 1965, but in both winters some Redpolls (*C. f. cabaret*) also reached the Iberian peninsula (Erard 1966). British-ringed Redpolls are caught in Belgium each autumn, but in varying numbers, and marked annual fluctuations also occur in the number of *C. f. cabaret* captured in Holland, though as yet few British-ringed birds have been recovered there. Maps of the recoveries of British Redpolls were given by Evans (1966a).

To summarize, the southeastward migration of Redpolls from Britain may involve movements of up to 500–600 miles in most years, but sometimes considerably further and sometimes less. Such distances are of course small by comparison with the long-distance migrations of some small insectivorous passerines. Nonetheless, considerable fat reserves (at least 2 g) would be required if the movements were to take place as nonstop flights. Information on this latter point is almost impossible to obtain. Recoveries of ringed birds can give only maximum journey times, but these suggest that Redpolls from northern Britain reach the general area in which they will winter within a week or two. Thus they probably make the journey as a series of short southward flights, stopping each day to feed when suitable food sources are reached. In support of this, 25 Redpolls, ringed in late September and October in parts of southeastern England where the species is not known to breed, have been recovered a few days or weeks later in Belgium.

ADVANTAGES OF MIGRATION

Lesser Redpolls are partial migrants; some birds remain to winter in northern Britain in areas where the species also breeds, while others move south and then southeast away from the breeding grounds. In this way the high population of late summer is spread over much larger feeding grounds in autumn and winter. However, it is not known whether an individual which migrates in one year migrates every year of its life, though recoveries of ringed birds suggest that at least some do. Six Redpolls ringed in southern England (where they do not breed) in the months of December, January, and February were recovered in Belgium in later autumns.

Those birds which move south (particularly those which reach southern England or the

Low Countries) gain the advantages of longer days, shorter nights, and almost untouched birch crops. The effect of longer days is both to increase the birds' potential feeding time and to reduce the length of night for which they have to accumulate a food reserve. Some advantages of moving south from 57°N to 51° N are shown in figure 4. However, since in at least some years, some Redpolls remain through the winter in northern Britain, there must also be disadvantages in moving south from the breeding areas. Among these are the necessity to find suitable feeding areas en route (particularly as the fat reserves for migration are small) and the massive bird-catching industry in Belgium in October and early November (which annually removes several million finches to provide cage-birds, and has provided most of the recoveries of Redpolls ringed in Britain). As I suggested earlier (Evans 1966a), the importance of finding suitable feeding areas en route may possibly explain why juvenile Redpolls migrate with adults even though some juveniles have finished molt several weeks earlier. The birch crops reached by migrant Redpolls may be taken in part by Bullfinches (chiefly in winter, Newton 1967b), though not to an important extent. In years when birch is scarce, Redpolls may have to take other foods, but the birds' movements are much more closely related to the birch crop than to other food supplies. For example, among the tree seeds which might be taken, only those of alder (*Alnus*) are available throughout the winter and are small enough for Redpolls; however in southern England, Newton (1967a) noted that in a winter when birch seeds were not available but alder seeds were plentiful, few Redpolls stayed in his study area. On the other hand, he noted that alder seeds were preferred to those of birch by wintering Siskins (*Carduelis spinus*). Also, in Finland the heavier-billed Mealy Redpoll took about equal proportions of birch and alder seeds in its diet in the one winter for which data are available (Peiponen 1962).

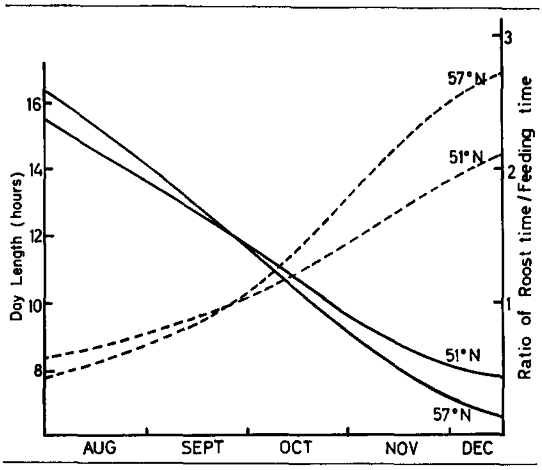

FIGURE 4. Decreases in daylength (sunrise to sunset) in autumn at different latitudes (solid lines), and corresponding increase in the ratio of time spent roosting to maximum possible time for feeding (dashed lines).

Redpolls which stayed in northern Britain in winters with poor birch crops could take the seeds of herbaceous plants, but these are more likely to be covered by snow, and hence unavailable, than seeds remaining on trees, which can be taken in almost all weather conditions. Thus heavy mortality of non-migrant birds would be expected in poor birch years, particularly in those with prolonged snow cover. Indeed, it might be thought most advantageous for Redpolls to stay in years of good birch crops and to move south whenever the crops are poor, but this speculation is untested.

It may be noted that those birds which winter in southern England, and more particularly those which winter on the continent of Europe, would not experience appreciably warmer weather than those which stay in northern Britain (table 1). Since all winter temperatures to which Redpolls are exposed in Britain are below their presumed thermo-

TABLE 1. Temperatures[a] (°C) in the wintering range of Lesser Redpolls.

	Dec.		Jan.		Feb.	
	Max.	Min.	Max.	Min.	Max.	Min.
Aberdeen (57°N 2°W)	6.0	2.0	5.0	0.5	6.0	0.5
Glasgow (56°N 4°W)	6.5	2.0	6.0	1.5	6.5	1.5
York (54°N 1°W)	6.0	3.0	6.0	1.5	6.5	1.5
London (51½°N 0°W)	7.0	3.0	7.0	3.0	7.0	2.5
Brussels (51°N 4°E)	5.5	0.5	5.5	−0.5	6.0	−0.5
Frankfurt (50°N 9°E)	4.0	−0.5	3.0	−1.5	5.5	−0.5

[a] These are long-term average temperatures; the British data refer to 35-year averages and are given to the nearest 0.5°C.

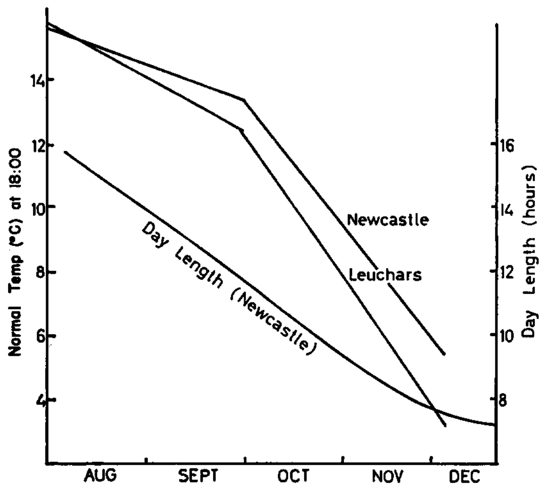

FIGURE 5. Decrease in temperature at 18:00 with date at two weather stations on the northeast coast of Britain: Newcastle (55°N) and Leuchars (56½°N), about 100 miles apart. The temperature data are based on 7-year averages.

neutral zone (the lower critical temperature of newly-caught *C. f. flammea* in Norway in winter was about 10°C; Steen 1958) they could have reduced their daily food requirements by wintering in warmer areas, but clearly they have not done so. Probably it would have required movement beyond the southern limit of distribution of birch, which hardly reaches the Iberian peninsula or Mediterranean Europe (Vedel and Lange 1960).

TIMING OF MIGRATION

At first sight there seems no good reason why most Redpolls should leave northern Britain each year as early as the end of September, particularly as abundant food was available in October and later in some years, both in the Cheviot birchwoods and at the coast. Migration in advance of the failure of food is well known in insectivorous birds, whose food is always least available in the northern winter, but it has not been emphasized in discussions of the movements of seed-eating species. In these species migration at a fixed date would be least expected, since the abundance of their food may fluctuate markedly from year to year, and thus also the date to which food remains available varies.

As shown in my earlier paper, adult Redpolls leave Northumberland as soon as they have finished their wing molt. Indeed, in 1961 and 1963 when males molted slightly faster on average than females, the first groups to depart contained chiefly males (Evans 1966a). In contrast, the juveniles left at the same time as the adults in all years, even though some had finished molt as much as two weeks earlier. However, the timing of migration cannot have been evolved to occur in late September primarily because the adults finished molt then, for molt could have been timed to occur much later, particularly in those years in which food was abundant. Other factors must determine that migration should take place then, and breeding must end in time to permit molt. Birds late to complete molt may delay migration slightly to avoid flying with missing or growing secondaries (Evans 1966a). It is extremely rare, in Britain, to catch migrating passerines of any species in wing-molt, although in Finland and Russia Chaffinches and other migrants at high latitudes apparently begin migration while molting (Dolnik and Blyumental 1967), and high-Arctic waders arriving in northern England in July and August have been found with primaries in molt (Chapman 1907).

In the Redpoll, timing of migration is probably related chiefly to the ease with which energy reserves for short migratory flights can be accumulated at different dates in autumn. Since the diet of the Redpoll is restricted chiefly to one type of seed, and its food intake per hour is limited by its feeding efficiency, the rate at which it can store energy will depend on time available for feeding, time lost in roosting, environmental temperature, and perhaps other subsidiary factors.

Temperature data for northern Britain in figure 5 show that temperatures fall from late summer onward, but more rapidly after the end of September. For this reason, each day's delay after early October makes energy storage steadily more difficult to achieve by comparison with a similar delay earlier in the season. The potential daily food intake is also reduced as the hours of daylight shorten, and after the autumnal equinox (23 September), daylength shortens more rapidly in northern Britain than in the south. Hence if a Redpoll were faced with food shortage in late autumn or winter, it would have less chance of accumulating fat for movement (to search for other feeding areas) if it had stayed in northern Britain than if it had moved south earlier in the autumn. Also, irrespective of the availability of food, a Redpoll which had to move at some time during the autumn or winter could deposit the necessary fat reserves most easily up to the end of September, and with progressively greater difficulty thereafter, particularly since daily movement would reduce potential feeding time.

DISTANCES TRAVELED IN RELATION TO FOOD SUPPLIES

Some species of long-distance migrants have been shown to travel between constant breeding grounds in Britain (where they are chiefly insectivorous) and constant wintering grounds in Africa (references in Evans 1966b). Similar information is not available for most seed-eating species, most of which move (if at all) much shorter distances from their breeding areas in Britain. However, I have shown earlier (Evans 1966a) that some Redpolls returned to the same breeding area near Craster (from which they are totally absent in winter) in subsequent summers, and that in several cases individuals returned to molt at Craster each year. There are as yet only two examples of individuals wintering, both in Germany, in the same area in successive years (Mohr 1967). Such behavior may not be common, if only because the numbers wintering in any one locality fluctuate markedly from year to year. Also, the six recoveries quoted earlier (p. 319) indicated wintering in southern England one year but in Belgium the next. However, individuals may possibly move south by the same route each year, as suggested by the recovery of a Redpoll, ringed at Craster in August 1962, at Rumes, Belgium, in November 1963 and then again at Rumes in October 1966.

As mentioned in my earlier paper, there is some evidence that the average distance moved by British Redpolls in each year is related to food availability, for the number of recoveries on the European continent of ringed British-bred birds is usually high in those years when the birch crop in southern England is poor, and vice versa. The recoveries come chiefly from Belgium during the bird-catching season, which extends for six weeks from 1 October, and they include birds in transit as well as potential winterers. It is now possible to examine the correlation over 11 years, and the results are presented in table 2. It was noted earlier that migration enables the high number of Redpolls in late summer to distribute themselves over larger feeding grounds in autumn and winter than if they had remained in the breeding range. Thus one might reasonably expect that the average distance moved might be related not only to food abundance but also to the population size after the breeding season.

TABLE 2. Birch crops and Lesser Redpoll emigration.

Year	Redpolls ringed	Birch pollen fall (% of avg.)	Winter[b] recoveries on the continent	
			Number[c]	Percentage[c]
1957	137	63	3	2.20
1958	170	142	1	—
1959	343	18	4	1.17
1960	476	157	0	—
1961	607	69	15	1.81
1962	840	28[a]	2	0.24
1963	922	359	6	0.11
1964	2369	26	31	0.97
1965	1984	59	30	0.91
1966	1884	75	32	0.78
1967	1935	175	16	0.46

[a] Reported in error as 375 in Evans (1966a).

[b] Winter refers to that season occurring at the end of the calendar year in the first column and extending into the following calendar year.

[c] The recovery percentages are calculated from the number of Redpolls ringed in a given year and recovered in the winter immediately following ringing. The numbers recovered refer to all Redpoll recoveries reported in a given winter, irrespective of the year in which the birds were ringed.

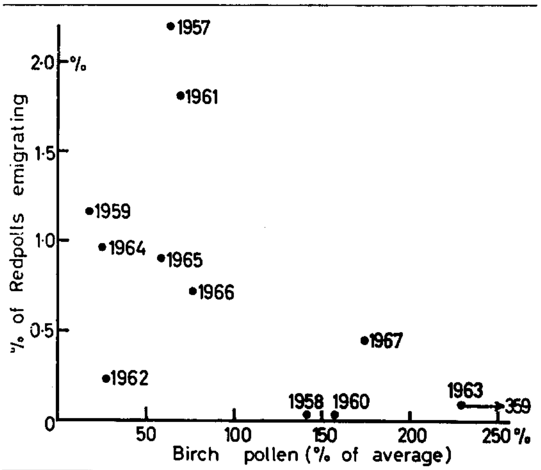

FIGURE 6. Emigration of Lesser Redpolls from England related to birch seed crops in southern England in the years 1957–67. The seed crops are those predicted from pollen fall (Hyde 1963; in litt.), expressed as percentages of the average pollen fall. Emigration has been assessed by the number of recoveries on the European continent (chiefly Belgium) in autumn and winter, expressed as a percentage of the number of Redpolls ringed in Britain earlier during the year.

It has proved impossible to assess accurately fluctuations from year to year in the size of the early autumn population, though the sudden rise in numbers ringed in 1964 (table 2), together with many reports of Redpolls moving by day in eastern England that autumn, and the large numbers caught at Craster (fig. 3) all point to a very high population in that year. (Before 1962, numbers ringed per annum cannot be used as a reliable guide to population size, as the use of mist-nets was not general in Britain before that date, and they are by far the most effective traps for Redpolls.)

Figure 6 shows in general an inverse relationship between the size of the birch crop in southern England (as estimated by pollen fall, Hyde 1963; in litt.) and the percentage of British-ringed Redpolls recovered beyond southern England. Certain limitations in the data on which figure 6 is based must be borne in mind. Although there is usually a good correlation between the size of the pollen fall in spring (late April and early May) and the subsequent autumn seed crop, late spring frosts could devastate a potentially good crop, and such might have affected the anomalously high 1963 figures. Since most of the recoveries are from Belgium, it must be assumed that the chance of capture of a Redpoll reaching Belgium is the same from year to year. However, it seems likely that in the two years (1959 and 1964) when the birch crop in southern England was very poor, and when Redpolls reached as far south as southern France and Spain, they may have passed through Belgium more quickly than in other years. In support of this, the numbers recovered in the first week of October compared to the rest of the month were 8:8 (1964), 1:15 (1965) and 3:16 (1966). These differences are significant (1964 vs. 1965: $\chi^2 = 7.8$, 1 df, $p < 0.01$; 1964 vs. 1966: $\chi^2 = 4.8$, 1 df, $p < 0.05$). Thus birds may have moved through unusually quickly in 1964. Such an effect would reduce the apparent emigration percentage.

Allowing for these limitations, the general picture of poor birch crop, high emigration, seems tenable. (No explanation can be given of the anomalously low emigration in 1962 since it is not known whether the population was very low in this year.) When the data are split into years with birch pollen fall above 75 and below 70 per cent of average (table 2), there was significantly more emigration in poor birch years than in good (mean per cent of emigration = 1.22 ± 0.31 and 0.27 ± 0.15, respectively; $t = 3.5$, $p < 0.01$). This indicates that those Redpolls which move south in autumn each year from their breeding areas in northern Britain move on until they reach abundant food supplies. In support of this, data collected in Wytham Woods, Berkshire (I. Newton, pers. comm.) have shown that while in several years the size of the birch crop there did not correspond to the estimate for the average crop over southern England (table 3), the numbers of Redpolls wintering in Wytham were much more closely correlated with the size of the birch crop there than with the countrywide estimate. When the crop in Wytham was good, some individuals were known to have stayed through the winter from the time of their arrival in September and October until at least February, as proved by retraps. On the other hand, in 1965 when the birch crop was rather poor, a Redpoll trapped on 4 October did not stay in Wytham, but moved on southeast to Belgium where it was recovered 11 days later. Even in years of good birch crops in Wytham some Redpolls move out of the woods in January, when most of the seed falls from the trees, but others remain to feed on the ground beneath the trees. The ideas outlined above on autumn movement and food supply are similar to those of Svärdson (1957), who studied the movements of Siskins in Scandinavia, although he was concerned chiefly with east-west rather than north-south movements and did not know when birds left their breeding areas. The behavior of Redpolls in Britain now allows the species to be classed as an irruptive migrant (Ulfstrand 1963).

IRRUPTIVE MOVEMENTS AND THEIR CONSEQUENCES

While Lesser Redpolls are regular winter visitors to Belgium, southern Holland, extreme north France, and certain areas of western Germany, they occur outside these areas occasionally (notably to the south, in France).

TABLE 3. Birch seed crops and wintering areas of Lesser Redpolls.

	Southern England[b]			Wytham[c]	
Year	Birch pollen fall (% of avg.)	Presumed birch seed crop	Redpoll emigration (%)	Birch seed crop	Redpolls wintering
1961	69	Mod.	1.81	Nil	None
1962	28[a]	Poor	0.24	Good	Many
1963	359	V. good	0.11	Mod.	Some/many
1964	26	Poor	0.97	Mod./good	Many
1965	59	Mod.	0.91	Poor/mod.	Some
1966	75	Mod.	0.74	Good	Some/many

[a] Reported in error as 375 in Evans (1966a).

[b] Data for southern England as in table 2.

[c] Categories of winter abundance in Wytham: some = few tens; many = few hundreds.

Erard (1966) has documented two such invasions, in the autumns of 1959 and 1964, respectively, the former definitely, and the latter probably, reaching Iberia. These were years of extremely poor birch crops in southern England. The 1964 invasion may also have followed a high breeding success in northern Britain, as large numbers of birds were seen moving down the east coast of England in late September that year (Davis 1964). After the invasion of autumn 1959, Redpolls of the race *cabaret* established themselves as breeding birds in the Frisian Islands, Holland, in 1960 (Blok and Spaans 1962), and a juvenile ringed on the east coast of England during the large emigration of September 1964 was caught on the Frisian Islands in July 1965, and may well have bred there. Perhaps the isolated Alpine breeding populations of Redpolls, which are morphologically very similar to the British race, were established in a similiar manner, rather than by remaining in the coniferous zone when this retreated up the mountains after the last glaciation, as suggested by most authors (summarized by Voous 1960). Even if the Alpine Redpolls were originally a relict population, they may have been supplemented at intervals by invasions of British birds.

PREMIGRATORY FAT DEPOSITION AND BODY COMPOSITION

Even a short migration requires that birds gather food in excess of their normal metabolic needs and store the surplus energy prior to flight. This is done most economically as fat (rather than glycogen), and most migrants lay down deposits of fat subcutaneously and increase in total weight. The extent of fat deposition before migration in Lesser Redpolls was uncertain, as I recorded in my earlier paper that there was little or no increase in the total body weight of Northumberland birds before they departed. To obtain further information it was necessary to determine the body composition of birds for several weeks prior to migration and again after their movement south. Accordingly 76 specimens (15 adults) were taken in Northumberland in August and September 1965, and 37 (9 adults) in Wytham Woods near Oxford in October and November 1966, under license from the Nature Conservancy. For each specimen, weights of dry plumage, fat, water, and lean dry material were determined by standard methods (Odum 1960).

Since Redpolls were in molt for up to eight weeks prior to migration, this study incidentally provides information on changes in body composition during molt. It will be shown that Redpolls normally lay down small fat stores during the day to provide the necessary maintenance energy by night, but that some individuals carry much more fat just before migration from Northumberland, and also soon after their arrival in Wytham (where, although some remain to winter, others move on to winter quarters further south or southeast). Unless otherwise stated, all data on body composition in the following sections refer to birds in their first autumn of life (hereafter called "juveniles").

THE DIURNAL PATTERN OF FAT DEPOSITION

In midwinter, Redpolls staying in southern England or the Low Countries need to store enough energy before going to roost to last for about 16 hr at temperatures around freezing-point. From the limited data given by Steen (1958), it may be calculated that in these conditions a Redpoll would require 5–6 kcal in 16 hr. As will be shown below, this energy cannot be supplied by stored glycogen or by food stored in the gullet before roosting, but must be stored as fat.

It is possible to estimate the maximum glycogen reserves which could be carried in the liver and muscles of a Redpoll by analogy with the data of Farner et al. (1961) on the White-crowned Sparrow (*Zonotrichia leucophrys*). Using their figures for maximum storage of glycogen (22 per cent of dry liver weight and 4 per cent of pectoral muscle weight), it may be calculated that a Redpoll could store at most about 0.3 kcal as glycogen, an insignificant part of its energy requirements.

As in most European finches and buntings, the gullet of the Redpoll is expandable, and can hold up to 0.8 ml of food (Newton 1967a). (Photographs of the full gullet are given by Fisher and Dater, 1961, who call the gullet "esophageal diverticula.") Thus a Redpoll could take to roost at most a gram of wet birch seed, which would provide perhaps 2 kcal, assuming the caloric value of birch seed to be 3.8 kcal/g dry weight (Turček 1961) and metabolizable energy to be about 70 per cent of the gross energy intake (Sturkie 1965). Clearly, the food reserves in the gullet are also quite inadequate to last the bird through the night in midwinter. Thus Redpolls must store some energy each day as fat, enough in winter to provide at least 3 kcal (i.e., at least 0.3 g). Maximum fat storage in liver and muscle,

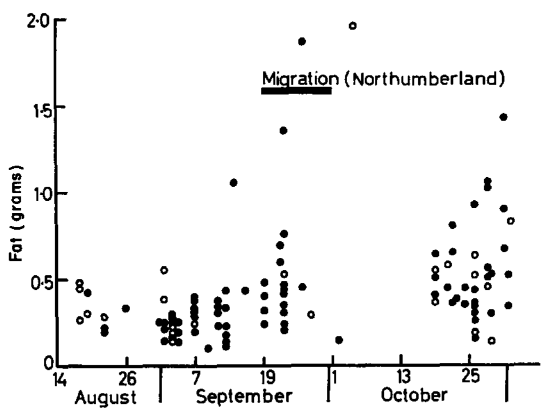

FIGURE 7. Fat contents of Redpolls at different dates in autumn. August and September data from Northumberland (55½°N); October data from Wytham, Oxford (51½°N). Open circles = adults; filled circles = juveniles.

again by analogy with the White-crowned Sparrow, would be about 0.05 and 0.1 g respectively (30 per cent of the dry weight of each). Thus, at least in winter, diurnal fat storage and utilization must involve also subcutaneous and retroperitoneal depots (as detailed in McGreal and Farner 1956). Nonmetabolizable fat in starved Redpolls is probably about 0.1 g, so even in midwinter the maximum fat deposits required in the evening are probably no more than 0.5 g. Weights of fat above this have been found in Redpolls just before and during migration (fig. 7).

Demonstration of a diurnal fat cycle in birds without migratory fat is found in the following data. Mean and SE of fat content (g) before and after noon were found to be 0.259 ± 0.017 ($n = 27$) and 0.316 ± 0.021 ($n = 25$), respectively, with the difference between these means significant at the 0.05 level. These differences in fat content are, of course, much less than those which occur in an individual bird between dawn and dusk. There were no significant differences in the fat contents of small (wing 65–68 mm) and large (wing 69–72 mm) Redpolls compared at the same times of day.

FAT DEPOSTION AND VARIATION IN LEAN DRY WEIGHT

In my earlier paper, I suggested that, as the total weight of Redpolls increased very little before migration, they had not deposited any appreciable amount of fat, but figure 7 now shows that some of them do. One feature distinguishes the birds with high fat contents from others: fat birds have significantly greater lean dry weights (without feathers) than lean birds, both before and during the migratory period (table 4). (It was checked that this did not result from incomplete fat extraction.) It is not known which components of the lean dry weight, whether skeleton, protein, or both, were heavier than average in these fat birds, but it seems very probable that it might result from an increase in size of the flight muscles, as an adaptation to migration.

These differences in lean dry weight with migratory condition are at variance with the conclusions of Odum et al. (1964) and Hicks (1967) that during preparation for migration there is no alteration in the body components of a bird, except by deposition of fat. The significance of the drop of lean dry weight of both fat and lean birds between the premigratory and migratory periods (table 4) is not understood, but it raises the possibility that some protein is used up during flight. The possibility that the October samples of Redpolls contained smaller birds than did the September samples is unlikely, as body size (measured by wing length) bears little relation to lean dry weight; only 10 per cent of the variations in lean dry weight of the 60 lean September birds can be attributed to variations in wing length.

TABLE 4. Lean dry weights (excluding plumage) of Lesser Redpolls before, and during and after migration.

	Fat birds > 0.5 g fat		Lean birds < 0.5 g fat	
	$\bar{x} \pm$ SE	(n)	$\bar{x} \pm$ SE	(n)
Before migration (September)	3.73 ± 0.171	(9)	3.21 ± 0.034	(60)
During and after migration (October)	3.21 ± 0.057	(17)	2.95 ± 0.047	(18)

Difference between means are all significant:
fat/lean before migration $t = 4.7$, $p < 0.001$
fat/lean during migration $t = 3.6$, $p < 0.01$
fat before/during migration $t = 3.6$, $p < 0.01$
lean before/during migration $t = 3.9$, $p < 0.001$

BODY COMPOSITION DURING AND AFTER MOLT

Figure 8 shows that the total fat content of Redpolls was correlated with total body weight more closely in October (after molt) than in August and September (during molt), which suggests that the weights of some other body components varied more in the earlier months than later. Not only the average lean dry weight but also the water content was higher in August and September than in October (table 5). Unlike the situation in lean dry weights, the water contents of fat and lean birds in the same month did not differ significantly. It might be thought that the higher water content before migration was associated directly with the higher lean dry weight, but this is not so. When water contents are expressed as percentages of lean dry weight, adult Redpolls in molt (in September) still had significantly higher water contents than those (in October) which had finished molt (table 5). Also, juveniles which were still in body molt in August and September had significantly higher water contents than those which had completed molt but had not yet migrated, and also than those which had migrated south to reach Oxfordshire by October (table 5). The fall in water content after molt was about 30 per cent, and it is probable that the high water content during molt was associated with heavy protein turnover. Keratin synthesis must involve the intake of a considerable surplus of protein in order to obtain sufficient of the rare amino acids, particularly those containing sulfur (Spearman 1965), and the surplus amino acids are presumably deaminated and excreted. A similar increase in water content during molt has been noted in other finches by Dolnik (1965), and the extra water in the Bullfinch has been shown to be localized chiefly in the growing feathers (Newton 1968).

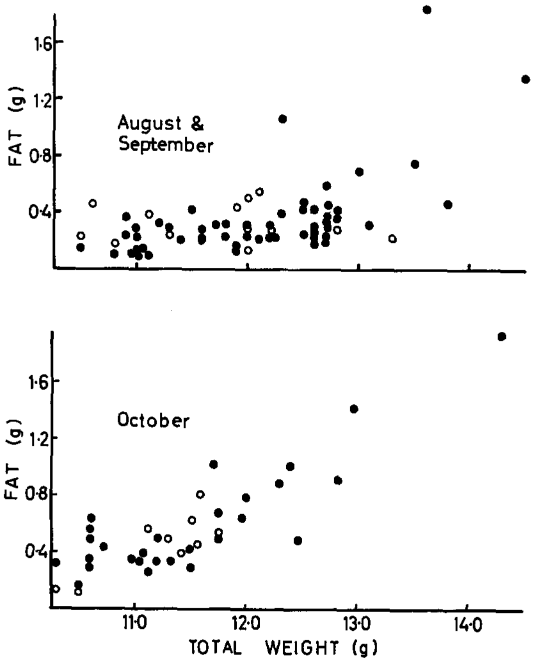

FIGURE 8. Fat contents of Redpolls of different total body weights (a) in August and September (most birds in molt); (b) in October, after the molt. Open circles = adults; filled circles = juveniles.

VARIATIONS IN TOTAL BODY WEIGHTS

It is now possible to reassess the weight data given in my earlier paper, in which it was noted that the average total body weight of adult Redpolls fell slightly at the start of molt but rose towards the end. Measurements made in this study (table 6) show that the dry plumage of adults weighs about 0.2 g less during the first than during the second half of the molt so that the drop of an average of about 0.15 g in total weight of adults at the start of molt (Evans 1966a: table 13, 14) may be attributed entirely to feather loss. Furthermore, most of the subsequent gain in weight

TABLE 5. Water contents of Lesser Redpolls.

	$\bar{x} \pm$ SE	(n)	Test of significance of difference
Grams water			
All ages August and September	7.69 ± 0.085	(70)	$t = 7.2$, $p < 0.001$
All ages October	6.91 ± 0.066	(35)	
% of lean dry weight			
Adults in wing and body molt	250.3 ± 3.3	(13)	$t = 4.4$, $p = 0.001$
Adults after molt	227.0 ± 6.4	(8)	
% of lean dry weight			
Juveniles after molt, before migration[a]	214.3 ± 4.7	(16)	
Juveniles in body molt before migration	251.6 ± 2.9	(34)	$t = 7.3$, $p < 0.001$ $t = 6.5$, $p < 0.001$
Juveniles after molt, during and after migration	224.8 ± 3.1	(27)	

[a] The difference between the average water contents of juveniles before (214.3) and after (224.8) migration is not significant at the 5% level.

TABLE 6. Weights (g) of body plumage and flight feathers of Lesser Redpolls during and after molt.

Age of birds	Month and molt score[a]	Body plumage		Flight feathers	
		$\bar{x} \pm$ SE	(n)	$\bar{x} \pm$ SE	(n)
Adults	Aug. and Sept.: 1–24	0.315[b] ± 0.029	(8)	0.162 ± 0.014	(8)
Adults	Aug. and Sept.: 25–45	0.506[b] ± 0.057	(7)	0.181 ± 0.011	(7)
Adults	Oct.: after molt	0.581 ± 0.019	(9)	0.194 ± 0.008	(9)
Juveniles	Aug. to Oct. inclusive	0.575 ± 0.008	(83)	0.194 ± 0.002	(83)

[a] Molt scores based on method described in Evans (1966a).

[b] The difference in weight of the body plumage of adults between early and late in the molt period (0.191 g) is highly significant ($t = 9.8$, $p < 0.001$). No other differences are significant at the 5% level, and there were no differences between the weights of juvenile body plumage (or flight feathers) in the three months: August, September, October.

probably resulted from growth of new feathers, leaving an increase in average weight of, at most, a few tenths of a gram to be accounted for. But as shown in figure 8, total weights (and therefore average weights) of Redpolls before migration give little indication of the fat contents of the birds. This may result from the loss of water at the end of molt offsetting some of the gain in fat, so that the resultant change in total weight is very small. Not all Redpolls caught in the second half of September carried much fat (fig. 7). Possibly they accumulated fat quickly in a few days just before departure, so that fat birds were less likely to be caught than lean ones. This would mean that average total body weights, based on non-random samples, would underestimate any weight increases in individuals due to fat. But it is equally possible that not all Redpolls deposit much fat before departure from Northumberland.

A lowering of lean body weight before migration has been noted in the White-crowned Sparrow by King et al. (1965), who suggested that it was an adaptation to reduce the weight to be carried on migration and hence the energy demands of the flight. However, it is unlikely that this is true for Redpolls, since the water content of lean birds and fat birds did not differ significantly, and birds caught during and after migration in October and November had almost as low a water content as those which had finished molt but had not yet migrated (table 5). Furthermore, nothing is known of the changes in water content of the White-crowned Sparrows, since the investigators examined changes only in overall lean weight. As their birds also molted just before migration, the reduction they noted in lean weight may simply have reflected, as in the Redpoll and also in the non-migratory Bullfinch (Newton 1968), the lowering of a high water content associated with molt, rather than an adaptation to migration.

STUDIES ON CAPTIVE BIRDS

In autumn 1965, 11 Redpolls caught at Craster were held in an aviary and given unlimited water and food, viz. unripe seeds of meadowsweet and dry mixed seeds of suitable size. It was hoped to establish the weights that would be attained and the rate of fat deposition of individual Redpolls kept under such apparently favorable conditions. Unfortunately, in spite of the abundant food, five birds did not adjust to captivity and died (apparently from starvation) one to seven days after capture; four others were released after a few days, when they began to lose weight suddenly.

The remaining two birds gained weight, reaching 12.7 and 13.2 g on the evening of 4 October. On 7 October their weights were slightly less, and they were released next day, some 10 days after most Redpolls had left Craster in 1965. (In spite of this late start to their migration, it was evidently successful, since one of the two was taken at Craster again in autumn 1966.) Each of these two birds gained about one gram, one of them in as little as two days. Both carried some subcutaneous fat in the interclavicular fossa at their maximum weights, which were little higher than most of those of Redpolls caught at Craster in the few days prior to their migration (fig. 7). Thus fat deposition in the wild was probably not restricted by food availability in September 1965.

Starvation has often been named as the cause of most deaths of wild birds. Some information as to changes in body composition associated with starvation may be gained from the five birds which died in captivity (though the three rapid deaths may have resulted in part from the shock of handling and captivity).

Three died about 24 hr after capture, in which time they had lost between 0.9 and 3.1 g, dying at weights between 8.7 and 9.2 g (about 80 per cent of the average weight of a Redpoll at this time of year). The other two died seven days after capture at weights of 8.4 and 7.8 g (about 70 per cent of normal) after losses of 3.3 and 4.2 g, respectively. As expected, all five birds carried little or no fat (petroleum ether extracted only 0.07–0.19 g). Their lean weights were also low, between 1.74 and 2.56 g, about 1–1.5 g below average. The low lean dry weights presumably resulted from metabolism of muscle protein when other energy sources had failed. While the water contents of starved birds were also lower than average (between 5.1 and 6.5 g), with one exception they decreased in proportion to the decrease in lean dry weight (i.e., water remained between 250 and 270 per cent of lean dry weight, as in normal molting birds). The exception was the Redpoll which died with the lowest lean dry weight, and in this bird the water content was 336 per cent of the lean dry weight. This was the only indication that abnormal fluid retention had occurred, and these results, therefore, support those of Newton and Evans (1966) that abnormally heavy weights of Bullfinches in winter are not usually due to high water contents, *contra* Mackay's (1965) suggestions that nutritional edema might occur regularly during starvation.

THE OVERLAP OF MAJOR EVENTS IN THE ANNUAL CYCLE

It is generally recognized that breeding, molt, and migration each demand energy above the normal metabolic requirements, and their temporal separation in many passerines of the North Temperate Zone has usually been explained in such terms. It seems worth pointing out, therefore, that in terms of food requirements, these three processes require different materials. During the later part of the breeding cycle, the adults must bring to their young food rich in protein (for growth) but containing enough fat or carbohydrate for maintenance of body temperature once thermoregulation has begun. Also, during molt, most of the extra food requirements of the adults must be protein for feather growth, although they may also need some extra fat or carbohydrate to maintain their body temperature while their feathers are being replaced. For migration, the energy stored as fat before departure requires the intake chiefly of extra carbohydrate or fat, as the conversion of protein to fat is not as efficient a process.

Thus in terms of the basic food constituents, protein, fat, and carbohydrate, there is little overlap in the demands of molt and fat deposition for migration, and one may speculate that their temporal separation results partly from the disadvantage of migration with defective plumage, since to maintain normal flight speed, more fat will be required if the wing area is reduced by loss of feathers. However, Dolnik and Blyumental (1967) have shown an antagonism also on the metabolic level between molt and migration, with carbohydrate metabolism predominating in the former state and fat metabolism in the latter. The reasons for the separation of breeding and molt are perhaps more obvious, for full flight efficiency during the breeding activities, particularly food-gathering, must be advantageous. Yet, the protein requirements for the two events may well be very different. For the synthesis of feather keratin, cystine might well be the scarcest amino acid relative to its abundance in vegetable protein, as Newton (1968) has argued. On the other hand, for growth of musculature in the nestlings, the total food intake may have to be increased so that enough lysine, histidine, and tryptophan are available (assuming that analogy with the needs of poultry chicks is fair, Biester and Schwarte 1952). Thus one would expect that Redpolls, taking the same type of seed for feeding their young, during molt, and before migration, must vary their daily food intake through summer and autumn much more than would be predicted from considerations solely of the energy requirements for the different activities in the annual cycle.

SUMMARY AND CONCLUSIONS

In Britain Lesser Redpolls (*Carduelis flammea cabaret*) are influenced in their movements by the size of the seed crop of birch *Betula* in two main ways. (1) In August and September, when adults have a complete molt and juveniles a partial molt, a poor birch crop in the breeding areas in northern England results in local movements by juveniles, but in a change of diet by the adults. (2) After their migration south at the end of September, a poor birch crop in southern England results in fewer wintering birds, and thus produces more emigration to the continent (especially to Belgium). In two years of very poor crops, 1959 and 1964, emigration reached as far as southern France and Spain.

The time of year at which movement south occurs is independent of the amount of birch seed available on the breeding grounds. Those birds which move south gain the advantages of longer days, shorter nights, and almost untouched birch crops, but they do not reach warmer wintering areas. They migrate in late September, probably by a series of short flights, because days shorten and temperatures drop more rapidly after the autumnal equinox than before, so that energy storage for the flights becomes steadily more difficult as the autumn progresses.

Fat is stored not only for migration, but also daily to provide existence energy during the night. The maximum fat contents recorded were insufficient to allow Redpolls to reach Belgium from northern England in a single flight. The fattest birds had lean dry weights higher than average, both before, and during and after migration, so may have developed extra flight musculature in association with the fat deposits.

Redpolls had higher water contents during than after molt. The loss of water after molt is associated with the end of protein synthesis, and not with fat deposition or migration, though adult Redpolls depart from northern Britain as soon as they finish molt. As a result of starvation, five captive birds used up not only their fat and carbohydrate reserves, but also some protein. In spite of this, abnormal water retention occurred in only one bird.

Redpolls often take birch seed as their sole food, so that their food requirements (by weight) must vary much more during the annual cycle than would be predicted solely in terms of energy costs, since different food constituents are important at different phases of the cycle.

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