Energy flow through a population of great tits, with notes on blue tits

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ENERGY FLOW THROUGH A POPULATION OF GREAT TITS, WITH NOTES ON BLUE TITS.

by

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being a thesis submitted as part of the
requirements for the degree of M.Sc. in
Ecology in the University of Durham 1968.

page.

CONTENTS.

INTRODUCTION

The Great Tit (Parus major L.) is a bird characteristic of temperate broad-leaved woodlands, and is found in most of the Palearctic Region. It is the largest of the Paridae in all parts of its range and has the largest distribution of all the Palearctic species and in many areas is the only member of the genus present. It is also the most atypical of the Paridae having the size and proportions more of a finch (Fringillidae), and like finches feeds much on the ground.

It was K. Wolda in Holland in 1912 who first recognized the value of Great Tits for population research, and this Dutch study has been continued by H.N. Kluijver and his research students up to the present in a wood at Orange Nassaus Oôrd near Wageningen and after 1944 in the nearby Velue. A parallel study has been carried out by members of the Edward Grey Institute, (Oxford University) under the direction of D. Lack in Marley Wood in the Wytham estate, Oxford, England, since 1947, first by J.A. Gibb, and later by D.F. Owen, P.H.T. Hartley, Miss M.M. Betts, T. Royama and C.M. Perrins. Supplementary studies were carried out by this group in the Brecklands and the Forest of Dean. The present work is the first intensive study of the species in the North of England.

The advantage of the Great Tit is that the whole population of a wood will readily use nest-boxes when provided and the number of pairs, the clutch size, and the number of young raised can be accurately and simply determined. Also the bird is common, conspicuous, diurnal in habits, easily trapped and marked in Winter, and in Oxford it was resident throughout the year, ringed birds seldom moving more than a mile from the study area (Lack 1966), in contrast to the Dutch population in which a proportion of the birds move for considerable distances in some years (Kluijver 1951).

In consequence the population dynamics of Great Tits has been investigated at greater length than most studied species of birds. The abundance of published data on Great Tits forms an excellent background for a more fundamental study such as that of population energy flow. As in all studies of the Great Tit, it was found instructive to collect parallel information about Blue Tits (P.caeruleus) a species with a similar ecology.

The investigation of population ecology and the study of energy flow are interdependent and fundamental to the concept of food webs. Energy flow is unidirectional, being channelled into two uses in whatever biological component is under consideration. The study of energy flow refers to organic production (i.e. the storage of energy in the form of tissues or other organic materials) and also respiration (i.e. the expenditure of energy in the maintenance of the life processes of the organism, which is eventually lost as heat).

The energy flow approach is applicable to any level, to the ecosystem as a whole, to a major trophic level, or a specific population. During the past fifteen years broad patterns of community metabolism have been worked out for a number of ecosystems, but energy flow at the population level has until recently received comparatively little attention.

In the case of birds there are many laboratory studies on their bioenergetics in the literature, including : Benedict 1938; Brody 1945; Kendeigh 1944, 1949; Seibert 1949; Pearson 1954; Wallgren 1954; Davis 1955; West 1960; Cox 1961; King 1961; Kahl 1962, 1964; Lasiewski 1963; Lefebvre 1964; Tucker 1966. However, few attempts have been made to estimate total energy flow through an avian population in its natural ecosystem. The first study in this direction was perhaps that by Pearson (1954) who determined the daily energy requirements of a wild Anna Humming bird (<u>Calypte anna</u>). Connell (in Odum, Connell and Davenport 1962) studied the population flow in Savannah Sparrows (<u>Passerculus sandwichensis</u>) wintering in old fields of South Carolina, U.S.A. Kahl (1964) estimated the energy flow in the Wood Stork (<u>Mycteria americana</u>) populations of south Florida. Uramoto (1961) made preliminary estimates of respiratory energy and food consumption in populations of adult birds in a deciduous forest in central Japan. Brenner (1963) studied the energy flow in two breeding populations of Red-winged Blackbirds (<u>Agelarus phoeniceus</u>) in fresh water marshes in Pennsulvania. Kale (1965) estimated the energy flow through a population of Long-Billed Marsh Wrens (*Telmatodytes palustris*) in Georgia salt-marshes.

The present work was an attempt to measure the food consumption of a population of Great Tits throughout the year in deciduous woodlands in Co. Durham, England. Measurements were also made of standing crops by estimating the average density and energy content of the population, and also production from natality and mortality rates in the literature. The study was of added interest since very few attempts have been made to study the bioenergetics of insectivorous birds like the Great Tit because of the difficulty of keeping such birds for long periods in captivity.

GENERAL METHODS.

Study Area

The field work was carried out in a 44½* ha. continuous stretch of woodland about a mile south of the centre of Durham City, most of it on sloping ground immediately to the west of the flood plain of the River Wear. Within this study area three distinct types of woodland are found, differing in their structure and composition (Fig.1).

Area 1 comprises 33 ha. of predominantly broad-leaved woodland, the dominant species being Oak (*Quercus robur*) and Beech (*Fagus sylvatica*). This area, forming the northern and central parts of the study area, is subject to standard forestry activities, with the result that there are only a few isolated patches of secondary vegetation (Plate 2a).

Area 2 was 6½ ha. of mainly Larch (*Larix decidua*) plantation approximately twenty years old, again with little secondary vegetation (Plate 4).

Area 3 was 5 ha. of mature undisturbed broad-leaved woodland forming the southernmost part of the study area and situated on the steeply sloping bank of the River Wear. The dominant tree species were Oak and Beech, but there was a considerable covering of secondary vegetation, mainly Bramble (*Rubus fruticosus*), Hawthorn (*Cataegus* sp.), and Elder (*Sambucus nigra*) etc. (Plate 2b).

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* 1 ha. = 1000m^2 = 2.471 acres)

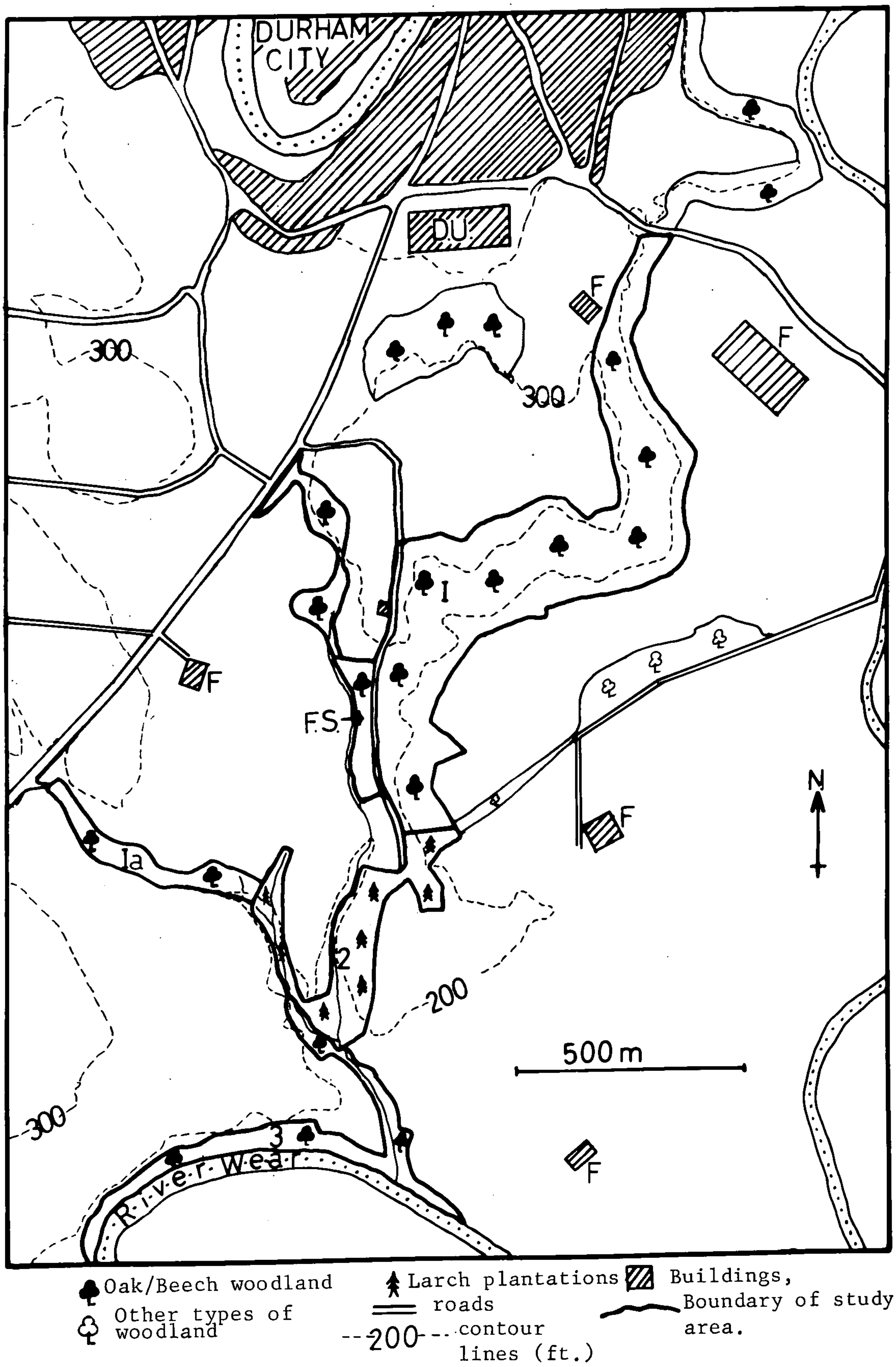
Fig.1. Map of the study area, Co. Durham.

I (inc. Ia), 2 and 3 major subdivisions of study area (see text)

D.U. Durham University Science Laboratories

F.S. Field Station

F. Farms


DURHAM CITY
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200
500 m
N
3
River Wear
300
F
Oak/Beech woodland
Other types of woodland
Larch plantations
roads
--200-- contour lines (ft.)
Buildings,
Boundary of study area.

In December 1967 forty nest boxes were put up, the majority being placed in trees (at a height of 10 ft) in the grounds of the Durham University Zoology Department Field Station situated near the centre of the Study Area (see Plate 3a and b), Fig.1). It was expected that these boxes would attract both Great Tits and Blue Tits so that one could gain information about the timing of the breeding season. In fact only Blue Tits (eleven pairs) used the boxes, Great Tits preferring to use natural holes in trees.

Meteorological data relevant to the study was obtained from Durham Observatory which is half a mile to the north-west of the field station. The mean daily, mean daily maximum and mean daily minimum temperatures for each month of the year are shown in Fig.2, and the average climatic cycle of Durham summarized in Table 1.

Table 1. The annual climatic cycle in Durham over the past 120 years

	Mean Temperature (°C)	Monthly rainfall (cm)	Daily sunshine (hr)
Jan - Feb	3.3	4.3	1.9
Mar - Apr	5.6	4.6	3.9
May - June	11.0	5.2	5.5
Jul - Aug	14.5	6.7	4.9
Sep - Oct	10.4	5.7	3.6
Nov - Dec.	4.4	5.8	1.7

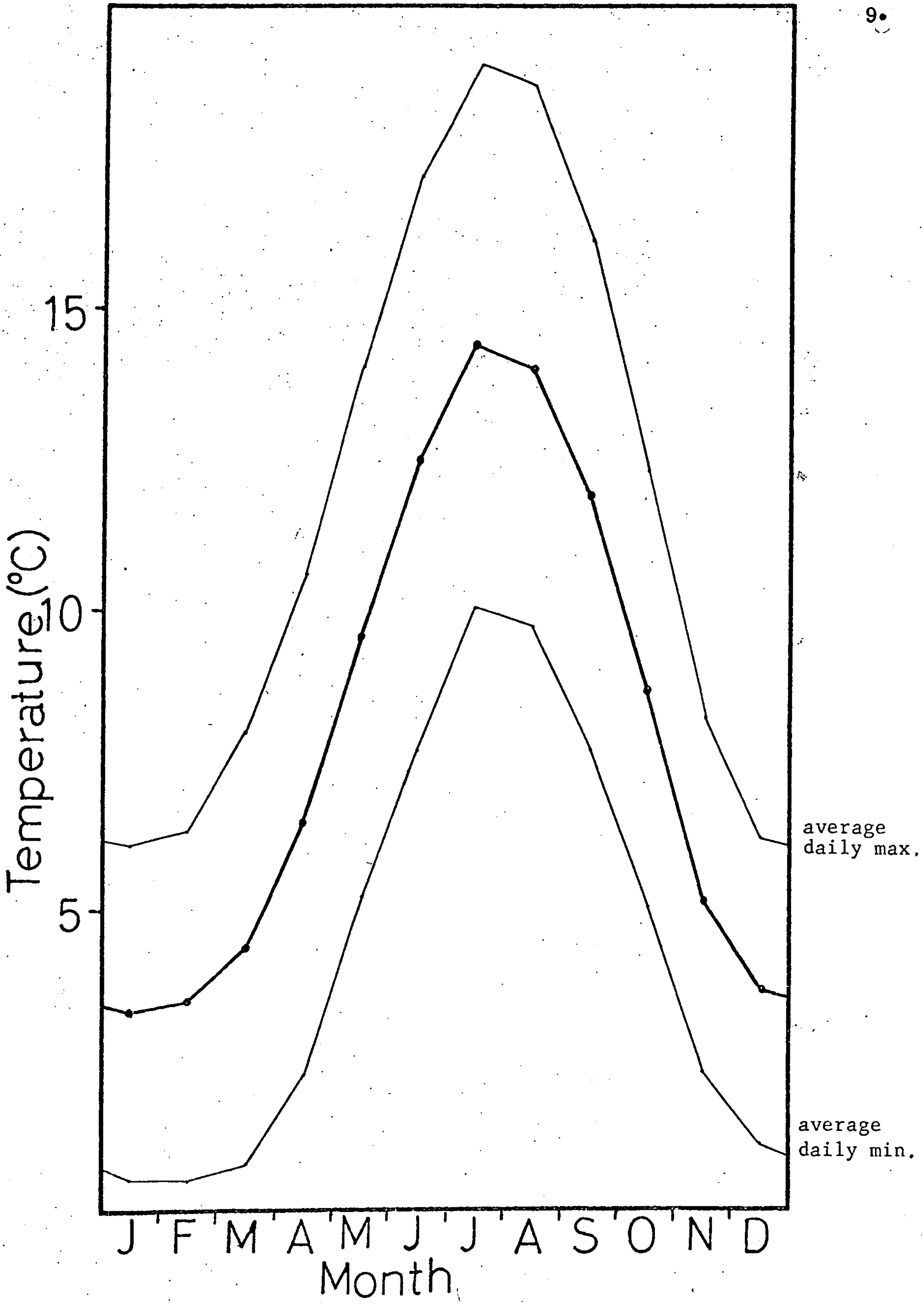


Fig.2. Average monthly temperatures in Durham, with average daily maximum and minimum temperatures, recorded over the past 120 years.

Census Techniques.

The size of the population of both Great Tits and Blue Tits was determined during the breeding season. Transects were made throughout the study area two or three times a week from mid-April to the end of June, and the positions of territorial pairs were plotted on a six-inch Ordnance Survey map. Censuses were made at random times throughout the day.

During the breeding season the nest boxes were visited once a week to record their contents. Those containing nests were visited more frequently, to determine dates of the first egg, of the completion of clutch, of hatching, and of fledging. To determine the average wet weight, dry weight, dimensions, lipid content, and calorific value of eggs, two were taken at random from each clutch within two days of the completion of the clutch. This analysis was completed on 22 eggs belonging to the Blue Tit, but only 2 from the Great Tit. Most of the nests of the Great Tit were inaccessible and those that were located were usually found after the clutch was complete.

After the eggs were taken they were weighed and measured before being dried to constant weight. The drying was carried out in an oven at 60°C and the sample re-weighed. Each egg was then thoroughly ground with an agate pestle and mortar and stored in a dessicator to await analysis of lipid-content and calorific value (method described later).

Great Tits and Blue Tits were intensively trapped and ringed during the Winter months (January and February 1968) and the Summer months (July and August 1968) in the grounds of the field station. During the Winter the birds were mainly caught by using a six-foot square house trap baited with fat, grain, peanuts and bread, while all the trapping in the Summer was done with mist nets set across the stream running through the field station grounds. In addition, during the Winter, birds were taken as specimens for body tissue analysis and for feeding trials in Little High Wood, a small isolated wood to the north of the main study area. There was no reason to believe that either of the trapping methods used was selective.

Each of the Great Tits ringed was also individually marked with two colour rings on the other leg in an effort to track their movements in and around the study area. A colour ringing sequence employing seven colours (Red, Yellow, Blue, Light Green, Dark Green, White and Black) was used, which allowed 78 different combinations for either leg. The colour rings could be easily read in the field at a distance of 40 yards with a pair of 10 x 50 binoculars.

All the birds caught were aged and sexed by the methods described by Cornwallis & Smith (1963). Only the Great Tits could be sexed on secondary sexual characters, while both the Great Tits and Blue Tits could be separated into first year and older birds "Adults"). Each bird was weighed on a beam balance accurate to 0.02gm and the wing length measured with a rule by the "Fair-Isle Method" (Stewart 1963) - the carpal joint being pressed lightly against the stop, the wing not pressed flat - giving the "chord" measurement. Observations were also made on the amount of visible subcutaneous fat using a system of fat-classes adapted from Weise (1956) :-

Class 1.	No Visible Fat.	No visible fat in the depression, or on the abdomen.
Class 2.	Little Fat.	Fat lining the furcular depression, visible fat in the abdomen between the intestinal folds.
Class 3.	Medium Fat.	Fat filling the furcular depression, visible fat in the abdomen between the intestinal folds.
Class 4.	Heavy Fat.	Furcular depression bulging with fat, peritoneal fat filling in between the intestinal folds.
Class 5.	Very Heavy Fat.	Furcular depression bulging with fat, abdominal region bulging with peritoneal and subcutaneous fat.

The whole classification was later put on an approximate quantitative scale when the amount of ether extractable lipid was measured from birds of known fat class during the analysis of the body tissue of the specimens taken. All birds caught during the Summer were also examined for moult, and the method of measuring the stage of moult developed for the British Trust for Ornithology Moult Enquiry was used. The ten primaries were numbered descendently (i.e. from mid-wing outwards) and the secondaries and ascendentally (i.e. from mid-wing inward). The following notation was used to describe the stage of moult of each of the remiges and rectrices :-

0 = old feather remaining.
1 = feather missing or new feather in pin.
2, 3, or 4 = new feather up to one-third, two-thirds, or nearly full grown, respectively.
N (or 5)= new feather fully developed.

Also the presence or absence of actual moult in the greater coverts, bastard wing, lesser and median coverts, underwing coverts, upper and underparts, was also noted.

Birds were caught throughout the day in an effort to determine the average daily fluctuation in weight of the population and also as a crude measurement of daily activity patterns during the Winter and Summer months. (Subsequently trapping was usually restricted to days when the weather permitted a full day's work in the field). It was found that the average weight of the birds showed a marked and significant increase throughout the day but with a three to four hour period around mid-day when it remained reasonably constant, and it was subsequently decided to take the mid-day weight as the average for the population for each particular time of the year. This method is preferable to that used by Kluijver (1952) and Van Balen (1967) who caught birds shortly after dusk while roosting in nest boxes and took the mean monthly weights of these in their respective studies of the seasonal variations in body weight of Great Tits in Holland (see Results). All specimens used for body-tissue analysis were taken within this period of the day. These were taken under a licence from the Natural Environmental Research Council, and comprised six adult Great Tits and two adult Blue Tits in Winter and three adult Great Tits and three adult Blue Tits during the Summer. In addition, three adult Great Tits died in captivity, presumably from starvation caused by stress, while they were being allowed to adjust to cage conditions prior to both the feeding trials held in mid-Winter and mid-Summer. These were kept for body-tissue analysis to give some indication of absolute minimum lipid content.

All specimens taken were stored in a deep freeze (-20°C) before analysis. Total feather weight was determined after completely plucking each specimen, and their body and feather components were subsequently analysed separately. The body and feathers of each specimen were then dried to constant weight in a vacuum oven at 60°C (a temperature at which no volatile lipids are lost) to measure the total dry weight before being ground up in an electric rotary mill, bottled and stored in a desiccator prior to determination of calorific and body-lipid content.

Feeding Experiments

Daily energy requirements were determined for wild caught Great Tits in January and July 1968 in order to investigate seasonal differences. The methods of measuring food consumption and excrement loss, initiated by Kendeigh (1949), and subsequently followed by Siebert (1949), Davis (1955) and West (1960) were followed. Metabolised energy was obtained by subtracting the calorific energy of the excreta from that of food consumption (gross energy intake). The difference represents existence energy when birds maintain constant weight and the only energy demands are for standard metabolism, chemical heat regulation, specific dynamic action of food assimilation, and the securing of food and water. Productive energy is the energy metabolised beyond that required for existence.

Six adult Great Tits, including birds of both sexes, were used in the experiments. The birds were placed in small individual wooden cages measuring 51 x 50 x 38cm, the front side of which had bars with perches and a simple shelter in one corner. The birds were allowed to adapt to these conditions for at least a week before experimentation. The cages were kept in the field station building where environmental conditions were not controlled, the birds living under the natural photoperiod and the same fluctuating temperature conditions as they were outside. The temperature in the field station building was measured with a recording thermometer. On the floor of each cage was a removable tray, on which a sheet of pre-weighed aluminium foil was placed to collect faeces and remains of food during the experiments.

While the Great Tits were adjusting to experimental conditions they were fed on meal worms, sheep's fat, bread and peanuts. During the feeding trials weighed amounts of meal worms in excess of the birds' actual needs were given at the start of each day of the trial, and the uneaten meal worms collected each evening at dusk and weighed and the total amount eaten obtained by subtraction. The average weight of the Great Tits during the feeding trials was obtained by weighing them every morning and evening. During the winter the feeding trial was run on the six captive Great Tits, for six consecutive days, while during the Summer two separate feeding trials were run, each of three days' duration, using three different birds in each.

Every three days the aluminium foil with the faeces was removed from the cages and dried to constant weight in a vacuum oven at 60°C and weighed and the total dry weight of faeces was obtained by subtracting the original weight of the foil from this. The dried faeces were then removed from the foil, finely ground up with an agate pestle and mortar, and stored in bottles in a calcium chloride desiccator. A sample of the meal worms was taken during both experiments, dried to constant weight in a vacuum oven and stored. The calorific value of the food and faeces were determined using the 'Durham' oxygen bomb calorimeter (described later).

From these results the total number of kilocalories of food eaten and faeces produced was calculated, and from this the digestive efficiency of each Great Tit. Assuming that this did not vary significantly from day to day during each of the three day feeding trials, the total number of kilocalories of energy metabolised each day was calculated.

The quantitative estimation of lipid content using the Soxhlet apparatus

Samples of finely ground egg and body tissue were put through a lipid extraction process, using the Soxhlet extraction method. In this thesis the term "lipid" is used where the more accurate term would be 'ether' extracted material, since extraction by ether removes not only true lipids, but also oils and waxes, but this is unimportant in the present context. The Micro-Soxhlet apparatus used is shown in Plate 5. It consisted of three sections, a reflex condenser at the top, an extraction chamber with a siphoning device in the middle, and a flask half-filled with ether (with a few glass beads to stop bumping) at the bottom.

In the extraction, finely ground material was placed in a weighed, special quality lipid-free filter paper thimble, and the whole re-weighed, and this was then placed in the extraction chamber. The flask was then heated on an electrically heated water-bath, causing the ether to volatilise and rise into the extraction chamber and condenser where it liquefies again and collects in the extraction chamber where it comes into contact with the material. On reaching the level of the siphon the ether siphoned off and drained into the flask carrying the extracted lipid with it. On re-entering the flask the ether volatilises again, but the lipid remained in the flask. The ether was allowed to siphon off at least twelve times to ensure that all the lipid was removed from the sample. The thimble with the lipid-free material was then dried to constant weight in a vacuum oven and re-weighed. The percentage of lipid contained in the original sample was calculated using the following formula :-

$$\% \text{ of lipid in sample} = 100 \frac{(y-x) - (z-x)}{(y-x)}$$

where x = wt. of thimble

y = wt. of thimble & original material

z = wt. of thimble & extracted material

Determination of calorific values using the "Durham" bomb calorimeter

The calorific values of finely ground eggs, feathers, body tissues, meal worms and faeces were all determined using the "Durham" bomb calorimeter (Phillipson 1964) (Plate 6). Pelleted samples of approximately 20mg were weighed on an electro-microbalance in a weighed pan made from 0.1mm platinum sheet.

Plate 6

The pan and pellet were then placed on the sample-holding tray in the bomb calorimeter, and a 3cm length of 0.1mm diameter platinum wire secured between the two terminals, and arranged so as to be pressing against the pellet. The two halves of the bomb were then screwed together with a spanner, the lower half of the bomb being held in a vice. The bomb was pressured to 30 atmospheres with oxygen and then cooled in running tap water, dried and seated in the copper ring of the stand, before the leads of the firing circuit were connected. The stainless steel jacket was placed over the assembly and the recording system switched on.

On reaching equilibrium, the condenser was charged and the sample ignited. The potentiometer recorded the heat rise in the bomb via thermocouples and a maximum reading was obtained after approximately seven minutes. When cooling became apparent the operation was stopped, the apparatus dismantled, and the bomb de-pressurised. The small platinum pan was removed and weighed so that the ash content of the sample could be determined.

The maximum reading in millivolts recorded on the potentiometer chart was used in conjunction with the calibration factor, and the total weight of the sample to determine the calorific content of the sample. With the samples used it was found unnecessary to make any corrections.

The bomb was periodically calibrated using benzoic acid.

Plate 1a.

Aerial photograph of central and southern parts of study area.

Plate 1b.

Aerial photograph of northern part of study area (both photographs taken looking westwards).

Plate 2a.

Detail of Area 1. Oak-Beech woodland with only a few isolated patches of secondary vegetation. Habitat most favoured by Blue Tits (see text).

Plate 2b.

Detail of Area 3. Oak-Beech woodland with an extensive secondary vegetation. Habitat most favoured by Great Tits (see text).

Plate 3.

Grounds of Durham University Zoology Department Field Station.

a. Field Station building and house trap used for catching Great and Blue Tits during Winter.

b. Detail of Oak woodland where the nest boxes were provided.

Plate 4.

a. Looking north over central part of study area. In foreground part of Larch plantation of Area 2. Habitat least favoured by Great and Blue Tits (see text). In middle distance - grounds of field station.

b. Looking north over Area 2, with part of Oak - Beech woodland of Area 3 in foreground.

Plate 4.

The Micro-Soxhlet apparatus used for lipid extraction.

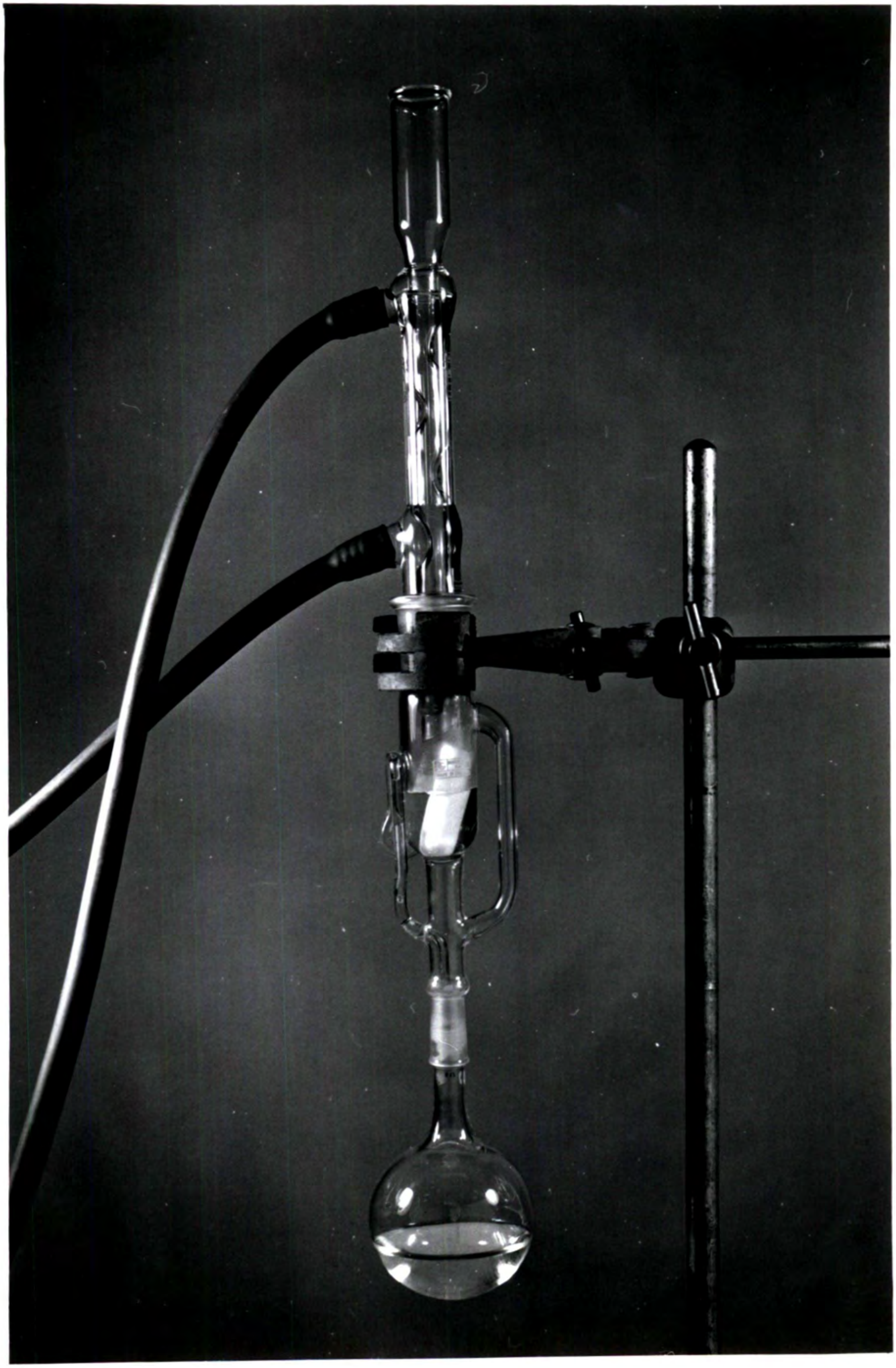
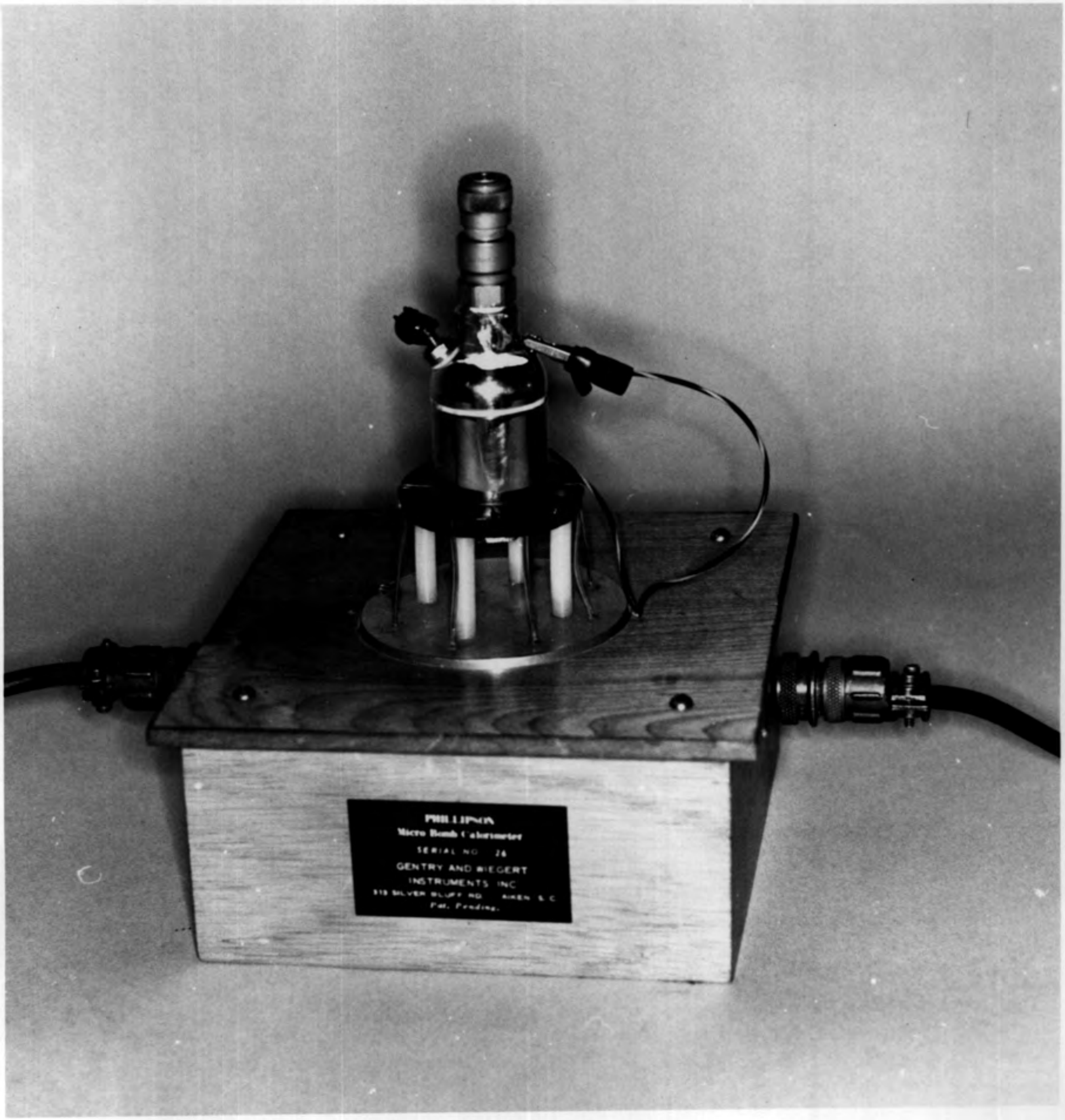


Plate 5.

The "Durham" bomb calorimeter, seated in the copper ring with the thermocouples.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RESULTS.

I. POPULATION DYNAMICS.

1. Census of Winter Population

During the Winter a large proportion of both the Great Tit and Blue Tit populations in the study area were caught and ringed. The actual numbers caught, together with the age ratios of both species and the sex ratio for Great Tits, are shown in Table 2. The percentage of first year Great Tits in the total population was 50%, while that for Blue Tits was 67%. These figures give an approximate measure of the annual recruitment rate of first-year birds into the population, since it has been shown by many authors (e.g. Lack 1946) that the mortality rate of first-year passerine birds is very similar to that of adult birds after they reach their first Winter. These figures, therefore, also give an indication of adult annual mortality rates, but this is only valid if the population is stable from year to year. Perrins (1965) used similar age ratios to show that the survival of juvenile Great Tits before their first winter is of critical importance in determining the size of the breeding population the following Summer. Perrins found that when the percentage of first year Great Tits in the Winter population was above 50% there was generally an increase in the size of the breeding population the next Summer, and vice-versa.

Table 2. Numbers of Great and Blue Tits caught in the study area during Winter 1968

Species		No.		No.	Total
GREAT TIT	Adult Males	10	Adult Females	9	19
	1st Year Males	11	1st yr Females	8	19
	All Males	21	All Females	17	38
BLUE TIT	Adults	26			
	First Year	54			
	Total	80			

At present there is no published data concerning mortality rates of British Great Tits as have been determined from ringing recoveries for a number of bird species. However, Kluijver (1951), working on the continental race of Great Tit (Parus m.major) in Holland, has found the average annual mortality rates to be 87% in the first year of life, and 49% for older birds. Kluijver also found that mortality rates among resident Great Tits were not significantly higher in Winter and Spring than in Summer and Autumn, except in severe winters. Snow (1956) showed that the annual adult mortality rate of British Blue Tits was about 70%. The close similarity between the published adult annual mortality rates for Great and Blue Tits and the annual recruitment rates estimated for these species in this study gives an indication of the stability of their respective populations in the study area.

2. Breeding Density and Habitat Selection

The breeding densities of Great and Blue Tits in the study area, and its three subdivisions, are shown in Table 3.

Both Great and Blue Tits favoured the mixed, broad-leaved woodland in Areas 1 and 3 to the largely coniferous woodland of Area 2. The most favoured habitat of Great Tits was Area 3 which had an extensive secondary vegetation (Plate 2), and in Area 1 they were generally restricted to areas with patches of secondary cover. In consequence it was only in Area 3 that the woodland was anything near saturated with Great Tit territories, whose average size was 0.9 ha. Great Tit territories in Areas 1 and 2 appeared also to be approximately of this size.

Blue Tits, on the other hand, had their highest density in Area 1, probably because this area had the tallest and most complete closed canopy (see Plates 1 and 2). The average territory size of Blue Tits in Area 1 was 0.6 ha.

Table 3. Breeding Density of Great and Blue Tits in the study area.

	GREAT TIT			BLUE TIT	
Area	Total area in hectares.	Total no.of breeding pairs	Density (prs/10 ha.)	Total No. breeding pairs	Density (prs/10 ha.)
1	33	11	3.3	57	17.3
2	6.5	1	1.5	5	7.7
3	5	6	12.0	5	10.0
	44.5	18	4.0	6.7	15.1

The densities of Great and Blue Tits in the different types of woodland were fairly consistent with those given by Lack (1966) (Table 4). It should be noted that the breeding density of Great Tits in Marley Wood varied considerably from year to year, reaching its highest level of 33 pair/10 ha. in 1961, and having its lowest level of 3 pair/10 ha. in 1947 at the start of Lack's study. It is possible that the provision of nest boxes may increase the breeding densities of Tits in some woodlands if suitable natural nesting sites are of limited abundance.

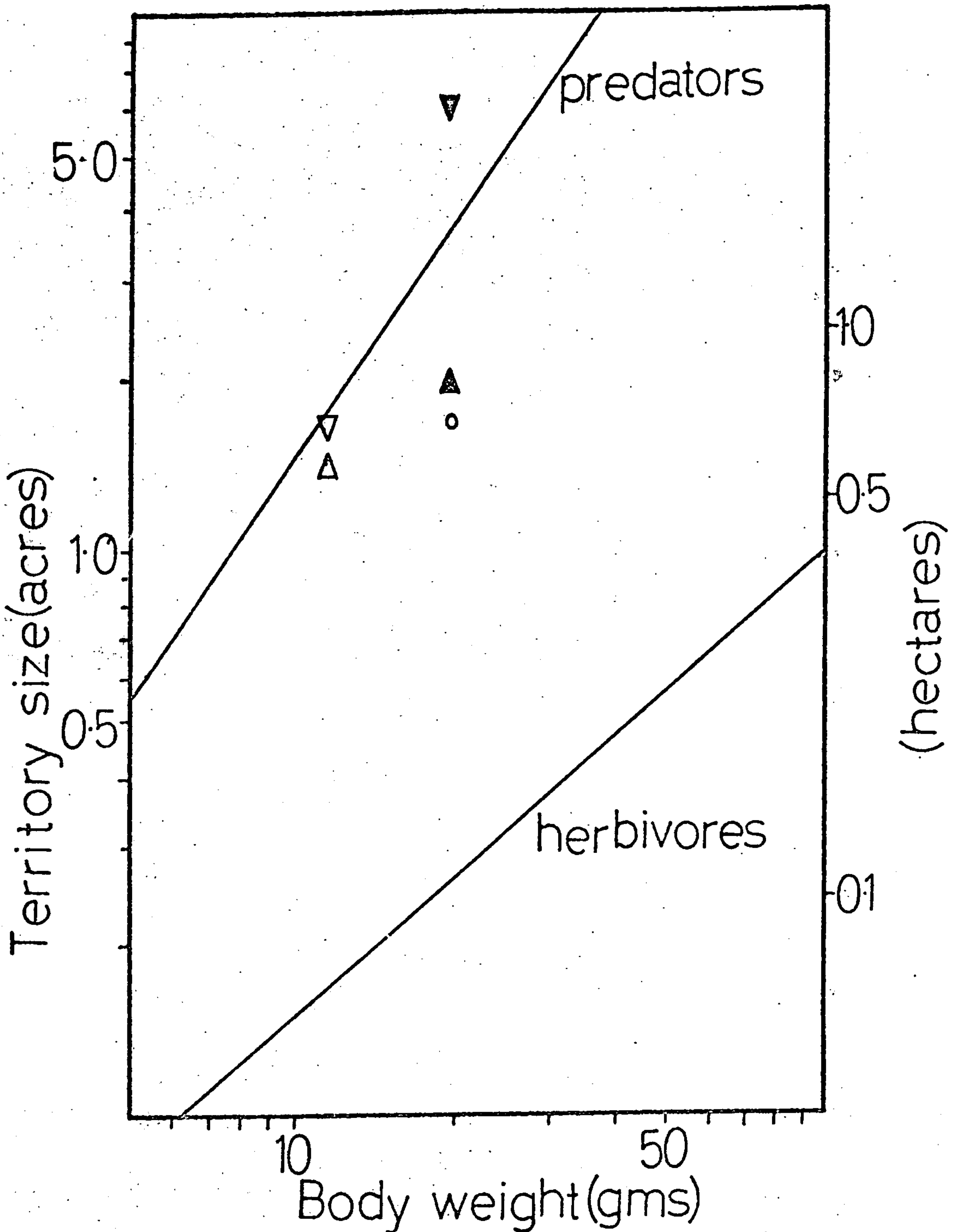
Table 4. Breeding densities of Great and Blue Tits in different habitats in southern England (after Lack 1966).

	GREAT TIT	BLUE TIT
Habitat	Mean density (pairs/10 ha.)	Mean density (pairs/10 ha.)
Pure Oak	c 12	20+
Marley	c 14	9+
Scots Pine	2.5	1.2
Corsican Pine	1.3	0.6
Gardens	c 9	-

In the rather poor mixed coniferous and broad-leaved woodlands in the Veluve, near Arnhem, Holland, Kluijver (1951) found the mean breeding density of Great Tits to be 2.5 pairs per 10 ha., very similar to the density found by Lack in the Breckland pine plantations, and the larch plantation used in this study.

In Fig.3 the densities of Great and Blue Tits discussed above are plotted against their respective average body weights and compared with average values found by Schoener (1968) for predatory and herbivorous birds. As can be seen, the densities found in this study for both species of Tit are very close to the average values for predatory birds.

Fig.3. Relationship of breeding density to body weight of Great and Blue Tits compared with Schoener's equations (1968) relating territory size to body weight of predatory and herbivorous birds.



▼ av. density of Great Tits in whole study area (ha/pair)
▲ " " " " " " area 3 of " " " "
o " " " " " " Marley Wood (Lack 1966)
▽ av. density of Blue Tits in whole study area (ha/pair)
△ " " " " " " area 1 of " " " "

3. Dispersal of Great Tits from Winter Quarters

During the Winter Great Tits were only observed moving around in mixed flocks of Tits when the weather was severe, and usually split off from these either individually or in pairs as soon as conditions improved, and the majority of these birds showed signs of being territorial. However, of the 29 colour-ringed Great Tits (17 males and 12 females) present in the Winter, only 10 (7 males and 3 females) were still present in the breeding season. Assuming a constant annual mortality rate for these birds of 50% (Kluijver 1951), 24 of the colour-ringed birds would be expected to survive until the Summer, so that 14 birds (58%) of the Winter population left the study area. However, since the breeding population of 36 birds in the study area was approximately of the size expected from the Winter trapping results, any movement of Great Tits out of the study area must have been largely balanced by movement of birds into it during late Winter and Spring.

While the figure of 58% for the percentage of the Winter population "emigrating" is probably inaccurate because the sample size was small, it does give an indication of movements of Great Tits between neighbouring populations. The nearest woodland population of Great Tits to the study area was situated half a mile away on the south side of the River Wear, while to the north, east and west there were no suitable woodlands within at least a mile, although a few copses harboured isolated pairs of birds. It seems likely that at least some of

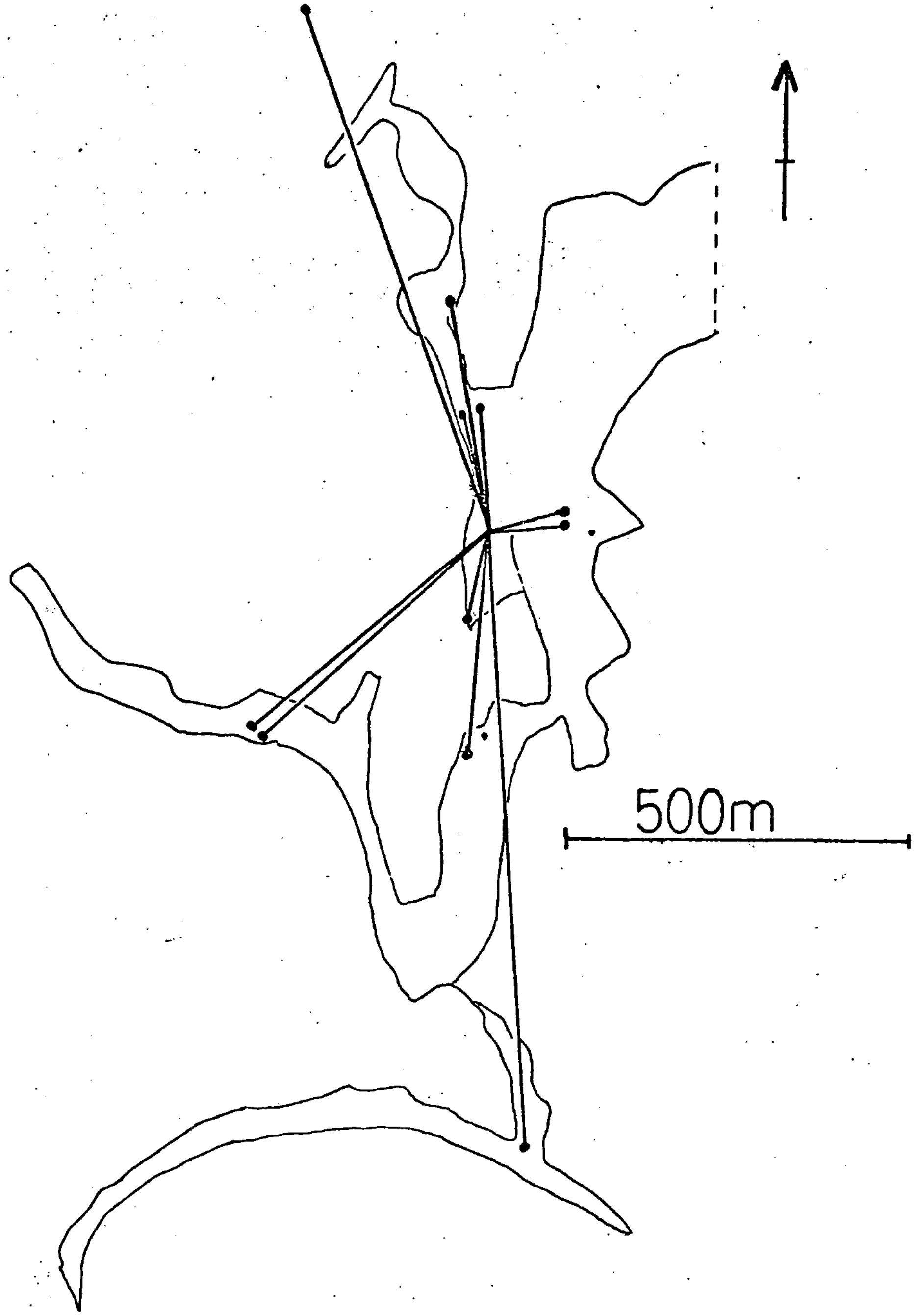


Fig.4.

Movement of Great Tits caught and colour ringed at field station in Winter 1968 to their breeding territories in May 1968.

the "immigrant" Great Tits were birds which were attracted into Durham City during the Winter in search of food, and returned to the woods to breed.

The actual movement of Great Tits from the ringing point in the Field Station to their breeding territories is illustrated in Fig.4 (which includes one bird which was located outside the study area to the north). It is of interest that a higher proportion of colour-ringed females than males left the study area. Although the figures are not significant, it is usual in birds for females to be less territorial than males, and also to search for territory-holding males before the breeding season.

4. Breeding Season

Although only three nests of Great Tits and eleven of Blue Tits were found, the data obtained gives an approximation of the timing and duration of the breeding season (Table 5 and Fig.5). In Durham the Tits began nest building approximately 7 - 8 days before egg laying started, but there was much variability with season - one of the last Blue Tits to start nesting laid her first egg in a box with no nesting material at all. Once egg-laying started, one egg was usually laid on each day until the clutch was complete. The average incubation period was 13.3 days for Blue Tits and 14 days for Great Tits, and the fledging period was 18.8 days for Blue Tits and 20 days for Great Tits.

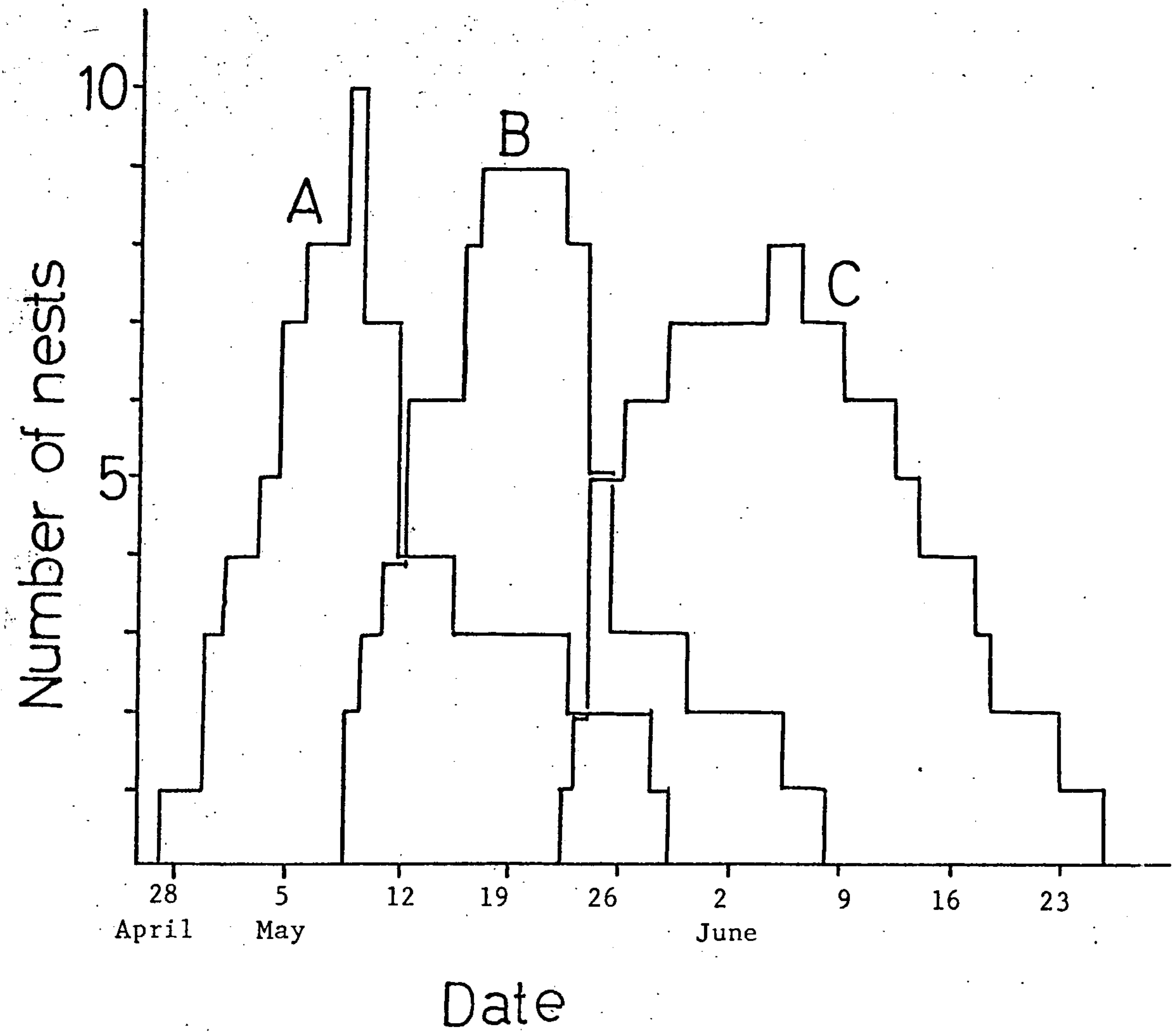


Fig.5.

Breeding season of Blue and Great Tits (combined) in Durham 1968.

A = Number of nests with eggs being laid.

B = " " " " clutches being incubated.

C = " " " " broods present.

Table 5. Egg laying Season and average clutch size of Great and Blue Tits in Durham 1968

	BLUE TIT		GREAT TIT	
Week ending	No.clutches started	Average Clutch size	No.clutches started	Average Clutch size
14 April				
21				
28	1	13		
5 May	4	9.0	2	8.5
12	3	7.3	1	8
19	3	8.7		
26				
Total	11	8.8	3	8.3

So far as one can see from the data, it would appear that the breeding both by individuals of the same species and by the two species was fairly synchronous. This was also found by Gibb (1950) for Tits nesting in Wytham Wood, Oxford, where it was shown that the maximum food requirements of the broods coincided with the period of greatest abundance of "defoliating" moth larvae upon which the young are fed.

The data in Table 5 indicates that there was a tendency for clutch size to decrease as the breeding season progressed, but the sample size was too small to test this statistically. The average clutch size of Blue Tits in Durham of 8.8 was significantly lower ($P < 0.001$ using methods described by Bailey (1966) for comparing the mean of a single small sample of size n 30 with a known standard, assuming a normal population) than the average clutch size at Oxford of 12.3 (Gibb 1950). The average clutch size of Great Tits in Durham of 8.3 was also significantly lower ($P < 0.02$) than the average of 11.1 at Oxford (Gibb 1950).

In Durham the mean date of laying of the first egg for both species of Tits was 8th May, which was eleven days later than the mean date of 27th April in Wytham Wood, Oxford this year (P. Jones pers.comm.). This is probably a function of the difference in latitude of the two places, Oxford being situated 206 miles due south of Durham. No second clutches were found in Durham, while they commonly occur in the Oxford area.

5. Breeding Success

The breeding success was remarkably high (see Table 6), and the maximum breeding success was very similar to the figure of 91% obtained by Gibb (1950). Human interference was probably the main factor causing the minimum breeding success to be as low as 67% (compared with Gibb's figure of 80% (1950)), including three Blue Tit clutches and one Great Tit brood which were deserted. As two eggs were removed from most clutches found, the data was corrected on the assumption that each of these eggs would have given rise to free-flying young in successful nests.

Table 6. Summary of breeding success in Durham 1968, Blue and Great Tits combined

Number of Eggs		Number of Young		Breeding Success	
Hatched	Infertile	Successfully reared	Died in nest	Maximum	Minimum
90(92.8%)	7 (7.2%)	82 (98.8%)	1 (1.2%)	92.1	67.2

(These figures discount all losses resulting from human interference, excepting the figure for minimum breeding success which includes all losses including deserted clutches and broods.)

6. Egg Weights and Dimensions

Table 7 shows the average wet and dry weights, length and breadth of Blue and Great Tit eggs, the analysis being made on the two eggs taken from each clutch found. The average wet weights obtained were almost identical to those given for the same species by Gibb (1950) of 1.75gms for Great Tit eggs and 1.11gms for Blue Tit eggs. There was a tendency for average egg weight of Blue Tits to increase as the season progressed, but this could not be tested statistically because the sample size was too small. Nevertheless there was also a tendency for the total weight of clutches to decrease with date since clutch size decreased with date.

Table 7. Weights and dimensions of Blue and Great Tit eggs

Species	Sample size	Average wet wt. (gms)	Average dry wt. (gms)	Av. Length (cm)	Av. Breadth (cm)
Blue Tit	22	1.114	0.259	15.40	11.80
Great Tit	2	1.711	0.351	18.80	13.98

7. Lipid content and calorific value of eggs

Table 8 gives a summary of the average lipid content of Blue Tit eggs and Table 9 the calorific values of Blue and Great Tit eggs.

Table 8. Average Lipid content of Blue Tit eggs in Durham 1968

Species	Sample Size	Average dry wt. (gm)	LIPID CONTENT Total wt. per egg (gms)	% dry wt. = lipid
Blue Tit	5	0.2502	0.0574	22.96

There was a very marked correlation between the size of Blue Tit eggs and their total calorific content (Fig.6). However, the total lipid content of Blue Tit eggs was only very slightly greater in large than small eggs, while the percentage lipid was markedly lower in larger eggs (Fig.7). Assuming lipids have a calorific value of 9 Kilocalories/gm, the proportion of the total calorific value of eggs attributable to lipids was calculated and plotted in Fig.6. This would indicate that the size of the yolk (where all the lipids are found) is a much more constant characteristic of the species than the size of its eggs.

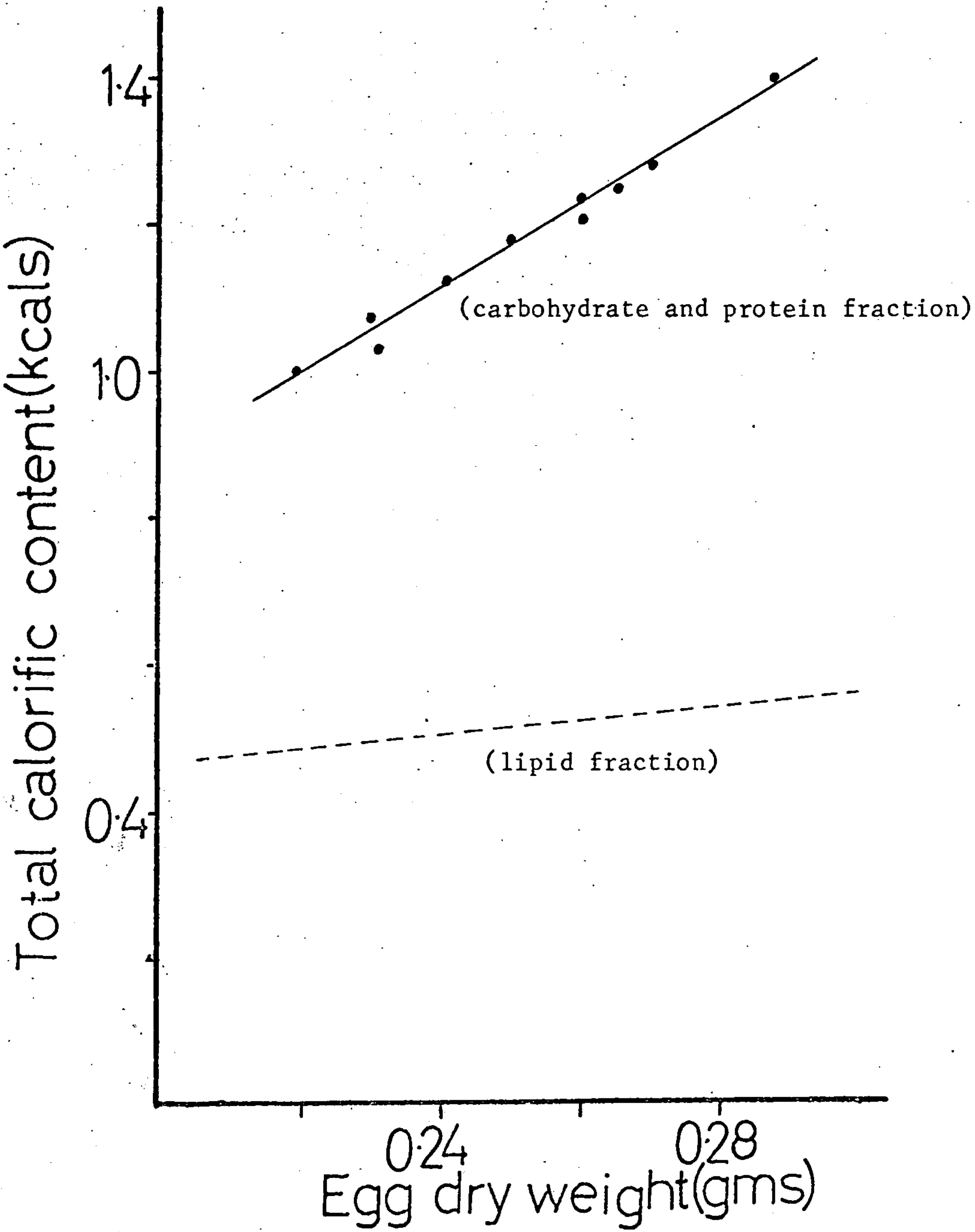


Fig.6.

Relationship of dry weight to calorific content of Blue Tit eggs, showing also the fraction of the calorific content attributable to lipids (see Fig.7), and the fraction attributable therefore to carbohydrates and proteins.

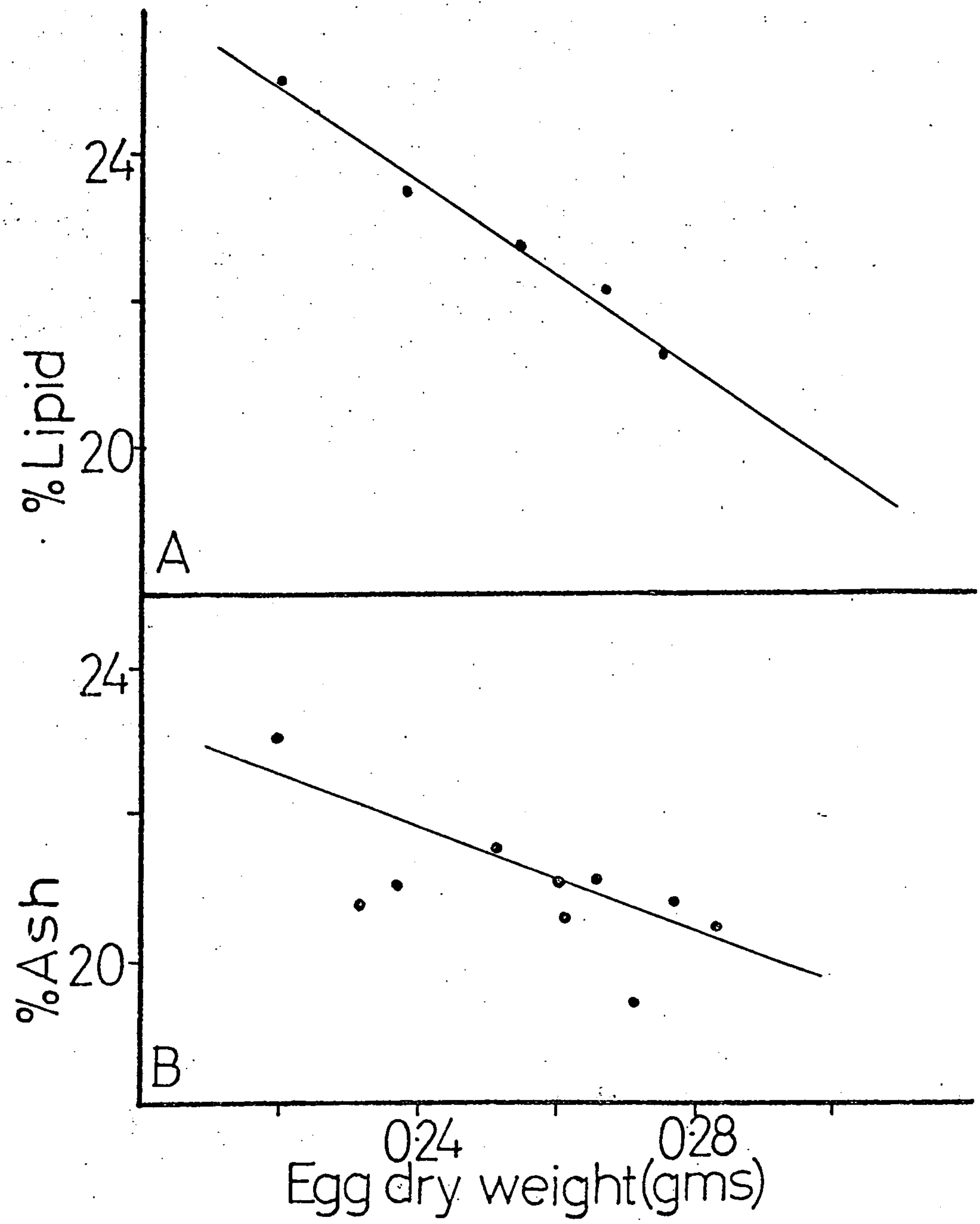


Fig.7. Relationship of % lipid (A) and % ash (B) to dry weight of Blue Tit eggs.

Table 9. Calorific content of Blue and Great Tit eggs, Durham 1968

Species	Sample size	Av.dry wt. of eggs (gms)	Av.calorific values Total K.cal/gm	Ash-free K.cal/gm	% of dry wt.= Ash	Av.cal.value of egg K.cal
Blue Tit	10	0.256	4.721	5.966	20.87	1.209
Great Tit	2	0.351	4.507	5.868	23.20	1.582

The total ash content, which is a measure of the shell size of the egg, varied from 20% of the dry weight of the largest Blue Tit egg analysed to 23% of the smallest. (Fig.7).

8. Seasonal fluctuation in population size of Great and Blue Tits in study area

From the preceding data, an attempt was made to calculate the seasonal population fluctuations of Great and Blue Tits that could be expected in the study area (Figs. 8 & 9). Having determined a breeding population of 36 Great Tits in June 1968 (point 'a' Fig.8), and assuming an annual adult mortality rate of 50% per year (Kluijver 1951), line A in Fig.8 can be calculated (since a linear relationship can be expected between the log of survivors and the length of time at risk in the environment if the mortality rate is constant). This gives the expected mid-January 1968 population size to be 50 birds, which is similar to the one determined by trapping.

Knowing that the average clutch size was 8.3 (this study) and taking the average minimum breeding success of Great Tit first broods of 80% found by Gibb (1950), the total number of fledglings present in mid-July produced by the 18 breeding pairs would be 120, giving a total population of 155 Great Tits (point 'b' Fig.8), and an adult : juvenile ratio of about 1 : 3.

In mid-Winter 1967-68 the adult : juvenile ratio was found to be 1:1, indicating that the juvenile mortality rate was much higher than that of the adults during Summer and Autumn. Perrins (1965) found that there was little change between the adult : juvenile ratio of Great Tits at the beginning of the Autumn and at the end of Winter in most years in Wytham Wood, and as there was no evidence to the contrary, the same probably applies in the Durham study area. Therefore in Fig.7, point 'c' is obtained simply by doubling the calculated adult population for the end of September.

Using similar reasoning, the seasonal population fluctuations of Blue Tits in the study area were calculated (Fig.9). From a breeding population of 67 pairs (point 'a' Fig.9), and an annual adult mortality rate of 70% (Snow 1956), seasonal changes in the adult population were calculated (line A Fig.9). The number of fledglings in July 1968 was calculated for the 67 pairs with an average clutch size of 8.8 eggs (this study) and using the average minimum breeding success for Blue Tit broods of 79%

found by Gibb (1950), giving a total of 466 juveniles and a total July population of 528 Blue Tits (point 'b' Fig.9). In mid-Winter 1967-68 the ratio of adults : juveniles in the study area was 1 : 2. Snow (1956) found that the mortality rates of juvenile Blue Tits was higher than that for adults in October and November, but from December onwards juvenile and adult mortality were about equal. Therefore point 'c' Fig.8 was calculated simply by trebling the calculated adult population at the beginning of December.

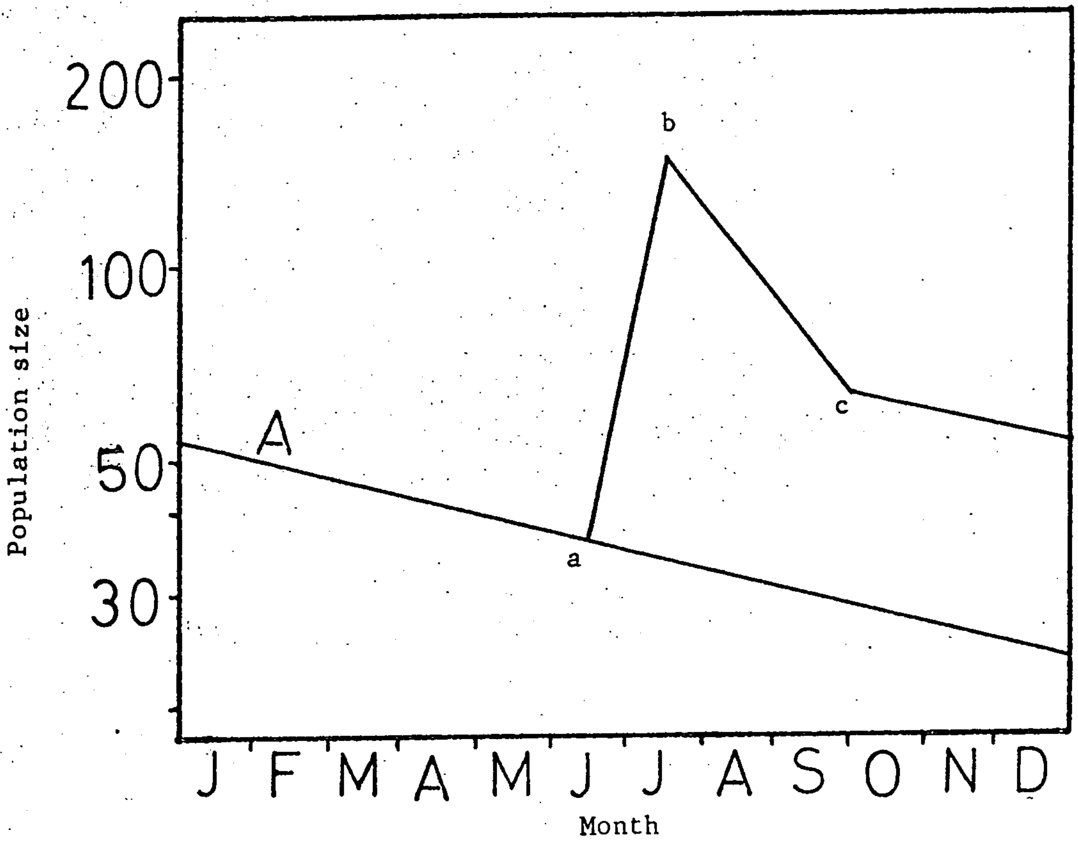


Fig.8. Seasonal fluctuations of Great Tit population in study area (see text)

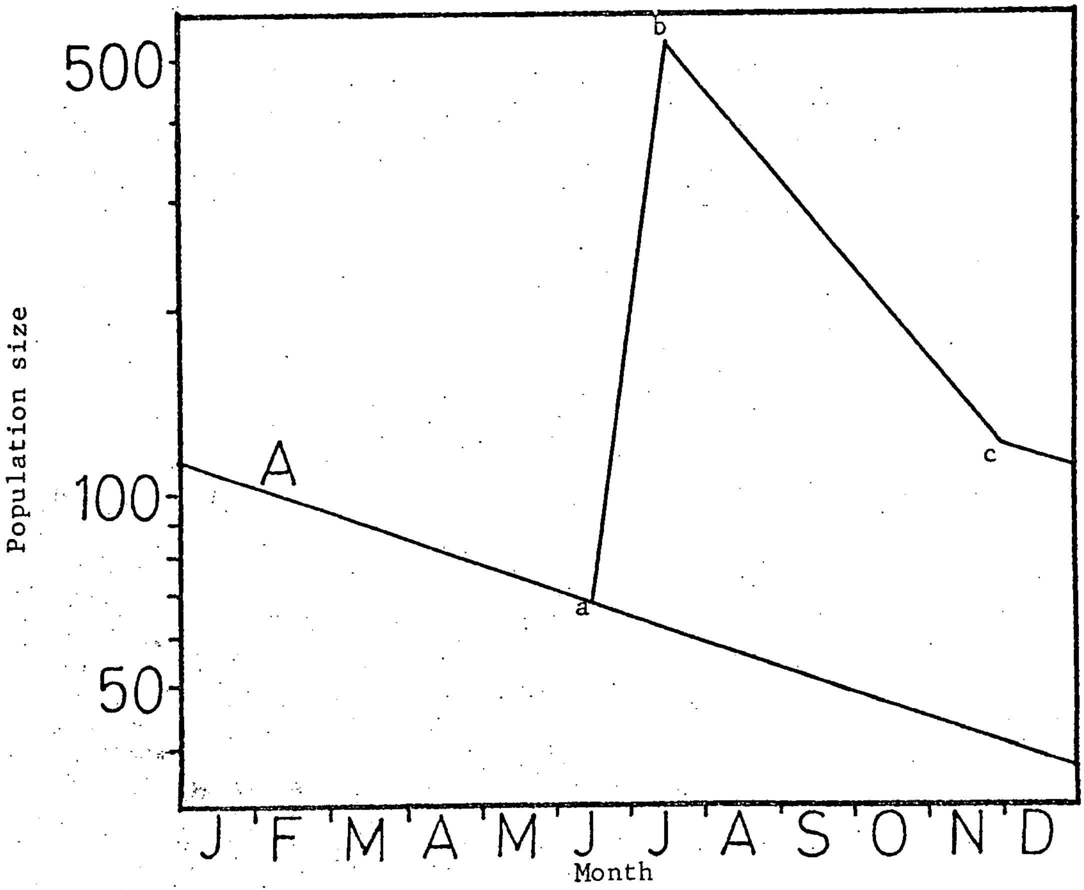


Fig.9. Seasonal fluctuations of Blue Tit population in study area (see text)

II. POPULATION BIOMASS

1. Daily and Seasonal Variations in Weight

Table 10 is a summary of the average weights of wild Great and Blue Tits caught during the Winter and Summer. The weights used were the average of birds caught at all times of the day, the mean time of trapping being very close to noon for mid-Winter, and in the early afternoon in mid-Summer (see Figs.12 & 13).

The results show that there was very little seasonal variation in the weights of adult male Great Tits, while adult female Great Tits were distinctly heavier in mid-Summer than in mid-Winter - due, no doubt, to an increase in size of their gonads etc. during the breeding season (Kluijver 1952). The average weights of all adult Blue Tits were slightly lighter in mid-Summer than in mid-Winter.

In Figs.10, 11 and 12 the average weights of all male and female Great Tits and all Blue Tits respectively caught during the Winter are plotted for each hour, and a regression line was calculated for each series of weighings against time of day. In Fig.13 the average weights of all Blue Tits caught during the Summer are plotted for each two hours.

The graphs show that during the Winter both species tended to put on weight most rapidly in the morning and late afternoon, the rate falling off between 11.00 and 14.00hrs.

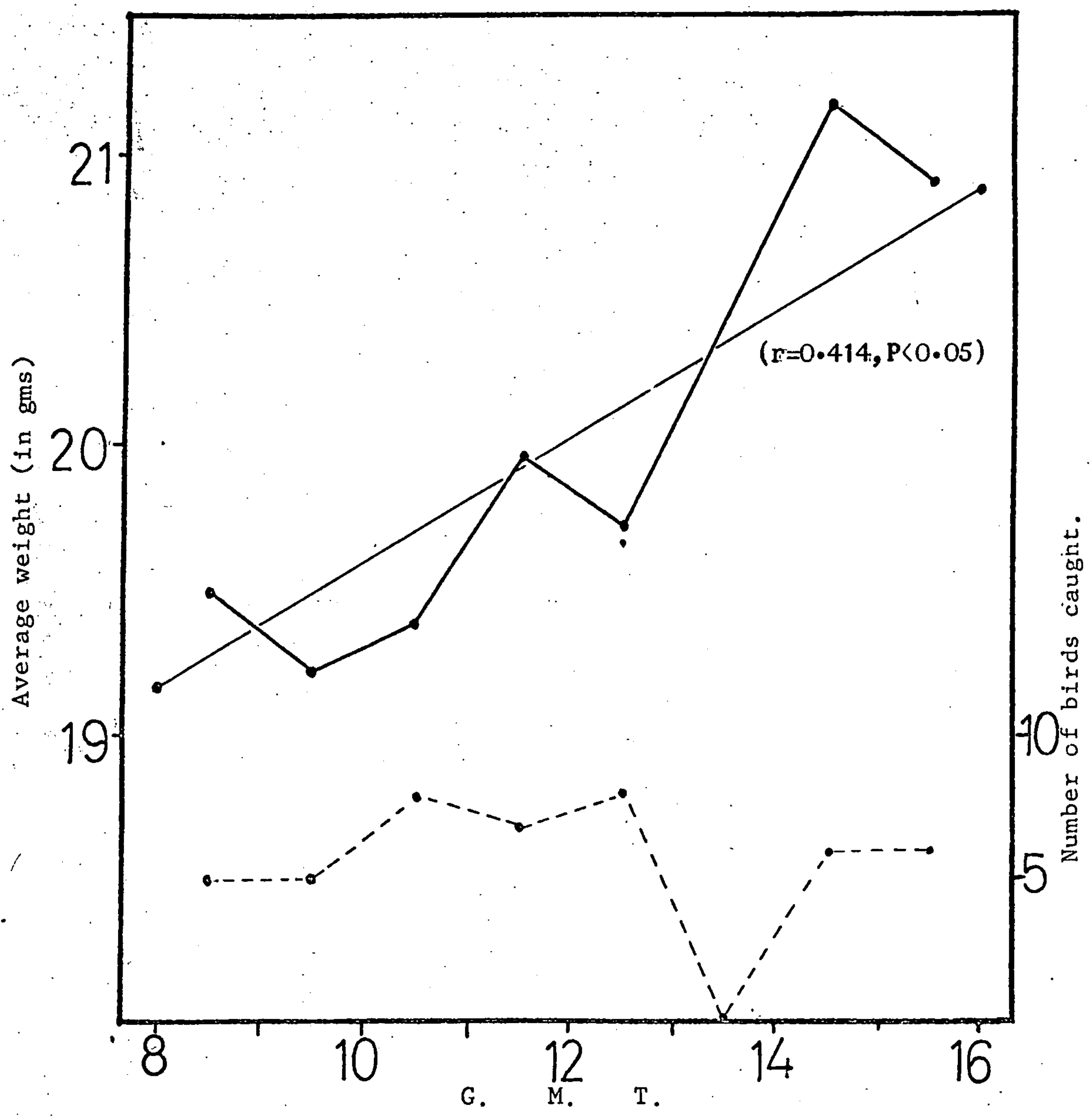


Fig.10. Average diurnal variation in weight of male Great Tits in January - February 1968, with a regression line for all weighings (solid lines), and feeding activity as indicated by number of birds trapped in each hour (broken line).

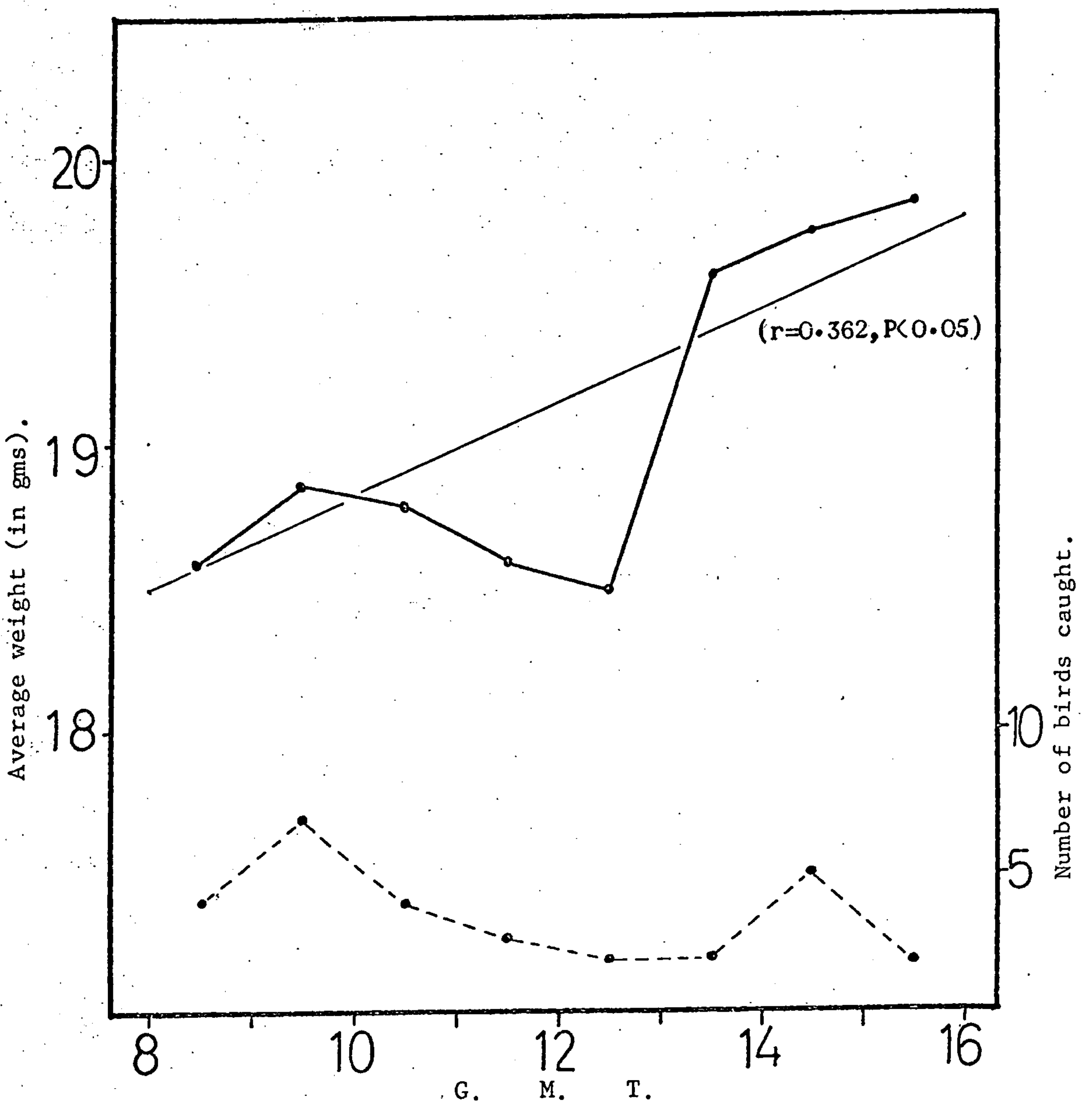


Fig.11. Average diurnal variation in weight of female Great Tits in January - February 1968, with a regression line for all weighings (solid lines), and feeding activity as indicated by number of birds trapped in each hour (broken line).

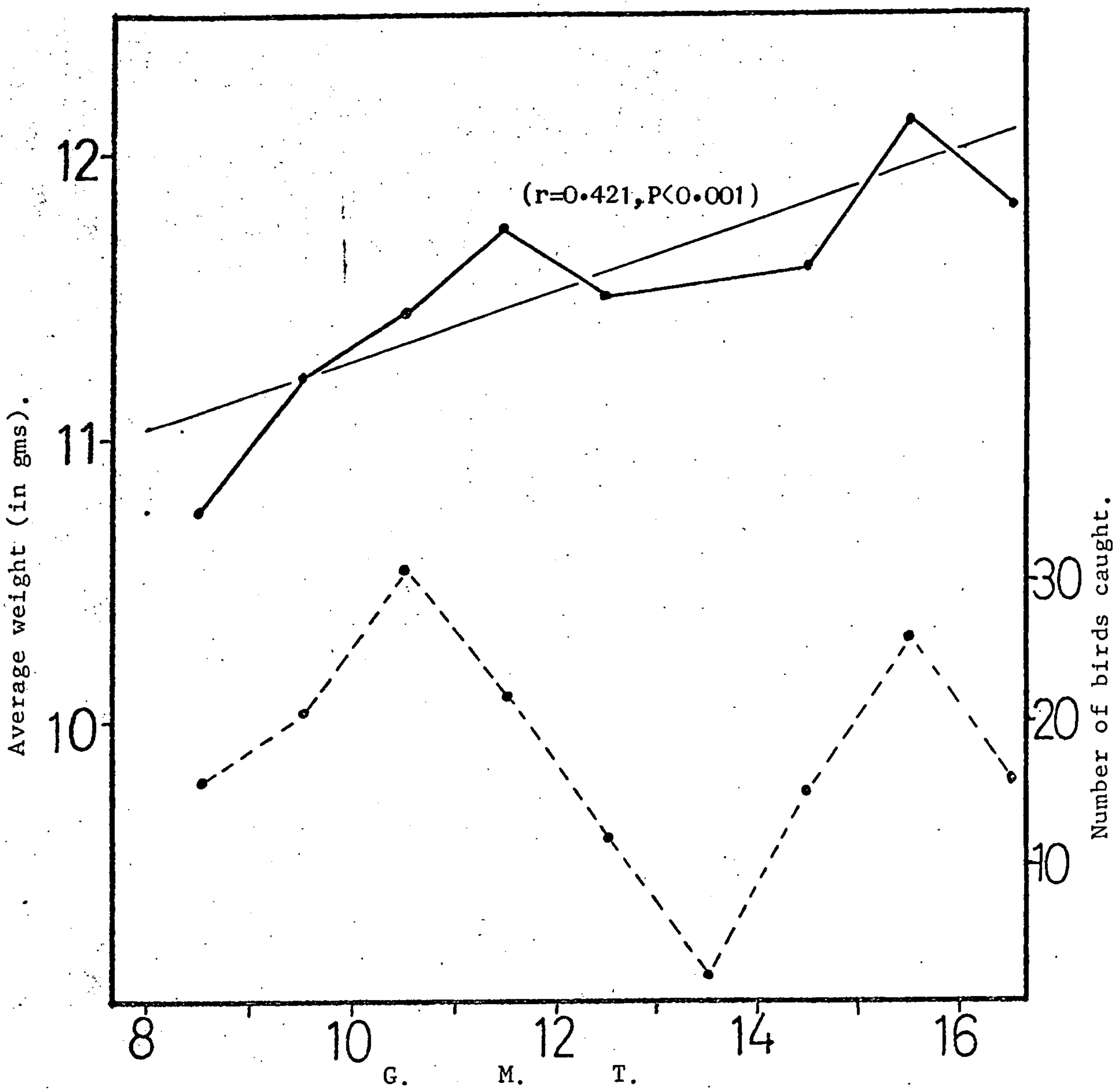


Fig.12. Average diurnal variation in weight of Blue Tits in January - February 1968, with a regression line for all weighings (solid lines), and feeding activity as indicated by the number of birds trapped in each hour (broken line).

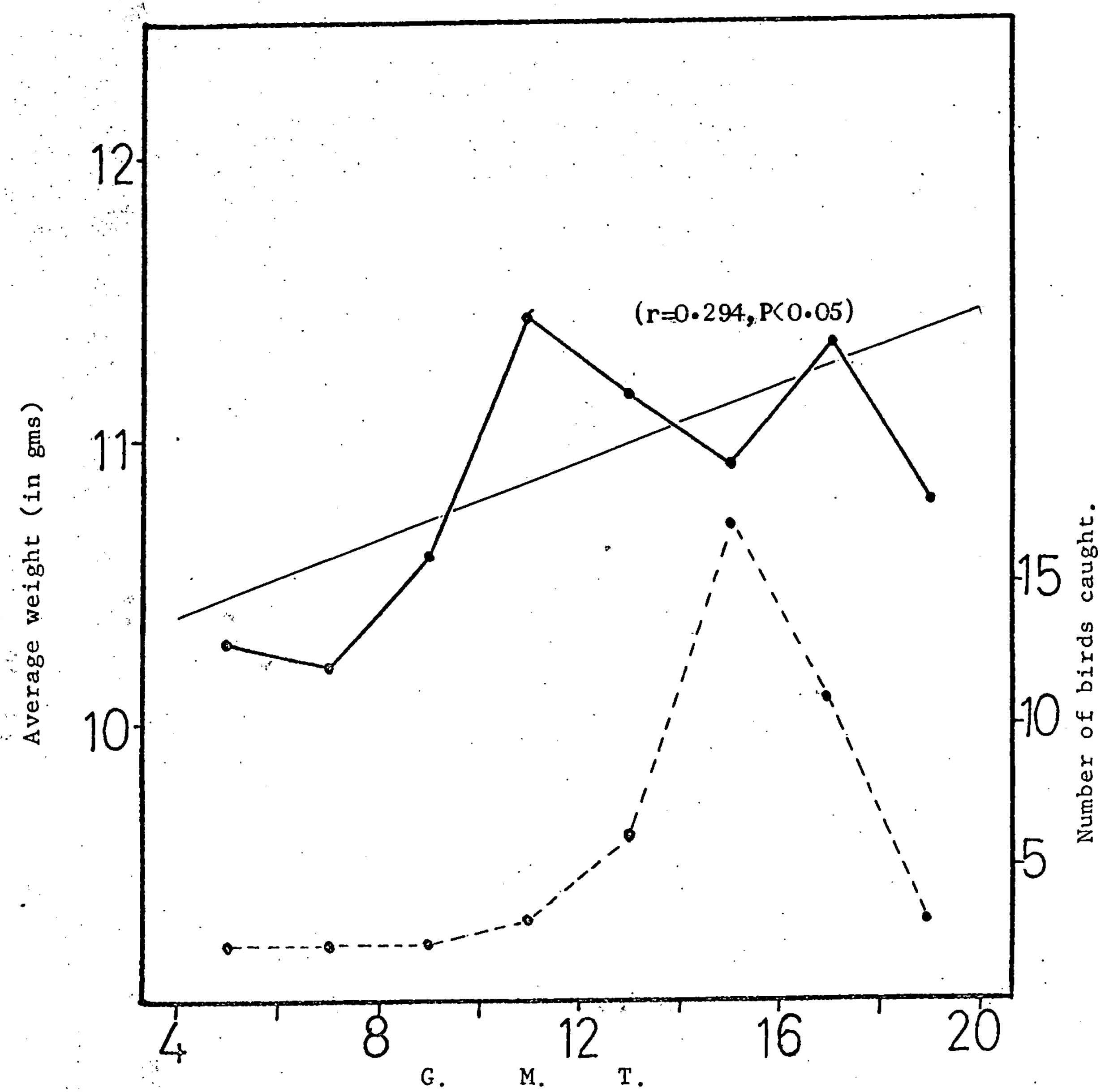


Fig.13. Average diurnal variation in weight of Blue Tits in June - August 1968, with a regression line for all weighings (solid lines), and activity (see text) as indicated by the number of birds trapped in each two hours (broken line).

Table 10. Average Weights of Great and Blue Tits in Durham in Winter and Summer 1968

		WINTER		SUMMER	
Species	Age & Sex	Sample Size	Av. Wt. ± S.E. (gms)	Sample Size	Av. Wt. ± S.E. (gms)
GREAT TIT	Adult Males	12	20.62 ± 0.34	8	20.54 ± 0.44
	1st Year Males	33	19.79 ± 0.25		
	Juvenile Males			3	19.62 ± 0.39
	All Males	45	20.01 ± 0.21	11	20.32 ± 0.38
GREAT TIT	Adult Females	13	19.07 ± 0.21	4	19.72 ± 0.39
	1st Year "	16	19.01 ± 0.27		
	Juvenile "			4	17.70 ± 0.32
	All Females	29	19.04 ± 0.17	8	18.71 ± 0.14
BLUE TIT	Adults	36	11.43 ± 0.09	18	11.15 ± 0.20
	1st Years	130	11.59 ± 0.07		
	Juveniles			29	11.01 ± 0.12
	All	166	11.55 ± 0.06	47	11.11 ± 0.10

The diurnal variations in feeding activity at this time of the year, measured by the number of birds caught in the house trap during each hour, shows that the periods of greatest feeding were also the periods of most rapid increase in weight. The results also show that Blue Tits were 12% heavier at dusk (16.00hrs G.M.T.) than at dawn (8.00hrs), while the daily percentage increase in weight of male and female Great Tits was 8 and 7% respectively.

In the Summer, Blue Tits increased in weight most rapidly during the morning, and showed, if anything, a slight fall between noon and dusk. The numbers of birds caught every two hours, in this case with mist nets, do not reflect feeding activity since the birds tended to feed in the tops of trees during the morning and came down to drink from a stream in the afternoon, at which time they were caught.

14 15 Figs. 14 and 15 show the average nightly weight loss during the Winter of ten Blue and four Great Tits respectively caught at dusk and kept in roost boxes overnight, being weighed at dusk, midnight and at dawn before being released. Both the Blue Tits and Great Tits were 11% lighter at dawn than at dusk, in keeping with the diurnal increase in weight. The most rapid weight loss occurred before midnight, probably because of the loss of the majority of the contents of the digestive tract at this time. Kluijver (1952) and Van Balen (1966) also measured nightly weight loss of wild continental Great Tits in Holland,

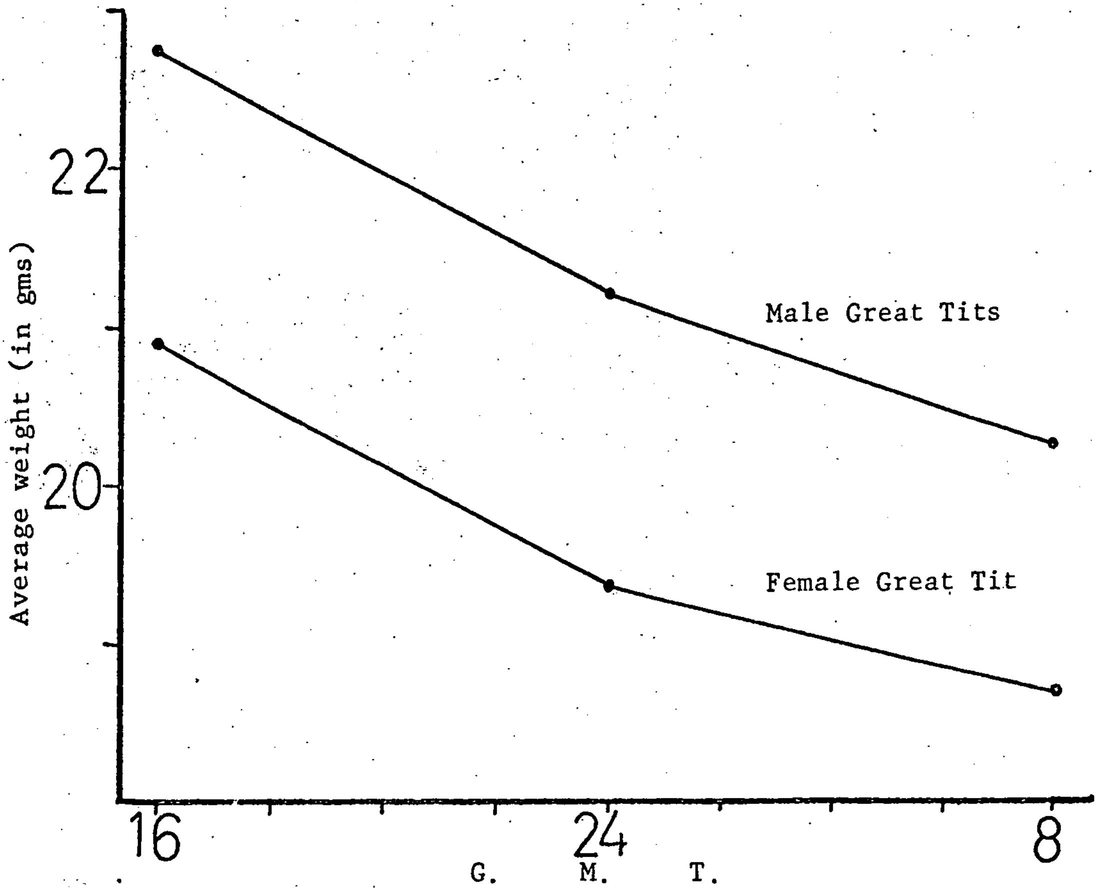


Fig.14. Nocturnal weight loss of Great Tits in Durham, January 1968.

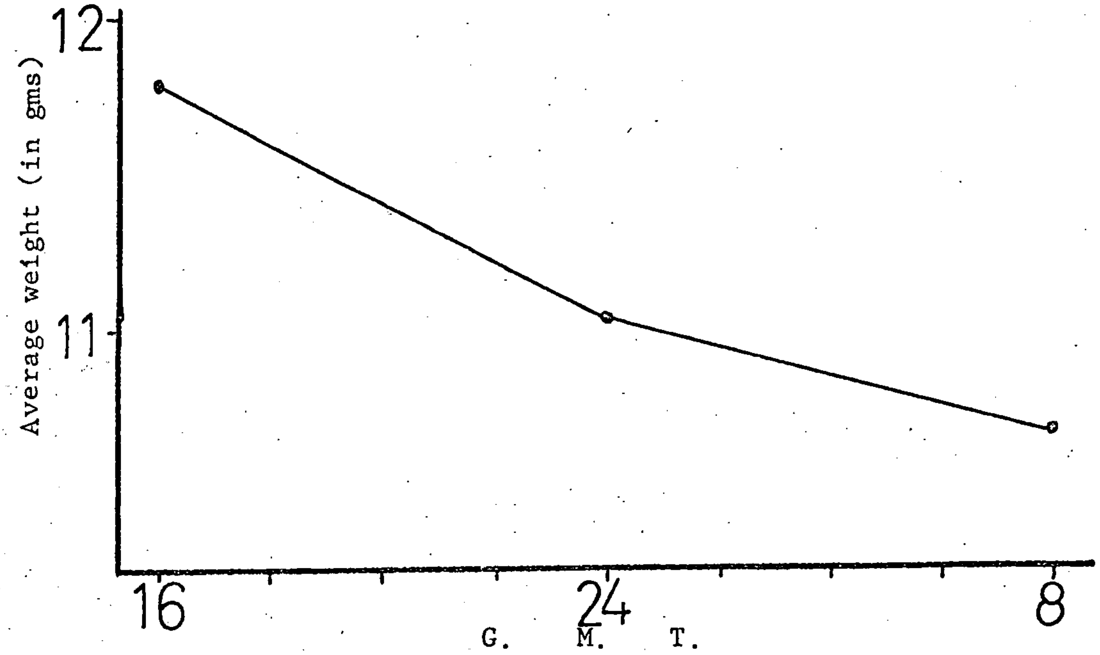


Fig.15. Nocturnal weight loss of Blue Tits in Durham, January 1968.

and found an average weight loss of nearly 10%, in good agreement with the findings of this study.

Comparing the actual winter weights of Tits caught in Durham with those given by Owen (1954) for birds caught near Oxford, Great Tits were on average 0.6gm heavier. The Winter weights of continental Great Tits given by Kluijver (1952) were on average 2gm lighter than the Durham Great Tits, highlighting one of the major differences between the Continental and British species.

2. Seasonal Variations in Wing Length

Table 11 gives a summary of the wing lengths ('chord' measurement) of Great and Blue Tits caught during the Winter and Summer. The adult Tits in Summer were all measured before their remiges were moulted, and were noticeably shorter than in mid-Winter, no doubt as a consequence of abrasion. There was also a significant difference ($P < 0.01$) between the wing lengths of male and female Great Tits (approximately 2mm) reflecting the difference in their body weights.

Table 11. Wing lengths of Great and Blue Tits during Winter and Summer

		WINTER		SUMMER	
Species	Age & Sex	N	Winglength ± S.E. (mm)	N	Winglength ± S.E. (mm)
GREAT TIT	Adult Males	7	74.80 ± 1.12	7	72.5 ± 0.48
	1st Year Males	11	71.72 ± 0.58		
	Juvenile Males			3	70.0 ± 1.48
	All Males	18	72.82 ± 0.67	10	71.75 ± 0.65
GREAT TIT	Adult Females	7	71.58 ± 0.72	3	69.17 ± 0.72
	1st Year "	8	69.90 ± 0.62		
	Juvenile "			4	70.63 ± 1.68
	All Females	15	70.82 ± 0.54	7	70.00 ± 0.88
BLUE TIT	Adults	16	61.20 ± 0.39	13	59.77 ± 0.62
	1st Years	37	62.04 ± 0.25		
	Juveniles			23	59.76 ± 0.34
	All	53	61.70 ± 0.24	36	59.76 ± 0.30

3. Feather Weight and Calorific Value

Table 12 is a summary of feather weight and calorific values of Great and Blue Tits taken for analysis during Winter and Summer 1968. This analysis was done to determine the seasonal differences in total insulation provided by feathers and to determine the actual amount of energy present as feathers and replaced each year during moult. It was found that the weight of down feathers per bird was variable and, expressed as a percentage, had a marked positive correlation with the weight of the bird, while the combined weight of rectrices and remiges per bird was very constant (Fig.16).

The water content of Great Tit feathers in Summer was twice as high as in Winter, no doubt because all the Summer birds analysed were in active moult. However, the water content of the feathers of Blue Tits in the Summer, all of which were taken before the moulting period, was not different from that in mid-Winter. The total weight of feathers of Blue Tits during the Summer was 32% lighter than in mid-Winter, the loss being attributed to wear, especially during the breeding season.

Table 12. Weights and calorific values of Great and Blue Tit feathers in Winter and Summer in Durham

Species	GREAT TIT				BLUE TIT	
Time of Year	Winter		Summer		Winter	Summer
Age and Sex	Adult ♂	Adult ♀	Adult ♂	Adult ♀	Adult	Adult
Sample size	4	5	5	1	2	3
Av.body wt.(gms)	20.53	18.63	20.84	20.55	11.23	10.64
Av.wet wt.of down/bird (gms)	1.393	1.163	1.112	1.152	0.958	0.552
" " " " rectrices and remiges/birds (gms)	0.406	0.399	0.362	0.350	0.213	0.189
Av.total wet wt. of feathers/bird (gms)	1.799	1.562	1.474	1.502	1.171	0.741
Av.total dry wt. of feathers/bird (gms)	1.579	1.368	1.073	1.098	0.956	0.612
% water in feathers	12.2	12.4	27.2	26.9	18.4	17.4
Calorific value of feathers K.cal/gm	5.123	5.079	5.384		5.242	
Ash free calorific value K.cal/gm	5.252	5.207	5.486		5.295	
% Ash (in feathers)	2.35	1.75	1.86		0.99	
Av. TOTAL K.cals of feathers/bird	8.088	6.946	5.777	5.788	5.010	3.209

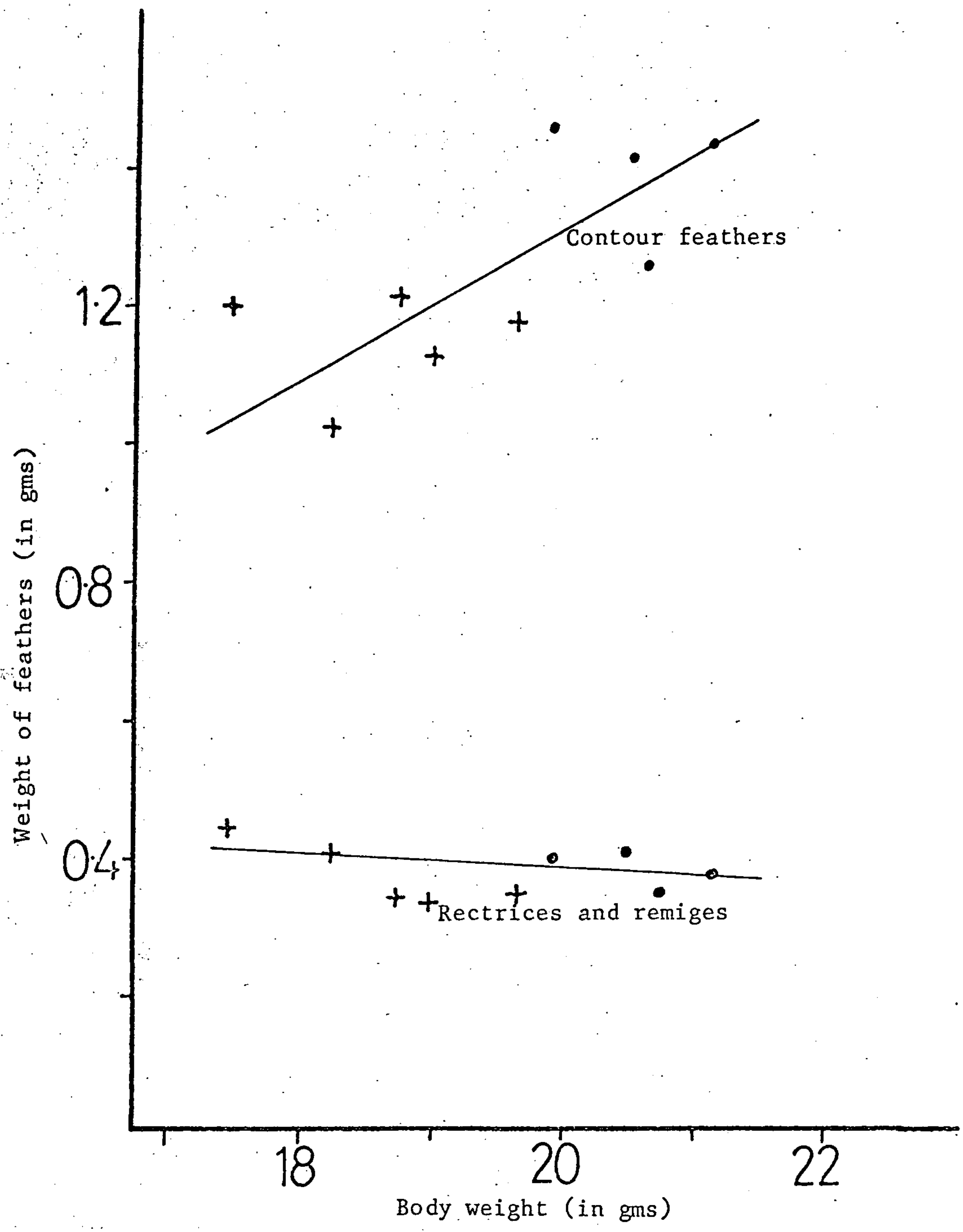


Fig.16. Relationship of body weight to weight of rectrices and remiges, and contour feathers of adult female (+) and adult male (●) Great Tits taken in Durham in January and February 1968.

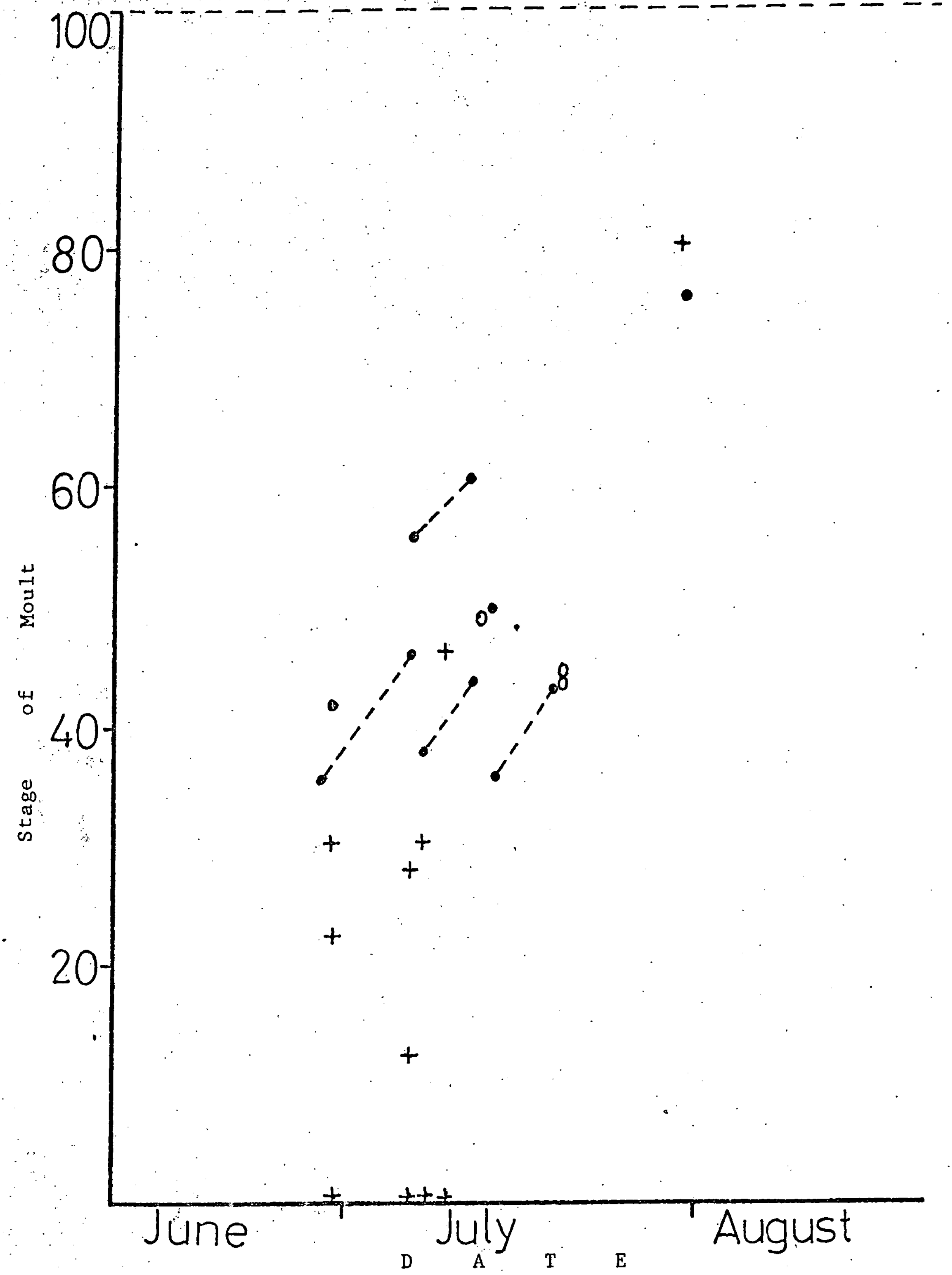


Fig.17. Timing of moult of Great and Blue Tits. Stage of moult of primaries expressed as a percentage of complete moult. (Broken lines join observations on the same bird).

● Adult male Great Tit + Adult Blue Tit

O Adult female Great Tit

4. Moulting Period

It has been found by many authors that the most accurate and least variable way of expressing the stage of moult of a bird is obtained by determining the stage of moult of the primary wing feathers, since the innermost primary is usually the first feather to be moulted, and the outermost the last (Snow 1967).

In this study, the timing and duration of moult was determined by expressing the stage of moult of the primaries as a percentage (100% = Moult completed) and plotting this against date of capture (Fig.17). As with breeding, both Blue and Great Tits appeared to moult synchronously, starting in mid-June and finishing towards the end of August, taking from start to finish an average of six weeks.

5. Daily and seasonal variations of body fat

The amount of ether-extractable lipid, expressed both as grams of lipid per bird (Fig.18) and as a percentage of the total live weight of the bird (Fig.19) was found to have a marked correlation with the fat class of the bird, i.e. the amount of visible subcutaneous fat. The correlation between fat class and amount of lipid appeared to have a steeper slope for Blue Tits than Great Tits (Fig.17) as would be expected from their difference weight. There was no difference in the slope of the correlations of birds taken in mid-Winter than mid-Summer, but for a given fat class the quantity of lipid in the

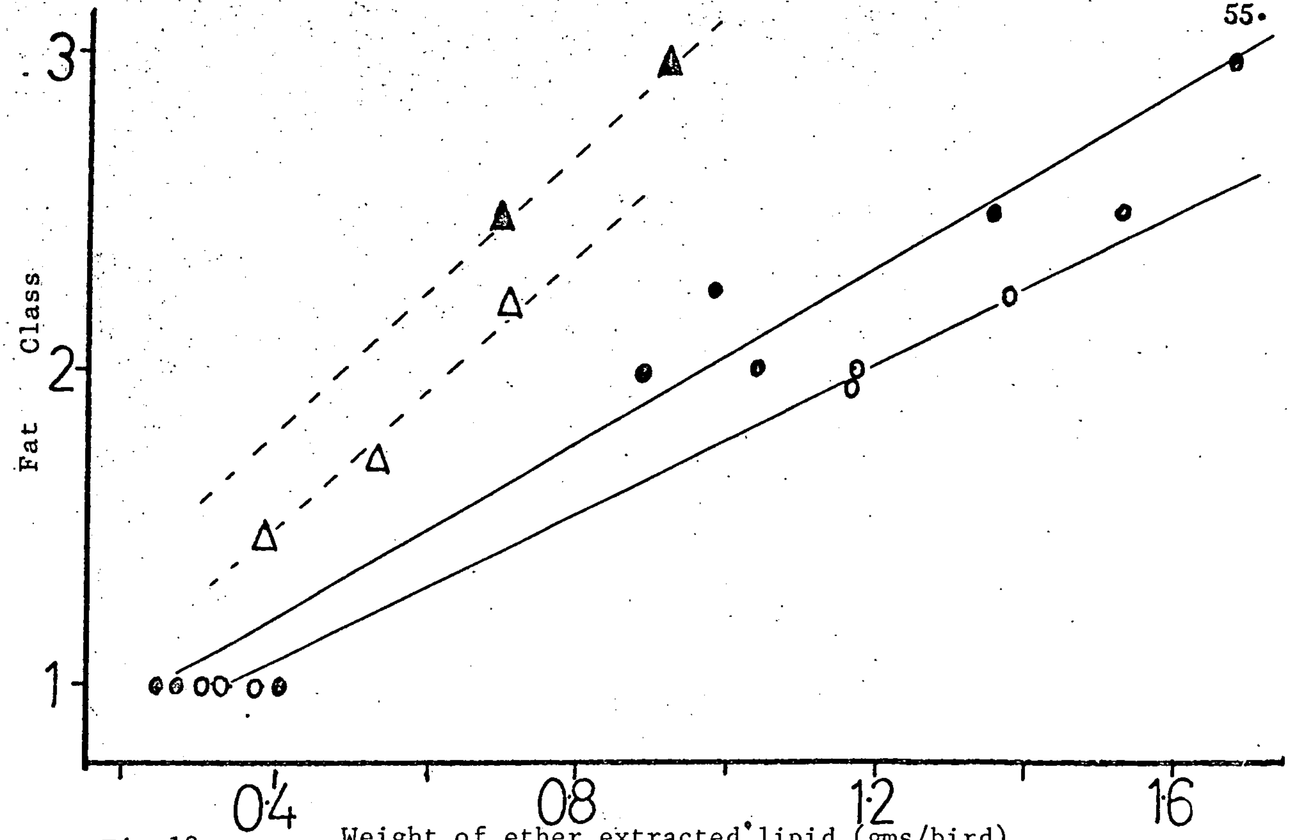


Fig.18.

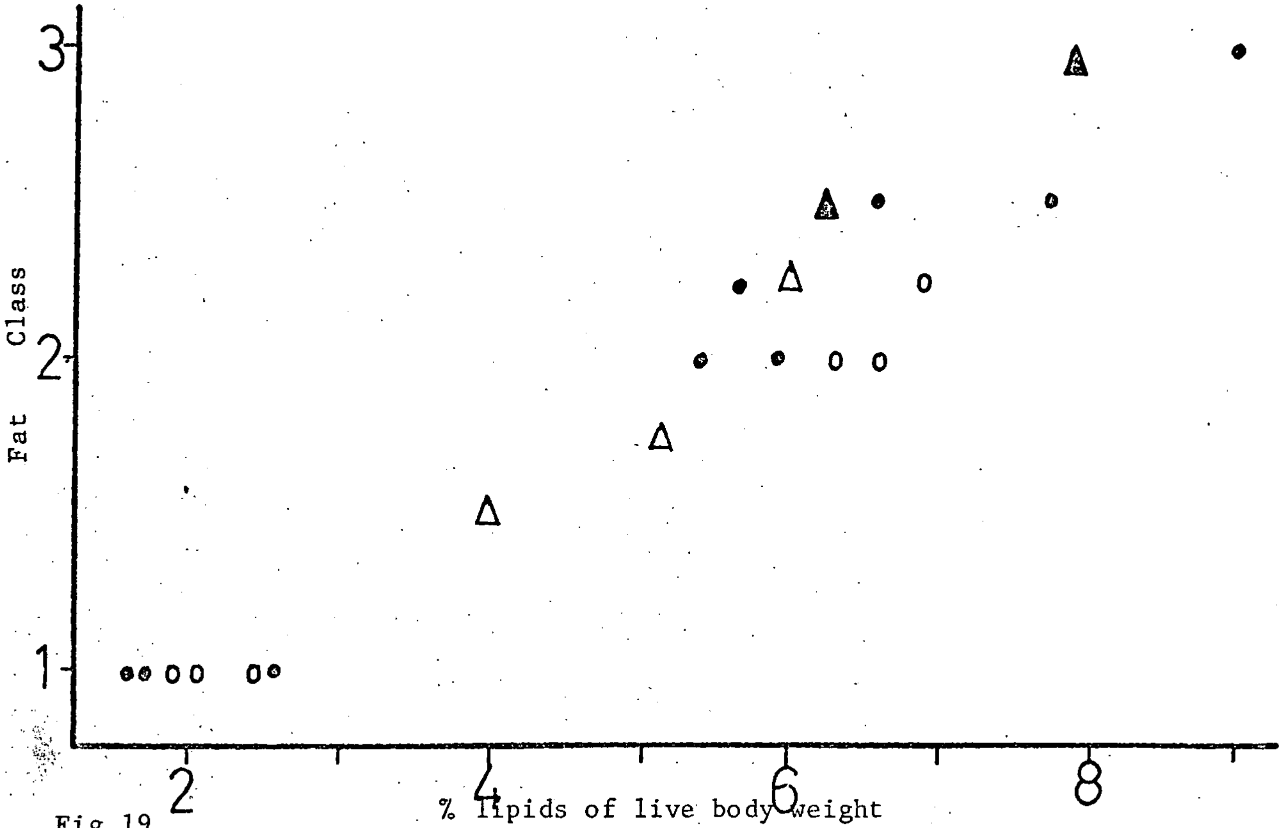


Fig.19.

Figs.18 & 19. Relationship of fat class to weight of ether-extracted lipid and percentage lipids of the live body weight of Great & Blue Tits.

● Great Tits taken in mid-Winter. ▲ Blue Tits taken in mid-Winter.
○ " " " " " Summer. △ " " " " " Summer.

body appeared to be slightly higher in mid-Summer, but the difference was not significant ($P < 0.1$).

From these relationships and the recorded fat classes of all birds caught in the Winter it was possible to determine the average percentage of lipid of Blue and Great Tits for each two-hourly interval of the day (Fig.20). As can be seen, the increase in percentage lipid to some extent reflects the increase in body weight during the day for Blue Tits (adults and first years combined) showing the most rapid increase in lipid deposition occurs in early morning and late afternoon, the rate being noticeably reduced between 11.00 and 13.00hrs G.M.T. Great Tits (adults and first years, males and females combined) showed a similar marked increase in percentage lipid during the morning at a very similar rate to Blue Tits, but levelled off around mid-day and showed a very slight decline in the afternoon, although finally finishing at a very similar level to that of Blue Tits.

Taken in conjunction with the graphs of daily weight increase during the day, Figs. 18 and 20 clearly show that diurnal variations in the weights of small birds are not solely due to the emptying of the digestive tract at night and the filling of it again during the day time. Of an average diurnal weight increase for Blue Tits of 1.35gms during the Winter (Fig.12), approximately 0.28gms (21%) can be attributed to lipid deposition, while for Great Tits 0.20gms (12½%) of the

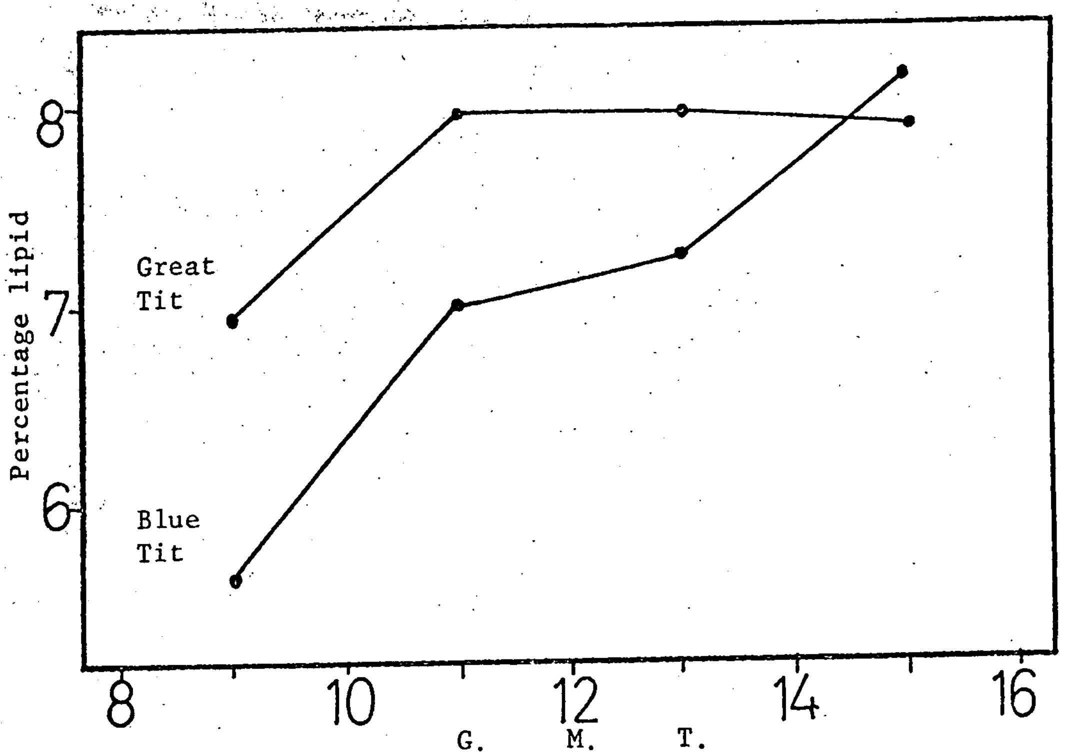


Fig.20. Relationship of percentage lipid of live weight to time of day for Great and Blue Tits in Durham, January - February 1968.

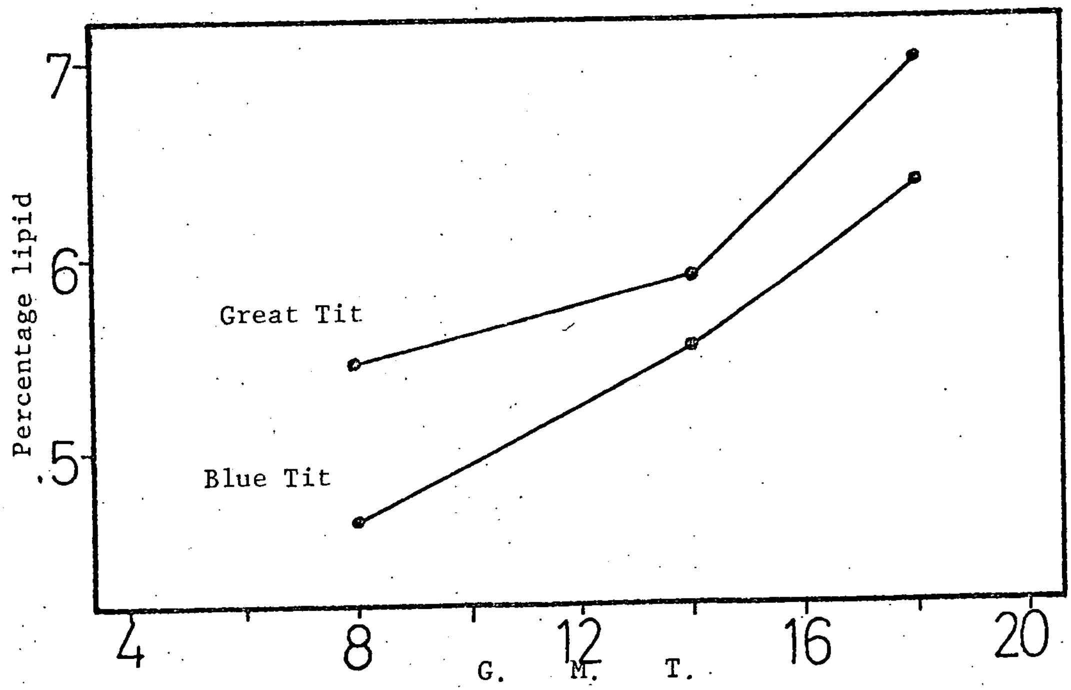


Fig.21. Relationship of percentage lipid of live weight to time of day for Great and Blue Tits in Durham, June - August 1968.

diurnal weight increase of 1.60gms was due to lipid.

These results indicate that the store of lipid in Blue and Great Tits is of the same relative size at dusk, but during cold Winter nights Blue Tits use up approximately 31% of their body lipids, while Great Tits use only 13% of theirs. This indicates that the metabolic rate of Blue Tits is much higher relatively than that of Great Tits as would be expected from their difference in body size.

Of course not all of the ether-extractable lipid in a bird will be available for metabolism, the minimal or starvation level being about 2% of live weight as determined from the experimental Great Tits which died in captivity. (It is significant that G.R. Potts (pers.comm.) has found a similar relative starvation level of body lipid of 2% for Shags (*Phalacrocorax aristotelis*)). Assuming that this minimal level applies both to Great and Blue Tits, Blue Tits used up to 41% of their metabolisable lipid store during Winter nights, while Great Tits used only 17% of theirs. As this was the amount of lipid burnt up in 16 hours, the length of time it would take for birds with the average dusk percentage of lipid (8%) to reach the minimal or starvation level of 2% would be 94 hours or 4 days for Great Tits and 39 hours or 1½ days for Blue Tits. These figures must be of critical importance in determining the mortality rates of the two species during the winter, since it is probable that Blue Tits could not go one full day without food before starving to death, while Great Tits could go 3 - 4 days without food. Blue Tits must therefore be much less secure than Great Tits in severe weather conditions in Winter, and this probably partly accounts for the higher annual adult mortality rates of Blue Tits of 70% (Snow 1956) compared with Great Tits of 50% (Kluijver 1951).

In Fig.21 the percentage body lipid of Blue and Great Tits in Summer against time of day is plotted. Because of the shortage of data the afternoon is divided into two four-hour periods, while the morning was represented as a single period. These again show a marked diurnal increase in percentage lipids, but at a noticeably lower level than in mid-Winter.

6. Calorific content of wild Great and Blue Tits

Mean calorific values of wild Great and Blue Tits taken in Winter are shown in Table 13. From these figures the average standing crop of Great and Blue Tits expressed in terms of Kilocalories per hectare can be calculated. The average population density of Great Tits in the study area throughout the year, taking the mean of the calculated monthly population densities (Fig.8) was 68 birds or 1.43 per hectare, giving an average annual standing crop of 55.97 K.cals/ha. For Blue Tits the average monthly population density was 180 birds or 4.05 per hectare, giving an average annual standing crop of 87.71 K.cals/ha.

Table 13. Calorific Values of Great and Blue Tits in Winter and Summer in Durham.

Species	Time of Year	Age & Sex	N	Av.Wet Wt.(gm)	Av.Dry Wt.(gm)	% Water	Calorific values (K.cal/gm)		% Ash	K.cals/ bird	Av.Fat Class
							Total	Ash-free			
GREAT TIT	WINTER	Adult male	2	20.26	7.793	61.5	5.408	6.049	10.60	42.141	2½
		Adult female	1	18.77	7.562	59.7	5.629	6.238	9.76	42.562	3
	SUMMER	Adult male	2	19.71	6.858	65.2	5.479	6.132	10.64	37.575	2
		Adult female	1	17.92	6.324	64.7	5.438	6.169	11.95	34.392	2
BLUE TIT	WINTER	Adult	2	11.323	4.124	63.6	5.781	6.412	9.84	23.841	2½
	SUMMER	Adult	3	10.639	3.7052	65.2	5.263	5.907	10.91	19.502	2

III. Energy Requirements

1. Weight of Experimental Birds

The body weight of all the birds used in the feeding experiments declined immediately after capture and levelled off at about 1.3gm lower than their original weight. There were no significant differences in the weight of these birds from day to day during the feeding experiments, indicating that all the digested food was being utilised for existence.

2. Calorific Content of Food

The meal worms used for food during the feeding experiments came from a culture maintained in the Department of Zoology, University of Durham. The water content and calorific values for these was determined from samples of 10gms each taken during each feeding experiment (Table 14).

The total calorific value is very similar to that determined by other workers, i.e. 6.6 K.cal/gm by Cummins (1967) and Gibb (1957).

Table 14. Calorific Value of Meal Worms used in the feeding experiments

	Sample size	% Water	Calorific Value (K.cal/gm Total	 Ash-free	% Ash
WINTER	9	62.22	6.599	6.723	1.84
SUMMER	9	64.95	6.708	6.877	2.46

3. Metabolic Rates

The metabolic rates determined for Great Tits during Winter and Summer by feeding trials are summarised in Table 15. It should be noted that all the birds used in the Summer experiment were in heavy moult so that the results obtained cannot be regarded as measuring only existence energy for that time of the year.

The results obtained during the Winter experiment were very similar to those found by Gibb (1957). His studies involved seven individual Great Tits of average weight, 19.4gm, kept in large experimental cages for a total of 45 days (between November 1955 and January 1956) at an average air temperature of 4.4°C, and using various kinds of nuts and seeds for food Gibb found the daily metabolised energy to be 1.015 K.cal/gm.bird/day, and the digestive efficiency to be 80.3%.

As can be seen, the mean daily metabolised energy represents about 50% of the mean calorific content of individual Great Tits.

Table 15. Summary of Winter and Summer feeding experiments on Great Tits in Durham.

	WINTER		SUMMER	
Age and Sex.	Adult Males.	Adult Females	Adult Males	Adult Females
Number of birds	3	3	5	1
Total bird feeding days	18	18	15	3
Average Air Temperature °C.	4.21	4.21	15.35	16.12
Average weight in gms	18.52	16.92	19.06	17.84
GROSS Food Intake (I) K.cal/bird/day)	21.914	20.378	23.806	26.063
FAECES output K.cal/bird/day	3.633	3.343	4.508	5.209
Metabolised Energy (A) (1) K.cal/bird/day	18.281	17.035	19.298	20.854
Metabolised Energy (2) K.cal/gm.bird/day	0.990	1.007	1.012	1.169
Digestive Efficiency A/I %	83.42	83.60	81.06	80.01

4. Calorific Content of Faeces

Bird excrement (faeces) consists of undigested food (including regurgitated pellets of meal worm mandibles etc.), digested but unabsorbed food, plus nitrogenous wastes from the kidneys. Fifty-four calorific tests were run on the faeces (Table 16), three duplicates being made on each sample to check for accuracy. Even allowing for a 1% inaccuracy attributable to

Table 16. Calorific Value of Great Tit faeces

	No. Birds	No. Tests	Av. Temp. (°C)	Calorific Value (K.cal/gm) TOTAL
WINTER	3	18	4.2	3.489
	3	18	4.2	3.523
SUMMER	5	15	15.4	3.608
	1	3	16.1	3.812

the calorimetry (Phillipson 1964), the faeces collected during the Summer had a significantly higher calorific value than those in Winter ($P < 0.01$). This was probably a consequence of the higher level of food intake by moulting birds and their lower digestive efficiency during the Summer.

5. Digestive Efficiency

The efficiency with which food is utilised as energy is affected by the type of food consumed, its protein content, and its balance of essential elements and vitamins (Hamilton 1939). The food which Great Tits consume in the wild (Betts 1955) is largely composed of Lepidoptera larvae and adult Coleoptera, in many respects similar to a diet of meal worms (larvae of the
o/ beetle *Tenebri~~s~~ molitor*) such as those used in these experiments. Therefore it would be expected that the utilisation of the two diets would be similar.

tr

Efficiency of food utilisation has been shown to increase from low to high temperatures (Kendeigh 1949, Siebert 1949, Davis 1955, West 1960), and from long to short photoperiods (Cox 1961), and appears to be related to the speed of movement of food through the digestive tract. At higher temperatures or longer photoperiods a higher efficiency can be maintained as a result of lower feeding rates which allow food to be digested more completely (Cox 1961). However, variation in assimilation efficiencies over a wide range of temperature has been found to be generally less than 10%, often less than 5%, and individual variation may be greater for a particular species at a single temperature, than variation for the species as a whole over a range of temperatures.

During the Winter feeding experiment, the digestive efficiency of male Great Tits was highest (83.9%) during the first period of three days of the experiment (average temperature = 6.6°C) compared with the second period (82.8% at 1.7°C). Female Great Tits however showed even less variation in digestive efficiency during this experiment. The digestive efficiency during the Summer experiment of 8.1% (average temperature 15°C) was therefore lower than expected, but this can be accounted for by the higher food intake at this time of the year associated with moulting.

The digestive efficiency for Great Tits in Winter found by Gibb (1957) of 80.3% was 3% lower than found in this study. This is probably because Gibb was using nuts and seeds as the food which, because they contain cellulose and have a lower water content than meal worms, were probably less easy to digest. However, Gibb did use meal worms in feeding experiments with Blue and Coal Tits and found the digestive efficiencies to be 84.1% and 86.1% respectively (very similar to the results for Great Tits found in the present study) while on a diet of nuts the digestive efficiency of Blue and Coal Tits was 76.8 and 80.8 respectively. Kale (1965) working on the Long Billed Marsh Wren (*Telmatodytes polistris griseus* (Brewster)) found the digestive efficiency of experimental birds fed on a meal worm - wren mixture diet to be 75.9%.

6. Relation of metabolic rate to body weight.

It is well known that an exponential relationship exists between standard energy metabolism * and body weight in organisms, that can be described by the generalised equation :

$\text{Metabolic Rate} = \underline{a}\,(\text{Body Weight})^{\underline{b}}$ where $\underline{a}$ and $\underline{b}$ are empirically derived constants. This equation can be re-written in the more convenient logarithmic form :

$\log \text{Metabolic Rate} = \log \underline{a} + \underline{b} \log \text{Body Weight}$, i.e. a mathematical expression of a straight line.

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* The term standard metabolism is preferred to that of 'basal metabolism which is sometimes used, because it has fewer clinical implications. Standard metabolism is metabolism at rest in the thermo-neutral zone. The thermo-neutral zone is that range of temperature which induces no change in metabolic rate (see Fig.22).

In a recent review of the relation between standard metabolic rates and body weights of birds, Lasiewski and Dawson (1967) showed that passerine birds have a higher weight compensated metabolic rate than non-passerines although the weight-metabolism regression coefficients ('b' values) are virtually identical. Their equations for all Passerine birds is :-

Standard Metabolic Rate = 129 $W.^{0.724}$

(K.cal/bird/day) (weight in Kg) (see Fig.21),

and this equation was used in preference to equations calculated by Brody and Proctor (1932) and King and Farner (1961) using combined passerine and non-passerine data, to calculate the standard metabolic rates of Tits. The calculated standard metabolic rates of Great Tits using this equation is very similar to some direct measurements of 0.451 K.cal/gm bird/day made by Steen (1958) using a respirometer.

In Fig.22, the metabolic rates of active Great Tits determined in this study and for active Great, Blue and Coal Tits determined by Gibb (1957) are compared with their standard metabolic rates. Also plotted is a regression line for all measurements of the metabolic rates of individual birds of these three species of Paridae, determined during Winter feeding experiments (giving a 'b' value of 0.75). It will be seen that the slope of this line is very similar to that for standard metabolic rate. However, the metabolic rates of Great Tits

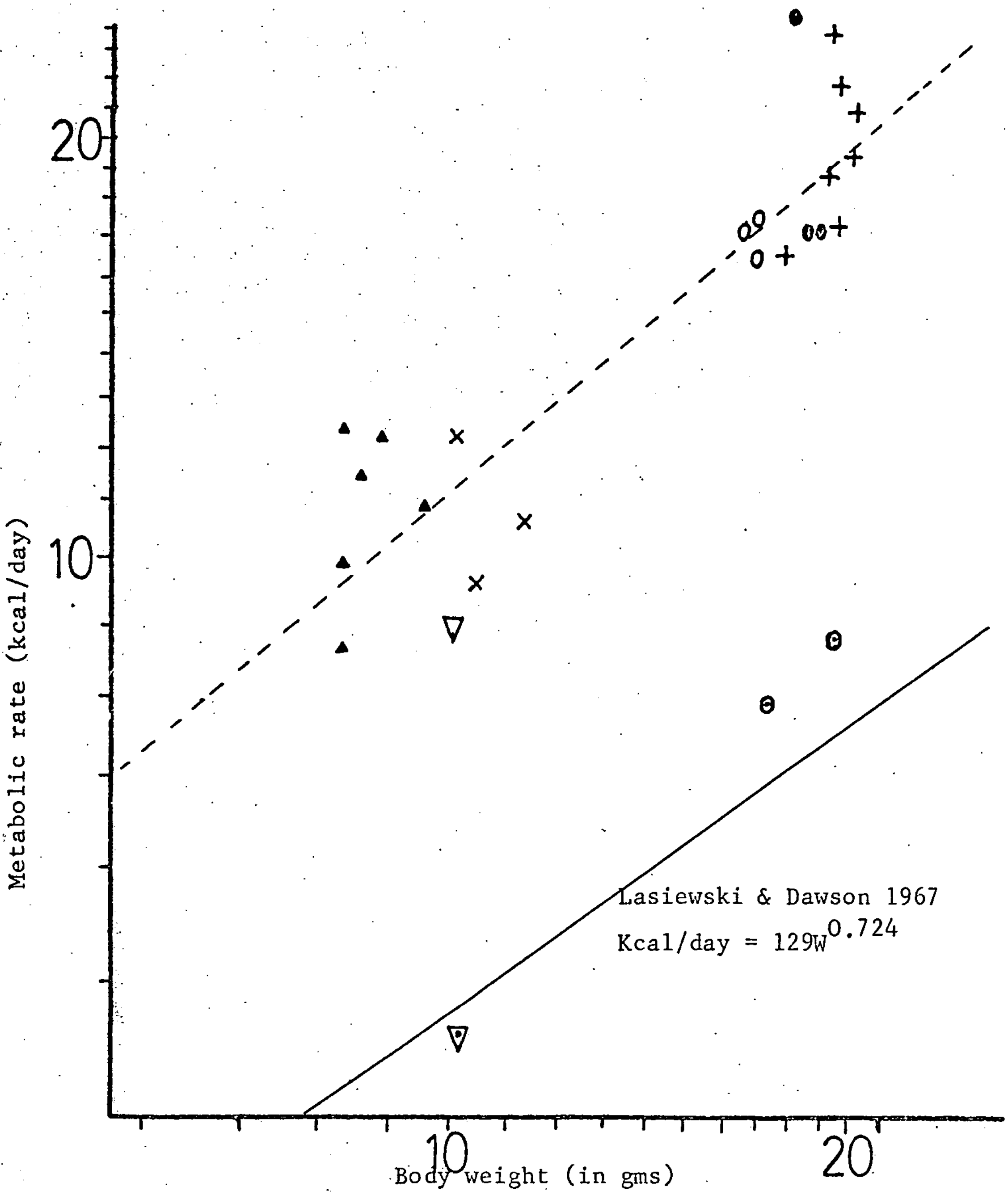

Fig.22. Relationship of metabolic rate of insectivorous passerines to body weight.

Key. ● Male Great Tits, active, Winter (this study).
○ Female " " " " " "
+ Great Tits, " " (Gibb 1957).
× Blue Tits, " " " "
▲ Coal Tits " " " "
⊙ Standard metabolic rate of Great Tits (Steen 1958)
▽ Long-billed Marsh Wrens, active, Summer, Georgia, U.S.A.(Kale 1965)
▽ Standard metabolic rate of Long-billed Marsh Wrens (Kale 1965).

determined by feeding experiments were two and a half times their calculated standard metabolic rates, and this is a measure of the energy used by activities such as feeding and keeping the body temperature at a high but very constant level (c. 40.0°C a/ Udv~~o~~rdy 1953 and 1955) when the ambient temperature of the environment is below that of the lower critical limit of the thermoneutral zone of the bird (av. 25 - 35°C for Passerines), King & Farner (1961).

7. Relation between metabolic rate and ambient temperature

Fig.23 shows the regression analysis between the metabolised energy in K.cal/gm bird/day for each male Great Tit on each day of the Winter and Summer feeding trials and the average daily temperature. The data for female Great Tits was not used as insufficient data was collected during the Summer, but their mean seasonal values are plotted and are very similar but slightly higher than for males (explained by their smaller size) but come within one standard error of the mean values for males indicating no significant difference. The Summer and Winter results were analysed separately because the Great Tits in the Summer experiment were all in heavy moult. In the Winter experiment the average daily temperature ranged from -0.25°C up to 10.75°C, while in the Summer the temperature range was 12.5°C up to 16.75°C. As can be seen, in both the Winter and Summer experiments, more energy was metabolised per

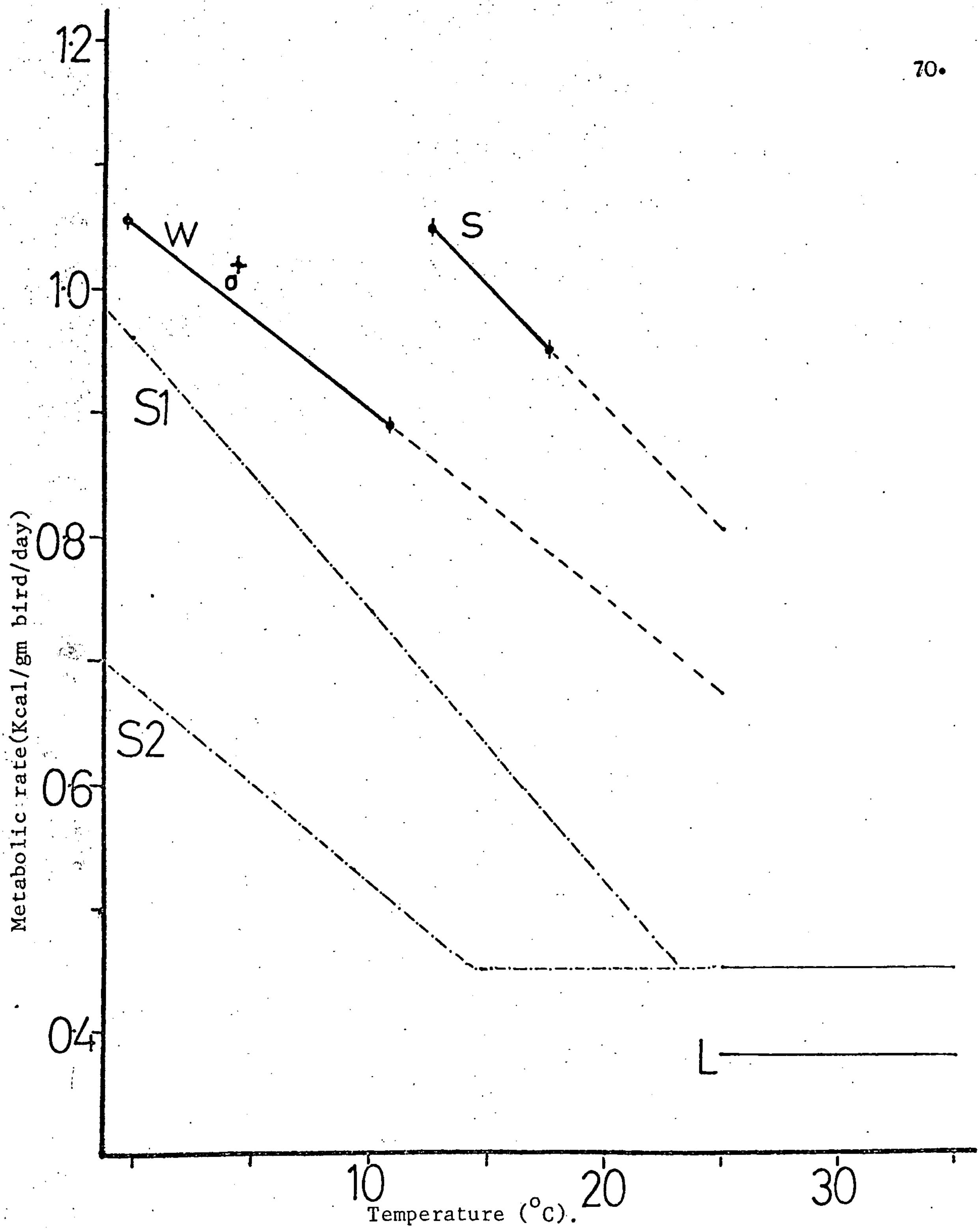

Fig.23. Relationship of metabolic rate of Great Tits and ambient temperature.

W Winter feeding experiment on males (this study)($r=0\cdot66, P<0\cdot05$)
S Summer " " " " " " ($r=0.24, P<0.05$)
o Winter " " " females " "
+ Winter " " (Gibb 1957)
S2 Night metabolism for birds acclimatised to -10°C (Steen 1958).
S1 Day metabolism (Steen 1958).
L Standard metabolism for passerines of similar weight to Great Tits (from Lasiewski & Dawson 1967).

day at low, than at high temperatures. However, the metabolic rate in the Summer experiment was much higher than expected from the Winter results, but this can be explained by the extra amount required by birds undergoing moult. As the moulting period started immediately after the breeding season in July, and lasted until September, it was not possible to run a feeding trial on Summer-adapted birds which were not moulting.

Fig.23 also shows the relationship between metabolic rate and temperature found by Steen (1958) for Great Tits using the indirect calorimetric method of measuring the oxygen consumption of inactive birds in a respirometer. As can be seen, Steen's results both for day-metabolism (Curve S1, Fig.23) and night-metabolism for birds acclimatised to -10°C (Curve S2, Fig.23) are for a given temperature at a considerably lower level than the results of the present study. If the regression lines obtained during both the Winter and Summer experiments are extrapolated to the lower critical limit of the thermoneutral zone, the metabolic rates obtained are 30% higher than the level of standard metabolism. The difference is probably because standard metabolism was measured on inactive birds, and was not a measurement of existence energy of active birds in the thermoneutral zone. Also, during the two experiments, birds were probably not acclimatised exactly to the average daily temperature, but probably to a lower one, but exactly what this was could not be determined, and needs further study. However, Van Balen (1967) found that the weight of Great Tits increased when the ambient temperature fell, as expected, but he obtained the best correlation when he plotted average weight against mean temperature in the preceding ten days.

Kendeigh (1949), Davis (1955), and West (1960), in their detailed studies of the relation between metabolic rate and temperature, obtained much better correlations in feeding experiments performed under various constant temperature conditions, than in controls run under natural fluctuating temperature regimes, although in both metabolic rate increased with decrease in temperature. In the controlled temperature experiments the metabolic rate of active birds at the lower critical limit of their thermoneutral zone was only slightly higher than the calculated standard metabolic rate. They subsequently used the controlled temperature results to predict the annual variation in existence energy, extrapolating values equivalent to the average monthly temperatures. However, it is probable that experiments run under fluctuating temperature conditions give a more realistic result.

While it is appreciated that the data presented is far from adequate to make an accurate interpretation of the seasonal variations in existence energy of Great Tits, it does at least give an indication of it. As Davis (1955) could find no significant difference in the relation of metabolic rate to temperature of Summer and Winter adapted House Sparrows (Passer domesticus) on their respective photoperiods, existence energy was therefore determined for each month for Great Tits from the equation describing the Winter results.

8. Food consumption of wild birds

The ultimate aim of measuring the food consumption of captive birds was the estimation of the food consumption of wild birds. The food consumption of wild birds has generally been considered to be higher than that of captive birds, but there is no precise information on this matter. Kendeigh (1949) assumed that the metabolised energy requirement determined at the lowest air temperature that the bird could withstand in captivity could be attained at higher temperatures when more energy was required for activity. This value was about 60% higher than the energy requirement of captive birds at 15°C. In the case of man, it is considered in the study of energy metabolism that a man at work requires about 30 - 50% more energy than that required at rest (Kleiber 1961). Uramoto (1961), after reviewing most of the previous literature available, tentatively assumed that wild birds would require 30 - 50% more energy than captive ones. Kale (1965), however, decided to add no correction factor to his estimations of metabolic rate, as his birds were very active in their cages.

Recently a number of papers have been published which give a fairly precise measurement of the metabolic rates of birds during flight. Le Febvre (1964), using a doubly-labelled water (D_2O^{18}) technique as well as measurements of fat loss, estimated that homing pigeons (Columba livia), weighing 384gm, metabolised 57 cal/gm/hour during a 500 Km cross-country flight. This figure is 13.4 times the standard metabolic rate calculated from Lasiewski and Dawson (1967) and eight times the resting metabolic rate. Tucker (1968), measuring oxygen consumption of budgerigars (Melopsittacus undulatus) (weighing 35gm) during level flight in a wind tunnel, found the metabolic rate was lowest at a flight speed of 35 Km/hour, with a mean value of 105 cal/g/hour or 12.8 times the calculated standard value. However, as both these birds were non-passerines, it was not possible to make a direct comparison with Great Tits, since their basal metabolic rate is approximately 66.7% higher than non-passerines of the same weight (Lasiewski and Dawson 1967).

To investigate the extra energy required for flight, a feeding experiment was carried out in which one male Great Tit was permitted to fly around in the field station building for a period of time equivalent to that estimated for wild birds for that time of year. The experiment lasted 3 days and followed immediately after the bird's 'resting' metabolic rate had been determined in mid-Summer.

The time that wild birds spend flying was taken from measurements of activity by Gibb (1954) from repeated standard observations. During the Winter the percentage of day time spent flying was approximately 10%, while in the Summer it was approximately 5%, or 45 minutes per day at each season (taking the Winter photoperiod as 8 hours and the Summer photoperiod as 16 hours). Therefore, in this feeding experiment, the Great Tit was allowed to fly for a total of 45 minutes per day, which were made up of short 15 to 30 second flights timed on a stop watch. During each day the bird was flown for 3 periods of about one hour, at mid-morning, mid-day and mid-afternoon, during which time it was allowed to fly for a total of 15 minutes, and then put back in its cage. Food consumption was measured by methods previously described, and the metabolised energy obtained from the digestive efficiency determined during the previous 3-day feeding experiment (Table 17). As can be seen, contrary to expectations, there was very little difference between the metabolised energy of when it was allowed to fly than when at "rest". Therefore it was thought not necessary at this stage to add any correction factor to the existence energy determined directly for caged birds, all of which were restless and fairly active.

From the results, an indication of the cost of flight of a Great Tit, expressed as a percentage of the "resting" metabolic rate, can be determined using the following equation :-

$$\frac{(0.931 - 0.912)\left(\frac{60 \text{ x } 24}{45}\right) + 0.912}{0.912} \text{ x } 100 = \underline{\underline{170\%}}$$

Therefore the cost of flight of Great Tits is approximately double the resting metabolic rate and five times basal metabolism.

Table 17.

Activity	No. of days	Av.Wt. of bird (gm)	Av.Gross Food Intake Kcal/bird/day	Digestive Efficiency	Metabolised energy Kcal/bird/day	Metabolised energy Kcal/gm bird/day
Non-Flying	3	19.75	21.939	81.2%	17.815	0.912
Flying (45")	3	19.20	22.093	-	17.932	0.931

This figure is comparable to those obtained for non-passerines, as their basal metabolic rate is 61% lower than for passerines. However, before any really definite conclusions can be drawn, much more work in this field is needed.

9. Energy requirements for fat deposition

It was found that Great Tits in Winter had an average of 40% more stored lipid in the body than in the Summer (or an extra 2.25% live weight (i.e. 0.4gm) of lipid (see Figs. 19 and 20). This is probably initially laid down in October or November when the ambient temperature falls and lasts until March or April. As the calorific value of lipid is 9.0 Kcal per gram therefore this initial accumulation of lipid = 0.4 x 9 = 3.6 Kcals or an average rate of 0.06 Kcals per day. The cost of depositing one Kcal of lipid is 1.67 beyond existence (Connell 1959), therefore the extra burden during October and November will be 0.16 Kcals/day. During the

Winter months it was shown (see Fig.19) that Great Tits deposit approximately 0.2gm of lipid per day (i.e. 1.8 Kcal of lipid/day) to be metabolised the following night and the total cost of depositing this lipid would therefore be 4.8 Kcals/day. In mid-Winter it was found that Great Tits metabolise c19.5 Kcal per day. Therefore 25% of this (4.8 Kcals) goes towards the total daily cost of depositing the lipid which is metabolised during the night.

10. Energy requirements for moult

As can be seen from Fig.22, Great Tits metabolised approximately 0.2 Kcal/gm bird/day (or $3\frac{1}{2}$ Kcal/bird/day) in excess of the predicted existence requirements during moult. As moulting takes approximately 42 days and it has been shown (Table 12) that the average calorific content of the feathers per bird in Winter was 8.0 Kcal, the net growth efficiency* of feathers =

$$\frac{8.0}{3.5 \times 42} \times 100 = \underline{\underline{5.4\%}}$$

This is much lower than most published net growth efficiencies (which vary from 5 to 60%, Phillipson (1966)), but it does not take into account the loss of insulative properties of the feathers during the moulting period (the weight of the feathers is 40% lower), or the synthesis of sheaths of developing feathers

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* Net growth efficiency = $\frac{\text{calories of growth}}{\text{calories assimilated}}$

which are lost when the new feathers are fully-grown. If the growth efficiency of feathers was corrected for these, it could well be greater than the calculated value.

11. Energy requirements for breeding

The energy requirements for reproductive activities in the Spring 1968 were estimated from egg production, incubation, and the extra activity recorded for adults during the nestling period. The average calorific content of Great Tits' eggs was 1.60 Kcals (see Table 9), and the average clutch size was 8.2 (see Table 5). Assuming a net growth efficiency for egg production by the female of 25% (Brody 1945), the increased burden on the female during May =

$$8.2 \times 1.60 \times \frac{100}{25} = 52.48 \text{ Kcals or}$$

3.50 Kcals/day during the first two weeks of May.

The energy requirements of incubation were calculated following West (1960). The average temperature of eggs during the day is 33.8°C for most passerines (Higgins 1941). The average body temperature of birds during the breeding season is 41.3°C (Baldwin and Kendeigh 1932). Therefore there is a 7.5°C average difference between eggs and birds throughout the day. Van't Hoffs law for biological functions states that the rate of a function decreases two or three times with a decrease of 10°C body temperature, Q_{10} (Heibrunn 1943). Assuming a decrease of 2.5 times per 10°C for Great Tits, the decrease would be 2.0 times for the 7.5°C difference between egg and body temperature.

Assuming that the energy necessary to maintain one gram of egg at incubation temperature is equal to maintaining one gram of bird at the same body temperature, the following equation applies :-

$$\frac{\frac{\text{Existence energy}}{\text{Bird wt. (gms)}}\text{ (Kcal/bird/day} \times \text{Total wt. of eggs (gms)}}{Q_{10}} = \text{Energy required for incubation (Kcal/day)}$$

In May female Great Tits, who do all of the incubating (Gibb 1950), require approximately 17.85 Kcal/bird/day for existence, average weight being 19.72 gms. Eggs weighed 1.72gm each and the average clutch size was 8.2.

Therefore :

$$\frac{\frac{17.85}{19.72} \times 8.2\ (1.72)}{2.0} = 6.396 \text{ Kcal/day}$$

As incubation lasts 14 days during the second half of May, the extra burden during May would be 6.396 x 14 = 89.544 Kcals.

If it is assumed that the burden of incubation is shared between the pair, for while the female Great Tit does all the incubating, the male feeds her on the nest, the added increment during the last two weeks of May is

$$\frac{6.396}{2} = 3.196 \text{ Kcal/day}$$

During the nestling and early fledging period in Durham it was found by repeated standard observations of activity that the percentage of time parent Great Tits spend flying was about 18.20% or approximately three and a half hours of the day.

As it has been shown that the metabolic rate of flight was approximately twice that determined for caged Great Tits, the energy spent on existence and bringing food for the nestlings in June can be calculated from the average existence energy at that time of the year.

$$\frac{17.1 \times 20\frac{1}{2}}{24} + \frac{17.1 \times 2 \times 3\frac{1}{2}}{24} = 19.60 \text{ Kcal/bird/day}$$

12. Total Expenditure of energy through the year

By adding values of reproduction and moult to the average monthly existence requirements, the total energy requirements for individual Great Tits can be plotted through the year. Fig.24 shows the average energy expenditure for males and females combined. The energy requirements for fat deposition are not shown as they were an intrinsic part of the daily measurements of existence energy.

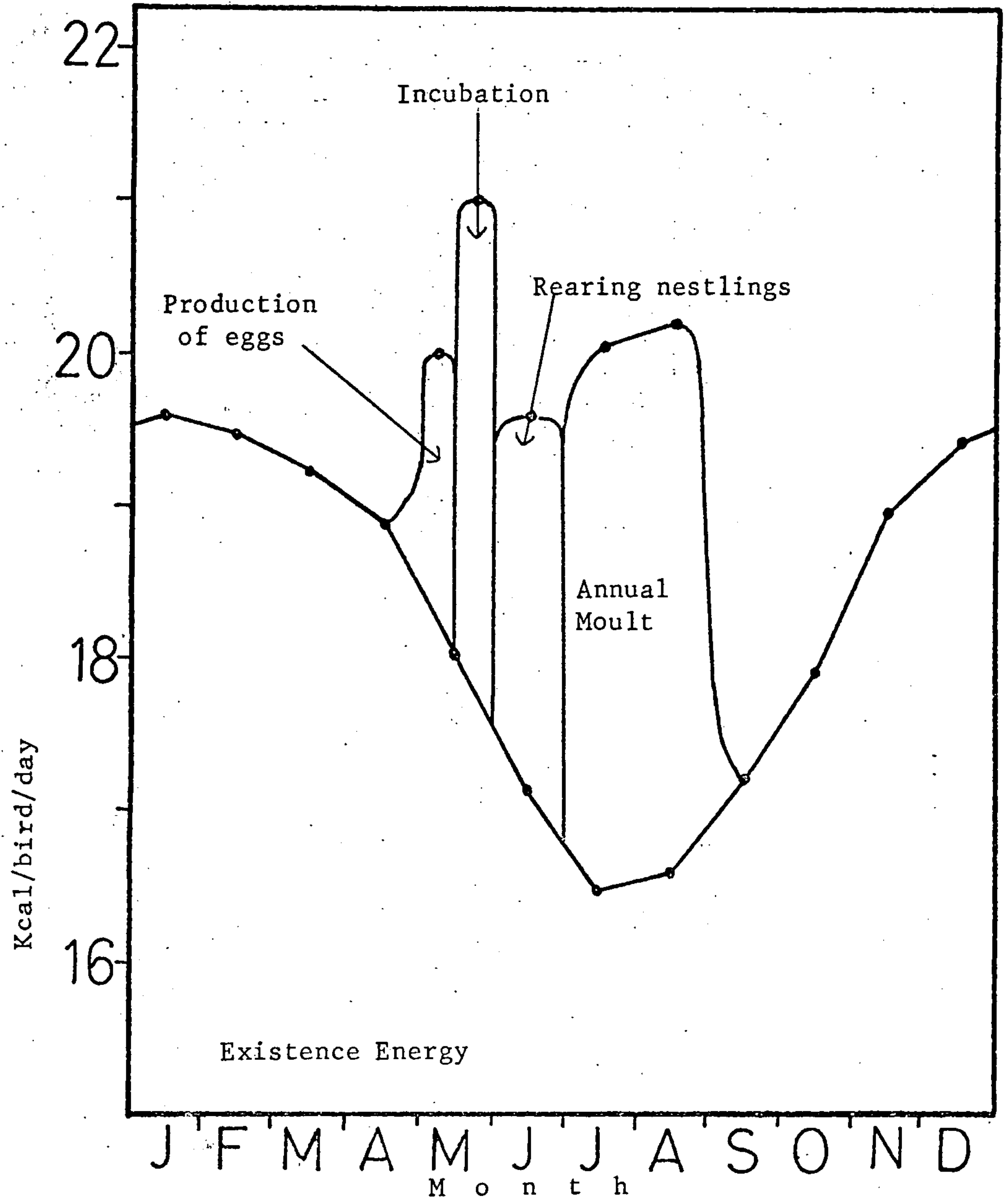

Fig.24. Total energy requirements of Great Tit's throughout the year. The lowest curve is that of existence energy to which the energy required by various activities has been added.

DISCUSSION

1. Population energy flow

The amount of energy metabolised by the population of Great Tits in the study area per month was determined from the preceding data (summarised in Figs. 8 and 24), and expressed in terms of Kcals/ha/month (Fig.25). Adult and juvenile existence (assuming juveniles metabolise the same amount of energy per day per month as soon as they leave the nest) was determined using the following formula :-

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$$\text{Kcal/bird/day/month}\ 30(\text{days})\ \text{x}\ \frac{\text{Population density/month in study area}}{\text{Total area (ha)}}$$

Increments for breeding and moulting were determined by using similar formulae (taking the average incubation period as the last two weeks in May and the nestling period as the first twenty days in June, see Fig.5).

The amount of food metabolised by nestlings was taken from Royama (1966) who found each nestling eats on average a total of 11.70gms (dry weight) of food for the whole of its period in the nest. As the calorific value of the food was 5.82 Kcal/gm dry weight (Gibb 1957), the total energy consumed by nestlings during June was :-

$$11.70 \times 5.82 \times \frac{\text{No.of nestlings in study area}\ \overset{(120)}{}}{\text{Total area (ha) (44.5)}} = 183.6\ \text{Kcal/ha}$$

The sum of the monthly averages gives an approximate figure for population metabolism of 9729. Kcals/ha/year, or 0.9729 Kcals/m^2/year. This is also a measure of the gross

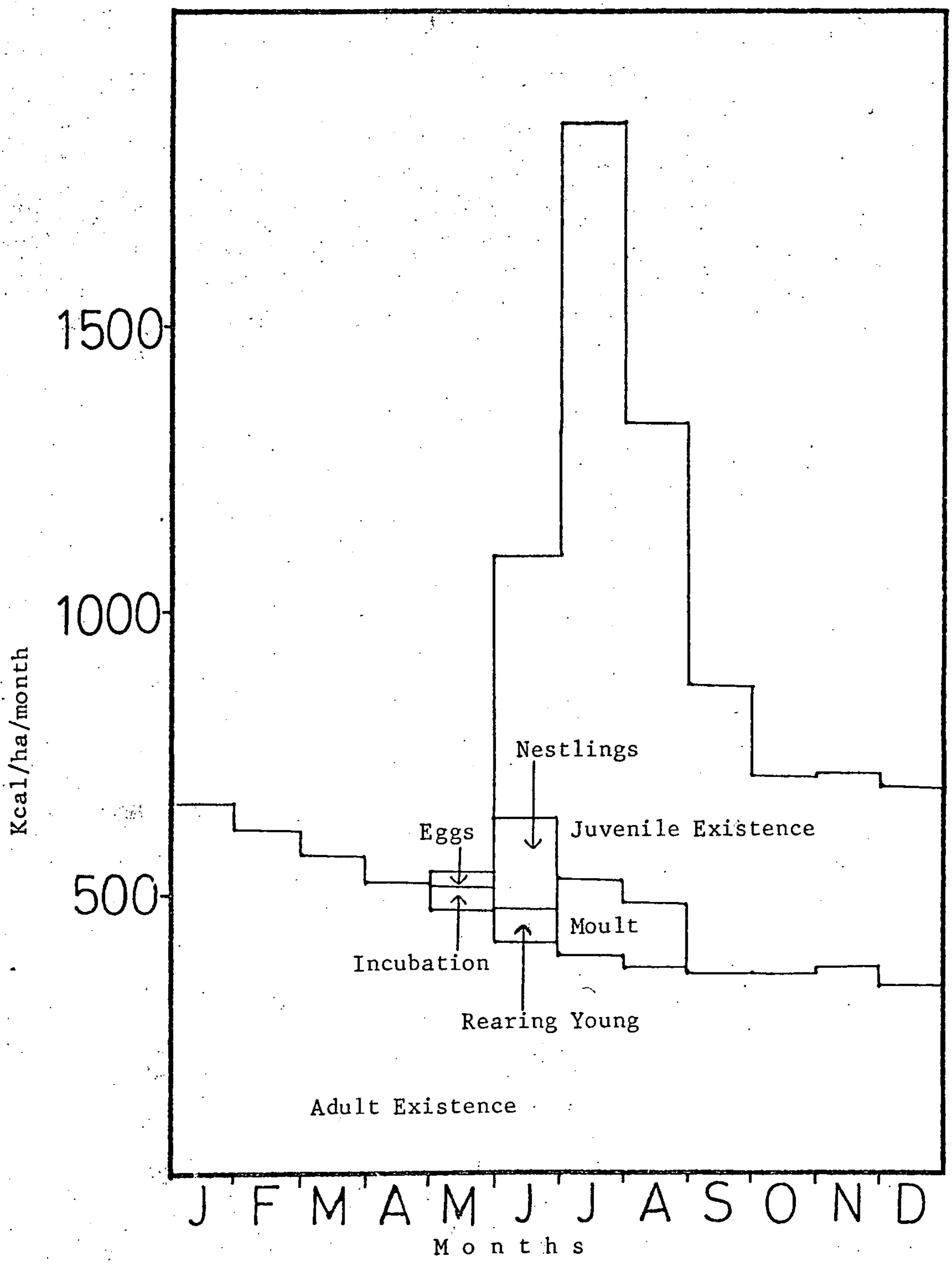

Fig.25. Estimation of the total energy metabolised by the Great Tit population in the study area during each month of the year.

productivity, defined as the total number of calories expended by the population in maintenance, i.e. respiration, plus the calories represented by numbers produced and increase in population weight or biomass (Englemann 1966). As the average digestive efficiency throughout the year was 82%, the total energy consumed was 1.1865 Kcals/m^2/year.

From the preceding data the net productivity of the population can also be calculated. Net productivity is defined as the number of calories represented by the new individuals and the increase in weight of the population per unit of time. If (Fig.8) is a true representation of the seasonal fluctuations in population density in the study area, the net productivity would be 120 birds plus the energy lost in moulted feathers by 35 adults in July and August and that lost through the 30 eggs which failed to produce free-flying young. As the average calorific value of individual Great Tits in Summer was 35.98 Kcals, that of moulted feathers 8Kcals and eggs 1.6 Kcals, the net productivity would be :-

$$\frac{120 \times 35.98 + 35 \times 8 + 30 \times 1.6}{44.5} = 104.2 \text{ Kcals/ha/year}$$

or 0.0104 Kcals/m^2/year.

From this the gross ecological efficiency of the Great Tit population can be calculated. Gross ecological efficiency is here defined as $\frac{\text{total yield}}{\text{total consumption}}$ (= Net production), the total yield including here production that goes to all other trophic levels (i.e. including decomposers). Therefore, Gross ecological efficiency $= \frac{0.0104}{1.1865} \times 100 = 0.88\%$

Net ecological efficiency, defined here as $\frac{\text{total yield (=Net production)}}{\text{total assimilation}}$

for the Great Tit population, can also be calculated: -

Net ecological efficiency $= \frac{0.0104}{0.9729} \times 100 = 1.07\%$

These figures compare favourably with those calculated from Kales results (1965) for Long-billed Marsh Wrens in Georgia salt marshes of 0.40% and 0.52% for gross and net ecological efficiencies respectively.

However, Slobodkin (1959) found the maximum gross ecological efficiency of Daphnia pulex populations to be 13%, and other workers studying invertebrates give values of the order of 10% (Phillipson 1966). Therefore, bird population may be considered more wasteful of energy (in the sense that they are less efficient producers) than invertebrate populations, and the explanation must be because of their different modes of life. Great Tits are homiotherms and are adapted to be very active, moving from one small source of food to another, and maintaining a very high metabolic rate, especially in Winter, when all invertebrates, being poikilotherms, are usually inactive, if not hibernating in a state of torpor.

The relationship between maintenance metabolism and net productivity of Great Tits is shown in Fig.26, and compared with the correlations found by Englemann (1966) for the same relationship for all the available data on both homiotherms

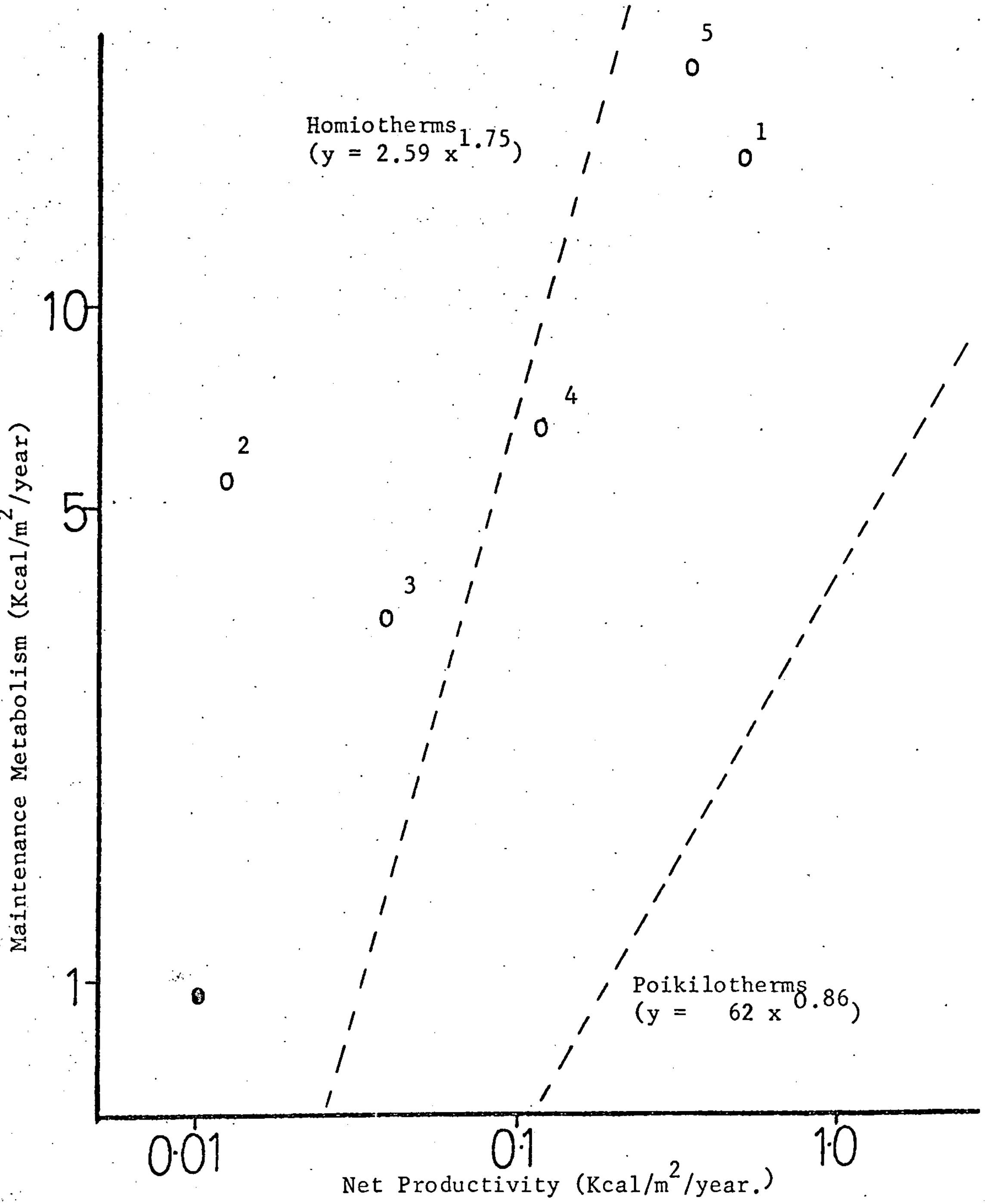

Fig.26. Relationship of maintenance metabolism to net productivity of Great Tits (●) in study area compared with Englemann's regressions (1966) for homiotherms and poikilotherms.

1. *Microtus agrestis*, Old Field, (Golley 1960).
2. *Mustella mustella*, " " " "
3. *Passerculus sandwichensis*, Old Field, (Odum, Connel & Davenport 1962).
4. *Peromyscus polionotus*, " " "
5. *Loxodonta africana*, Savannah, (Petrides & Swank 1965).

and poikilotherms. It seems probable that Englemann's regression for homiotherms is not entirely correct, partly because of the position of the Great Tits found in this study, and partly because he miscalculated the position of Passerculus from Connell's results (in Odum, Connel and Davenport 1960). In any case the figures for net annual production and annual maintenance metabolism for Passerculus are very tenuous, since they were only measured from birds wintering in old fields in Georgia, production simply being estimated from premigratory fat deposition. From Fig.26 it is suggested that the regression line for homiotherms parallels rather than diverges from that for poikilotherms, but at a considerably higher level of maintenance metabolism for a given net production.

2. Trophic position of the Great Tit

Betts (1955) described qualitatively and quantitatively the diet of Great and Blue Tits in each month of the year from the stomach contents of birds killed in the Forest of Dean. Re-classifying the food into four major trophic levels (vegetation, herbivores, carnivores and decomposers) and weighting the figures according to the calculated food intake in each month (Figs. 7 and 8), the annual diet of Great and Blue Tits is as follows :-

	GREAT TIT	BLUE TIT
Herbivores	81% (mainly Weevils, lepidopter-larvae, Hymenoptera imagoes)	84% (mainly Scale Insects, small larval and pupal forms)
Vegetation	10% (Beechmast)	10% (Oak galls and buds)
Carnivores	9% (Spiders)	6% (Spiders)
Decomposers	½%	½%

As there was no evidence to the contrary, this is probably similar to the diet of the Tits in the study area. From this and the preceding data an energy flow diagram for Great Tits can be constructed (Fig.27).

This can be compared with figures of productivity of temperate deciduous woodlands given by Muller et al (in press) for Beech woods in Denmark. The standing crop was 6200 Kcals/m^2/year, and the gross primary production 9400 Kcals/m^2/year of which 4000 Kcals/m^2/year are used in respiration and 5400 Kcal/m^2/year in net production. Of the net production an estimated 3800 Kcals/m^2/year was consumed by herbivores while 1600 Kcals/m^2/year went into the decomposer food chain. M. Hughes (pers.comm.) has found a similar figure for net production for deciduous woodlands in Co. Durham.

Since gross ecological efficiency is a measure of energy transfer from one trophic level to the next, and assuming it to be 10% for most herbivores (Phillipson 1966), a generalised tropho-dynamic model for woodlands can be calculated, with herbivores having a gross production of $\frac{3800}{3}$ Kcal/m^2/year*, and a net production

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* (assuming a digestive efficiency for invertebrate herbivores of 33% (Odum 1959))

of 127 Kcals/m^2/year. Great Tits therefore consume

$$\frac{0.9611}{127} \times 100 = 0.75\%$$

of the net production of herbivores in the woodland. This figure may appear insignificant, but it must be realised that only a small proportion of the herbivores present in a woodland are available to Great Tits. It may, however, be compared with other estimates made for food consumption by Tits in the literature. Betts (1955), who measured the caterpillar population during the breeding season, estimated that in different years and in different habitats Tits (of four species - Great Tit, Blue Tit, Coal Tit (*Parus ater*) and Marsh Tit (*P. palustris*)) took between 0.9 and 4.8% of the caterpillars.

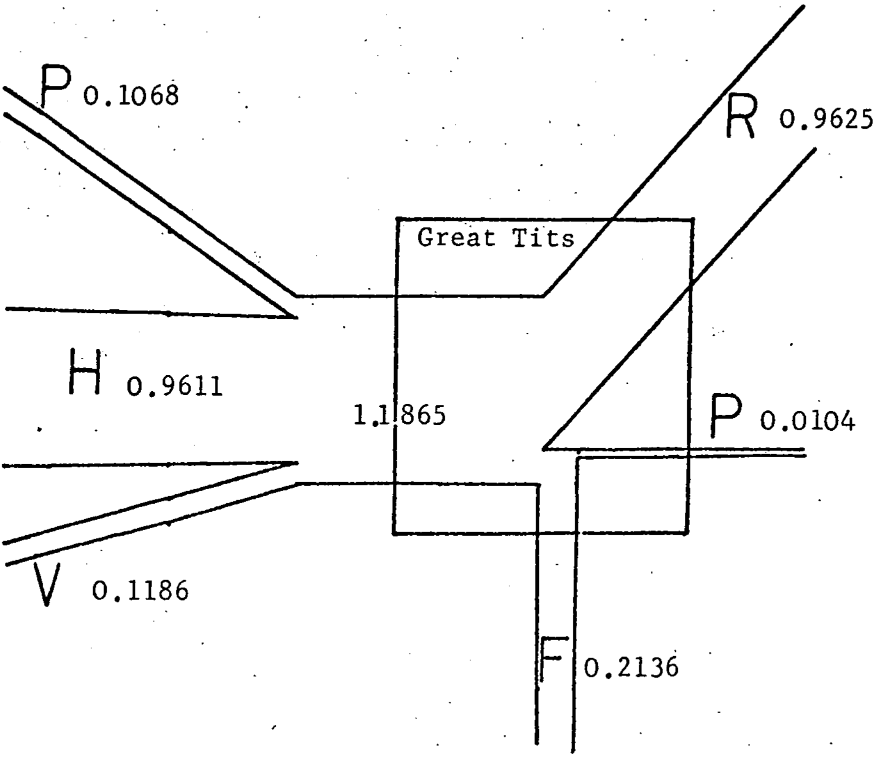

Fig.27. Energy flow diagram for the Great Tit population in the woodland study area (P = predators, H = herbivores, V = vegetation (beech mast), R = respiration, P = production, F = faeces). All figures expressed as Kcal/m^2/year.

3. Factors limiting population density

Many authors have commented on the fact that populations of birds are relatively stable from year to year (Lack 1954, Wynne-Edwards 1962). In this study, while the seasonal population fluctuations of Great Tits, from which the monthly energy flow diagram (Fig.25) was estimated, was calculated assuming a high degree of stability, it does give an impression of average seasonal trends and so highlights the most important periods of the year when population limiting mechanisms are operating. Many authors have tried to understand population stability by studying the causes of annual changes that occur in small natural populations which appear to oscillate around a stable mean. In this discussion, as well as citing the conclusions of this approach, a broader analysis from the energetic and trophodynamic viewpoint is attempted.

The basic problem in population ecology theory at the present time is whether the size of the natural populations of a species is limited by available energy or whether the density is kept below the energy "carrying capacity" by physical factors (weather etc.), intra - or interspecific competition, predation, disease, or other limiting factors not directly limited to energy flow. If energy is limiting, the intra - and interspecific competition for food should be density-governing and provide the major mechanism for population control. If other limiting factors control population size, then density governing competition may be of less importance.

Hairston, Smith and Slobodkin (1960) deduced that populations in different trophic levels differ in their methods of control. Populations of producers and decomposers are limited by their respective resources in classical density-governing fashion, because all the energy that is fixed by plants must be metabolised (except in peat bogs) or else fossil fuel would accumulate rapidly, and therefore all organisms, especially decomposers, must be limited by the amount of energy fixed. Herbivores are seldom food limited, appear most often to be predator-limited, and therefore are not likely to compete for the same resources, because in the wild there is very rarely an obvious depletion of green plants by herbivores, but there are temporary exceptions (e.g. plagues and the effect of predator removal). Carnivores probably control herbivore populations and are therefore limited by their own resources and therefore must be food limited. Populations of some carnivores are limited by territoriality, but this internal check cannot work for all, or else herbivores would expand to deplete the vegetation. Subsequently, interspecific competition must necessarily exist among the carnivores, as well as the producer and decomposer trophic levels. That herbivores are not necessarily food-limited is well illustrated by studies on closely related species of fat-eating mouse birds (<u>Colius colius</u>, <u>C.striatus</u>, <u>C.indicus</u>) in southern Africa (Rowan1967), in which no sign of competition could be detected, and even under the most adverse climatic conditions, the southern mouse birds never suffered any serious food crises.

From this one would expect that Great Tits, being primarily insectivorous, are probably limited ultimately by the available energy, but the many studies carried out on the species indicate that this is an inadequate simplication of the situation. Great Tits have only been studied intensively in the northern temperate zone which are subject to considerable seasonal changes in environmental conditions. They are also a component of the complex, although doubtless very stable (Odum 1959) climax woodland ecosystem. In addition, Great Tits take some of their food from the primary producer and carnivore trophic levels and are more accurately described as omnivores than carnivores.

It has been found that there are no significant seasonal variations in mortality rates of adult Great Tits in Holland (Kluijver 1951) except in severe Winters, while in England, even after the very severe Winter 1962/63 there was very little change in the Great Tit breeding population (Bailey 1967, Lack 1966). Therefore, weather cannot be regarded as a major density governing factor, but it probably has an important modifying influence. However, it is always possible for severe weather to be a major factor if intra - or interspecific competition is involved, as could occur if there was a shortage of adequate shelter, e.g. holes or cracks in trees etc. It is interesting in this respect that a large proportion of Great Tits in Velue, Holland, roost in nest boxes during the Winter (Kluijver 1957), while very few Great Tits in Marley Wood, Oxford (C.M.Perrins, pers.comm.), or in the Durham study area, do so, possibly reflecting the greater severity of Winters on the continent of Europe.

Great Tits are very territorial during the breeding season (Gibb 1956) and have a relatively large clutch size which is probably an adaptation to high adult and juvenile mortality rates. The clutch size is probably related to the number of young that can be reared (Lack 1947-48), but not necessarily to the food supply available for nestlings. From energetic considerations, the controlling factors in the Great Tit should include the size and number of eggs the female can incubate, and less importantly the number of eggs that can be synthesised (see Figs. 24 and 25), variations being caused by the different physical capacities of birds to keep them warm.

In mid-Summer the populations of insectivorous birds in woodlands increases considerably with the appearance of young, not only of resident birds like Tits (see Fig.25), but also of Summer migrants like Warblers. That this population can exert a considerable pressure on their food supply has been shown by several authors. For instance, Brian and Brian (1957) found that bird predation may effect a reduction of 75% of defoliating caterpillars. Also, Bruns (1960) found insectivorous birds may remove a substantial proportion of the insect population of forests, especially when it is low, and proposed that birds be conserved and protected for economic reasons of pest control.

In summarising the population data for Great Tits in Marley Wood, Oxford, Lack (1966) concluded that the annual fluctuations

> "were due primarily to corresponding variations in the juvenile mortality before the winter, most of which probably occurred in the first one to three weeks after the young left the nest. Circumstantial evidence suggests that the marked annual variations in this mortality were correlated with the availability of food soon after the young left the nest. Yet there was a strong correlation with the beech-mast crop, for reasons not understood, since Great Tits .... feed on beech-mast only when it is ripe, and hence after the critical period of juvenile mortality."

Gibb (1950), after a five year study of Tits in pine plantations, found the density of birds in Winter was closely related to their stock of food. However, Perrins (1961), in assessing the changes in the population of Great Tits in Marley Wood between Autumn and the breeding season, found no density dependence in the figures.

Lack (1966) also concluded

> "the average number of fledged young produced per pair varied inversely with population density, but probably had no influence in population regulation as this variation was swamped by much greater variations in juvenile mortality after the young fledged".

Kluijver (1951) similarly found an inverse relationship between clutch size and population density, the reason for which was most probably

> "that the more frequent meetings with other Great Tits and the resultant quarrels may have a direct unfavourable influence on fecundity in the densely populated habitats."

However, concerning the disappearance of juveniles from the population in the Dutch study area, Kluijver (1951) concluded :

> "It would appear that the percentage of young which emigrate is higher in years when the Summer population is higher. The stimulus for this emigration seems not to be direct shortage of food, but rather an innate mutual intolerance of other individuals .... The older individuals, which hold the most suitable habitats in Autumn, drive the young out of these suitable places so subjecting them to the greater risks .... For a young Great Tit it appears to be a matter of the utmost importance to establish a territory in a suitable habitat as soon as possible."

It has therefore been shown that population density of Great Tits in woodlands is controlled both by inter- and intra-specific competition, and also that juvenile survival during the July - September period is the main factor governing annual population changes. This study, using an 'energetic' approach in conjunction with population dynamics, highlights the need for much fuller study of this little understood phase of the life cycle. It would seem a reasonable conclusion that Great Tit population density is ultimately determined largely by interspecific competition, while intraspecific competition is an important internal factor in maintaining stability.

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SUMMARY

Field and laboratory studies of the Great Tit (*Parus major*) and the Blue Tit (*P. caeruleus*) were carried out from December 1967 until August 1968 on populations in a woodland about a mile south of Durham City.

Great Tits had a breeding density of 0.4 pairs/ha preferring areas of deciduous woodland with an extensive secondary vegetation. Blue Tits had a breeding density of 1.5 pairs/ha. The breeding season of Tits lasted from the end of April until the end of June. The average clutch size for Great Tits was 8.3 and for Blue Tits 8.8, and the combined breeding success was 67%. The average calorific content of Great Tit eggs was 1.58 Kcals and for Blue Tit eggs 1.21 Kcals.

In Winter the average weight of Great Tits was 20.0gms for males and 19.0gms for females, and the average diurnal weight increase was 1.60gms of which 12½% was attributable to lipid deposition. In Winter the average weight of Blue Tits was 11.6gms and the average diurnal weight increase was 1.35gms of which 21% was attributable to lipid deposition. In Summer the average weight of Great Tits was 20.5gms for adult males and 19.7gms for adult females, while for adult Blue Tits it was 11.1gms. In Summer the weight of feathers for both species was approximately 30% lighter than

in Winter. The two species of Tit had a fairly synchronised moulting period lasting from mid-June until the end of August. The average annual standing crop of Great Tits was estimated to be 1.43 birds/ha or 55.97 Kcals/ha, while for Blue Tits it was 4.05 birds/ha or 87.71 Kcals/ha.

Energy requirements of individual caged Great Tits was determined by feeding experiments in Winter and Summer. In Winter Great Tits on average metabolised an average of 1.00 Kcal/gm bird/day which represented about 50% of the mean calorific content of individual birds. In Summer Great Tits in heavy moult metabolised 1.01 Kcal/gm bird/day. It was found that the metabolic rate of Great Tits was higher at low than at high temperatures during both feeding experiments.

Population energy flow was estimated for Great Tits by calculating the production and respiration of the standing crop for each month of the year.

Mean annual production was estimated at 104 Kcal/ha/yr. and mean respiratory energy flow 9605Kal/ha/yr. Mean gross energy intake based on an average assimilation efficiency of 82% was 11865Kal/ha/yr. The gross ecological efficiency for the Great Tit population was 0.88% and the net ecological efficiency was 1.07%, being representative of a small, active homiotherm.

Of the possible population limiting factors, the disappearance of juvenile Great Tits during the July - September period caused by both inter- and intra-specific competition was considered very important.

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