THE TEMPERATURES, WEIGHTS, AND BODY COMPOSITION OF MOLTING BULLFINCHES

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Although most birds molt at seasons when food is plentiful, it is commonly assumed that the replacement of the plumage imposes a strain. In captivity, at least, adult birds often lose weight during molt, and many more die then than at any other time of year. Apart from hormonal aspects (Assenmacher 1958; Voitkevitch 1966), however, the physiology and nutritional state of birds in molt have received surprisingly little attention. One might expect that extra food would be required then both for feather synthesis and to compensate for the additional heat lost because of reduced insulation and increased peripheral blood flow through growing feathers.

The aims of this paper are (1) to assess the effects of molt in wild Bullfinches (*Pyrrhula pyrrhula*) through analyses of their weights, body composition, and temperatures; (2) to discuss the wear and replacement of the plumage; and (3) to show a diurnal cycle in the protein content of birds in heavy molt. The paper is based mainly on birds caught from six weeks before to four weeks after molt in Wytham Woods, near Oxford (lat. 51° 80′ N), England, in August–November 1966. Not all birds caught were killed, so more information was obtained on weights and temperatures than on other aspects, and weights from earlier years have also been used. Except where otherwise stated, there were no differences in any of the data between males and females, so results for both groups have mostly been combined. On samples of less than 30, standard deviations are "best estimates" (see Fisher 1950).

THE MOLT

The molt takes place in late summer and autumn after breeding (Newton 1966, 1967). The complete molt of adults lasts 11–12 weeks, and the partial (body) molt of juveniles 7–9 weeks. In both, five stages were distinguished; in adults stage 1 covers birds in molt to the 2nd primary, stage 2 to the 4th, and so on to stage 5 which covers the entire growth of the 9th (and last) primary. The postjuvenal molt was subdivided according to molt in the body feathers (Newton 1966). In 1966 most Bullfinches at Wytham began molting between late July and early September, and birds at each stage of molt were therefore caught over several weeks; on the average, individuals at successive stages were caught progressively later in the year.

BODY TEMPERATURE

Body temperature during molt has previously been investigated only in Yellow-eyed Penguins (*Megadyptes antipodes*), in which the temperature of molting birds was 0.8°C higher than in nonmolting, nonincubating ones (Farner 1958). I caught Bullfinches in flight in mist nets in which they hung and sometimes struggled until removed. Their body temperatures were then taken rectally to the nearest 0.1°C, noting the level after a steady reading for at least one minute. (The thermometer bulb was warmed slightly in the hand beforehand.) The values obtained were within the range reported for other small passerines (Kendeigh 1934), but are not comparable with published figures for resting birds in which body temperature is often slightly lower than after recent activity (*e.g.*, Farner 1956). Handling may raise a bird's body temperature, but all temperatures used here, from molting and nonmolting birds, were recorded under similar conditions and so should be comparable within themselves. When the birds were caught, there was a steady drop in air temperature from an August mean of 15.5°C to 4.4°C in November; these temperatures were well below the body temperatures of Bullfinches, which were always over 39°C.

Body temperature in adults did not change significantly from before molt started until near the end, when there was a marked drop (fig. 1). The mean over the whole molt period (41.7°C) was 1°C higher than within a month after completing molt (40.7°C) ($P < 0.001$). In juveniles, body temperature at the start of molt was lower than in adults, but in the middle of molt (stage 3) was significantly higher by about 1°C than at both the start

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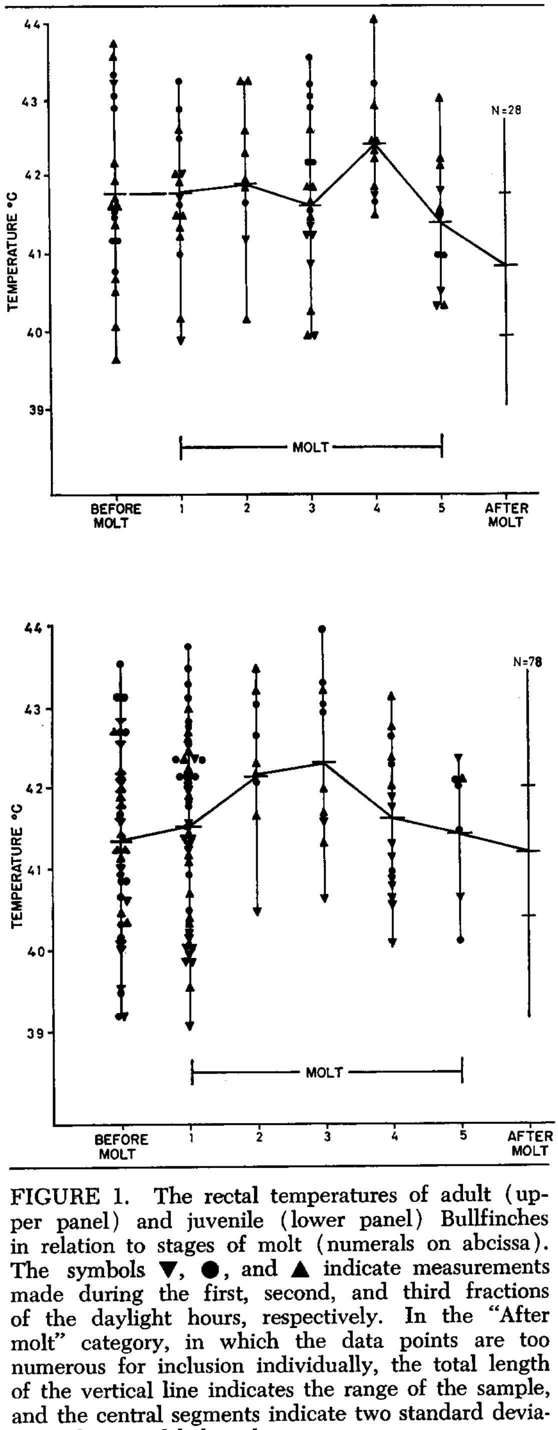

FIGURE 1. The rectal temperatures of adult (upper panel) and juvenile (lower panel) Bullfinches in relation to stages of molt (numerals on abcissa). The symbols ▼, ●, and ▲ indicate measurements made during the first, second, and third fractions of the daylight hours, respectively. In the "After molt" category, in which the data points are too numerous for inclusion individually, the total length of the vertical line indicates the range of the sample, and the central segments indicate two standard deviations above and below the mean.

($P < 0.05$) and end ($P < 0.001$). The higher mean temperature of adults before, and in the early stages of, molt may result because most of them are then very active feeding late young (Newton 1966). This could explain why they do not show the temperature increase that occurs at the start of molt in juveniles.

Adults and juveniles in molt differed in diurnal rhythm of temperature change from those that had completed molt (table 1). During molt, the mean temperature was significantly higher, by up to about one degree, in the middle third of the day than in the morning or evening, but there was no significant diurnal variation before or after molt.

Many species are known to increase their metabolic rate during molt (refs. in King and Farner 1961), and their deep body temperature depends on the balance between the rates of metabolism (heat production) and heat loss. In Bullfinches, the heat produced during molt more than offsets an extra loss caused by reduced plumage efficiency (as shown by the rise in body temperature). This implies that in this species the energy requirements of molt are not set primarily by the need to balance extra heat loss, for if this were the case, there is no reason why heat production should continue beyond the point at which body temperature reached its "normal" level. The higher temperatures during molt must therefore be the result of metabolic processes occurring primarily for reasons other than heat production (presumably feather synthesis), though I can suggest no reason why the diurnal metabolic rhythm should differ during molt.

WEIGHTS AND BODY COMPOSITION DURING MOLT

Body weights in adults and juveniles were similar to one another at the start and end of molt, and both were heaviest when they had most feathers in growth (stages 3–5). While both groups lost weight slightly toward the end of molt, they were still 1.5 g heavier then than at the start ($P < 0.001$) (table 2 and fig. 2). Changes in weight during molt may merely reflect the growth of new feathers, which initially contain blood and are enclosed by a protective sheath. To check this, I examined the weights of some birds without feathers. The plumage of each bird was removed within two hours of death, weighed and reweighed after drying for 24 hours at 80°C. The rest of the carcass was also weighed soon after plucking (to minimize error due to water loss) and after any food in the gullet had been removed; the carcass was analyzed later by standard methods (Odum 1960) to determine the contributions to its total weight of water, fat, and lean dry material (mainly muscle and skeleton). Petroleum ether was used as fat solvent.

TABLE 1. Rectal temperatures of Bullfinches at different times of the day in relation to molt.[a]

	Mean rectal temperature (± SD), °C		
	Before molt[b]	During molt	After molt[c]
ADULTS			
Morning	(a)	(d) 41.3 ± 1.25 (14)	(h) 40.5 ± 1.61 (10)
Midday	(b) 41.7 ± 1.15 (9)	(e) 42.0 ± 1.11 (17)	(i) 40.3 ± 1.22 (9)
Evening	(c) 41.7 ± 1.21 (12)	(f) 41.5 ± 0.56 (33)	(j) 41.2 ± 0.90 (9)
JUVENILES			
Morning	(k) 41.1 ± 0.83 (10)	(n) 40.9 ± 0.86 (31)	(q) 41.2 ± 0.97 (34)
Midday	(l) 41.3 ± 1.12 (13)	(o) 42.1 ± 0.59 (30)	(r) 40.7 ± 0.66 (14)
Evening	(m) 41.2 ± 0.86 (11)	(p) 41.7 ± 1.09 (29)	(s) 41.4 ± 1.05 (30)

[a] The day has been divided into three periods of approximately equal duration. Sample sizes are in parentheses. For tests of significance between means see footnote (d).
[b] Up to six weeks before molt.
[c] Up to four weeks after molt.
[d] Tests of significance between means (t-test): (n) vs. (o) and (o) vs. (r), $P < 0.001$; (e) vs. (i), $P < 0.01$; (d) vs. (e), (o) vs. (p), and (p) vs. (s), $P < 0.05$. The other differences are not significant ($P > 0.05$).

PLUMAGE WEIGHTS

The dry body plumage in juvenile Bullfinches (acquired in the nest) weighs only two-thirds as much as in adults of similar body weight, because their individual feathers are softer and weaker, with fewer barbs and barbules. These light feathers of juveniles are carried for only 3–9 weeks (depending on date of fledging), while adults carry theirs for about a year. Probably feather production in both age groups is as economical as is compatible with the period for which the feathers are normally carried. In nestlings, it is presumably advantageous to divert most protein toward body growth (to minimize the nestling period) and as little as possible into temporary plumage to be replaced soon after leaving the nest. In contrast, juvenile flight and tail feathers, which are not replaced at postjuvenal molt, weigh only slightly less than those of adults (table 3); and in both groups they remained in good condition for the 12 months or more between molts.

Plumage wear does not seem to have been studied in any other species. To give some idea of its normal extent in Bullfinches each year, the plumage weights of different birds caught just before molt and just after are set out in table 3. The flight and tail feathers of both adults and juveniles lost little or no weight over the year, but the body plumage of adults lost one-third in weight between the end of one molt and the start of the next, presumably with reduced potential as insulation. Body feathers were not only more susceptible to wear than the stiffer flight and tail feathers, but in captive birds any lost in summer were not replaced. The more important flight and tail feathers were always replaced by captive birds whenever they were lost.

In adults, the plumage increased during molt by up to two-thirds of its weight at the start, while that of juveniles doubled; in both groups this amounted to an increase of more than one gram (fig. 3 and table 4). There was then a drop in plumage weight near the end of molt (through the withdrawal of blood and loss of sheaths from newly grown feathers). At the end of molt, the plumage of both groups weighed and looked the same. Because there is blood in growing feathers,

TABLE 2. The live body weights of Bullfinches at different stages of molt.[a]

	Before molt[b]		Stage of molt					
	Male	Female	1	2	3	4	5	After molt[c]
ADULTS								
No. weighed	48	57	79	56	64	37	59	14
Mean wt., g	21.5	22.5	22.0	23.0	23.6	24.0	23.7	23.5
SD	1.0	1.2	1.5	1.5	1.7	1.2	1.2	1.3
JUVENILES								
No. weighed	127[d]		251	71	89	78	60	72
Mean wt., g	21.3		21.9	22.3	22.8	23.6	23.9	23.4
SD	1.3		1.5	1.2	1.2	0.8	1.0	1.0

[a] From Newton (1966), plus additional data.
[b] Up to six weeks before molt. Adult females averaged heavier than adult males during the breeding season but with the onset of molt the difference disappeared.
[c] Within 10 days after completion of molt, as indicated by the presence of sheaths on newly grown feathers.
[d] Sexes combined.

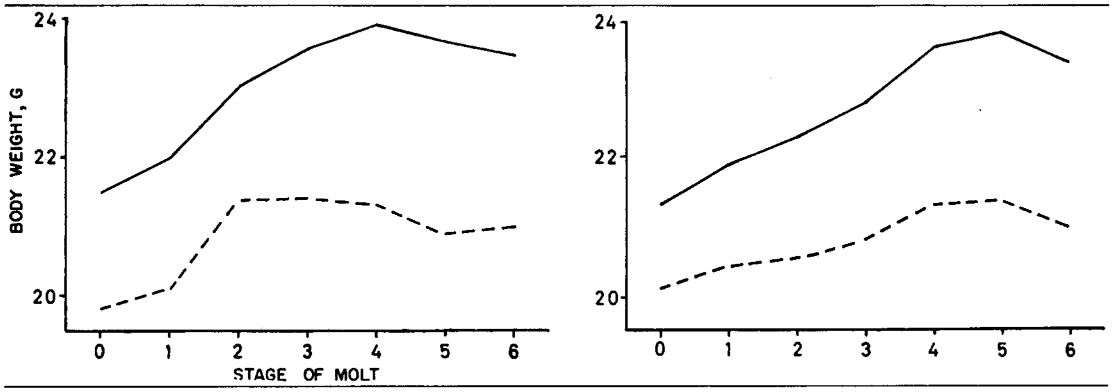

FIGURE 2. The weights of adult (panel at left) and juvenile (panel at right) Bullfinches in relation to stage of molt (numerals on abcissa). The continuous lines show the total body weights, and the broken lines show the body weights minus feathers.

the moisture content of the plumage was much higher during molt than at other times. In adults, the feathers weighed up to 2.8 g during molt, compared with 1.7 g before and 2.4 g just after. At peak molt they contained up to 1.1 g (7 per cent) of the total water in the bird. Since growing feathers weigh more than complete ones, changes in insulation during the molt itself cannot be assessed from wet or dry plumage weights.

BODY COMPOSITION

Excluding the feathers, the weight changes occurring during molt were reduced, but adults still gained an average of one gram during their 11- to 12-week molt, and juveniles 0.7 g in their 7- to 9-week molt (fig. 2). Moreover, juveniles started molt weighing, on the average, 0.5 g more than adults, but this was masked completely by weighing bodies plus plumage.

In both adults and juveniles, the increase in body weight (excluding feathers) during molt entailed an increase in lean dry material, in water, and in fat (fig. 4 and table 5); but the fat increased proportionately more than the others. At all stages of molt, and whatever the fat content, the water and lean dry material remained in approximately the same proportion to one another (table 5). These same trends continued after molt (see also Newton, in press).

It is possible that the volume of a bird's blood increases during molt to supply the growing feathers, in which case this should be reflected on the water content. Although growing feathers contain much more water than complete ones (see above), table 5 shows that Bullfinches did not contain proportionately more water in the rest of their bodies during molt than at other times. Further, individuals in molt varied no more in water content than did others.

In the White-crowned Sparrow (*Zonotrichia leucophrys*) King, Farner and Morton (1965) also found that fat-free weight increased during molt, but they did not distinguish among water, lean dry material, and feathers. Expressing my data like theirs (according to mean fat and nonfat fractions of the carcass), the increase in nonfat weight during the molt of Bullfinches is of the same order as in

TABLE 3. Dry weights of fresh and worn plumage of Bullfinches.

	Adults			Juveniles	
	Wing	Tail	Body	Wing	Tail
NEW PLUMAGE (October)					
No. examined	13	22	36	57	59
Mean wt., g	0.300	0.115	1.61	0.285	0.103
SD	0.014	0.011	0.14	0.017	0.008
WORN PLUMAGE (August)					
No. examined	28	31	18	6	11
Mean wt., g	0.296	0.106	1.05	0.288	0.111
SD	0.018	0.008	0.08	0.014	0.005

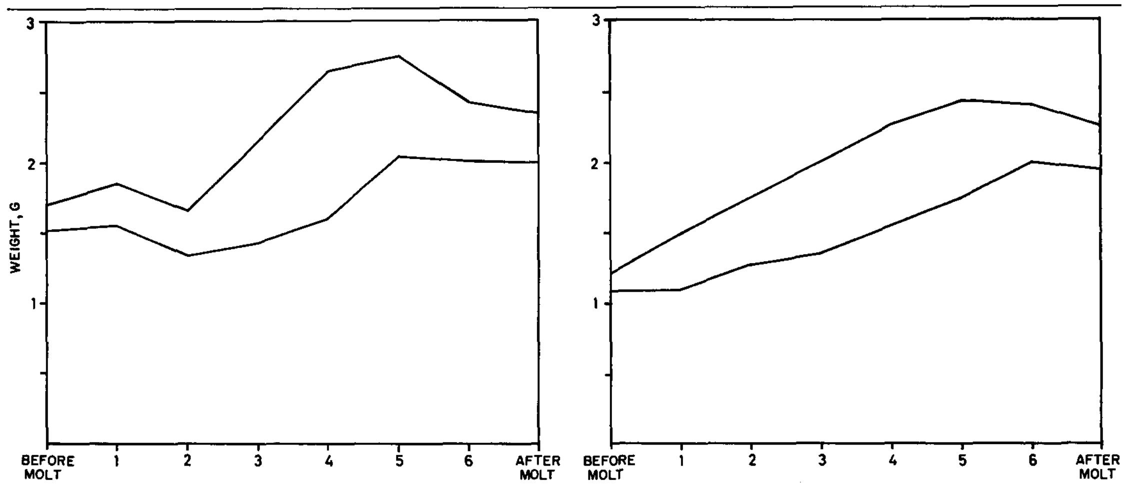

FIGURE 3. Total weight (upper line) and dry weight (lower line) of the plumage of adult (panel at left) and juvenile (panel at right) Bullfinches in relation to stage of molt (abcissa). Stage 6 of molt denotes birds that had completed the molt within 10 days before capture, as indicated by the presence of sheaths on the bases of the newly grown feathers.

Zonotrichia. In *Zonotrichia,* however, there is a drop in nonfat weight at the end of molt associated with the deposition of migratory fat. The results for nonmigratory Bullfinches also differ from those of Evans (in press) for migrant Redpolls (*Carduelis flammea*) in which there is an increase during molt in the proportion and absolute weight of water in the plumage-free body; in the Bullfinch the extra water is localized in the feathers.

DIURNAL VARIATION IN BODY COMPOSITION

Each month, all groups of birds, whether molting or not, were heavier in the afternoon than in the forenoon, by one gram or more (table 6). The fat increased proportionately much more than the lean dry matter and water, which, though also increasing, remained in approximately the same ratio to one another. Thus, similar changes in body composition took place each day as occurred in long term over the whole molt period (excluding changes within the feathers).

Fat evidently served partly as an overnight food reserve; and the afternoon values, especially, tended to be higher in all birds (whether molting or not) as the season advanced and nights became longer and colder. Diurnal variation in other material is more difficult to account for. The lean dry component consisted of skeletal material, protein, and carbohydrate from the bird's body, and dried food from the gut. At dusk, the contents of the digestive tract from the gizzard

TABLE 4. Plumage weights (in grams) of Bullfinches at different stages of molt.

	Before molt[a]	Stage of molt 1	2	3	4	5	6[b]	After molt[c]
ADULTS								
No. examined	18	12	5	11	14	12	4	36
Total weight	1.67	1.86	1.66	2.14	2.67	2.75	2.42	2.37
Dry weight of body feathers	1.05	1.14	0.98	1.12	1.27	1.67	1.61	1.61
Dry weight of wing feathers	0.30	0.29	0.25	0.25	0.25	0.27	0.29	0.30
Dry weight of tail feathers	0.12	0.12	0.11	0.06	0.08	0.11	0.11	0.12
Total dry weight	1.47	1.55	1.34	1.43	1.60	2.05	2.01	2.03
Water weight	0.20	0.31	0.32	0.71	1.07	0.70	0.41	0.34
JUVENILES								
No. examined	22	33	11	20	13	10	22	47
Total weight[d]	1.22	1.51	1.76	2.00	2.26	2.43	2.40	2.27
Dry weight[d]	1.08	1.10	1.27	1.35	1.55	1.72	1.98	1.94
Water weight	0.14	0.41	0.49	0.65	0.71	0.71	0.42	0.33

[a] By up to six weeks.
[b] Molt just finished, as indicated by the presence of sheaths on the newly grown feathers.
[c] By up to four weeks.
[d] Includes, as well as the body feathers, the weight of the flight and tail feathers which are not molted and therefore stay the same weight throughout.

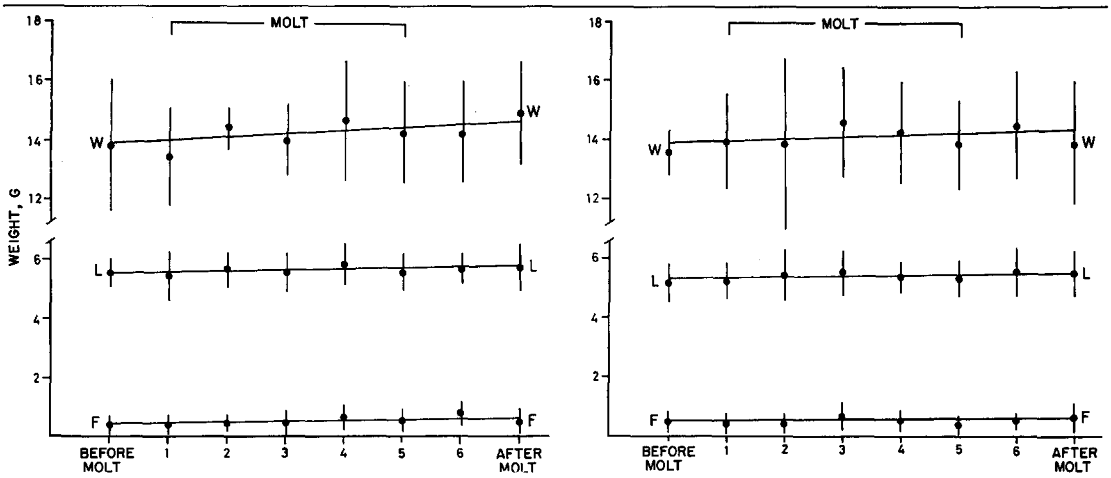

FIGURE 4. The weights of water (W), lean dry material (L), and fat (F) in the carcasses of adult (panel at left) and juvenile (panel at right) Bullfinches in relation to stages of molt (abcissa; see fig. 3). Vertical lines depict two standard deviations above and below the means.

down (those above were removed before analysis) weighed 0.3 g when dry, and at dawn 0.2 g (12 birds examined each time). The gut does not completely empty at night and most of the birds collected at "dawn" (*i.e.*, within one hour of sunrise) had already fed. Diurnal change in lean dry weight might also be due partly to the accumulation during the day of carbohydrate for use overnight. From data for *Zonotrichia* (Farner *et al.* 1961), I conclude that the total carbohydrate reserve of a Bullfinch would weight at most about 0.2 g. Thus, overnight loss of gut contents and carbohydrate together would amount to 0.3 g lean dry weight, and this was the most recorded in Bullfinches outside molt.

In Canada Geese (*Branta canadensis*), fat breakdown is sometimes accompanied by

TABLE 5. The weights (in grams) of lean dry material (excluding feathers), water, and fat in Bullfinches killed at different stages of molt.

	Before molt[a]		Stage of molt						After molt[c]
	Male	Female	1	2	3	4	5	6[b]	
ADULTS									
No. examined	10	5	11	5	10	13	11	4	13
1. Lean dry, mean	5.52	5.87	5.35	5.71	5.56	5.86	5.59	5.66	5.74
SD	0.21	0.42	0.42	0.32	0.28	0.35	0.29	0.18	0.38
2. Water, mean	13.83	14.64	13.44	14.53	14.02	14.68	14.29	14.28	15.05
SD	1.10	0.81	0.83	0.32	0.64	1.02	0.85	0.86	0.86
% of lean dry weight	251	250	251	254	252	251	255	252	262
3. Fat, mean	0.43	0.39	0.37	0.45	0.50	0.67	0.60	0.85	0.53
SD	0.17	0.16	0.12	0.12	0.17	0.21	0.18	0.18	0.24
% of lean dry weight	7.8	6.6	6.9	7.9	9.0	10.5	10.7	15.0	9.2
4. Total (1 + 2 + 3)	19.78	20.90	19.16	20.69	20.08	21.21	20.48	20.79	21.32
JUVENILES									
No. examined	12[d]		30	11	15	13	10	20	22
1. Lean dry, mean	5.18		5.27	5.52	5.61	5.40	5.38	5.58	5.51
SD	0.34		0.29	0.38	0.35	0.22	0.31	0.39	0.36
2. Water, mean	13.59		14.01	13.92	14.68	14.13	13.92	14.50	13.94
SD	0.37		0.82	1.40	0.94	0.85	0.68	0.87	1.05
% of lean dry weight	262		266	252	262	262	259	260	253
3. Fat, mean	0.40		0.43	0.42	0.66	0.50	0.44	0.45	0.65
SD	0.18		0.19	0.22	0.18	0.17	0.16	0.15	0.23
% of lean dry weight	7.7		8.1	7.6	11.8	9.3	8.2	8.1	11.8
4. Total (1 + 2 + 3)	19.17		19.71	19.85	20.95	20.05	19.74	20.53	20.10

[a] Adult females averaged heavier than adult males during the breeding season but with the onset of molt the difference disappeared.
[b] Within 10 days after completing molt, as indicated by the presence of sheaths on some newly grown feathers.
[c] To mid-November.
[d] Sexes combined.

TABLE 6. The weights (in grams) of lean dry material (excluding feathers), water, and fat in the carcasses of Bullfinches in relation to time of day and stage of molt.

	Befort molt[a]		Stage of molt 1 and 2		3 and 4		5 and 6		After molt[b]	
	AM	PM	AM	PM	AM	PM	AM	PM	AM	PM
ADULTS										
No. examined	6	11	8	8	9	13	6	9	9	4
Lean dry, mean	5.47	5.77	5.46	5.47	5.40	5.95	5.35	5.78	5.70	5.82
SD	0.20	0.41	0.49	0.24	0.23	0.47	0.22	0.19	0.46	0.20
Water, mean	13.80	14.36	13.56	13.92	13.78	14.80	13.83	14.59	15.06	15.03
SD	1.00	0.73	0.62	0.93	0.42	0.69	0.86	0.68	0.74	0.63
Fat, mean	0.33	0.46	0.34	0.46	0.36	0.75	0.43	0.77	0.38	0.86
SD	0.15	0.19	0.08	0.11	0.11	0.14	0.20	0.17	0.11	0.19
Total wt., mean	19.60	20.59	19.36	19.58	19.54	21.50	19.61	21.14	21.14	21.71
JUVENILES										
No. examined	3	5	20	19	10	16	16	14	10	19
Lean dry, mean	4.86	4.98	5.25	5.47	5.44	5.59	5.46	5.59	5.56	5.77
SD	0.36	0.19	0.60	0.46	0.23	0.32	0.34	0.43	0.29	0.43
Water, mean	12.96	13.72	13.90	14.21	13.93	14.77	14.19	14.50	14.13	14.30
SD	0.16	0.38	1.00	0.71	0.72	0.93	0.55	0.66	1.20	0.47
Fat, mean	0.44	0.61	0.29	0.57	0.48	0.64	0.35	0.55	0.43	0.78
SD	0.13	1.00	0.15	0.22	0.18	0.17	0.09	0.21	0.22	0.19
Total wt., mean	18.04	19.31	19.44	20.25	19.85	21.00	19.00	20.64	20.12	20.85

[a] By up to six weeks.
[b] By up to four weeks.

breakdown of protein (Hanson 1962). If this occurs overnight in Bullfinches, one might expect that it would be more extensive during molt, when feathers are growing, than at other times of year. (In this species, the feathers grow at the same rate by night as by day [Newton, unpublished].) Tables 7 and 8 were therefore prepared from data for the few birds caught at either dawn or dusk, so as to get a better indication of the full extent of the overnight loss of lean dry material and fat, respectively, than is provided by table 6. Birds were divided into three groups: (1) those that had either not started molt or were in the first stage (with few feathers growing); (2) those in heavy molt; and (3) those that had completed, or almost completed, molt. (Data for some birds caught in December are also included for comparison.)

While the overnight fat loss increased with increase in length of night and decreasing air temperatures (table 8), the overnight loss of lean dry material was significantly greater during peak molt than before or after. About 0.7 g lean dry material was lost overnight at the peak of molt in both adults and juveniles, *i.e.*, over 0.4 g more than at other times (table 7). This must have been due to extra

TABLE 7. Comparisons of the weight of lean dry material (excluding feathers) in Bullfinches killed within one hour of dawn ("AM") or dusk ("PM") at different stages of molt.

ADULTS	Molt not started[a] or advanced only to 2nd primary AM	PM	From shedding of 3rd primary to complete growth of 8th primary AM	PM	Molt beyond full growth of 8th primary, or completed entirely (to mid-November)[b] AM	PM
No. examined	7	5	15	12	4	7
Mean, g	5.35	5.45	5.36	6.07	5.68	5.77
SD	0.18	0.38	0.21	0.45	0.06	0.26
Difference	0.10	(not sig.)	0.71	($P < 0.001$)	0.09	(not sig.)
JUVENILES	**Molt not started or at stage 1 AM**	**PM**	**Molt at stages 2–5 AM**	**PM**	**Molt complete (to mid-November) AM**	**PM**
No. examined	9	8	8	11	21	24
Mean, g	5.23	5.30	5.17	5.90	5.55	5.80
SD	0.23	0.23	0.51	0.36	0.38	0.37
Difference	0.07	(not sig.)	0.73	($P < 0.01$)	0.25	($P < 0.05$)

[a] Includes birds up to six weeks before starting molt in August and early September.
[b] Includes birds caught within four weeks of completing molt. Birds caught in December (molt completed) and not distinguishable on weight data as adults and juveniles, gave values as follows: AM, 5.74 ± 0.39 g ($N = 11$); PM, 6.05 ± 0.43 g ($N = 9$). The difference was not statistically significant ($P > 0.05$).

TABLE 8. Comparisons of the weight of fat in Bullfinches killed within one hour of dawn ("AM") or dusk ("PM") at different stages of molt.

ADULTS	Molt not started[a] or advanced only to 2nd primary		From shedding of 3rd primary to complete growth of 8th primary		Molt beyond full growth of 8th primary, or completed entirely (to mid-November)[b]	
	AM	PM	AM	PM	AM	PM
No. examined	7	5	15	12	4	7
Mean, g	0.28	0.46	0.37	0.79	0.38	0.93
SD	0.11	0.09	0.12	0.16	0.11	0.14
Difference	0.18 ($P < 0.05$)		0.42 ($P < 0.001$)		0.55 ($P < 0.001$)	
JUVENILES	Molt not started or at stage 1		Molt at stages 2–5		Molt complete (to mid-November)	
	AM	PM	AM	PM	AM	PM
No. examined	9	8	8	11	21	24
Mean, g	0.23	0.57	0.30	0.70	0.33	0.62
SD	0.12	0.22	0.20	0.14	0.08	0.20
Difference	0.24 ($P < 0.05$)		0.40 ($P < 0.001$)		0.29 ($P < 0.001$)	

[a] Includes birds up to six weeks before starting molt in August and early September.
[b] Includes birds caught within four weeks of completing molt. Birds caught in December (molt complete), and indistinguishable on weight data as adults and juveniles, gave values as follows: AM, 0.60 ± 0.18 g ($N = 11$); PM, 1.23 ± 0.26 g ($N = 9$). The difference was statistically significant ($P < 0.001$).

breakdown of protein overnight in midmolt, and to its replacement during the daytime. It is, however, far more than would be required for feather synthesis alone (see later), even allowing for the fact that to produce a given weight of feathers, a much greater weight of muscle would need to be degraded. At more than 0.4 g, this may seem a large amount of dry protein to be laid down daily in a bird of this weight (*ca.* 10 per cent of the total dry protein in a morning-killed bird); it is, however, much less than the amount accumulated daily by growing nestlings, which can double their protein contents from one day to the next.

PROTEIN REQUIREMENTS FOR FEATHER SYNTHESIS

The amino acid composition of the keratin, of which feathers are almost entirely composed, has been given by Ward and Lundgren (1954) from several studies on chicken feathers, and of proteins in general by Tristram (1953). Of the 20 or so amino acids in feathers, the sulfur-containing cystine (or cysteine) is the most difficult to get enough of from dietary proteins, since it is exceptionally concentrated in feathers. Thus, by weight, cystine (plus cysteine) is the fifth commonest amino acid in feathers, at 6.8–8.2 g per 100 g total protein, but is one of the four least common of the 21 amino acids in most other animal proteins (between 0 and 6.3 g per 100 g total protein) and in vegetable proteins (0–2.9 g per 100 g total protein).

Adult Bullfinches produce about 2.0 g dry feathers during molt and juveniles about 1.5 g. (The examination of extra birds has enabled me to revise slightly some values published earlier [Newton 1966].) Since this is equivalent to 32 and 25 per cent of their total dry protein contents at the start of molt, the feathers cannot be formed merely by degradation and redistribution of proteins already in the body, but must come primarily from food eaten during their growth. However, as discussed above, feather growth in this species is probably maintained at night by breakdown of other body proteins, which are replenished during the day.

Adult molt lasts 11–12 weeks and postjuvenal molt (in which fewer feathers are replaced) 7–9 weeks, so that the mean rate of feather synthesis is about 27 mg per day in both (though it must at times exceed 40 mg per day [see Newton 1966]). (The rates must be twice as high in species, such as the Snow Bunting [*Plectrophenax nivalis*], Lapland Longspur [*Calcarius lapponicus*], and Sprosser [*Luscinia luscinia*], which are of similar size to the Bullfinch, but molt in less than half the time [Stresemann and Stresemann 1966]; and the rates for the nestlings of all species, in proportion to body weight, must greatly exceed those of the adults themselves.)

Bullfinches live on seeds during molt (Newton 1966). The protein content of plant seeds varies between 8 and 15 per cent by dry weight in cereals to nearly 50 per cent in certain leguminous plants (Haurowitz 1963). Seed proteins typically contain about 1 g cystine per 100 g total protein (Tristram 1953). Thus about 7 g of such protein would contain the same amount of cystine as the 2 g of feathers on an adult Bullfinch (assuming the same proportion of cystine as in chicken feathers). From figures on the digestibility of plant proteins in Haurowitz (1963), it may be calculated that to yield the cystine (cysteine) required for feather production, this 7 g plant protein must be increased by 33–100 per cent; or about 5–7 times the weight of the feathers themselves. The bird might be able to lighten this demand for cystine by producing it within the body from the other (essential) sulfur amino acid, methionine, if this were available in excess of normal requirements. Either way, the sulfur-containing amino acids needed by Bullfinches for feather growth alone do not seem excessive when spread over several weeks. But without precise knowledge of all the nutritional requirements of molt and of the composition and availability of the various foods, it is not possible to judge by this approach how easy it would be for Bullfinches to meet these demands. An alternative method is to examine the condition of the birds themselves, and this is discussed below on the basis of the carcass analyses.

CONCLUSIONS: THE EFFECTS OF MOLT ON BULLFINCHES

Bullfinch carcasses were analyzed partly to see if there were any evidence from changes in body composition that molt represented a nutritionally difficult time for the birds. One might have thought, for instance, that any birds unable to meet the demands of molt by extra feeding would have abnormally low fat content or lean dry weight. In fact, no birds in obviously poor condition and markedly below average weight were caught; so whatever the effects of molt, all individuals were affected similarly.

There was also no evidence from the mean changes in weight and body composition that Bullfinches lost condition during molt: they did not incur the long-term protein debt associated with the molts of certain species (see for example, Hanson 1962), and the fat contents of birds in molt were just as high as in nonmolting birds killed at the same time. In fact from July/August to January/February (the coldest months) Bullfinches became steadily heavier through increases in all three main body components (fig. 3 and Newton, in press) and, apart from changes within the feathers themselves, this trend was not interrupted during molt.

Further evidence that most of the Bullfinches examined did not suffer even temporary food shortage during molt is provided by the rarity of "fault bars" on the feathers. These are lines of weakness across the feather, where the rachis is "pinched" and the barbs are deficient in barbules; they are supposedly caused by food shortage and are usually formed at night. They were noted on the feathers of only 2 per cent of the birds killed for this analysis.

A diurnal cycle in the fat content of small birds has been established by several workers (*e.g.*, Helms and Drury 1960). A similar protein cycle, by which feather growth of birds in heavy molt could be maintained at night, does not seem to have been suggested previously. It is now desirable that the body proteins are examined separately, and not (as here) in conjunction with other lean dry material.

SUMMARY

The mean rectal temperature of adult Bullfinches remained fairly stable from before the start of molt until near its end, when it dropped by about 1°C. Body temperature in juveniles was about 1°C higher in midmolt than at the start and end. In molting birds of both age groups, the temperature in the middle part of the daylight period was higher (by up to about 1°C) than in the morning or evening, but this trend was absent before and after molt.

The body feathers of juveniles serve for only 3–9 weeks (till postjuvenal molt) and are weaker (with fewer barbs and barbules) than those of adults, which last a year. On the other hand, the flight and tail feathers of juveniles, which are not renewed at postjuvenal molt, are just as substantial as those of adults. Between the end of one molt and the start of the next, nearly a year later, the body plumage of adults lost one-third of its weight; but in the flight and tail feathers the loss was negligible. The plumage was at its heaviest at that stage of molt when most feathers were growing.

Both adults and juveniles increased in weight during molt, and for some weeks afterward, through increases in all three body components: lean dry material, water, and fat. In addition, the water content of Bullfinches was higher during molt than at other times; the extra water was localized in the growing feathers, which, at peak molt, contained up to 7 per cent (1.1 g) of the total water in the bird.

A diurnal cycle was superimposed on the seasonal trends. Whether molting or not, birds lost water, lean dry material, and fat overnight and replaced them during the day.

Moreover, the diurnal fat cycle increased in amplitude, irrespective of molt, as the season advanced and nights became longer and colder. In contrast, the diurnal cycle in lean dry material was much greater in amplitude during heavy molt than at other times. It is suggested that at peak molt the breakdown of body protein occurred overnight (and was replaced during the day), and that the amino acids so released might be used partly to support feather growth which continued at the same rate as by day.

By analogy with data from chicken feathers, the total amino acids required for feather synthesis by molting Bullfinches was calculated. It is concluded that the total protein required for feather growth is probably set by its cystine content, for this amino acid is present in feather keratin at much higher concentration than in the proteins of plant seeds, on which Bullfinches feed during molt. Possibly the birds can lighten the demand for cystine by synthesizing it from surplus methionine.

Adult Bullfinches produced about 2 g of feathers during a molt of 11–12 weeks, and juveniles 1.5 g in 7–9 weeks; in both, keratin was synthesized, on the average, at 27 mg per day.

From carcass analyses, it seems that Bullfinches were able to meet entirely the nutritional demands of molt from food eaten at the time; they did not show the long-term protein deficit associated with the molts of certain species, and had fat contents as high as did nonmolting birds caught at the same time.

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