Seasonal weight changeof the house sparrow, passer domesticus. L

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SEASONAL WEIGHT CHANGE OF THE HOUSE SPARROW, PASSER DOMESTICUS, L.

by

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SECTION I.

I. Introduction.

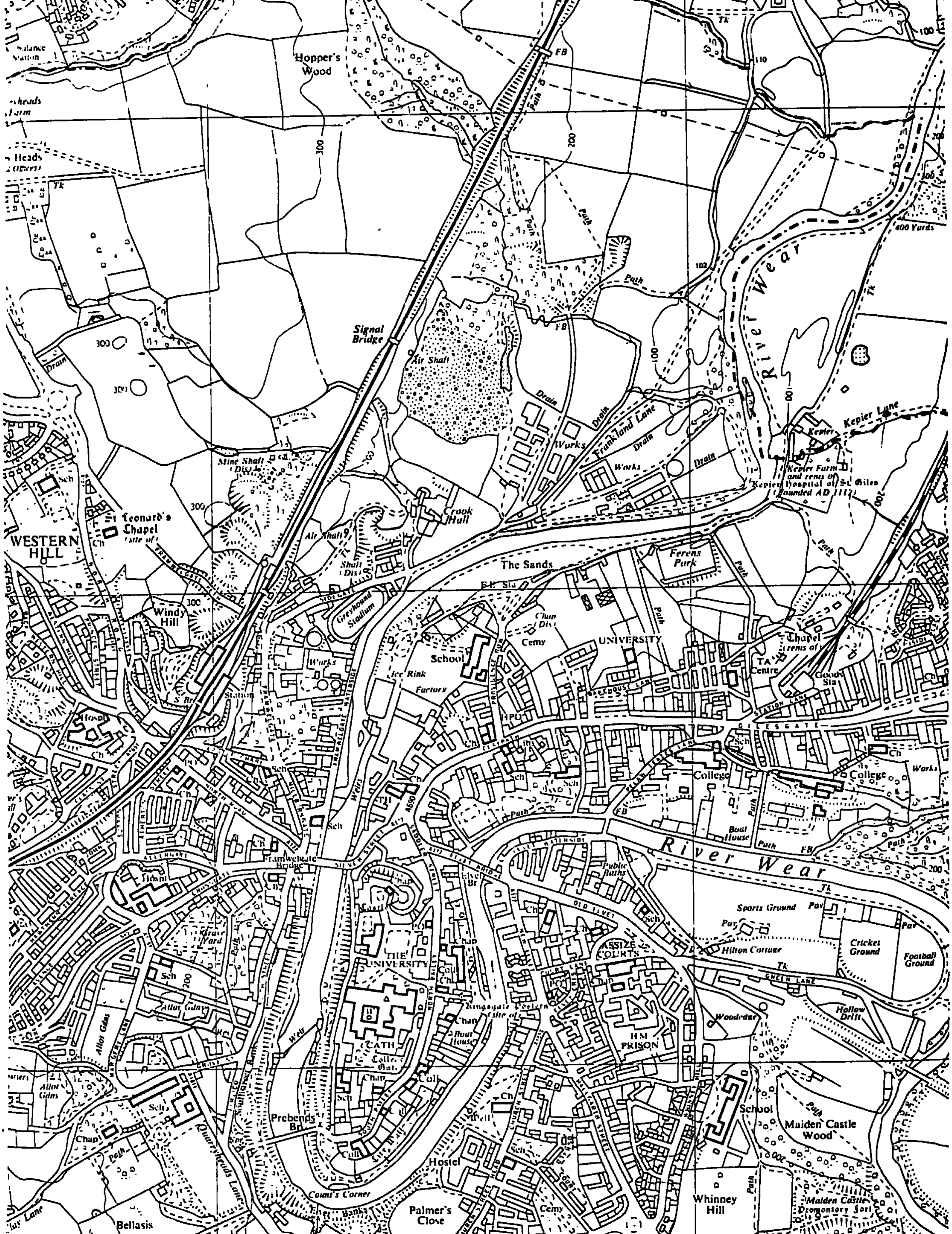
A bird will maintain a constant weight over a period of days when its daily energy intake balances the energy it requires for its daily activities. The energy required for these varies during the year; also the food sources available to a bird vary both in amount and in quality at different times of the year. Since passerine birds feed only by day, they must store energy for use overnight, partly as fat which has the highest calorific value of the normal body components. They may also lay down deposits of fat to be used as an emergency resource in times of need, e.g. during very cold weather. For migration, the extra energy required for long, non-stop flights is stored prior to take-off, again as fat. The amount laid down is related to the energy needed for the bird to complete its flight (Odum 1960). Although non migratory birds do not have heed of such short-term energy reserves, they nevertheless store fat each day in winter and use it overnight.

The breeding season is also a time of increased energy demand for adult birds, through egg production, incubation and feeding of nestlings. For most birds the breeding season is timed ultimately to coincide with food abundance; this permits each pair to raise larger broods than it could at any other times of the year. The strain of breeding may lead to alterations in the body composition (muscle protein, fat etc.) of birds. Thus the cyclic variation in body weight of the tropical bulbul, *Pycnonotus goiavier* is associated with breeding and also moulting (Ward 1969). Newton (1966) also found a drop in weight in the lean dry weight (i.e. body protein and skelaton of Bullfinches (*Pyrrhula pyrrhula*) after the breeding season. The present study set out to investigate the seasonal changes in body weight and composition of the House Sparrow (*Passer domesticus*) in view of its extended breeding season. Mortality in the adult House Sparrow is known to be highest in mid-summer (Summers-Smith 1963), at a time when the higher temperatures would be expected to impose the least maintenance energy requirements on birds (Kendeigh 1949, Davis 1955). This mortality could be due to a relative food shortage or possibly to a very high energy expenditure throughout the long breeding season.

II. Study Area.

Observations were carried out in various habitats in and about Durham City. The areas chosen (Fig.1.) consisted

Fig 1 Study area



HAM (DURHAM AND FRAMWELGATE) MB

of houses interspersed with parks, gardens and allotments; and included quite large areas of wasteland. As many of the buildings were old and in bad repair, there were plenty of sites for nesting and roosting.

During the winter small flocks of House Sparrows from the study area fed in the neighbouring field or collected in the City where scraps were available. In the breeding season, however, birds fed in parks and gardens, searching for insects. Towards the end of the breeding season, flocks of up to fifty birds fed on grass seeds on the allotments and wasteland.

III. Food.

Sparrows have, to a large extent, become dependent on food provided directly or indirectly by man. Their population density is related to the availability of food such as kitchen scraps, grain and food of domestic animals (Summers-Smith 1963). These items form the major part of their diet at all times of the year (Southern 1945), but more especially in the winter.

During the breeding season some proteinaeuous food is essential for the nestlings' growth. The amount and nature of the animal food eaten varies widely. There is no shortage of insects in fruit growing areas, and therefore in these localities insects comprise 40% of the adult's diet. The adults feed mainly on Lepidopteran larvae (23.5%) but Diptera (5.5%), Coleoptera (4.5%) Hemiptera (1%) and earwigs (5.0%) were also eaten. The nestlings diet was similar, but contained a higher proportion of aphids. It is not known how relevant these figures are to conditions in rural areas in 1969. In urban areas, where fewer insects are available, Collinge(1924) found that adults and nestlings also ate slugs, earthworms and spiders. The amount and kind of animal food taken depended on the amount available.

In Durham, I found no evidence of food shortage during the winter. Sparrows fed on grain and scraps which were available throughout the coldest periods.

To investigate the changes in insect numbers, catch records from a light trap situated just outside Durham were analysed. These included totals for Tipulida Diptera, Hemiptera Lepidoptera and Coleoptera (Fig.2.). A peak in total number of flying insects occured in June-July followed by a slow decline. The numbers of Lepidopterans trapped decreased in August (Fig. 3.) since sparrows feed primarily on larvae their availability presumably decreased before the decline of the imaginos.

The breeding season of most insectiverous birds has evolved to coincide with the period when most insects occur (Lack 1954). Sparrows, although primarily graminiverous birds, breed at this time when insects are readily available as food.

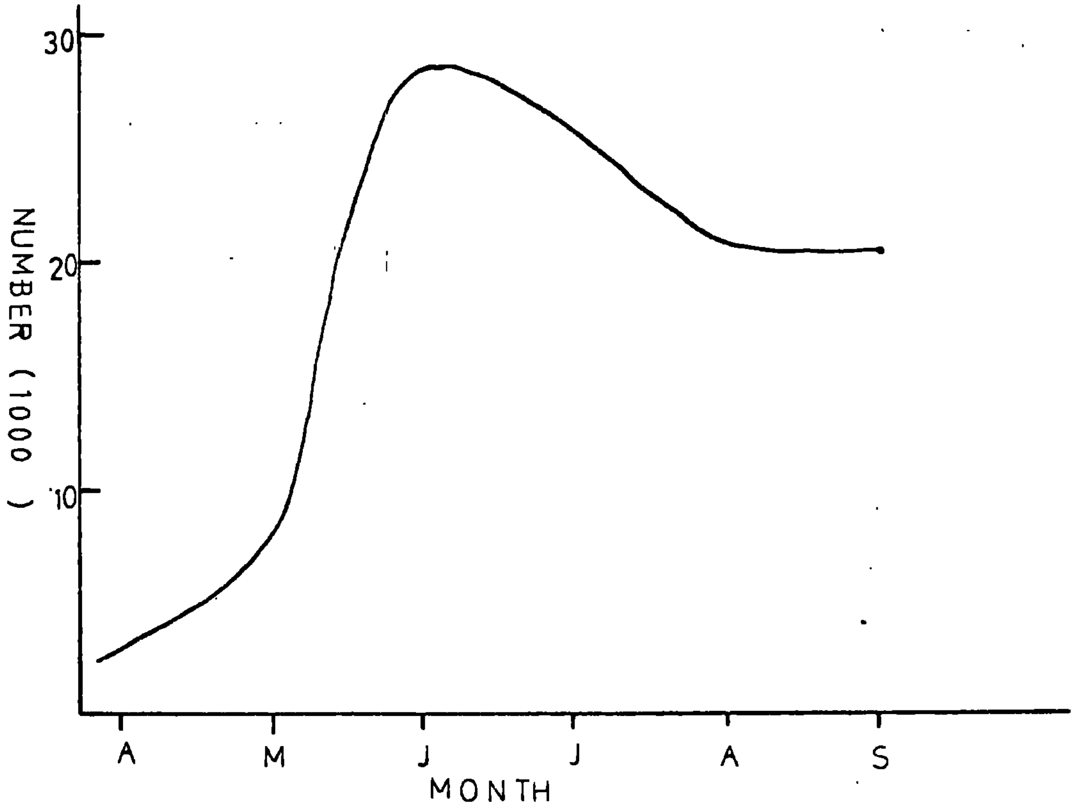


Fig.2. Change in total number of flying insects from April to September (based on light trap records 1966-9).

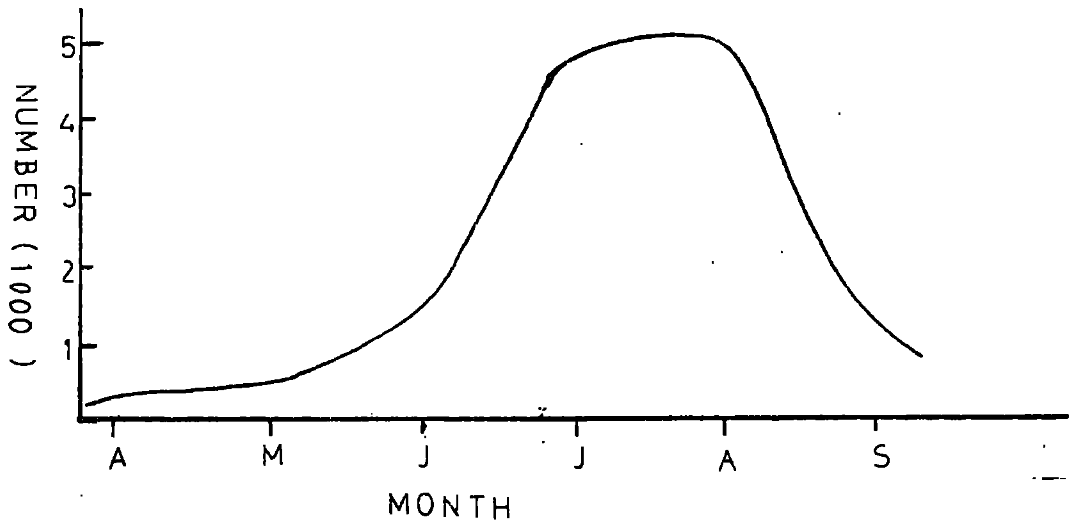


Fig.3. Change in number of adult Lepidoptera from April to September (based on light trap records 1966-9).

IV. Climate.

Meteoroligical data was obtained from the Durham University observatory, situated a mile from the centre of Durham city. The change in the mean temperature from November, 1968 to August, 1969 is shown in figure 4.

Temperatures throughout the beginning of winter were above the average recorded over the last 120 years, but decreased towards the end of December (Table 1). After a mild January, it was the coldest February since 1963. Snow lay on the ground for most of the month and persisted into March. Temperatures increased towards the end of March, and the mean temperature in April was a little below the mean.

TABLE I

MONTHLY TEMPERATURES IN DURHAM FROM WINTER 1968 - SUMMER 1969

Month	TEMPERATURE (°C)		
	Mean Daily	Mean Daily Maximum	Mean Daily Minimum
November	7.0	7.9	6.2
December	3.4	4.8	2.0
January	4.5	7.1	1.0
February	2.0	3.1	-2.8
March	2.1	4.9	0.6
April	6.4	10.7	2.2
May	9.4	13.1	5.7
June	13.1	18.1	8.1
July	15.9	20.4	11.4

TABLE II

MONTHLY TEMPERATURES IN DURHAM FROM WINTER TO SUMMER (Based on the last 120)

Month	TEMPERATURE (°C)		
	Mean Daily	Mean Daily Maximum	Mean Daily Minimum
November	5.2	8.2	2.3
December	3.7	6.3	1.0
January	3.3	6.1	0.5
February	3.5	6.4	0.5
March	4.4	8.0	0.8
April	6.5	10.6	2.3
May	9.6	14.0	5.2
June	12.5	17.2	7.7
July	14.6	19.1	10.1

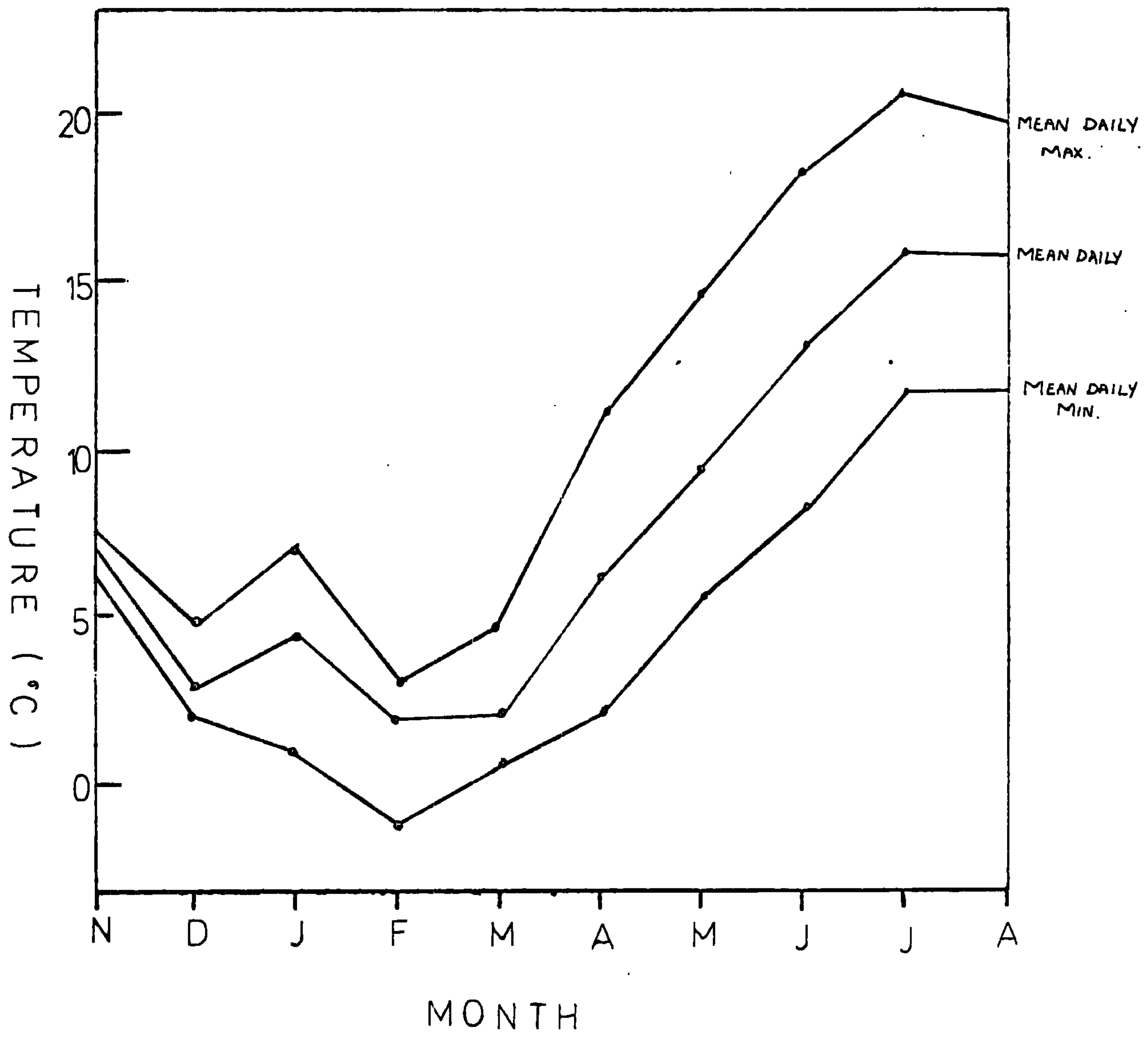


Fig. 4. Mean monthly temperatures in Durham from November 1968 to August 1969.

SECTION II.

1. Introduction.

The energy required by a wild bird for its daily activities is difficult to measure directly, a notable study is that on the lilied Anna Hummingbird (<u>Calypte anna</u>), by Pearson, (1954). Because of the difficulties, indirect measurements are usually employed.

Energy requirement may be divided for convenience into "existence energy" defined by Kendeigh (1949) as energy required "in maintaining standard or basal metabolism, in chemical heat regulation, in securing food and drink and in the heat increment of digestion and assimilation", and "productive energy" required for activities above the minimum leval of existence, such activities are flying, moulting, and breeding. In the present study, existence energy was estimated from measurements on birds in captivity and by observations of daily activity rhythms of sparrows. Productive energy was also estimated from observations of activity rhythms.

11. Methods.

a) Energy requirements of House Sparrows in captivity.

Birds were kept in captivity in a ventilated wooden hut under natural light conditions. Since the temperature was only slightly higher in the hut than outside, the conditions of captivity should not have altered the birds' energy requirements from those in the wild, apart from the obvious restrictions in flight and activity. Each bird was confined in a wire cage, 8" x 9" x 12", with a shelter at one end. These cages did not prevent the birds from feeding and moving quite freely, though they did restrict flying or excessive activity. Birds were weighed every morning.

The base of the cage was lined with preweighed foil, and a weighed amount of crushed oats (in excess of the birds' requirements) was provided each day. The apparent amount eaten each day was measured by subtracting the weight of food remaining the following day. The aluminium foil was changed daily, and any spilled food removed and weighed; this weight was subtracted from the apparent amount eaten to give a corrected figure for the daily intake. The foil was then dried to a constant weight at 55°C and the weight of the faeces produced per day obtained by subtracting the original weight of the foil.

Calorific values of the food and faeces were obtained bombing dry-weighted samples in a Ballistic Bomb caloumeter. Hence the energy ingested and egested was estimated, and therefore the energy required for each bird per day was calculated. Feeding experiments were carried out on four birds in early April before the breeding season, and in early June during moult.

(b) <u>Daytime activities of House Sparrows.</u>

To measure the energy normally expended, in excess of that measured in captivity the amount of time spent in various activities was recorded:

i) time spent in flight

ii) time spent in feeding or drinking

iii) time spent perching, calling, preening, roosting, etc.

As sparrows are gregarious, it was impractical to follow any one bird, and Gibb's (1954) method of repeated standard observation was used. Observations were made by walking at a set pace through the study area, and recording the nature of each sparrow's activity when first seen. To avoid overestimation of the time spent flying, birds were counted only within a radius of approximately twenty yards. Any birds disturbed during observation were not recorded to avoid encouraging a bias in results.

These observations were carried out on two successive days, with similar weather conditions in early April, before the breeding season, and then repeated in mid-May and in early June when the fledglings were being fed. In July, as sparrows were feeding in flocks of up to fifty birds, this method became unreliable and was discarded.

II.

RESULTS.

a) Daily energy requirements of the House Sparrow.

Before experimentation, four birds were allowed to adapt to conditions of captivity for a week. Their weight fell initially, then levelled at 5-7 gms. below their original weight. During the six day experimental period in April, the birds' weight did not change by more than 0.5 gms. during any one day. Hence, a mean value for the daily energy required was calculated. (Table III). The mean energy required for the sparrows (irrespective of sex), was 21.0 K.cals per day at a mean temperature of 6.4°C. The mean energy required by females (22.6 K.cals per day) was slightly, but not significantly higher than that required by males (19.4 K.cals per day).

This experiment was repeated on four birds of both sexes in July (Table II). The mean energy requirement was calculated as 19.8 K.cals per bird per day, at a mean temperature of 13.1°C. Again the females utilised more energy (20.8 K.cals per bird per day) than the males (18.8 K.cals per bird per day), but this difference was not significant.

b) Daily activities of the House Sparrow in the Wild.

Field work was carried out between the hours of 0.500 to 21.00, and over a total of 45 hours in the months of April to June. During this time approximately 4,000 spot observations of behaviour

TABLE III

ENERGY REQUIREMENTS OF CAPTIVE HOUSE SPARROWS IN APRIL (Mean Temp. 6.4°C)

Sex	Weight (in grams)	Food Intake (Kcals/day)	Faeces (Kcals/day)	Percentage Assimulation	Energy required (Kcals/day)
Female	22.92 ∓ .11*	25.90 ∓ .63	3.48 ∓ .03	87.2	22.60 ∓ .57
Female	25.46 ∓ .52	26.08 ∓ .55	3.39 ∓ .07	86.9	22.67 ∓ 1.10
Male	20.76 ∓ .03	23.24 ∓ .82	3.32 ∓ .20	84.9	19.75 ∓ .37
Male	23.35 ∓ .26	21.76 ∓ .91	2.99 ∓ .01	88.0	19.15 ∓ .37

TABLE IV

ENERGY REQUIREMENTS OF CAPTIVE HOUSE SPARROWS IN JUNE (Mean Temp. 13.1°C)

Sex	Weight (in grams)	Food Intake (Kcals/day)	Faeces (Kcals/day)	Percentage Assimulation	Energy required (Kcals/day)
Female	23.73 ∓ .13	25.96 ∓ .91	3.65 ∓ .10	85.9	21.31 ∓ 1.20
Female	23.82 ∓ .29	24.43 ∓ .56	3.59 ∓ .21	85.3	20.34 ∓ .91
Male	22.97 ∓ .18	22.81 ∓ .06	3.25 ∓ .06	85.5	19.52 ∓ .65
Male	22.94 ∓ .17	21.71 ∓ .74	3.51 ∓ .11	83.7	18.19 ∓ .34

*The variance indicated with measurements is the standard error of the mean.

were made; and the results are shown in Table V.

TABLE V. DAYTIME ACTIVITIES OF SPARROWS.

Month:	Mean Temp.	Day length (hrs).	Estimate* of Total Time spent: - (Hours) (1) Flying:	(2) Feeding	(3) All other activities.
April	6.4°C	14	3.8	3.1	7.1
May	9.4°C	15	4.1	5.7	5.2
June	13.1°C	16	5.0	6.8	4.2

* Estimate calculated by multiplying day length by percentage of time spent in different activities.

At the beginning of the breeding season, sparrows had little difficulty in obtaining food. In early April (Fig.V), feeding was carried out in a leisurely manner throughout the day. In this month, cock sparrows spent as much as 16% of the day calling outside the nests; and both sexes passed a large part of the day in non-essential activities (such as preening, dust-bathing, sunbathing, etc). As the breeding season progressed, a larger part of the day was devoted to obtaining food. This also required an increase in the time spent flying (to reach feeding stations).

In June, when the birds were feeding fledglings, adults fed for 42% of the day. Birds showed marked peaks of feeding activity

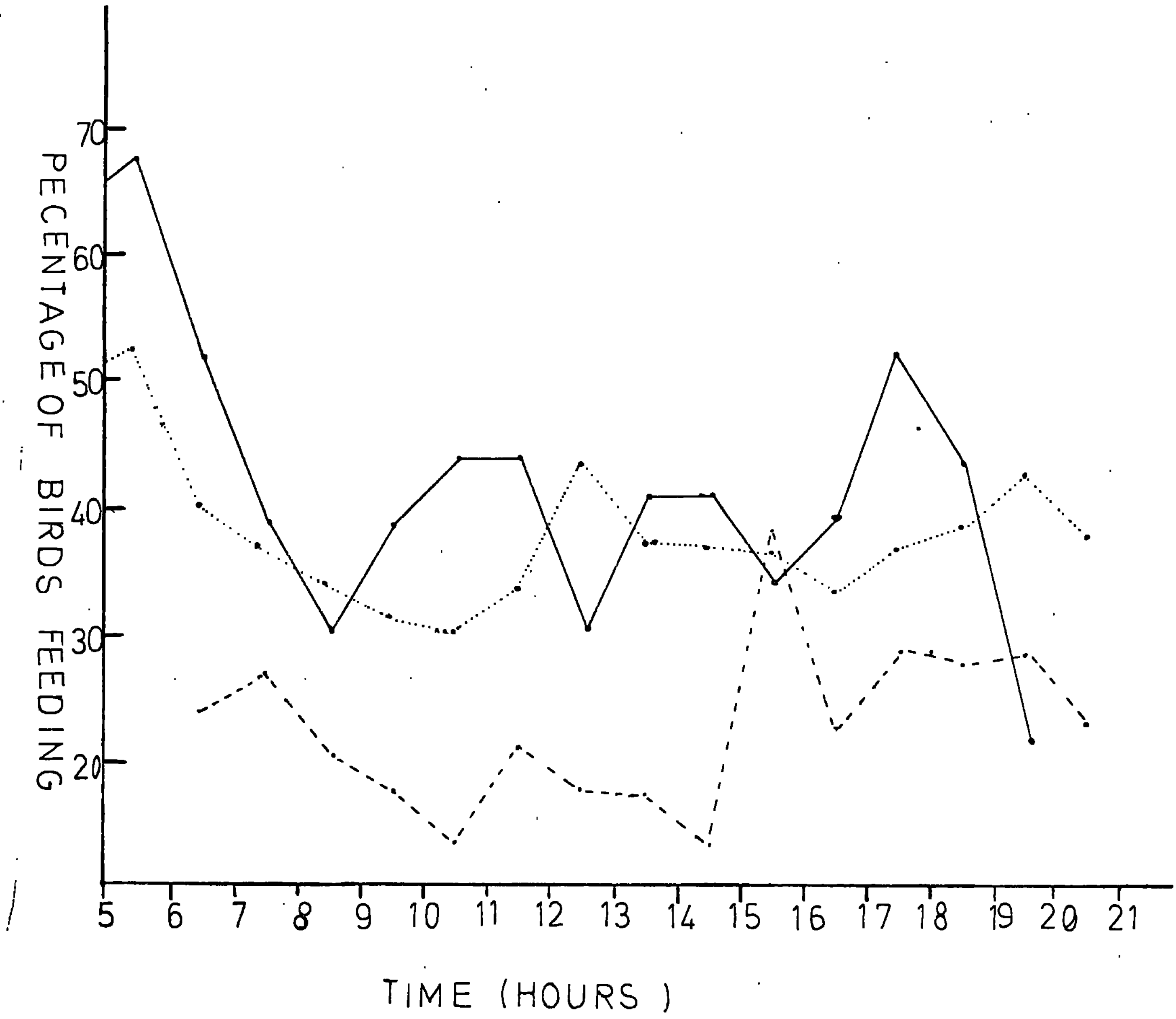


Fig. 5. Changesin feeding activity rhythms of House Sparrows

---- April

······ May

—— June.

just after sunrise, just before sunset and at other times of the day (Fig.5).

c) Field energy requirements of House Sparrows.

Sparrows kept in captivity could move and excerbise quite freely. Therefore, the energy required in the wild for feeding and activities other than flight is assumed to be equal to that measured in captivity. To estimate field energy requirements of birds, a correction was applied for the 27% of daylight hours spent in flight, i.e. 3.8 hours in a fourteen hour photo-period.

Lefebre (1964) estimated that the energy required by the homing pigeon Columbia livia for rapid flight was eight times the resting metabolic rate. This figure agrees with Tucker's (1968) value for flight energy requirements of the budgerigar (Melopsittacus indulatus). However, pigeons flying at moderate speeds required only three times the energy utilised in resting metabolism. As sparrows do not fly very fast, or very far, it will be assumed that their energy requirements for flight are three times their resting Metabolic rate.

My results of the measurements of the energy requirements of House Sparrows in captivity were similar to those obtained by Kendeigh (1949) using the same method, and so it may be assumed that his values for resting metabolism (obtained by measuring the rate of respiration) may also be applied to this study. In April, with a mean temperature of 6°C, the energy utilised for resting metabolism was approximately 0.84 K.cals per bird per hour. Hence, correcting for the flight energy requirements the total energy required by House Sparrows at that time:

$$= 21.04 + (84 \times 2 \times 3.8)$$

$$= 21.04 + 6.38$$

$$= 27.42 \text{ K.cals per bird per day.}$$

In June, with a mean temperature of 13°C the resting metabolic was 0.75 K.cals per bird per day. Field energy requirements of sparrows calculated as above equaled 27.31 K.cals per bird per day. However, at this time the birds spent an extra 3.7 hours collecting food. Assuming that in moderate activities a bird utilised twice the energy necessary for resting metabolism, the field energy requirements of sparrows in June

$$= 27.31 + (0.75 \times 3.7)$$

$$= 27.31 + 2.77$$

$$= 30.08 \text{ K.cals per bird per day.}$$

DISCUSSION.

If the daily activities of House Sparrows (i.e. percentage of day spent in flying, feeding, etc), in June equaled those in April, field energy requirements in a sixteen hour photoperiod would

$$= 19.84 + 0.75 \times 2 \times 4.32$$

$$= 19.84 + 6.48$$

$$= 26.32 \text{ K.cals.}$$

Thus, the House Sparrow requires approximately 3.8 K.cals for activities due to breeding.

The mean energy metabolised by captive sparrows in both April and June, was higher than the mean energy required for resting metabolism at temperatures of 6°C and 13°C respectively (Kendeigh, 1944). This difference was greater by approximately 1 K.cal in June. The assimilation ratio (i.e. energy metabolised expressed as a percentage of energy intake) was lower in June (compare Table III, Table IV), while Kendeigh (1949) found that this increased with increasing temperature. These differences although not significant, may reflect the changes in metabolism due to moulting. Davis (1955) also found a slight increase in the energy requirements of moulting birds.

Since these values for energy requirements of sparrows are estimates, and cannot be regarded as numerically exact, but are reliable for purposes of comparison. T hey show that the extra activity required for feeding fledglings, results in a higher energy requirement in June compared with April by a factor of about 10%.

SECTION III.

1. Introduction.

Sparrow carcasses were analysed to investigate the variation through the spring and summer in the major body constituents: lipid water and lean dry weight (chiefly skeleton and muscle protein. The skeletal weight was assumed to remain constant.

Lipid levels in the flight muscles of birds have been investigated for the study of fat metabolism before migration (King and Farner 1965), but muscle weights are also a valuable indication (Ward 1969) of the amount of protein in the body. Any protein deficiency would be expected to result in a decrease in the lean (i.e. fat free) weight of the pectoral muscles. The present study was carried out to find how energy reserves carried by House Sparrows varied during the year.

2. Methods.

81 birds were caught by mist netting at approximately fortnightly intervals from January to July, 1969. During the winter months (January to March inclusive), birds were caught prior to roosting. The birds were killed, weighed immediately, and stood in deep freeze for analysis at a later date.

Each carcass was plucked and the feathers weighed:

The breast muscles, i.e. pectoralis major and pectoralis minor, were dissected out carefully and the sternum and coracoid were scraped clear of any remaining tissue. These were weighed and extracted separately. The contents of the crop, the proventiculus and the gizard were removed. The length of the testes were measured.

a) <u>Soxhlet extraction.</u>

The breast muscles were dried to a constant weight in a vacuum oven at 55-60°C. The material was allowed to cool in a dessicator, then ground finely and returned to the vacuum oven overnight to ensure that all the water in the tissue had been removed. The dried material was placed in a paper extraction thimble and weighed before extraction with technical petroleum ether in the soxhlet apparatus (c.f. diagram), which permits continuous extraction.

The dried breast muscle was extracted for 6 hours; after this time no further weight loss occured. The thimbles were dried and reweighed to give the amount of lipid present by difference from the initial weighing.

b) <u>Direct extraction with petroleum ether.</u>

The rest of the carcass (i.e. minus pectoral muscles), was chopped, dried to a constant weight in a vacuum oven at 55-60°C and then ground finely prior to extraction.

Extraction by this method may not be as complete as by the soxhlet method, so it cannot be used for estimation of small amounts of fat. However, it is much quicker and where larger volumes of material or appreciable weights of fat are to be extracted, it has proved sufficiently accurate for measurement of lipid levals in birds (Odum 1960, Newton & Evens 1966, Brusbin, 1969).

Direct extraction was carried out in crystalising dishes warmed over an electrically heated waterbath. Several extractions of each portion were made with solvent decanted off and filtered between each. Finally the mixture was filtered through a weighed filter paper and dried to a constant weight. As before, the amount of lipid present was calculated by subtracting the weight of residue from the original dry weight.

111. Results.

Live weights of both male and female House Sparrows trapped in late afternoon were highest in mid-winter and decreased thereafter until April, when weights of females rose slightly (Table VI; FigVI.) Weights of both sexes rose in May but dropped in June. The mean live weight of females was higher than that of males in all months, though (because of the small samples available) this difference was significant at the 5% level only at the end of the breeding season. This significance of changes in total weight will be discussed later.

The weight of plumage dropped steadily throughout the sampling period (Table VII). In winter the down feathers act as an insulating layer, helping the bird to maintain a constant temperature without increased metabolism. When the temperatures rise in spring, such extra insulation becomes unneccessary, and down feathers lost are not replaced. This explains some of the decrease in weight of the plumage in the spring; a further contributing factor is abrasion of the tips of body feathers.

During January and February, the weight of food stored, just prior to roosting remained at about 1 gm. (approximately 14% of the lean dry weight) despite a long period of harsh weather (Table VII). In March the weight of undigested food fell to 0.6gm.

TABLE VI

SEASONAL VARIATION IN LIVE WEIGHTS OF HOUSE SPARROWS

Month	Time of Capture	No.of Males	Weight of Males (in gms)	No.of Females	Weight of Females (in gms)
January	1630-1730	3	29.16 ∓ .65	9	30.30 ∓ .31
February	1630-1730	10	28.70 ∓ .58	3	30.76 ∓ .57
March	1630-1800	4	28.19 ∓ .44	2	28.59 ∓ .27
April	1600-1800	9	27.40 ∓ .60	3	29.08 ∓ .84
May	1600-1800	8	27.65 ∓ .43	4	29.93 ∓1.10
June	1600-1800	6	26.48 ∓ .10	5	27.52 ∓ .91
July	1600-1800	7	25.80 ∓ .64	6	27.82 ∓ .69

TABLE VII

WEIGHTS OF PLUMAGE AND STORED FOOD

Month	Time of Capture	No. of Birds	Weight of Plumage (Gms)	Weight of Undigested Food (Gms)
January	1630-1730	12	2.38 ∓ .03	.88 ∓ .10
February	1630-1730	13	2.32 ∓ .29	1.00 ∓ .10
March	1630-1800	6	2.06 ∓ .02	.60 ∓ .10
April	1600-1800	12	1.99 ∓ .02	.24 ∓ .16
May	1600-1800	12	1.82 ∓ .02	(.17 ∓ .10)
June	1600-1800	11	1.67 ∓ .02	(.25 ∓ .12)
July	1600-1800	13	1.70 ∓ .05	(.14 ∓ .02)

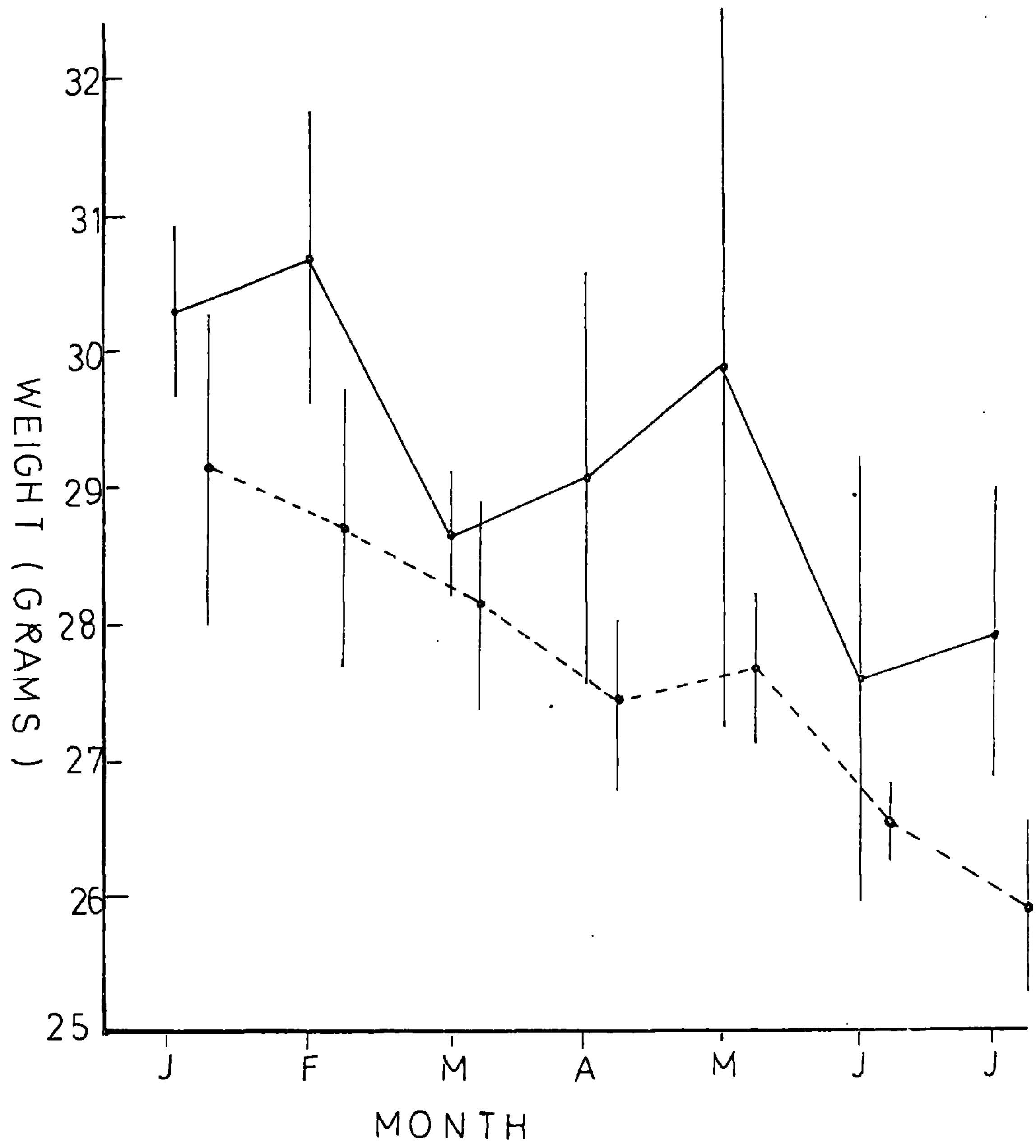


Fig.6. Variation in live weights of House Sparrows circle = means ; vertical lines = 95% confidence limits ; males ---- females —— in Figures 6 - 16.

(8% of the lean dry weight). From April onwards the birds were not trapped immediately before roosting and the weight of food in their gut and gizzard was more variable.

The decrease in weight of plumage and stored food was one of the causes of the overall drop in live weight of sparrows throughout the spring and summer. When weights of plumage and food are subtracted, the residual body weights showed a clearer difference between the sexes (Table VII. Fig.VII.) Female sparrows fluctuated more in mean body weight than males, but the apparent decrease in mean weights of females between January and July was not significant at the 5% level. Their highest mean body weight was recorded in May, when it was greater than their lowest mean weight recorded in June. Not even this drop was significant however, due to the small sample sizes.

At the end of the breeding season, females were significantly heavier ($P = 0.05$) than the males. The mean body weight of the males remained approximately constant until May and then dropped in June and July ($P = 0.02$) at the end of the breeding season.

a) <u>Variation in the major body components.</u>

Analysis of the body into the major components (Table VIII) lipid water and lean dry weight (i.e. chiefly skelaton and muscle protein) revealed the following changes.

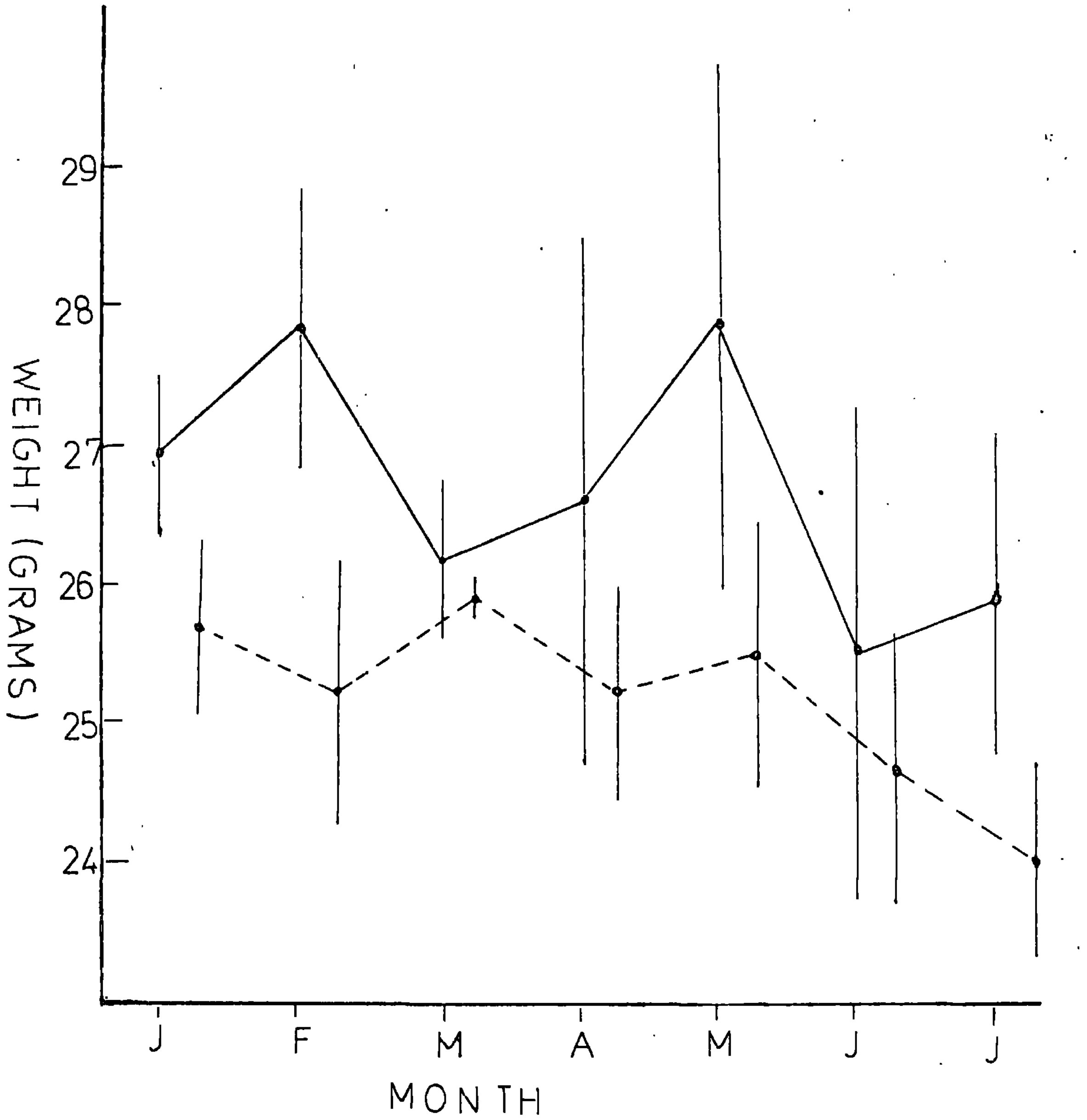


Fig. 7. Change in body weight of House Sparrows (excluding plumage and stored food).

TABLE VIII

SEASONAL VARIATION IN BODY CONSTITUENTS OF FEMALE SPARROWS (in Grams)

Date	No. of Birds	Wet Weight Excluding Plumage and stored food	Water	Lipid	Lean Dry Weight
January	9	26.97 ± .24	18.42 ± .24	2.51 ± .20	6.04 ± .03
February	3	27.83 ± .53	18.16 ± .53	2.60 ± .22	7.09 ± .13
March	2	26.03 ± .29	17.39 ± .13	1.91 ± .08	6.73 ± .02
April	3	26.64 ± .98	18.14 ± .64	1.45 ± .14	7.05 ± .22
May	4	27.91 ±1.10	19.32 ± .60	1.30 ± .08	7.29 ± .17
June	5	25.49 ± .92	17.48 ± .74	1.02 ± .03	6.99 ± .14
July	6	25.89 ± .78	17.66 ± .46	1.32 ± .10	6.91 ± .25

TABLE IX

SEASONAL VARIATION IN BODY CONSTITUENTS OF MALE SPARROWS (IN GRAMS)

Date	No. of Birds	Wet Weight Excluding Plumage and stored food	Water	Lipid	Lean Dry Weight
January	3	25.71 ± .24	17.41 ± .66	2.02 ± .20	6.28 ± .20
February	10	25.22 ± .50	16.57 ± .13	1.94 ± .10	6.71 ± .12
March	4	25.98 ± .18	17.43 ± .46	1.68 ± .12	6.87 ± .14
April	9	25.58 ± .48	17.12 ± .13	1.25 ± .06	6.85 ± .13
May	8	25.67 ± .42	17.56 ± .10	1.11 ± .06	7.00 ± .12
June	6	24.69 ± .37	16.75 ± .28	1.04 ± .04	6.90 ± .14
July	7	24.02 ± .40	16.51 ± .30	.91 ± .03	6.60 ± .12

Water content of sparrows was highest in May during the early part of the breeding season (Fig.VIII). The mean weight of water in females decreased in early spring, although total mean weight increased at this time. Water content than rose in April and May, but fell again in June and July. The mean weight of water in males varied less than in females. The highest mean weight was also recorded in May. In February and May the females had a significantly higher water content than the males. Since the weight of water in any indicidual was partly related to the weight of fat present (R = 0.4209), this difference was, in part, associated with the greater fat content of the females mentioned below.

A marked decrease in the weight of lipid present in both males and females also contributes to the decrease in live weight in spring (Fig.IX). Hens had a higher fat content than cocks in all months; this difference in mean weight of fat was significant ($P < 0.001$) in February and July. During the early part of the breeding season (i.e. April and May), the weight of fat present varied more in the females than in the males. This variation may have been due to the developing eggs present in some of the females analysed. Lipid levels dropped in June and at this time the mean weight of fat carried by hens was about the same as that of the cocks. The fat contents of the males

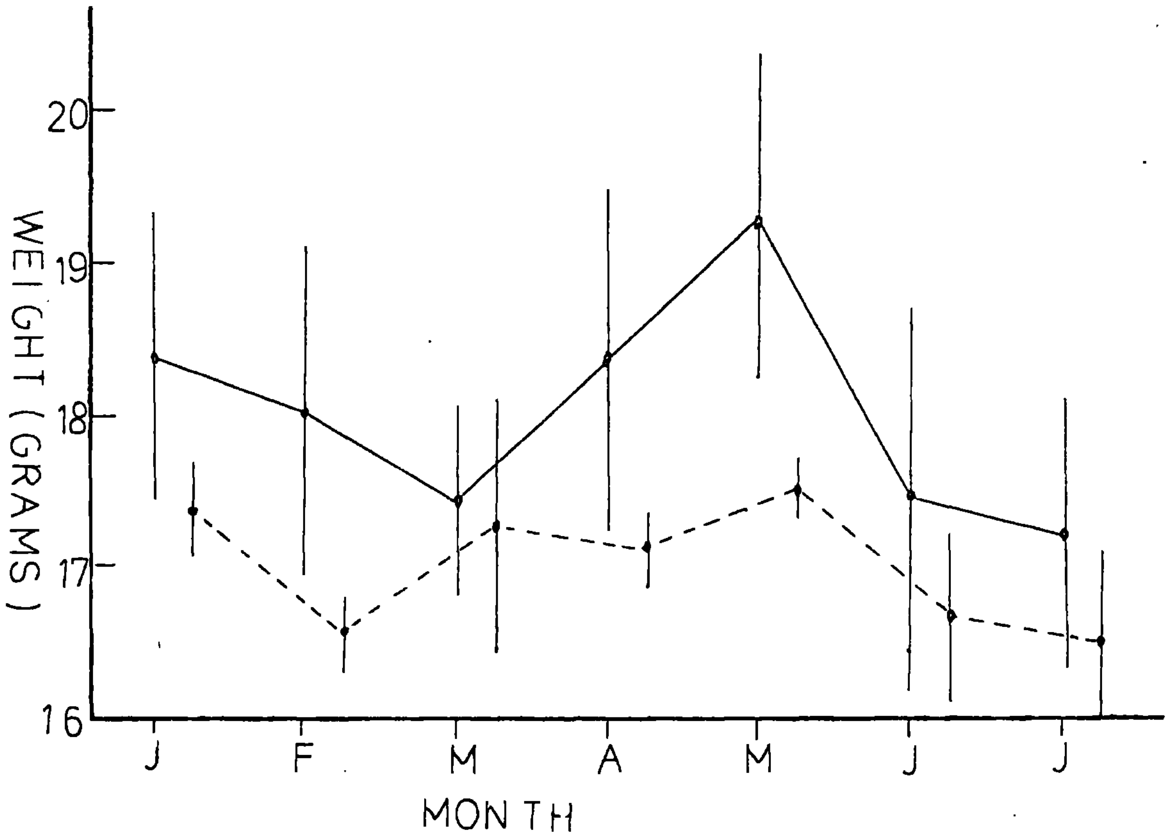


Fig. 8. Seasonal variation in water content of House Sparrows

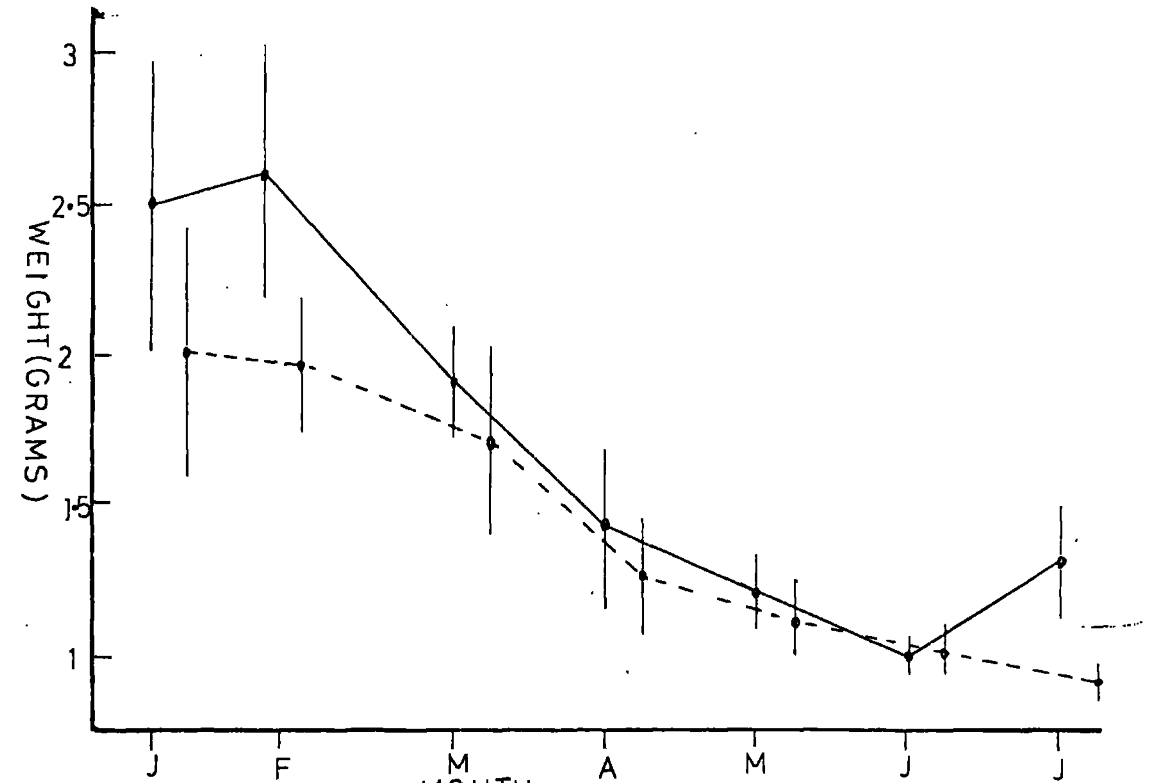


Fig.9. Seasonal variation in lipid content of House Sparrows

dropped steadily from mid-winter to July.

In House Sparrows of both sexes the lean dry weight increased significantly during spring and remained constant until a decrease occurred towards the end of the breeding season (Fig.X). The lean dry weight of the females increased in early spring but fell in March to a level below that of the males. Throughout the breeding season, from April to July the lean dry weight of the females remained approximately constant. The mean fat-free (= lean dry) weight of male sparrows increased more slowly than that of females, remained constant until May, but then decreased significantly (P 0.001) to a level just above the mean weight in January. The variation in lipid index (lipid expressed as a percentage of lean dry weight) is shown in FigureXI. The lipid index provided a measure of the lipid levels in an animal independent of any change in lean dry weight. The lipid index of female House Sparrows droped sharply in spring, due to both an increase in lean dry weight and a decrease in fat content. From April to May the lean dry weight increased further (Figure X), and the lipid index still dropped. The lipid index of male sparrows fell in spring and then levelled out during the breeding season to a value almost identical with that of females. This suggests that the higher weight of fat carried by females during the breeding season was needed to provide energy to maintain the body temperature of the larger lean dry weight chiefly metabolically active tissue.

b) **Variation in weight and major constituents of pectoral muscles.**

Analysis of the flight muscles of sparrows showed that total weight and composition varied in parallel with the rest of the body (Table X & XI). Muscle protein is believed to be a better indicator of protein levels in the whole body than lean dry weight, as the tissue is homogeneous.

The mean wet weight of the flight muscles of the females decreased in spring (Fig.XII), rose again in April and then dropped significantly and steadily until July. The highest mean weight (in January) was 11% higher than the lowest mean weight in June. The mean weight of the flight muscles of males was highest in February and then remained fairly constant until May when it dropped significantly ($P < 0.001$) to a July mean weight 15% lower than that in February.

Water content of the flight muscles varied in parallel with mean total wet weight, in both females and males (compare Fig.XII & Fig. XIII). However, lipid levels in the muscles dropped steadily throughout the sampling period in both sexes. The hens had a significantly higher mean weight of fat in their muscles (Fig. XIV) than did the cocks, but a lower weight in May

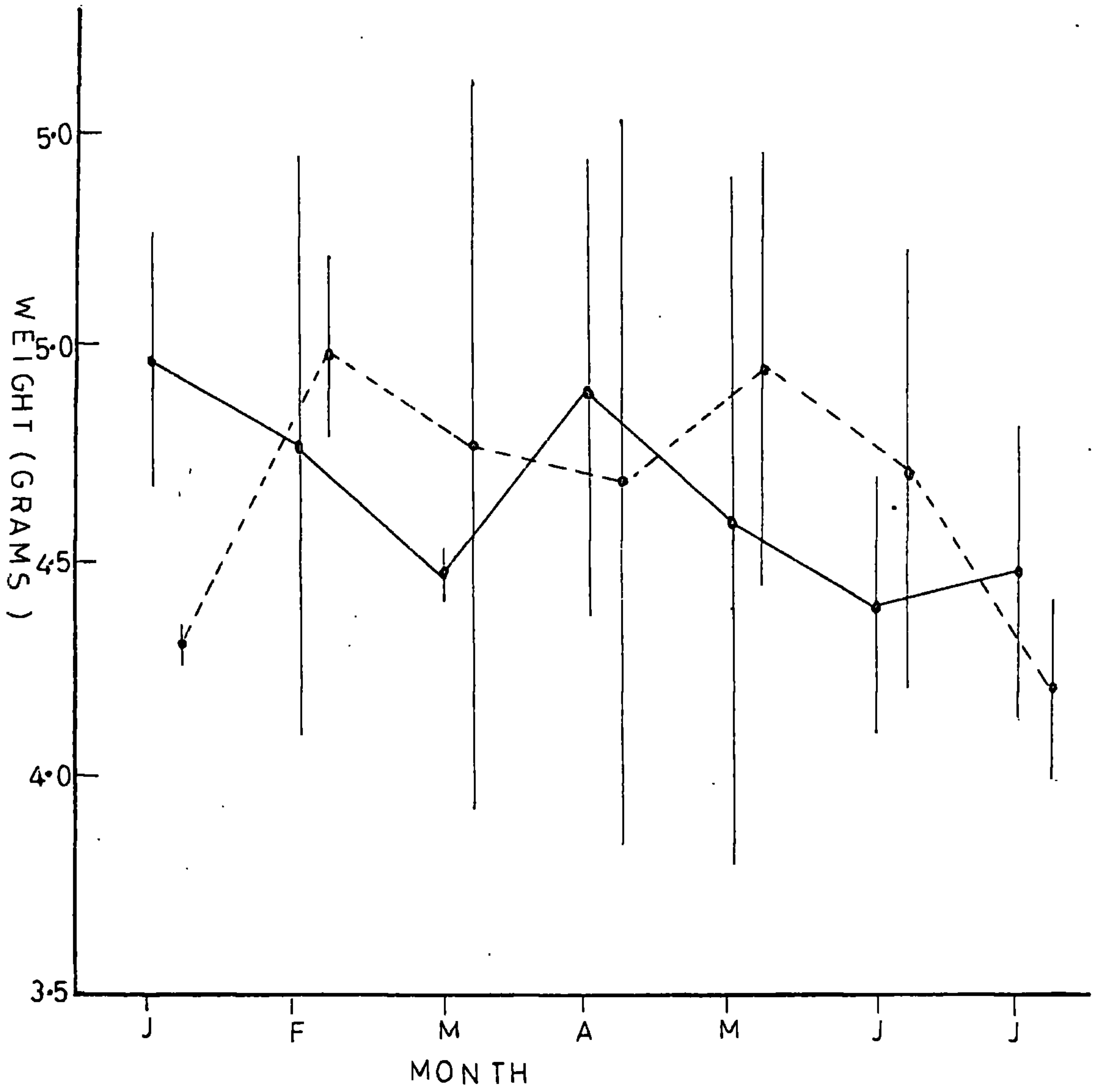


Fig.12. Total weight of flight muscles of House Sparrows.

TABLE X

CONSTITUENTS OF FLIGHT MUSCLES OF FEMALE SPARROWS (IN GRAMS)

Month	Number	Wet Weight	Water	Lipid	Lean Dry Weight
January	9	4.94 ∓ .16	3.48 ∓ .13	.192 ∓ .002	1.26 ∓ .03
February	3	4.78 ∓ .34	3.24 ∓ .06	.142 ∓ .002	1.39 ∓ .03
March	2	4.47 ∓ .01	3.05 ∓ .07	.086 ∓ .001	1.33 ∓ .02
April	3	4.84 ∓ .29	3.38 ∓ .12	.075 ∓ .006	1.38 ∓ .03
May	4	4.60 ∓ .47	3.21 ∓ .10	.049 ∓ .008	1.34 ∓ .03
June	5	4.41 ∓ .15	3.09 ∓ .12	.040 ∓ .006	1.27 ∓ .02
July	6	4.56 ∓ .18	3.19 ∓ .15	.063 ∓ .004	1.31 ∓ .04

TABLE XI

CONSTITUENTS OF FLIGHT MUSCLES OF MALE SPARROWS (IN GRAMS)

Month	Number	Wet Weight	Water	Lipid	Lean Dry Weight
January	3	4.36 ∓ .02	3.05 ∓ .07	.142 ∓ .020	1.16 ∓ .04
February	10	5.02 ∓ .10	3.57 ∓ .06	.126 ∓ .001	1.32 ∓ .04
March	4	4.78 ∓ .31	3.25 ∓ .01	.106 ∓ .001	1.43 ∓ .02
April	9	4.66 ∓ .30	3.21 ∓ .08	.058 ∓ .006	1.40 ∓ .01
May	8	4.95 ∓ .13	3.51 ∓ .08	.055 ∓ .003	1.39 ∓ .02
June	6	4.71 ∓ .16	3.32 ∓ .08	.057 ∓ .004	1.33 ∓ .02
July	7	4.26 ∓ .09	3.01 ∓ .08	.043 ∓ .006	1.20 ∓ .04

and June. The rate of decrease in the weight of fat present in the flight muscles was not as rapid in males as females. Weights of fat in the males' pectoral muscles decreased significantly ($P < 0.001$) from January to April, but remained constant thereafter.

The protein content (lean dry weight) of the flight muscles of females increased during the early spring and remained constant throughout the early part of the breeding season (Fig. XV). From May to June, weights dropped significantly but a slight increase was noted in July. Lean dry weights of the males' muscles showed greater variation than those of females, reaching a maximum in March significantly higher than that of the females. Weights remained constant until May when the mean weight dropped significantly to a weight just above that recorded in January.

The ratio between fat and lean dry weight (i.e. the lipid index), was slightly more variable in females than males (Fig. XVI). The lipid index dropped sharply from January to March, indicating a marked drop in the proportion of fat stored in the muscle tissue prior to roosting. During the breeding season the lipid index dropped further, even though from April onwards the lean dry weight was decreasing. The lipid reached its lowest value in June. The lipid index of the flight muscles of males varied in almost exact parallel with that of females.

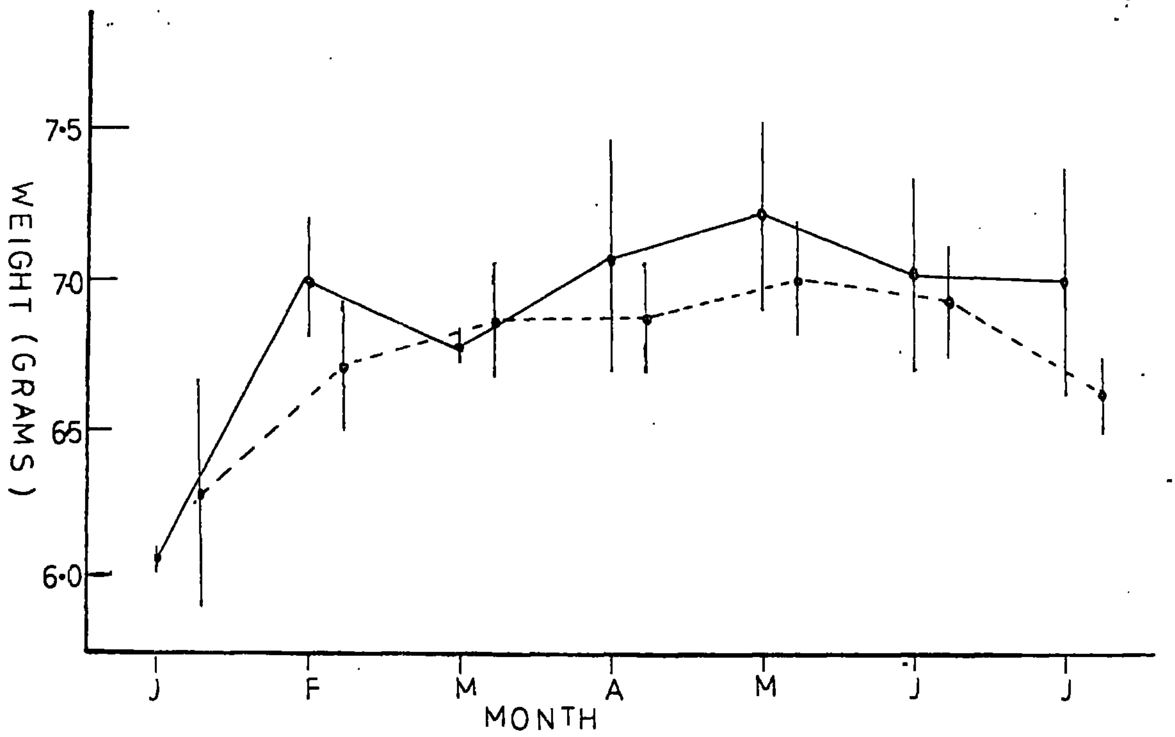


Fig.10. Seasonal variation in lean dry weight of House Sparrows.

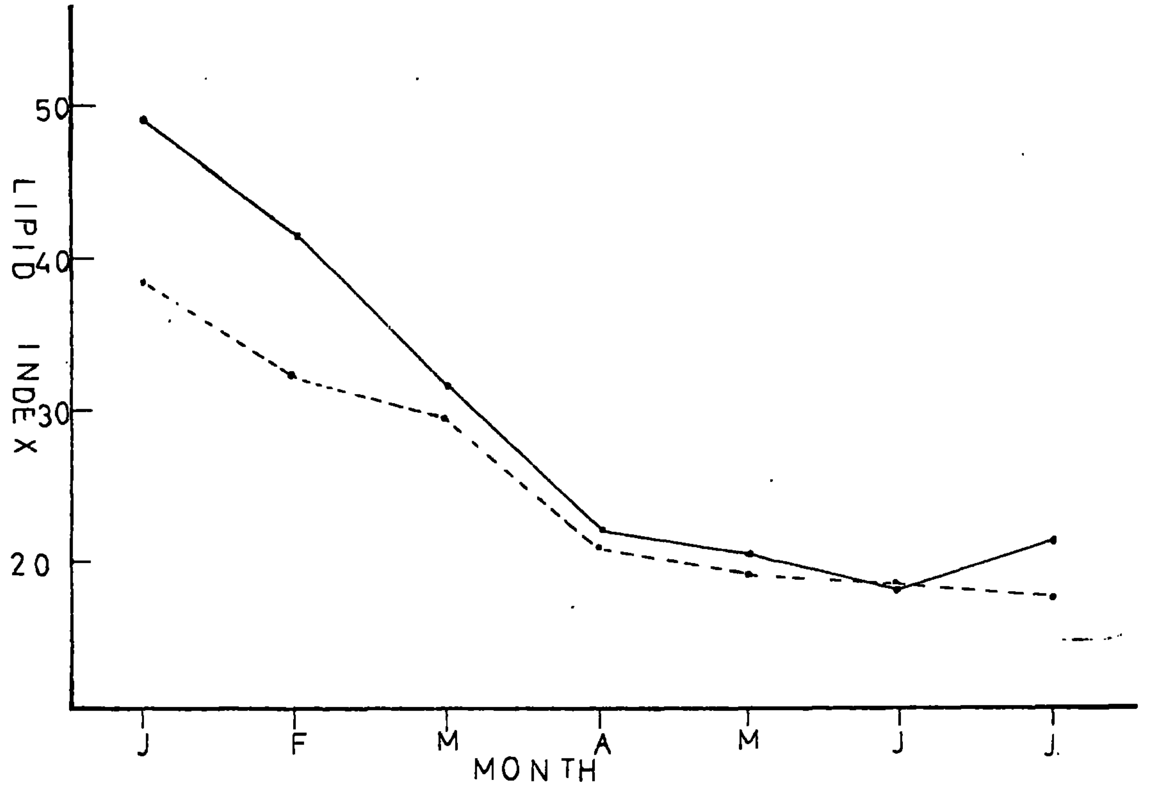


Fig.11 Seasonal in lipid index of House Sparrows (i.e. fat content expressed as a % of lean dry weight.).

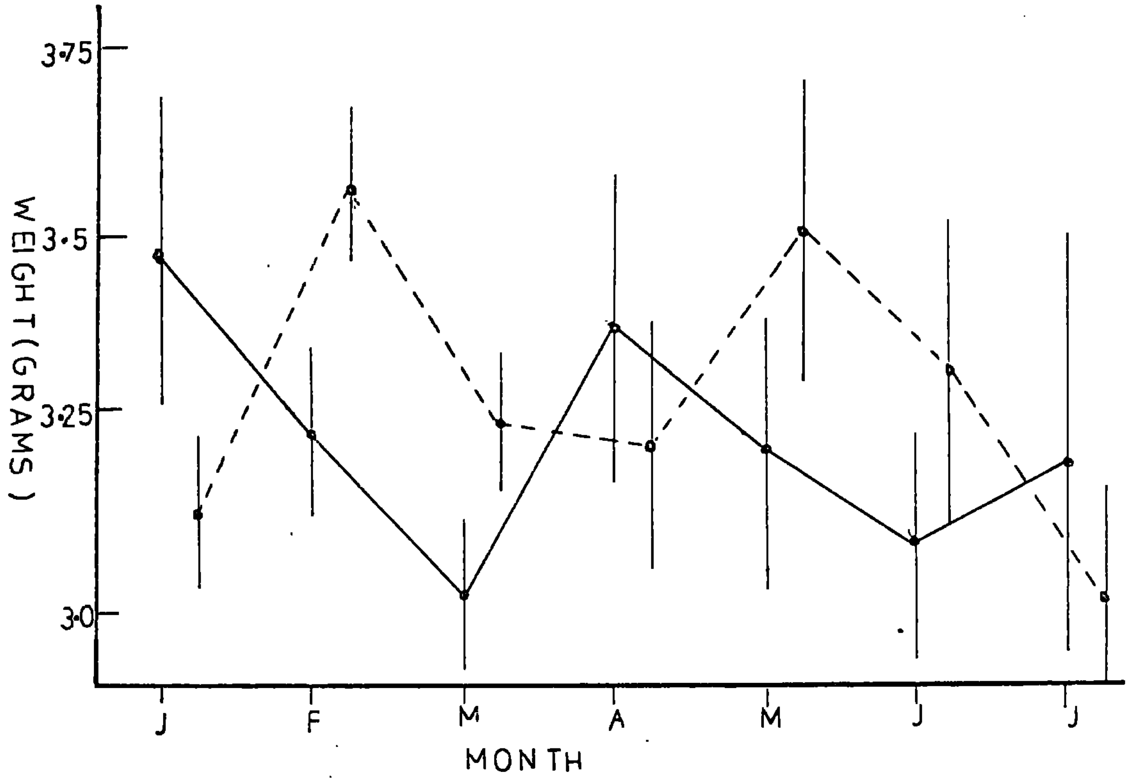


Fig.13. Water content of flight muscles of sparrows.

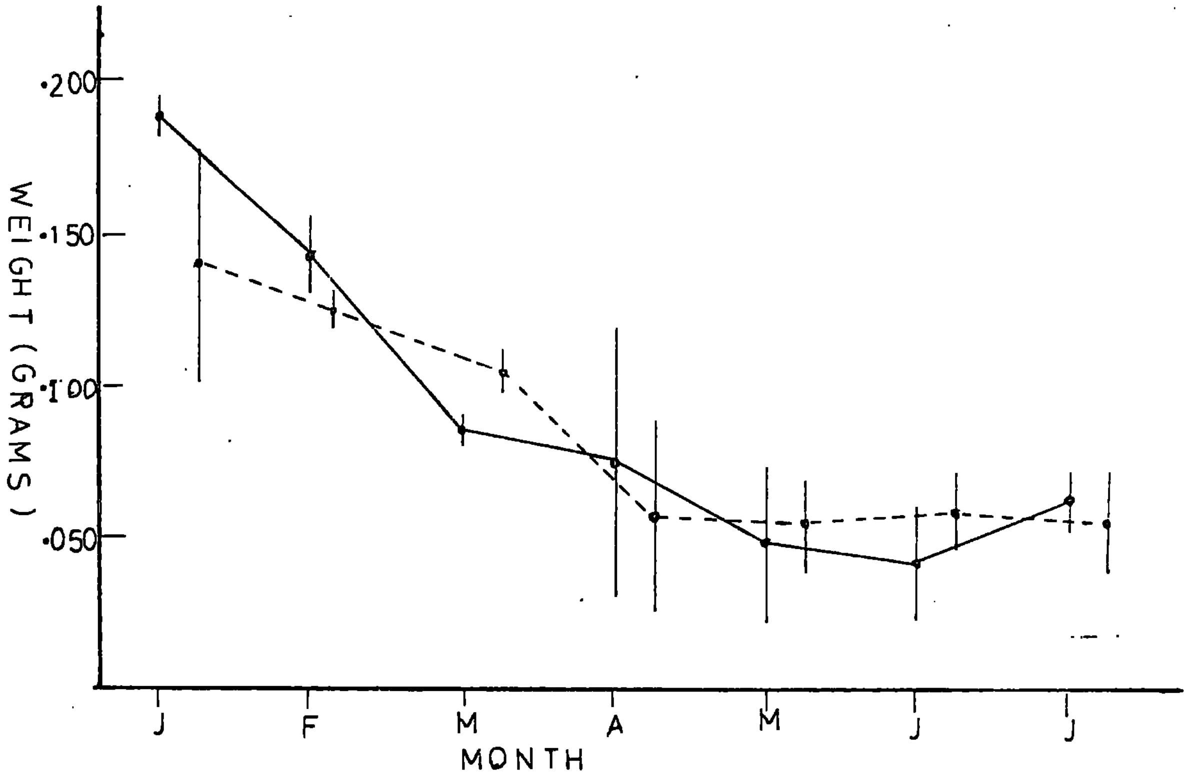


Fig.14. Lipid content of flight muscles of sparrows.

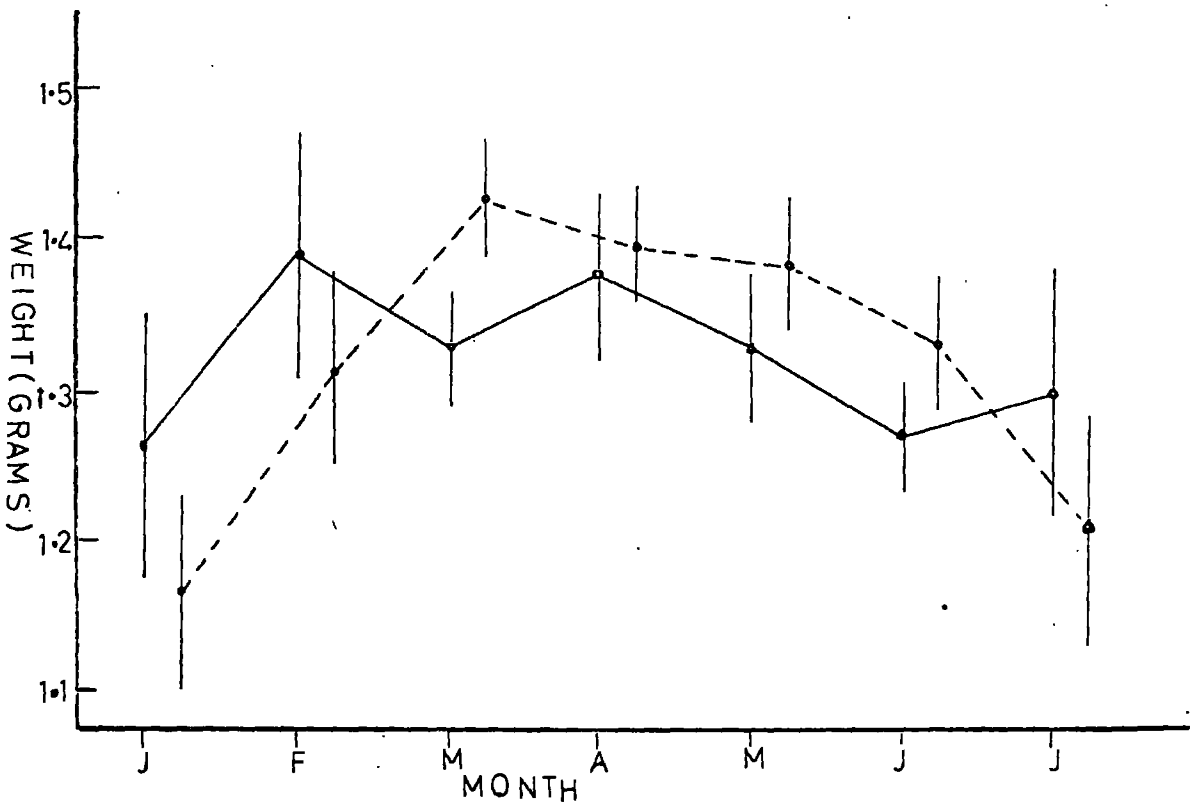


Fig.15. Lean dry weight of flight muscles of sparrows.

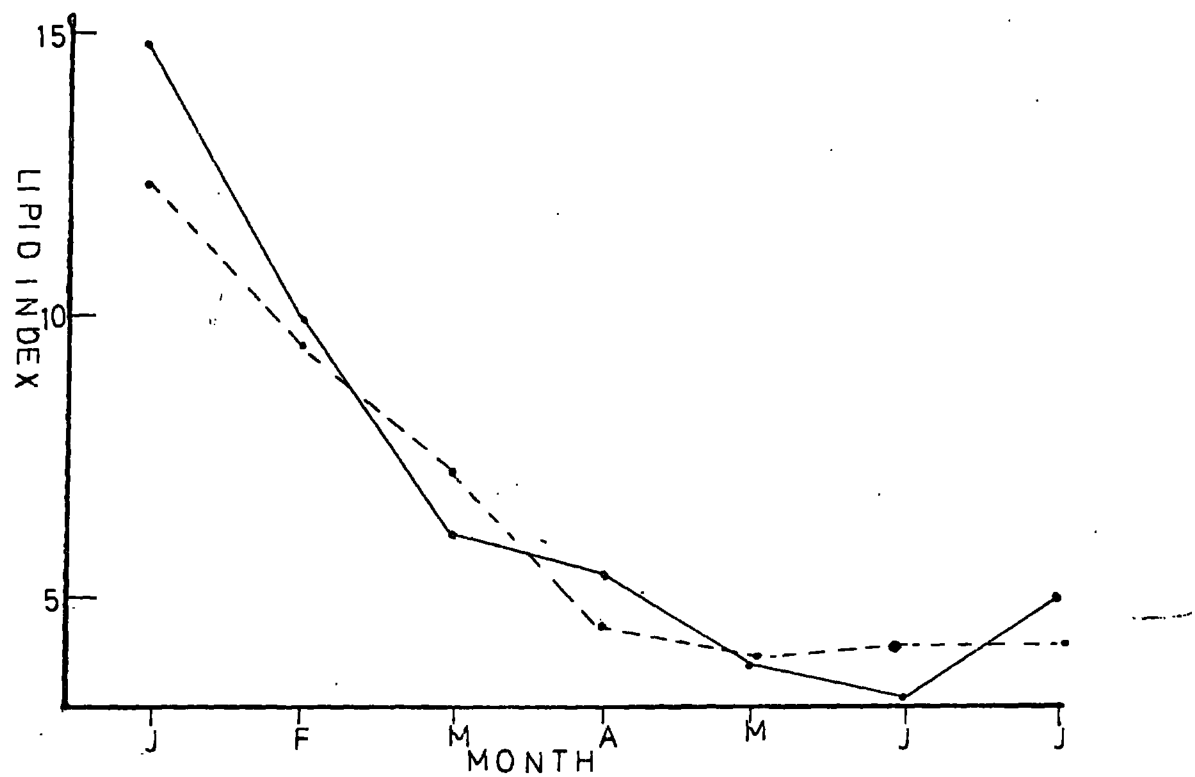


Fig.16. Change in lipid index (fat expressed as a % of lean dry weight.) of flight muscles of sparrows.

<u>General Discussion</u>.

Live weights of sparrows were highest in midwinter and lowest in midsummer. The pattern of weight change was similar to that found in Bullfinches in Wytham Woods, Oxford, where variation in weight was related to temperature rather than food availability (Newton, 1966) It will be shown that the seasonal variation in the mean weight of sparrows was due primarily to changes in temperature and daylight in spring, while during the summer the effects of breeding were more important.

To ensure a stable body temperature, a bird must maintain a balance between heat loss and heat production. Within the sparrow's thermoneutral zone, 15-37°C (Kendeigh, 1934, Steen 1956) it can control heat loss entirely by physical thermoregulation, that is by altering the position of the body feathers relative to the skin. In this way, it can vary the insulation provided by the air spaces between the feathers. Above the higher 'critical temperature', 37°C, heat loss may be facilitated by activities such as panting. Below the lower critical temperature, increased heat loss requires increased heat production, approximately proportional to the decrease in environmental temperature.

In Great Britain, mean daily temperatures are below the termoneutral zone through most of the year, so sparrows can maintain a constant body temperature only by increasing metabolic activity at lower temperatures. Hence, in cold weather, their energy requirements are correspondingly greater.

To survive periods of cold weather, birds have evolved both physiological and behavioural adaptions, for example, summer-adapted sparrows in captivity were able to survive only in temperatures above 0°C, whereas winter-adapted birds could tolerate temperatures down to approximately - 30°C. This acclimatisation was achieved partly by the thicker plumage of the winter-adapted birds, and partly by a change in the pattern of energy intake at lower temperatures. Thus the maximum energy intake of summer-adapted birds was only 23 K.cals, 9 K.cals lower than that of the winter-adapted birds. Energy intake at a constant temperature was also related to photoperiod, increasing with decreasing daylength (Davis, 1955).

The increased level of food intake during winter, enables a passerine bird to store enough energy, chiefly as fat, but also as undigested food to survive an obligatory starvation period overnight. In St. Paul's, Minneseota, winter feeding patterns of sparrows were related both to daylength and to temperature(Beer,1961). In the short days of November and December, feeding started immediately after sunrise and was most intense then and before sunset, with two smaller peaks of activity during the day. Similar feeding behaviour was observed at mean temperatures of - 9 to -14°C. When the mean temperatures dropped below - 20°C, the birds started feeding even before sunrise; between periods of intense feeding they sat perched in sheltered places, with feathers fluffed out. By this behaviour they conserved energy, both by reducing activity and increasing insulation. At mean temperatures between 2°C - 3°C (similar to the coldest weather in 1969 in Durham), birds fed in a more erratic manner with no distinct peaks of activity. Beer (1961) concluded that a large proportion of the sparrow population he studied in Minneseota, failed to survive due to the very low temperatures. High winter mortality has also been recorded in Germany (Fallet 1958), and Barrows (1889) and Stanchinsky (1927) have suggested that snow and low temperatures may set the northern limit of distribution of sparrows.

In Durham, conditions in Winter were considerably milder than these areas where winter mortality may limit the sparrow population. The mean total energy reserves carried by birds at roosting were calculated to discover whether they were sufficient to ensure overnight survival in winter. I also wished to investigate the effect of daylength and temperature on such energy reserves.

The total energy reserves carried by each bird at roosting were calculated by summing the fat content (9.3 K.cals/gm) and the stored food (2.2 K.cals/gm). These figures were then converted to cals. per gm. by dividing by the weight of the bird. A value of 13 cals/gm. (the mean fat content of two sparrows which died in captivity, presumably due to starvation), representing tisace liquids unavailable for metabolic use was deducted from the total energy reserves to give the available energy reserves (Table 12).

The energy required for thermoregulation during the roosting period was calculated from Kendeigh's (1944) values for resting metabolism of sparrows at different temperatures. Such estimates are in fact maximum values since they refer to measured air t temperatures, whereas sparrows roosted in holes, under eaves, or in outhouses where temperatures were probably somewhat higher. The mean energy reserves were sufficient to ensure survival of House Sparrows and allow sufficient energy for the birds to search for food the following morning. My results confirm observations (Summersmith,1963) that sparrows in urban areas can survive winters in Britain without hardship, since, despite an unusually cold month of February in 1969, sparrows could obtain ample food to survive.

The mean energy reserves for January, February and March were more closely related to the long term average temperatures in these months (recorded over the last 120 years) rather than to the mean temperatures in these months in 1969 (Fig.18. Table XIII). Energy reserves carried to roost by Yellow Buntings,

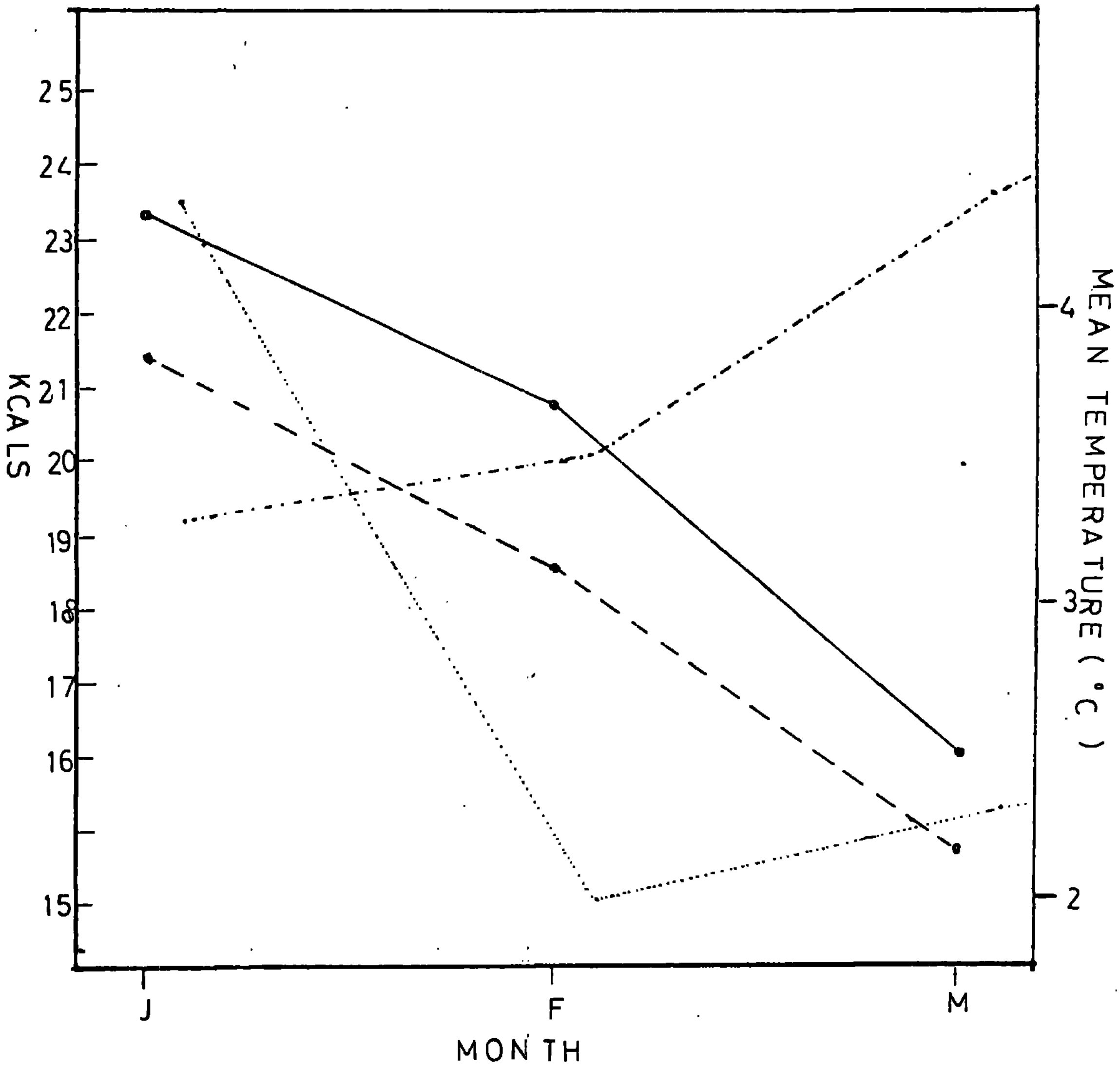
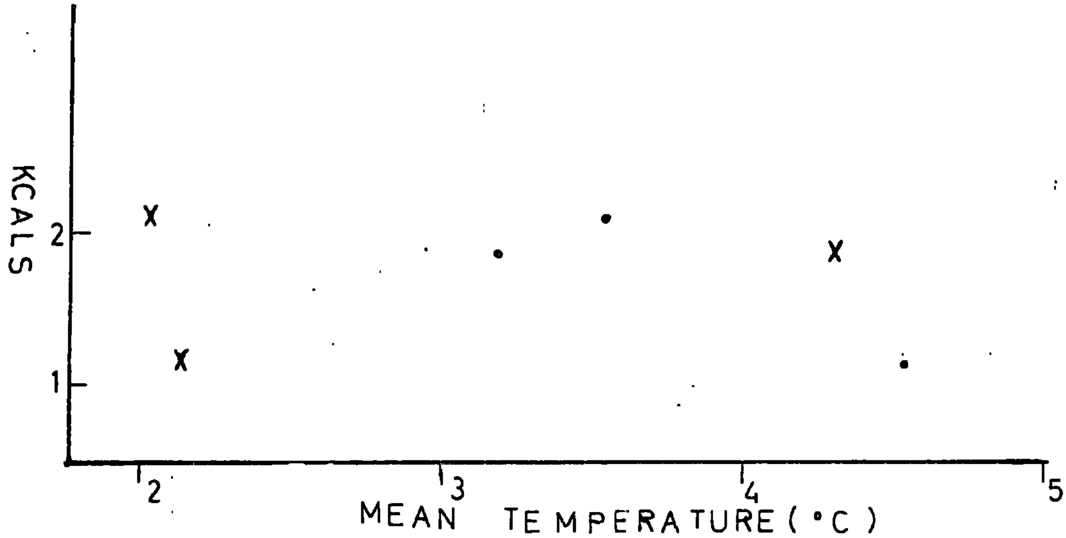
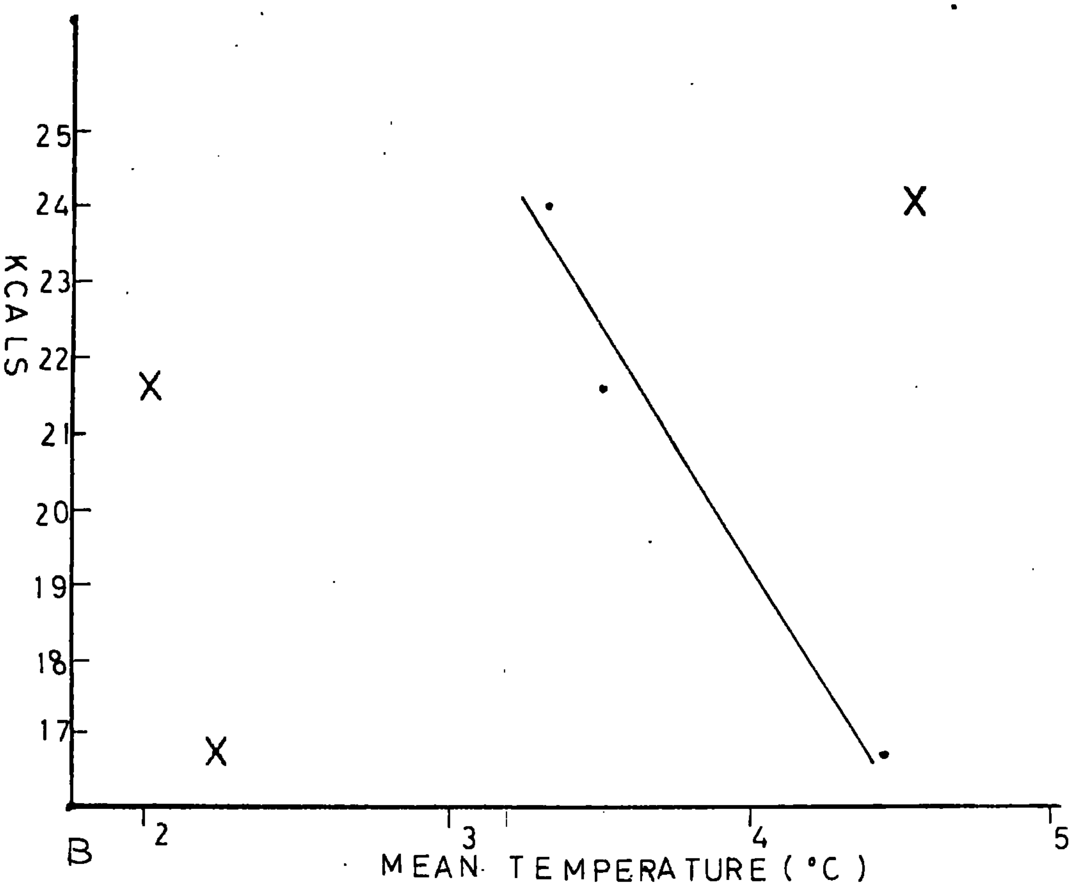


Fig17. Energy reserves (monthly mean) from January to March 1969.

—— Total energy reserves
- - - - Energy reserves (fat)
-·-·-·- Mean monthly temperature 1969
·········· Longterm monthly mean temperature.



A. Energy stored as food



B

Fig.18. Energy reserves of sparrows (monthly mean in relation to long term mean temperature — • and to mean temperature 1969 X

A. Energy stored as food
B. Total energy reserves.

TABLE XII

ENERGY RESERVES OF HOUSE SPARROWS AT ROOSTING

Date	Mean Temp.	Roosting Time	Total Energy Reserves Cals/gm	Mean Available energy reserve Cals/gm	Energy Requirements (Cal/gm)
10 January	1.9	$16\frac{1}{2}$	888 ∓ 53	875	627
30 January	2.3	$15\frac{3}{4}$	702 ∓ 43	689	580
9 February	-0.3	15	784 ∓ 84	771	615
28 February	1.8	14	690 ∓ 64	677	546
19 March	2.2	13	590 ∓ 51	577	481

* Variance indicated = Standard deviation of the mean.

TABLE XIII

ENERGY RESERVES OF HOUSE SPARROWS IN RELATION TO LONG-TERM TEMPERATURES

Date	Mean Temp. 1969	Long Term Temp.	Total Energy Reserves Cals/gm	Stored Energy /Food (Cals/gm)	Stored Energy /Fat (Cals/gm
Jan	4.5	3.3	805	65	740
Feb	2.0	3.5	741	76	665
Mar	2.2	4.4	590	45	545

Emberiza citrinella, each day in winter were shown to be closely related to the long term average temperature to be expected on that day (Evans, 1969) so that it is possible that the situation in the House Sparrow parallels this. However, the energy reserves carried on any day may have been affected by the mean temperatures on that day. (Fig. 19.), since they showed a suggestion of an inverse correlation with the temperature. With the small samples of sparrows caught on each day, it is impossible to assess how much of this variation in the energy reserves they carried is related to the actual temperature, and how much to the long term average temperature which may operate through the effect of daylength on feeding behaviour.

Marshall, (1959) has divided the breeding cycle of birds into several phases. Following the end of the breeding season, he believes that birds undergo a period of recovery, the 'regeneration phase', during which no sexual behaviour occurs. At this time the sex organs of both sexes regress before becoming functional. This phase is also called the 'refactory period' (Bissonette & Wadland, 1932) since during this time birds do not respond to photo-stimulation; it varies in duration between species, but ends in late October in the House Soarrow (Marshall, 1952B). Following this phase, gonadotrophins are once again released, the gonads recrudesce and the acceleration phase begins.

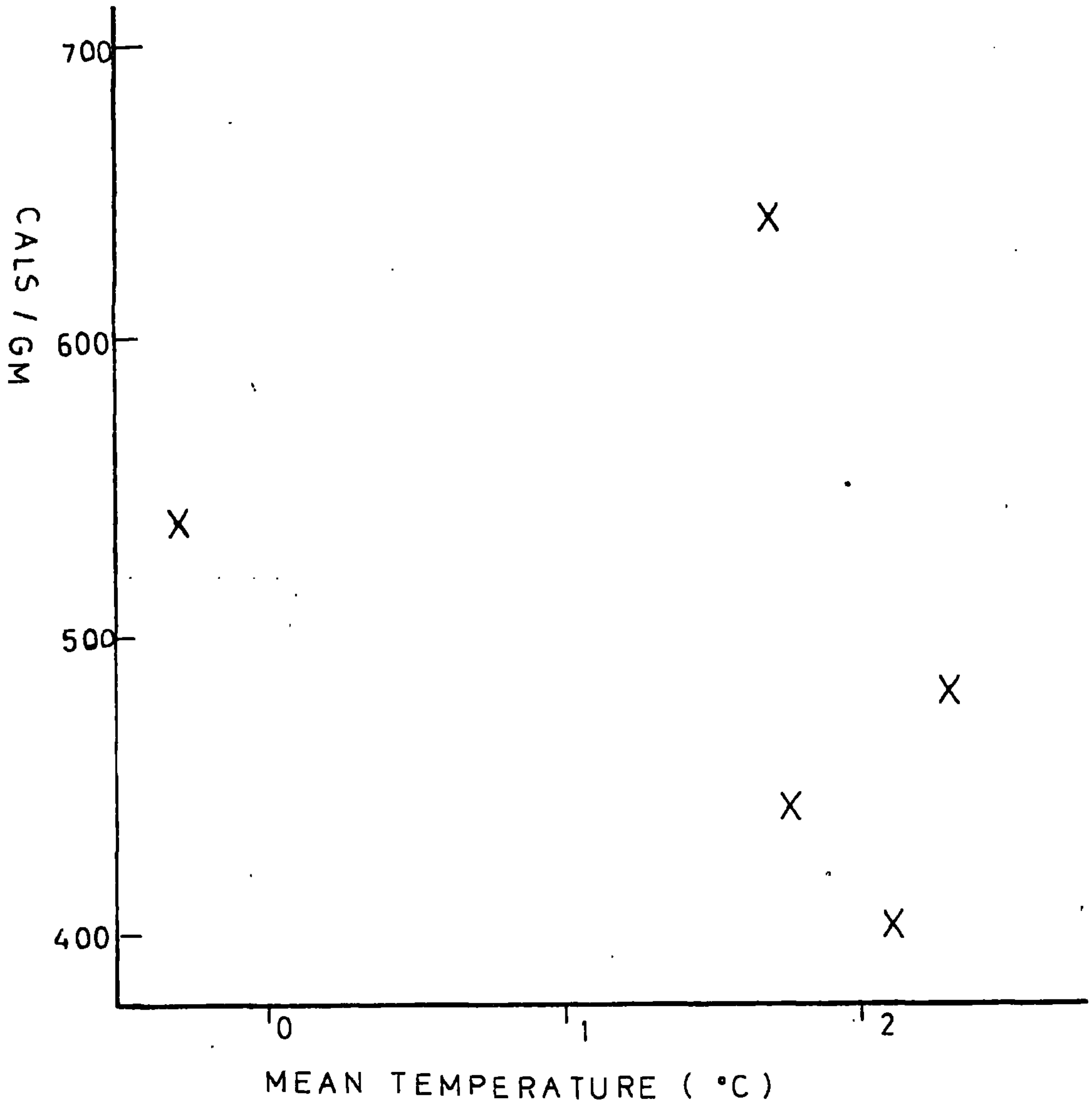


Fig 19. Energy reserves of House Sparrow in relation to mean temperature on day

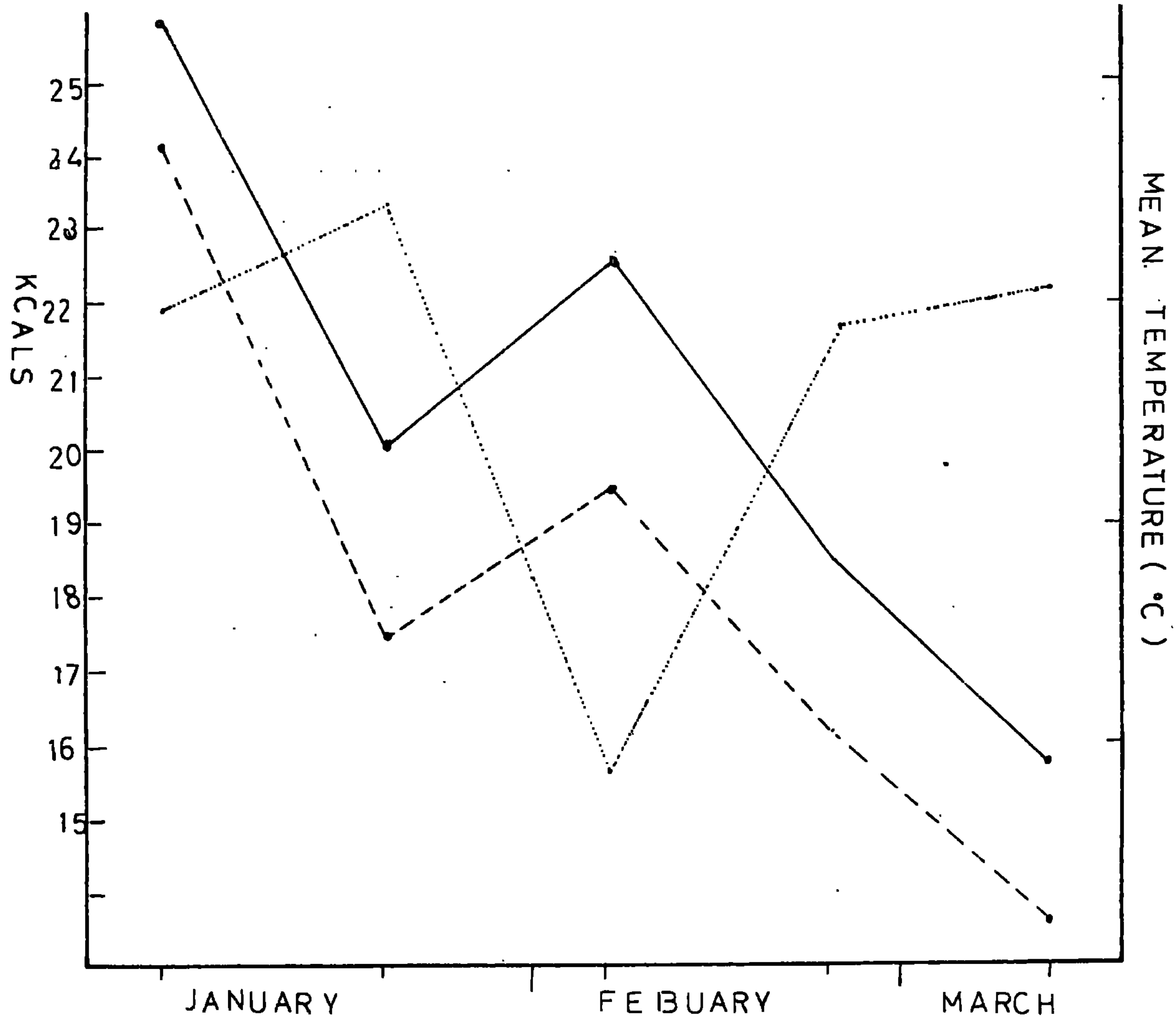


Fig.20. Energy reserves of sparrows

—— Total energy reserves

- - - Energy stored as fat

.... Mean daily temperature.

In temperate regions, sexual behaviour occurs in several species in Autumn, and birds often pair at this time. Definite sexual activity has been demonstrated in the testes of sparrows in autumn (Marshall, 1959) so that birds were then in potential breeding condition. However, winter conditions depresses or halts the development of the gonads. Following the winter solstice the increase of daylength reactivates (via the pitutary) the sex organs of many birds of temperate regions. While the gonads of male sparrows respond to photostimulation (Poilikarpa,1940) no marked effect was found in the ovary of the hen sparrow (Kirshbaum, et. al. 1939). Since sparrows and starlings (Marshall 1959) may nest in autumn. However, light cannot be the only factor regulating the spermatogenic cycle. It would seem that in Spring, after the initial stimulus of increase of light, the rate of development is related to a complex of factors.

By measuring the lengths of testis and ovary of sparrows caught in Durham, the rate of development of gonads was followed. The onset of sexual activity occurred in early January, 1969, and the development of the sex organs thereafter was paralleled by an increase in the mean weight of protein in the body (as reflected by lean dry weight of the flight muscle). There was, in fact, a significant correlation between the length of testes and the protein level throughout the season (r = 0.8870) though less correlation was found with the length of the ovaries. During a mild January, the ovaries increased significantly in size (Fig. 21). This spell

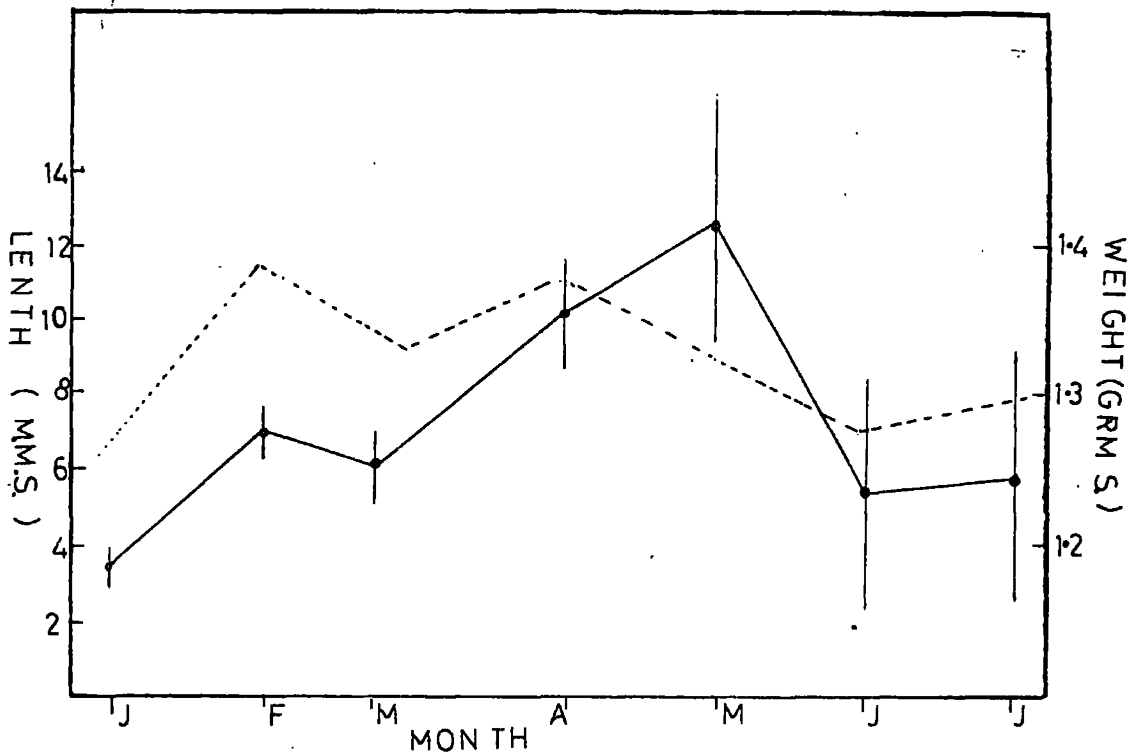


Fig.21. Change in lenth of ovary —— , compared with mean weight of muscle protein ----- . Circle = means vertical lines = 95% confidence limits.

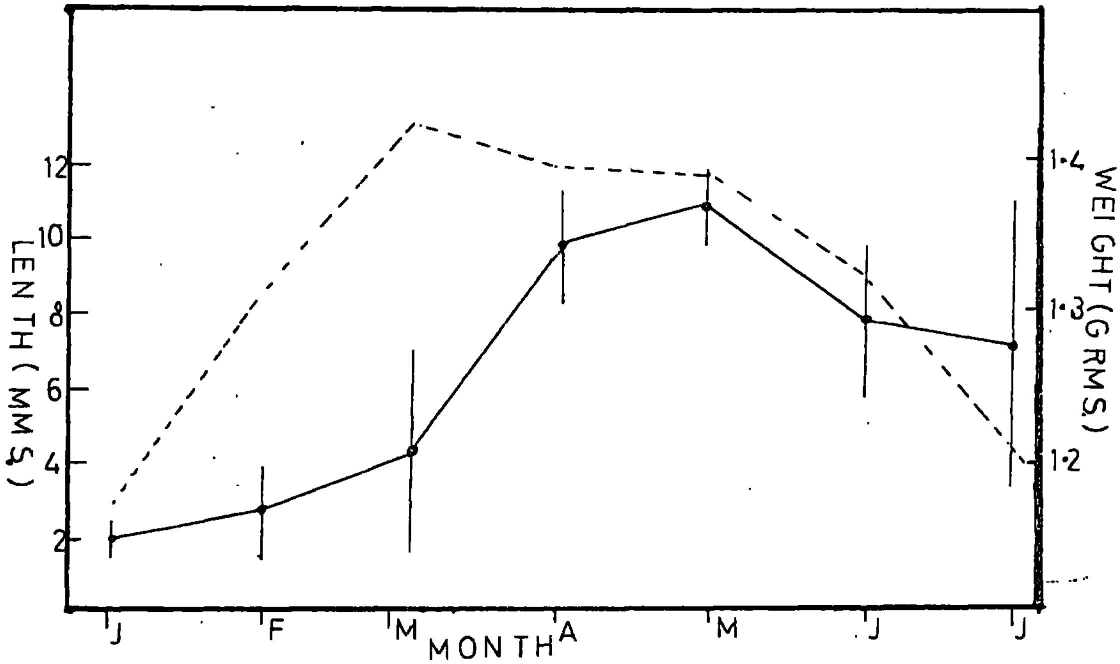


Fig.2 2 Change in lenth of testis —— compared with mean weight of muscle protein (i.e. lean dry weight of flight muscles of sparrows, of mild weather was sufficient to stimulate breeding in early February 1969 in the south of England. However, cold dull weather in February and the beginning of March delayed the sexual cycle. Weather may possibly act directly in the control of breeding as birds require less energy for survival in the warmer temperatures of late spring so that more energy may be diverted to reproduction. The increasing daylength at this time also increases the energy potentially available. Weather may also act indirectly on the timing of breeding by its effect on food availability. However, though animal food may be an important source of food for sparrows at the peak of the breeding season and during the fledgling period in early spring, it is not an important food item in their diet. The major food item of sparrows, i.e. scraps, waste is unaffected by the weather.

Behavioural interactions also determine the timing of sexual development and egglaying and in sparrows may be an important factor synchronising the 'culmination phase' (i.e. ovulation and fertilisation), Summersmith (1963) found the dates of laying of first eggs of different females within each colony were more closely grouped than between different colonies. He suggested that breeding within any colony was synchronised by display at the mutual feeding grounds. In Durham, 1969, judging by the time fledglings appeared, the majority of birds laid in the second week in May, while a second brood was started about a month later.

The breeding season places a heavy demand on the energy reserves of the House Sparrow. Each season, a pair of sparrows in Northern England, lay, on average, 2.3 clutches (Summersmith, 1963) each clutch containing eggs. As found in this study, the mean weight of a sparrow's egg is 2.99 gms. Hence, if the dry weight has a similar calorific value to that of a hen's egg (Brody, 1954) a sparrow's egg has a calorific value of 2.6 K.cals. The energy required by a hen to lay a clutch of three eggs would be 31.2 K.cals, assuming, following Brody (1954), that female sparrows have a 25% production efficiency. At the time of laying, the energy requirements of the male are considerably less than those of the female, although they are more active at this time of the year. The male helps to incubate the egg, but does not feed the female on the nest as found in some passerine species (Royama, 1966).

The fledgling period places the greatest strain on the parents. When the juveniles leave the nest they weigh 24-25 gms and have a total calorific value of approximately 30 K.cals. Thus, the brood of three fledglings increase by 60 K.cals over an average period of 15 days (Summersmith, 1963). If fledglings increased in energy content at a rate of 4 K.cals per day, then each parent must provide 2 K.cals per day.

At this time the field energy required for activities associated with breeding was 4.K.Cals. The efficiency of adult birds was 50%. The energy required by the hen may be higher since the hen plays a greater part in feeding the fledglings (Summersmith, 1963). After the fledglings leave the nest the cock continues to feed them while the hen starts another brood. Possibly the incubation may be a period of recovery (Newton, 1966) from any 'strain' incurred when feeding young.

The breeding season is a time when adults need protein for sperm or more important egg production and later for moulting, and breeding may be ultimately timed to coincide with the time when animal food is most readily available. Towards the end of the season such food may not be so readily available due to competition from other young birds. House Sparrows gradually show a drop in both lipid and protein, through May and June. The strain of breeding combined with a decrease in the availability of food leads to considerable depletion of their energy reserves. Towards the end of the breeding season one may speculate that the birds may not have enough fat to last overnight, and so may have to break down protein; but this needs further investigation.

In 1969, the breeding season at Durham, towards the end of June and birds began to moult. It was impossible to say whether birds which had started moulting were still in breeding condition without making microscopic examination. The regression of the gonads was closely paralleled by a sharp drop in body protein. This could be due to exhaustion of the androgens whose anabolic action may maintain a high protein level (Hanson 1962, William, 1964). The growth of feathers during moulting also requires protein.

The termination of the breeding season may be related to the considerable drop in energy reserves at this time. The energy requirements of House Sparrows may be so high that the production energy drops below a critical level and causes the regression of the gonods and the onset of moult.

The House Sparrow, though a highly adaptable bird, is partly dependent on man. Survival during winter was facilitated by the food and shelter readily available. During the long breeding season, birds require both protein and lipid for reproduction and the extra activity it entails. At this time the availability of insect food may be an important factor in determining whether the birds can withstand the strain of breeding, since their other food sources remain approximately constant throughout the year. In Durham there was no absolute food shortage, though towards the end of the breeding season there was a decrease in the relative availability of food. In large cities, where food such as wild grass seeds, grain, etc. is not within flying distance of the nest, and animal food is hard to obtain, a high summer mortality may occur. This may be the cause of the decrease in the sparrow population of London, reported from 1951-1965 (Cramp and Tomlins, 1966).

SUMMARY

A study was carried out on seasonal variation in weight and body composition of the House Sparrow in Durham City.

Seasonal variation in weight from winter to spring was associated with change in day length and temperature. Energy reserves were sufficient to ensure over-night survival.

Changes in weight during the latter part of the breeding season were related to the higher energy requirements at this time (30.0 K.cals per bird per day), associated with breeding activity. The strain of the prolonged breeding season combined with a possible decrease in the availability of food, leads to considerable depletion of energy reserves, which reached a minimum at the end of the breeding season.

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