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THE SIGNIFICANCE OF VARIATIONS IN BODY WEIGHT AND WING LENGTH IN THE GREAT TIT, PARUS MAJOR

by

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CONTENTS

I. Introduction

1. General remarks

Like many other bird species, the Great Tit (*Parus major*) occupies several different habitats. These include coniferous and deciduous woods and forests and various man-made habitats such as gardens, parks, and orchards. However, the breeding density of the Great Tit shows great differences according to the habitat. Deciduous woods and parks can be classified as habitats with a high breeding density, coniferous woods as one of those with a low density. The extent of this difference becomes clear if we realize that the mean density of breeding pairs in the years 1959-1965 in two of our oak woods amounted to 2.64 and 1.35 pairs per ha, and in two of our pine woods 0.21 and 0.18 pairs per ha.

When we study breeding populations in deciduous and coniferous woods, we usually find great differences in various aspects of the breeding biology, pointing to a more favourable situation in the former. Elsewhere we will demonstrate the importance of feeding conditions in explaining these differences.

For the comparison of different types of forests as habitats (more or less favourable) for a bird species, it is not sufficient to show that reproduction has greater success in a given habitat; feeding conditions in winter must also be studied. Gibb (1960) demonstrated the importance of winter food as a regulating factor in Coal Tit (*Parus ater*) populations in pine woods. We have studied winter feeding conditions with an indirect method, using the body weight and weight changes of the tits under different conditions. Feeding conditions can be expected to have an effect on the weight of the tits. Moreover, feeding conditions in the moulting period are assumed to have an effect on the wing length. With this in mind we analysed the variations in weight and wing length in several hundred tits from different habitats. Apart from variations due to differences in habitat, many other factors are found to influence weight and wing length.

Acknowledgements

My thanks are due to the various landowners who permitted me to work on their property, and to Messrs. A. Klaver, H. Th. G. Mutter, J. Visser, A. Blok, and H. M. van Eck who helped in the field work. Mr. C. W. Stam kindly made available data collected by him in Meyendell, near The Hague. I am particularly indebted to Dr. H. N. Kluyver, who initiated this study and did much to improve the manuscript. Part of the work was made possible by a grant from the *Nederlandse Organisatie voor Zuiver Wetenschappelijk Onderzoek* (ZWO), The Hague. Mrs. I. SEEGER-WOLF corrected the English text.

2. METHODS

Since 1955 many data on the winter weight of Great Tits were collected in our study areas. In these areas, a description of which follows below, each summer we caught and ringed all tits that nested in our nest-boxes, both adults and nestlings. During the winters all boxes were inspected at least once, mostly twice. By this method an appreciable percentage of the winter population is caught, but this does not provide a random sample of the population: KLUYVER (1957) has shown that a greater percentage of adults than juveniles roost in boxes, and a greater percentage of males than females.

From the roosting tits we recorded: ring number, sex, body weight, and wing length. In some winters we estimated the amount of subcutaneous fat. In later years we also estimated age by means of plumage characters. Because the nestlings were ringed in summer, we know the age of many of our winter birds. The other birds were first ringed as adults, either in the breeding season or while roosting in a nest-box in winter.

In many cases it is possible *to determine the age* of these birds with the characters given by DROST (1951). Originally we did not use this method, but since the autumn of 1964 many Great Tits have been aged and the reliability of this method has been tested. Table 1 shows the results obtained between September 1964 and March 1966, both by day and by night. The reliability of this method varies from 80 to 100%, depending on the sex and the real age of the birds and the conditions. By day all adult birds can be aged correctly, but by night (in artificial light) results are slightly inferior. From the figures in Table 1 the real age structure of a sample of birds of unknown age can be estimated, if these birds have been aged with DROST's method. Table 2 gives for five samples of unringed Great Tits the percentage of first-year birds according to the plumage characters and the percentage after a correction for the percentage of wrong determinations. It is clear that in these two winters some 70% to 100% of the immigrant tits were in their first year; this percentage tends to be higher in males than in females. The percentage of first-year birds among the immigrants is dependent on local conditions, e.g. on the size and the form of the study area, and the habitability for tits of the surrounding area. Moreover, it is reasonable to suppose that yearly differences occur, e.g. caused by annual differences in the extent of migration shown by yearling and adult birds, particularly between normal years and "invasion years" in which a great part of the tit populations over large areas migrates. However, as CRAMP (1963) points out, in the invasion years 1957 and 1959 a very high proportion of the migrants in Great Britain consisted of juvenile birds, a situation similar to that

TABLE 1

AGE DETERMINATION BY PLUMAGE CHARACTERS COMPARED WITH REAL AGE, KNOWN FROM RINGING

	A. By day				B. By night			
Sex	Males		Females		Males		Females	
Real age	*e*	*m*	*e*	*m*	*e*	*m*	*e*	*m*
Estimated as *e*:	73	0	38	0	33	11	4	2
Estimated as *m*:	7	37	7	9	2	56	1	34
% correct	91	100	84	100	94	84	80	95

NOTE: *e* = yearlings; *m* = adults.

found in normal winters in Holland (Table 2). Moreover, in our material there are no yearly differences in the emigration of adult birds, judged by the number of recoveries outside the study areas. From these facts we conclude that the proportion of first-year birds among the immigrants is rather constant from year to year, and that the age structure found in 1964-'65 and in 1965-'66 (Table 2) is more or less characteristic of the whole period. Thus, the proportion of first-year birds among the immigrants will generally vary from 70% to 100%.

We will find later that the average wing length and weight of the immigrants are in good agreement with those of the juveniles and differ markedly from those of the adult birds. For these reasons we will use the data from immigrants as if they were in their first year when they entered the study area, but we will restrict this procedure to those cases in which too few birds of known age are available.

Sex. It is nearly always possible to separate males and females according to plumage. In some difficult cases retrapping during a later breeding season usually gave the answer.

Body weight. The birds were weighed with a beam balance mounted in a metal box; this enabled us to weigh under many conditions. The accuracy reached with this balance (0.02 grams) is not always necessary in this type of work because the weight of birds is very variable owing to several disturbing

TABLE 2

AGE OF IMMIGRANT GREAT TITS, DETERMINED BY PLUMAGE CHARACTERS
Percentage of first-year birds in sample before (*a*) and after (*b*) correction

Sample	Males		Females	
	a	*b*	*a*	*b*
1. Caught by day Hoge Veluwe, winter 1964-'65	95	100	81	96
2. Roosting birds, Hoge Veluwe, winter 1964-'65	97	100	59	72
3. Roosting birds, Liesbosch, winter 1964-'65	75	76	70	86
4. Caught at nest, Hoge Veluwe, 1965	76	83	55	65
5. Caught by day, Hoge Veluwe, winter 1965-'66	90	99	97	100

factors such as wetness of the feathers, presence or absence of food in the stomach, defaecation, etc. But in some parts of this study, for instance for determining the nocturnal decrease in weight, an accuracy of this sort is undoubtedly required.

Observations on the amount of visible *subcutaneous fat* were carried out in the winters of 1959-'60 to 1963-'64. For all birds weighed during the routine inspections of nestboxes, the amount of fat from three parts of the body (in the furculum, at the abdomen and under the wing, where the wing joins the body) was estimated in one of four classes: fat absent or a small, medium, or large amount of fat. The resulting figures for the three body parts where added, and classified as:

0 = no fat on any of the three body parts,
1 = a small amount of fat on one of the three body parts,
2 = a medium amount of fat on one, or a small amount of fat on two body parts,
3 = a large amount of fat on one, or a small amount on three body parts, or a medium amount on one and a small amount on another of the body parts; etc.

Theoretically we may expect fat values of up to 9 (large amount of fat on all three body parts), but in practice we never found more than fat class 6 and most of the birds belonged to classes 1 to 3.

The *wing length* of a bird can be measured in several ways, with different results, as explained by STEWART (1963) and EVANS (1964). These methods differ in the extent to which the natural curvature of the wing is eliminated. Whereas in museum-skins it is not possible to determine the natural chordal length of a wing and consequently a method must be used in which the wing is pressed flat on a ruler, in live birds an attempt should be made to measure the wing in its natural position and retaining its natural shape. We achieved this by using a sliding rule, the ends of which are kept lightly against the carpal joint and the tip of the longest primary. The wing length can then be recorded to the nearest 0.5 mm. For a comparison of our results with data from the literature it is essential to know the size of the differences in wing length caused by the use of different methods. In 1963-'64 we tried to establish this by measuring the same individual Great Tits with each of the following methods:

a. With a sliding rule, as described above.
b. With a ruler: the carpal joint pressed lightly against the stop, the wing not pressed flat. This is the so-called Fair Isle method (STEWART 1963).
c. With a ruler: as in b, but the wing pressed flat with the thumb (recommended by CORNWALLIS & SMITH 1960).
d. With a ruler: as in c, but the lateral curvature of the primaries eliminated by straightening them with the fingers.

These measurements were all made by one observer, but in addition to this the results of several observers with the same method have been compared. Table 3 gives a summary of these results, which are expressed as the difference in mean wing length of a group of Great Tits obtained by some observer and method, compared with the mean of observer A with method *a*. For a comparison of the different methods the results of 4-13 March 1964 are most important. Combining the results of several dates, one can say that method *b* gives an average higher by 0.75 mm than method *a* (mean of 3 averages from A), for method *c* this difference is +1.53 mm (mean of 8 averages from A), for method *d* +2.84 mm.

TABLE 3

RESULTS OF WING LENGTH MEASUREMENTS WITH DIFFERENT METHODS AND BY DIFFERENT OBSERVERS (mean difference in mm)

Date	Locality	Observer	Number of birds	Difference in mean wing length with mean obtained by A with method *a*			
				a	b	c	d
12 Nov. 1963	Hoge Veluwe	A	16	0		+1.73	
12 Nov. 1963	Hoge Veluwe	B	16	—0.15			
14 Nov. 1963	Liesbosch	A	22	0		+1.52	
14 Nov. 1963	Liesbosch	B	22	—0.41			
3 Dec. 1963	Gent	A	43	0		+1.33	
19 Febr. 1963	Arnhem	A	11	0	+0.68	+1.73	
27 Febr. — 3 March 1964	Arnhem	A	16	0	+0.78		
27 Febr. — 3 March 1964	Arnhem	B	16	—0.06	+0.96		
4-13 March 1964	Arnhem	A	39	0	+0.80	+1.67	+2.84
25 March 1964	Meyendell	A	16	0		+1.47	
3 Dec. 1963	Gent	A	43	0		+1.33	
3 Dec. 1963	Gent	H	43			+1.95	
25 March 1964	Meyendell	A	16	0		+1.47	
25 March 1964	Meyendell	S	16			+1.58	

NOTE: Observers A and B (J. H. VAN BALEN, A. KLAVER) made most of the measurements discussed in this paper. H = Prof. Dr. J. HUBLÉ (Gent, Belgium). S = C. W. STAM (The Hague).

These rather large differences show the necessity for exactly describing the method used in wing length measurements. When different workers use the same method, they usually get slightly different results. The difference between observers A and B with method *a* amounted to about 0.2 mm. With method *c* a considerable difference was found (between A and H). In practice it is not always easy to distinguish between methods *b*, *c* and *d*, and there are gradual differences between them. This makes the use of these methods less reliable, and forms another reason why the use of method *a* is preferable, at least with live birds.

In section II. 4 another aspect of the reliability of wing length measurements will be treated. There we will find that a difference of 0.5 or 1 mm between successive measurements of the same bird, by different observers using method *a*, is quite common.

In the tables and figures of this paper we will use the following symbols as indication of age classes:

e = yearlings (less than 1 year old),
m = adults (at least 1 year old),
m2 = between 1 and 2 years old,
m3 = between 2 and 3 years old, etc.

FIGURE 1. Map showing the position of the study areas; numbers refer to the descriptions on page 8-9.

In the tables n is the number of observations on which an average, $\bar{x}$, is based, and s signifies the standard deviation of this average. Wing lengths are expressed in millimeters, body weights in grams. The statistical tests used to establish the significance of differences can be found in any statistical textbook, e.g. DE JONGE (1958-1960).

3. STUDY AREAS

Most of the work on which this paper is based was carried out in two areas, viz. the Hoge Veluwe in the central part and Liesbosch in the southern part of The Netherlands. In these areas nocturnal inspections of nest-boxes were made from December 1955 on. Data from the other areas cover shorter periods, as will be indicated below. For comparison with our data Mr. C. W. STAM has kindly lent us his data collected from

1958 in the dunes of Meyendell near The Hague, The position of the study areas is indicated by numbers on the map (Fig. 1).

Hoge Veluwe (1); the study area covers about 300 ha in the southern part of the National Park "De Hoge Veluwe". More than half of it consists of plantations of Scots Pine (*Pinus sylvestris*), the remainder is made up partly of Scots Pine mixed with many Birches (*Betula* ssp), and partly of poorly growing Oaks (*Quercus robur*) and some small Birch plantations. Along some roadsides Beeches (*Fagus sylvatica*) and Red Oaks (*Quercus borealis*) have been planted. Because of the sandy soil most of the vegetation is rather poorly developed. In the spring of 1955 we started with 70 nest-boxes (on 97 ha), in the autumn of 1955 extended to 90 boxes (on 132 ha), and in the autumn of 1958 to the present number: about 230 boxes on about 300 ha.

Oranje Nassau's Oord (2); (66 ha), described by KLUYVER (1951). Data from 1955-'56 to 1958-'59, but in some winters only from the northern part (27 ha).

Kreelsche Bosch (3); plantations of Scots Pine. Understory partly well developed, partly lacking. Deciduous trees nearby. About 95 nest-boxes on 64 ha. Data from 1955-'56 to 1957-'58.

Waterberg (4); Scots Pine is the most important tree, locally birches. Understory with Beech and Red Oak. About 85 nest-boxes on 110 ha. Data from 1955-'56 to 1958-'59.

Imbosch (5); pure plantations of Scots Pine of mixed ages, 41 boxes on 75 ha, started in 1960. Data from noctural inspections starting in 1962-'63.

These five areas are situated on the sandy soil of the Veluwe; the next two areas have a more fertile soil, resulting in a rich vegetation of deciduous trees and a well-developed understory.

Oosterhout (6); a small deciduous wood with mature oaks predominant. Dense understory. From 1956 12 nest-boxes (on 4 ha), in 1957 increased to 24 boxes on 9 ha, in 1959 to 29 boxes on 11.4 ha, and in 1964 to 48 boxes (11.4 ha). The wood is surrounded by orchards, meadows, and arable land, and is isolated from other woods.

Liesbosch (7); mature oak wood, with locally many beeches and clumps of conifers. Size about 180 ha, but only small parts used as study areas. Part A (18 ha) has carried 63 boxes since 1955 and 97 boxes since autumn 1957. This part can be characterized partly as *Violeto-Quercetum*, partly as *Querceto-Carpinetum* (LEYS 1965). In another part (B, 16 ha) 70 boxes were erected in the autumn of 1959. Vegetation more varied than in A, with patches of beech and conifers, but oak is still the most numerous tree.

Vlieland (8); the pine plantations on the island Vlieland were planted from 1902 onwards. The main tree is the Corsican Pine (*Pinus nigra*). Locally deciduous trees and Sitka Spruce are found. The plantations cover about 225 ha, in which 120-140 boxes were erected in 1955. This total area is composed of 5 plantations separated from each other by unwooded areas. Since the distance between these areas is only about 1 km and there is frequent interchange between them by the tits, we will treat the total wooded area as one study area.

Meyendell (9); the woods in the dunes near The Hague have a varied structure and composition. The total area is composed of many different parts, some of them rather isolated. Partly birchwood with dense understory, partly open wood with park-like appearance (pine, birch, poplar, oak).

II. Wing Length

The wing length of a bird is usually regarded as a good indication of its body size. Although, as we have pointed out, the use of different methods of measuring wing length compels us to be cautious when comparing the results of different authors, wing length is still a very useful measurement, for example for a comparison of the size of birds from different localities. Rand (1961) showed that wing length can be a reliable measure for the weight of a bird if intraspecific populations or populations from species with similar habits are compared. We will examine our material for possible differences in wing length among the populations of our study areas, and try to compare the results with data from the literature. Next, we will examine the possible sources of variation within the population of one area, such as the age of the birds. Before doing so we must consider a very obvious factor affecting wing length, viz. the sex of the birds.

1. Sex and wing length

Just as in many other passerine species, in the Great Tit the males have larger wings than the females. From Figure 2 it is clear that the wing lengths of males and females overlap to a great extent in both areas. The same can be said of the results from the other areas. However, the peak frequencies are so clearly separated that the difference in mean wing length of males and females in all years is very significant (data in Table 4; $P < 0.01$).

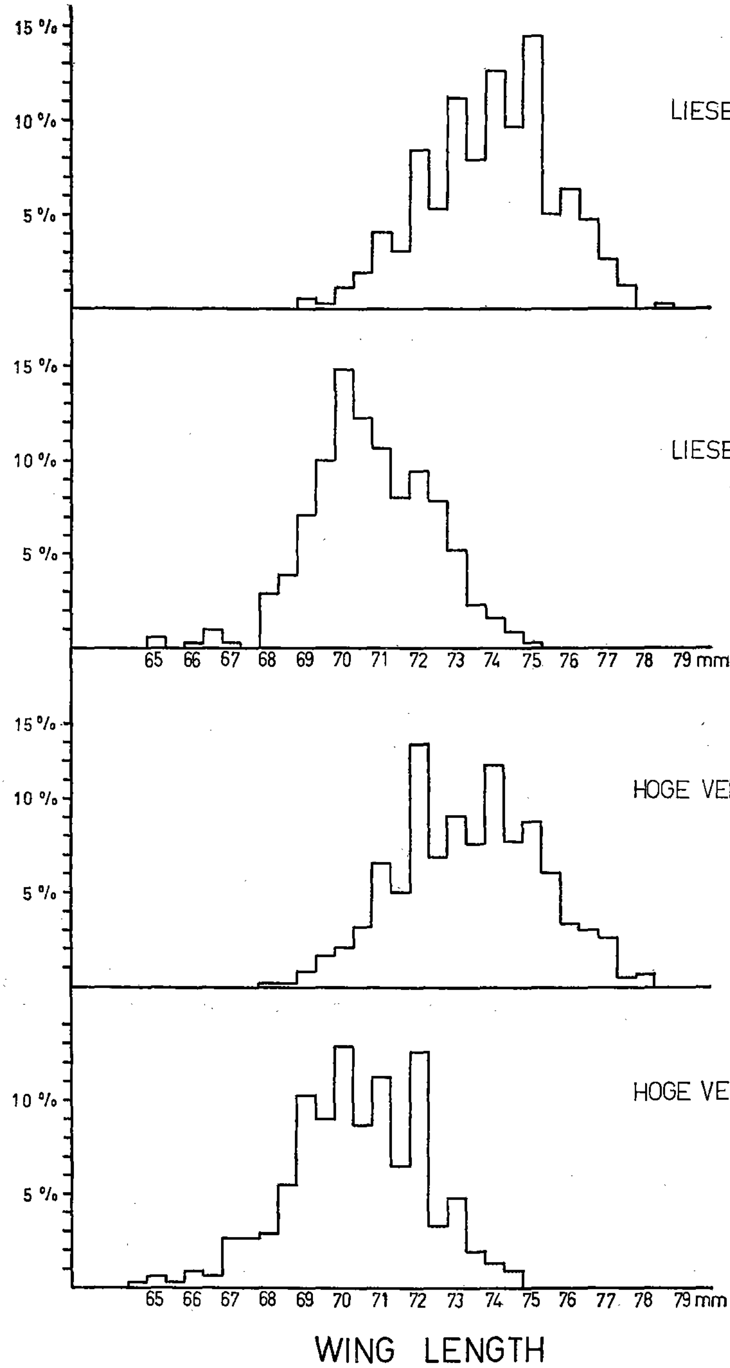

FIGURE 2. Frequency of wing lengths (in percent) of male and female Great Tits in the two main areas, all winters combined.

TABLE 4

WING LENGTH OF MALE AND FEMALE GREAT TITS FROM HOGE VELUWE AND LIESBOSCH

Year	Hoge Veluwe				Liesbosch			
	Males		Females		Males		Females	
	x̄	s	x̄	s	x̄	s	x̄	s
1955-'56	74.60	1.63	71.57	1.01	74.00	1.30	71.07	1.92
1956-'57	74.01	1.67	70.79	1.88	74.46	1.64	71.15	1.36
1957-'58	—	—	—	—	74.36	1.44	71.64	1.51
1958-'59	72.71	2.32	69.74	2.42	73.56	1.51	70.50	1.91
1959-'60	72.94	1.79	70.24	1.55	72.95	1.79	69.33	1.48
1960-'61	72.21	1.56	69.46	1.09	73.87	1.61	69.84	2.06
1961-'62	73.85	1.70	70.75	1.37	73.99	1.78	70.67	1.42
1962-'63	73.00	1.89	68.97	1.80	73.84	1.74	70.48	1.12
1963-'64	73.33	1.60	70.35	1.66	73.53	1.86	70.71	1.58
1964-'65	74.34	1.65	71.59	1.50	74.26	1.56	71.50	1.44
1955-'65	73.35	1.88	70.34	1.82	73.90	1.72	70.71	1.76
n	634		310		430		308	

TABLE 5

DIFFERENCE IN WING LENGTH BETWEEN MALES AND FEMALES OF ALL AREAS

Area	Males		Females		Difference in percent of wing length of females
	n	x̄	n	x̄	
Hoge Veluwe	634	73.35	310	70.34	4.3
Oranje Nassau's Oord	123	73.64	106	70.70	4.2
Kreelsche Bosch	46	74.13	43	71.42	3.8
Waterberg	91	73.83	54	70.81	4.3
Imbosch	32	74.13	25	71.46	3.7
Oosterhout	62	75.03	34	71.16	5.4
Liesbosch	430	73.90	308	70.71	4.5
Vlieland	178	74.08	103	71.02	4.3
Meyendell	152	74.45	42	71.31	4.4

On the average the wing length of the males exceeds that of the females by about 4%. A difference of this size was also found in the other areas (see Table 5). As Table 5 indicates the largest differences (in percent of the female average) were found in the deciduous woods Oosterhout and Liesbosch and the smallest in the coniferous woods Kreelsche Bosch and Imbosch. The biological significance of this effect of the habitat cannot be readily understood.

2. LOCAL AND REGIONAL DIFFERENCES IN WING LENGTH

For a comparison of the wing length of tits from different localities, the average of all birds, caught in these places could be used. A more exact procedure, however, is to compare birds of one age class, because, as we will show later, wing length is correlated with age. For this comparison we used the data from the adult birds, most of which were in their second year, a fair proportion in their third, and some older. To make the comparison as valid as possible we must take into account some other sources of variability such as differences in wing length within one winter (section II. 4) and differences between winters (section II. 5).

Table 6 gives the results from all areas, and compares these with the results from the Hoge Veluwe in the same period. There are only small differences between the results from the woods of the South Veluwe (1, 2, 3, 4). At Oranje Nassau's Oord, Waterberg, and Kreelsche Bosch the means are slightly lower than for the Hoge Veluwe. This justifies combining the results of these four woods, which differ only slightly in vegetation and in geographic position. Combining the four means gives a mean value for the whole area of the South Veluwe of -0.3 mm. The results from the Liesbosch are about 0.5 mm above this mean, those from Oosterhout somewhat higher again. This suggests that the conditions for the growth of primaries are more favourable in these deciduous woods. Since the growth of the primaries takes place in the period July-August the difference in conditions must occur in this period. It is logical to suppose that food is more plentiful in the deciduous woods, but data on this point are lacking.

A comparison of the wing length of the yearling tits in different habitats shows that here the same trend, i.e. longer wings in the broad-leaved woods, is present. These birds grow their primary feathers earlier in summer, before and shortly after fledging. Estimates of the feeding conditions during the breeding season show that the young tits grow up in much more favourable conditions in deciduous wood than in pine wood, but this will be discussed elsewhere (VAN BALEN in prep.).

Although several authors have published wing lengths of the Great Tit, most of these data are not comparable with ours because the method used for their measurements is not clearly stated. Dr. J. HUBLÉ (pers. comm.) found a mean wing length of 76.6 mm for ♂♂ and 72.4 mm for ♀♀ in some woods around Gent (Belgium). These averages require a correction of -2.0 mm, as established by Dr. HUBLÉ and the author in Gent (December 1963). Therefore the mean wing length of the males is 74.0 mm, for the females 70.4 mm, which corresponds closely to the averages for Liesbosch (73.9 and 70.7 mm), 90 km northeast of Gent. Another set of data is available from Möggingen (Southern Germany), kindly supplied by Dr. G. ZINK. Here the averages of wing length

TABLE 6

MEAN WING LENGTH OF MALE GREAT TITS FROM DIFFERENT LOCALITIES

Area	1955-'65		1955-'59		1962-'64		1963-'66		Difference from Hoge Veluwe values
	n	$\bar{x}$	n	$\bar{x}$	n	$\bar{x}$	n	$\bar{x}$	
1. Hoge Veluwe	245	74.4	21	75.3	35	74.9	100	75.1	—
2. Oranje Nassau's Oord			58	74.5					—0.8
3. Kreelsche Bosch			26	75.2					—0.1
4. Waterberg			36	74.9					—0.4
6. Oosterhout							35	75.7	+0.6
7. Liesbosch	210	74.6							+0.2
9. Meyendell					44	73.9			—1.0

NOTES: 1. Numbers before area names refer to the map (Fig. 1) and the description.
2. Adult birds only, from November to January.
3. Data from Meyendell obtained by Mr. C. W. STAM, corrected for difference due to method of measuring (1.5 mm).

were 76.2 mm for the males and 72.8 mm for the females. The correction factor, established by Dr. ZINK through a comparison of measurements with the method used by him (with a ruler) and with our method, amounts to -2.4 mm. Thus the wing length of the males is 73.8 mm and for the females 70.4, again very close to the Dutch averages. SNOW (1954) found a good correlation of body size with winter temperature in the Great Tits (Bergmann's Rule), but probably the difference in climate between the localities cited above is too small to result in differences in body size.

3. VARIATION OF WING LENGTH WITH AGE

In several passerine species the juvenile birds have shorter wings than the adult birds. This has been observed in the Greenfinch (*Chloris chloris*, SUTTER 1946), the Redstart (*Phoenicurus phoenicurus*, SUTTER *loc. cit.*), the Pied and Collared Flycatchers (*Ficedula hypoleuca* and *F. albicollis*, CREUTZ 1950, LÖHRL 1954), the House Sparrow (*Passer domesticus*, LÖHRL & BÖHRINGER 1957) and the Blue Tit (STEWART 1963). These species do not moult the juvenile primaries in their first autumn moult.

In the Great Tit KLUYVER (1939) observed this difference between yearling birds and birds at least one year old, and found in some birds an increase in wing length from their second to their third winter. The latter conclusion is based on a few measurements. CREUTZ (*loc. cit.*) found from his extensive material a substantial increase in wing length after the first complete moult (in the second autumn), and concluded that after this moult the maximal wing length had been attained; his data on the latter point suggest in my opinion a small increase from the second to the third winter. HINDE (1952) too found an greater wing length in adult birds than in yearlings. BJÖRN (1960), on the other hand, found no difference in wing length in yearling and adult tits from southern Sweden, whereas HUBLÉ (pers. comm.) recorded a considerable difference in his data from woods near Gent.

When studying fluctuations in wing length in the course of the tit's life one cannot expect wing length to reflect accurately any variation in the size of the bird's body. The greater part of the measured quantity is composed of feathers (the primaries) and the length of the primaries is subject to sudden changes, restricted to short periods, viz. abrasion during the breeding season and growth during moult, mainly in August. On the other hand, the bird's body probably reaches its final size gradually, but the period over which this growth extends is unknown. Therefore, an increase in wing length from the first to the second winter does not necessarily mean that the body size has increased over this period.

In our material the most extensive data on this point come from Liesbosch, the Hoge Veluwe, and Vlieland. In Figure 3 these data have been grouped according to age, i.e. first-year, second-year, third-year and older birds. In these graphs the effect of the factors habitat and sex have been eliminated and differences within one year have been allowed for by using only data from November to January (compare section II. 4). No allowance is made for differences between years, but probably these differences do not differ in effect on young and older birds (section II. 5).

For each age class two points are given, one for the whole sample and one for the part of the sample composed of birds whose age was known exactly. The difference between them represents the immigrant birds (compare section I. 2), which are supposed to have been in their first year at entering the study area. In a few cases there is a significant difference between the wing length of the immigrants and of the birds of known age, viz. among first-year males from Liesbosch, second-year females from Liesbosch, and second-year females from the Hoge Veluwe (tested with STUDENT's t-test).

Figure 3 demonstrates a great difference in wing length between the juveniles and the older birds. It is clear that—particularly for the males—there is no question of a consistent increase or decrease after the second year. When STUDENT's t-test was applied to the means of successive age

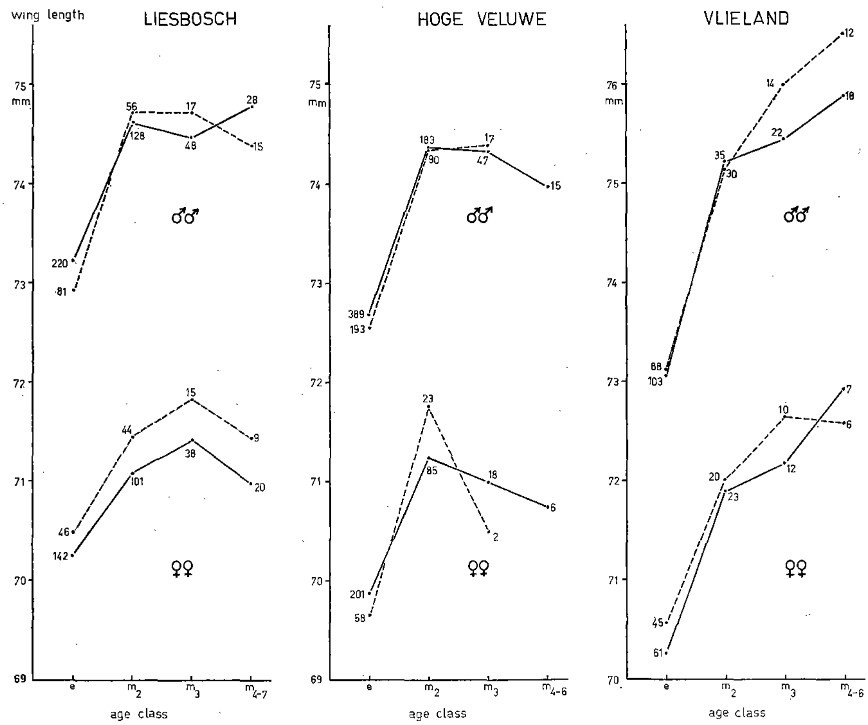

FIGURE 3. Mean wing length in different age classes. Numbers beside each point give the sample size.

classes, only the differences between the means of the yearlings and the second-year birds were significant (in most cases $P < 0.001$). It is therefore doubtful whether the small differences between the older age-classes are real.

On the island of Vlieland conditions differ from those in the other areas, mainly because of the experiments carried out since 1960 (see KLUYVER, 1966). These experiments implied a considerable decrease in the reproduction from 1960 to 1963, and resulted in a reduced density of tits after the breeding season, with a correspondingly increased survival among the yearling birds and especially among the older birds. These relatively favourable conditions in the years 1960 to 1963 are not responsible for the apparent deviation in the increase of wing length with age as compared with the two other areas (Fig. 3). In the first place, the differences in wing length between the older age classes on Vlieland are not statistically significant. In the second place this trend of wing length to increase with age (beyond *m*2) was most pronounced in 1964,

TABLE 7

RELATION BETWEEN WING LENGTH AND AGE (independent samples)

Area and Sex	*e*		*m*2 + *m*3		Result from t-test; P
	n	$\bar{x}$	n	$\bar{x}$	
Liesbosch ♂♂	71	72.87	55	74.81	< 0.01
Liesbosch ♀♀	37	70.70	40	71.58	< 0.02
Hoge Veluwe ♂♂	156	72.58	68	74.28	< 0.01
Hoge Veluwe ♀♀	50	69.58	16	71.66	< 0.01

when the reduction of the reproduction had been very small, as compared with the four preceding years. Consequently, we cannot attach special importance to the deviating results on Vlieland.

The results from several other areas (Oosterhout, Oranje Nassau's Oord, Meyendell) on this subject are in good agreement with the conclusions drawn above. It may therefore be said that the wing length increases considerably at the first complete moult, but that further changes are insignificant.

The conclusions drawn above are weakened by the fact that data from individual tits are included in more than one of the age classes, viz. where a bird was caught in the area and measured in more than one winter. Use of a statistical test becomes more meaningful if the samples are completely independent. Therefore, we made the samples from Liesbosch and the Hoge Veluwe independent by selecting one observation from each individual tit and dividing the selected values into a group of yearling birds and a group of birds in their second or third year. The difference in mean wing length of these two groups was found to be significant (t-test, see Table 7) in both areas and both sexes. This confirms the conclusions drawn above.

4. SEASONAL VARIATION IN WING LENGTH

Although most of our data come from a fairly restricted period (November — end of January), we also have some data about variations in wing length in the course of winter and spring. Abrasion of wing and tail feathers was sometimes observed, and it is interesting to know in which part of the year this occurs. To investigate this we combined all data of tits that have been measured more than once in the same winter and then calculated the mean change in wing length from the first to the second date. Table 8 shows the frequency of changes found in several groups of birds as well as their averages. The first line refers to birds

TABLE 8

SEASONAL VARIATION IN WING LENGTH

Area	Period elapsed between measurements	n	Frequency of differences in wing length from first to second date											Mean difference
			< -2	—2	—1.5	—1	—0.5	0	+0.5	+1	+1.5	+2	> +2 mm	
Hoge Veluwe	at most 30 days	253	4	8	10	23	50	73	49	22	10	3	1	—0.08 mm
Hoge Veluwe	2-3 months	156	6	2	11	34	25	30	23	16	6	2	1	—0.27 mm
Liesbosch	2-3 months	40	—	3	3	8	9	5	8	2	1	1	—	—0.34 mm
O.N.Oord	Dec.-March, April	73	1	1	—	12	6	29	13	10	—	1	—	—0.02 mm
Vlieland	winter to 1st brood	87	12	11	13	13	17	13	4	3	—	1	—	—1.22 mm
Vlieland	winter to 2nd brood	41	10	10	10	7	1	—	1	2	—	—	—	—1.80 mm

remeasured within a month of the first date in the period November to March. In such a short period there is no question of a decrease in wing length due to abrasion. These data give an impression of the reliabilily of the wing length measurements, and show that a difference of 0.5 mm to 1.0 mm between succeeding measurements is rather common. In 28% of all cases no difference occurred, in 39% of all cases the difference amounted to 0.5 mm, in 18% to 1 mm, and in 14% to more than 1 mm. When studying differences in wing length one must bear in mind that a difference of 0.5 mm may easily be caused by inaccurate measuring.

The second and the third line give data with a larger interval between the two measurements, the first date usually being in November or December, the second in January to March. Both groups of data show on the average a small decrease in wing length, mainly caused by a few extreme individuals with a decrease of 2 to 3.5 mm. In the Liesbosch the change in wing length differs significantly from zero ($P = 0.03$). In KLUYVER's data from Oranje Nassau's Oord no appreciable decrease occurred up to April. It is clear, however, that in the reproductive period, especially while the parent tits rear their young, the wings have been worn considerably. This is shown by the data from Vlieland in 1962, 1963, and 1965 in Table 8. Both differences, i.e. -1.22 mm during the rearing of the first and -1.80 mm during the rearing of the second brood, are highly significant. This means that abrasion of the primaries occurs mainly from April onwards. Presumably the increased activity of the parent tits in the breeding season plays a role in this phenomenon.

5. Annual variation in wing length

A further possibility for variation in wing length is indicated by differences in the averages for different winters. Examination of the annual averages for Liesbosch and the Hoge Veluwe, as shown in Figure 4, gives an idea of the rather strong fluctuations from year to year. The difference between the highest and the lowest average amounts to 1.7 mm (Liesbosch ♂♂), 2.4 mm (Hoge Veluwe ♂♂), 2.6 mm (Liesbosch ♀♀), and 2.6 mm (Hoge Veluwe ♀♀). The differences between these extremes are statistically significant (t-test, $P < 0.01$); moreover, the averages for males and females in the same habitat fluctuate in parallel, so this fluctuation is more than a chance effect.

As seen in section II. 3, the age of the tits has a considerable effect on wing length; therefore, at least a great part of the annual variations in wing length may be attributable to differences in the age structure of the

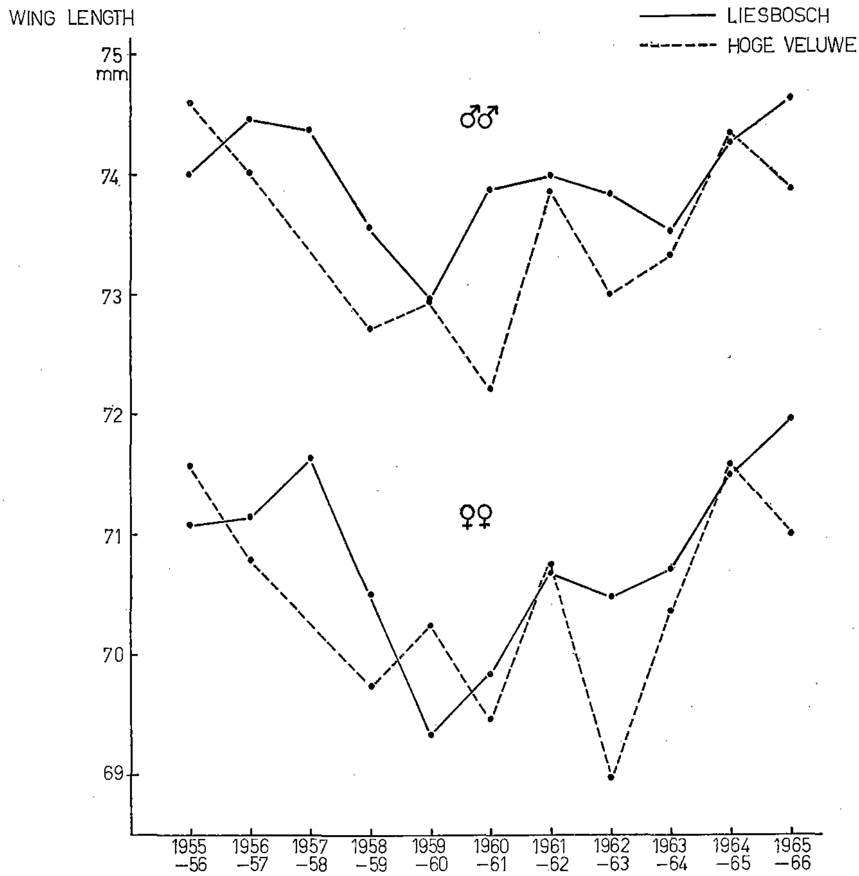

FIGURE 4. Annual fluctuations in average wing length in the two main areas.

tit population. We expect that in years with a high proportion of yearling and immigrant tits the mean wing length of the total sample will be lower than in years with a high proportion of older birds in the sample. A comparison of the mean wing length in a given year and the proportion of yearling birds in the sample did not reveal a correlation. There seem to be other factors reponsible for the annual differences in mean wing length in both yearling and older birds. One of these factors is probably the availability of food in the period of growth of the primaries. For the yearling birds this is the nestling period and a few weeks after it. For this period figures about caterpillar density in the pine wood at the Hoge Veluwe are available and these show a fairly good positive correlation with wing length at fledging time and in the first winter. For the older birds the period in which the primaries grow out is July-August. The data we have on caterpillar density are usually restricted to the period May-July, thus they do not cover the entire moulting period. There appeared to be no correlation between the caterpillar density in July and the wing length of the tits older than one year, but this does not mean that food plays no role in the growth of the primaries. Firstly, the caterpillar density in August can differ considerably from the figures of July; secondly, the caterpillar density was measured only in the pine wood at the Hoge Veluwe, and the wing lengths used here come from the whole Hoge Veluwe area, including pine and broadleaved woodland. Lastly in the moulting period other types of food may form a substantial part of the diet of the tits. BETTS (1955) showed that in the Forest of Dean (oak wood) the diet of adult Great Tits in July was composed of many types of insects, and spiders, but data from pine wood in this period are lacking.

Apart from the effect of food on the growth of the primaries, weather factors could be expected to exert some influence on primary growth, for instance when severe weather (heavy rains, low temperatures) interferes with feeding or increases the food requirements. To test this assumption we compared the mean wing length of the older tits in winter with the mean temperature and the rainfall in the preceding July and August. For both weather factors the deviation from the average value over a long period was taken. There appeared to be a weak negative correlation of wing length with temperature in August, but this correlation was not significant (KENDALL's Rank Correlation Test). A significant positive correlation with the amount of rainfall was found ($P = 0.045$) in one out of three cases (Liesbosch ♀♀). In the other two cases (Liesbosch ♂♂, the Hoge Veluwe ♂♂; for the Hoge Veluwe ♀♀ data were too scarce) the positive correlation was not significant. Temperature and rainfall in July appeared not to be correlated with primary growth. We must conclude that there are some indications that low temperatures and high rainfall in August are associated with long primaries, but the mechanism of this correlation, if it exists, is not clear.

EVANS (1964) found that the wing length of Dunlins (*Calidris alpina*) was affected by the dampness of the feathers at the time of measuring. Wing length increased with increasing wetness of an initially dry wing. A comparison of our results with weather data of the dates on which the tits had been measured did not suggest a correlation between the amount of precipitation and the wing length, so this effect cannot explain the correlation found above.

6. Conclusions

In this material the usual sources of variation in wing length, as described in the literature, have been demonstrated, viz. variation due to sex and age of the birds. In addition to this we found that seasonal variation in wing length occurs, due to the abrasion of the primaries during the breeding season. Annual differences in wing length were found to be partly caused by feeding conditions in summer, and possibly to be partly related to weather conditions in the moulting period. With respect to the main object of this study, differences in wing length and weight in relation to habitat, small but consistent differences occur in the average wing length of populations of different habitats. These differences indicate that conditions for primary growth are most favourable in the two oak woods Liesbosch and Oosterhout.

III. Body Weight

1. Introduction

In 1938 Baldwin & Kendeigh published their pioneer study on "Variations in the weight of birds". In this study they treated a large number of weight data from live birds of many species and formulated a number of rules which promoted a better insight into the usually large variation in body weight found in most birds. They found, for instance, a clear sexual difference in weight and a difference according to age. Moreover, a distinct diurnal rhythm in weight was demonstrated, related to the periods of feeding and resting. Daily differences in weight appeared to be correlated with changes in air temperature, and a seasonal trend occurred, resulting in a high weight in winter and a low weight in summer in most species. These and other phenomena have subsequently been found by other authors in a large number of species.

For the Great Tit and related species the following facts about body weight are known at present:

Haftorn (1951) weighed a number of Great Tits at a feeding station in Oslo, Norway, during five winters. The mean weights of males and females were 20.1 and 19.2 grams. Seasonal fluctuations in weight appeared to be considerable, with a maximum in December or January. In the months of November to January weight was negatively correlated with air temperature, resulting in the highest values in the coldest winters. In February weight tended to vary positively with temperature. Haftorn concluded that in the coldest period (January to February) feeding conditions become more and more critical, and that the tits were at last unable to react positively to cold (by putting on more weight) but, to the contrary, tended to loose weight.

In the weights of roosting Great Tits, collected by KLUYVER (1952) in the winter 1937-'38 at Oranje Nassau's Oord, the males gave the same picture as HAFTORN's tits: a maximal weight in December, with a steady decline, in this case up to June. The air temperature was minimal in December, and the weight of the males was clearly negatively correlated with the air temperature. The females showed a more or less constant weight from November to February, a decrease to March and a sharp increase in weight in April, in connection with the development of the gonads. During a period of heavy cold the weight of the tits regularly visiting a feeding station increased and that of the remaining tits decreased. During this period the overnight loss of weight amounted to 1.7 grams.

OWEN (1954) analysed a large number of weight data from Great Tits and related species. These birds had been trapped by day, on bait, in Wytham Wood near Oxford, England. The males averaged 1.5 grams more than the females. Weight increased during the day, and at 16.30 hours was more than 5% higher than at 9.30 hours. Great, Blue, and Coal Tits had their peak weight in November or December and continually decreased in weight until March. This decrease (in the mild winter of 1951-'52) reached large proportions in the Great Tit: from 20.0 grams in November to 18.2 grams in March (males). Thus there was no correlation witn air temperature in this winter (temperature was minimal in January and February), but weight differences between the two winters were clearly related to air temperature. OWEN explains the early weight peak found by him as a reserve for possible food shortage later, and considers the decrease in air temperature in autumn to be the stimulus for this increase in weight. On the other hand, OWEN states (p. 305) that food probably was never scarce and that it is unlikely that weight losses were due to food shortage. So it is difficult to see why his tits did not increase in weight up to the coldest mont (February), as is usually found in passerine birds, but to the contrary decreased sharply. I suggest that this decrease was still due to food shortage.

KEIL (1962) caught some Great Tits near Frankfurt (W. Germany) by day. The average weights of males and females were 18.75 and 17.86 grams respectively, giving a much smaller difference due to sex than the difference recorded by other authors.

Summarizing we can say, that the following facts about the body weight of Great Tits are known:

1. Males are heavier than females in the period November to March.
2. There is a marked diurnal rhythm in weight; the overnight weight loss can amount to 10% of the body weight.
3. The weight is usually maximal in December, in OWEN's birds in November.
4. Cold weather is associated with an increase in weight, when feeding conditions are favourable.

We will now examine whether these and other phenomena occur in

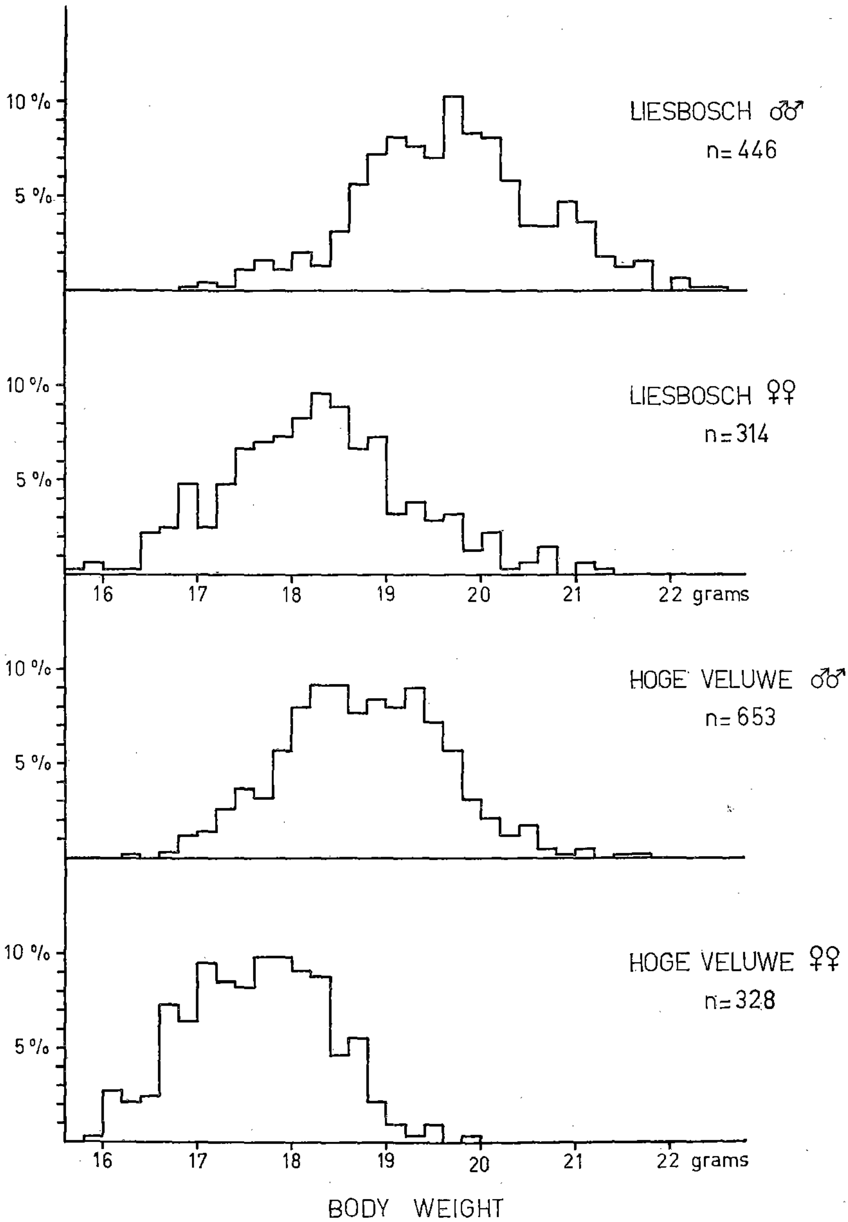

FIGURE 5. Frequency of body weights (in percent) of male and female Great Tits in the two main areas, all winters combined.

our material. In particular we will deal with the influence of different habitats on the winter weight. In discussing the effect of a factor on body weight we will eliminate the effects of other factors as much as possible; the data from each study area will therefore be presented separately.

2. Sex and body weight

In the two main study areas, the Hoge Veluwe and Liesbosch, a total of 1741 weights were collected in the winters of 1955-'56 to 1964-'65. These weights can be plotted graphically to show the percentual frequency of each weight class (classes of 15.01 to 15.20 grams etc.), as in Figure 5. These graphs indicate a considerable difference in the weight of males and females. Table 9 gives the average weights of males and females from these areas, and from the other areas with less extensive material. The difference in mean weight of males and females varies from 0.57 gm in the Imbosch to 1.58 gm in Meyendell, which is from 3.1% to 8.8% of the female weight. This percentual difference is somewhat larger than the sex difference in wing length given in Table 5. For wing length the difference between the sexes was largest in the deciduous habitats, but for body weight this is not the case. Here two of the deciduous woods, Liesbosch and Meyendell, show large differences, but the third one, Oosterhout, where the average weights of males and females are highest, has a small sex difference in weight. In the next section we will consider the differences in weight due to habitat, and then the conclusions reached here will be discussed more fully.

Table 10 shows that the sex difference in weight was very marked in each of the years at the Hoge Veluwe and Liesbosch. These differences were statistically significant in each case ($P < 0.01$). Moreover, in each year the sex difference in weight at the Liesbosch was larger than at the Hoge Veluwe. Comparison of the sex difference in weight in each of the years with the average weights of males and females shows that the sex difference in weight at the Hoge Veluwe was large in years with a low mean weight of the females and small in years with a high mean female weight. There was no relation with the mean weight of the males. This could mean that the weight of the females in this wood depends to a greater extent on food or other factors than that of the males. Although in the Liesbosch the sex difference in weight was larger than at the Hoge Veluwe, the variations in this difference from year to year were actually smaller, pointing to a more stable situation in the deciduous wood in winter.

TABLE 9

DIFFERENCE IN MEAN BODY WEIGHT OF MALES AND FEMALES IN ALL AREAS

Area	Males			Females			Difference between means (gm)	Difference in percent of female weight
	n	$\bar{x}$	s	n	$\bar{x}$	s		
Hoge Veluwe	653	18.76	0.84	328	17.65	0.74	1.11	6.3
Oranje Nassau's Oord	144	18.72	0.87	123	17.78	0.87	0.94	5.3
Kreelsche Bosch	46	19.05	1.00	43	17.87	0.94	1.18	6.6
Waterberg	109	18.94	0.90	65	17.80	0.94	1.14	6.4
Imbosch	38	18.87	0.75	28	18.30	0.73	0.57	3.1
Oosterhout	55	19.94	0.89	28	18.91	0.84	1.03	5.4
Liesbosch	445	19.68	0.96	315	18.28	1.00	1.40	7.7
Vlieland	176	19.03	1.12	102	17.92	1.15	1.11	6.0
Meyendell	359	19.43	1.09	132	17.85	0.79	1.58	8.8

TABLE 10

SEX DIFFERENCE IN WEIGHT IN THE TWO MAIN AREAS OVER A TEN-YEAR PERIOD

Years	Hoge Veluwe					Liesbosch				
	Males		Females		Difference in (gm). between means	Males		Females		Difference (in gm.) between means
	n	$\bar{x}$	n	$\bar{x}$		n	$\bar{x}$	n	$\bar{x}$	
1955-'56	30	18.33	20	17.05	1.28	21	19.42	13	17.91	1.51
1956-'57	34	18.93	19	17.74	1.19	39	19.19	27	17.55	1.64
1957-'58	2	—	5	—	—	33	19.95	14	18.50	1.45
1958-'59	64	18.83	41	17.99	0.84	32	20.50	31	18.96	1.54
1959-'60	56	18.59	39	17.52	1.07	28	20.16	27	19.03	1.13
1960-'61	87	18.98	45	17.55	1.43	49	19.59	41	18.13	1.46
1961-'62	124	18.59	50	17.54	1.05	69	19.40	51	18.04	1.36
1962-'63	55	18.93	20	17.60	1.33	54	20.16	28	18.65	1.51
1963-'64	103	18.67	49	17.61	1.06	48	19.13	37	17.88	1.25
1964-'65	96	18.84	40	17.95	0.89	73	19.67	46	18.33	1.33

In section II. 1 it was shown that the males have considerably longer wings than females. It is probable that the other body dimensions of the males are also larger. In section III. 4 it will be shown that there is a marked correlation of wing length and body weight in a group of birds of the same sex and habitat. Therefore, it is quite possible that the difference in weight of the two sexes can be accounted for by differences in body dimensions. This can be tested by comparing the weights of males and females with equal wing lengths. When this is done we find that the sex difference in weight persists and is still significant ($P < 0.01$). The extent of the sex difference decreased to about 1.10 grams in Liesbosch and 0.75 grams at Hoge Veluwe.

In the difference in weight between groups of male and female tits the age of the birds may play a role too. It will be shown below (section III. 5) that differences in weight according to age occur and that these differences remain when birds of equal wing length are compared. If the age structure of the groups of males and females differs, this may have an effect on the mean weight of the two groups. Therefore, we must compare males and females within each class of wing length and age. When this is done we still find considerable differences in the weight of males and females. In all samples with at least 10 observations of males and 10 of females the sex difference was statistically significant ($P < 0.05$). This result leads us to the conclusion that male Great Tits are heavier than females of equal age and wing length. This probably means that the males carry more fat.

As mentioned in the introduction, we estimated the amount of fat visible through the skin, during the winters 1959-'60 to 1963-'64. The results of these fat estimates should be considered critically because the method used is not accurate enough to exclude observational errors and differences in observation between observers. As the great majority of the observations at the Hoge Veluwe and Liesbosch were done by two observers, and their share of the work was about equal in all five years, we assume that differences between observers are unlikely to have played a role in the results given in Table 11. This is especially true of the differences between males and females, but also holds for the differences according to habitat discussed later. Table 11 shows that in nearly all years the mean fat value of the males is slightly higher than that of the females. However, the differences are small and statistically insignificant, except in 1963 at the Hoge Veluwe, when the sex difference was significant ($P < 0.01$; t-test). Application of the t-test to the total of all five years shows significant sex differences in both areas: $P < 0.01$ for the Hoge Veluwe and $P < 0.04$ for the Liesbosch. This result, and the fact that the

TABLE 11

AVERAGE FAT VALUES IN THE TWO MAIN STUDY AREAS

Year	Hoge Veluwe		Liesbosch	
	♂♂	♀♀	♂♂	♀♀
1959-'60	1.6	1.4	2.2	2.1
1960-'61	3.0	2.7	3.1	2.9
1961-'62	2.4	2.4	2.5	2.4
1962-'63	2.7	2.3	3.6	3.1
1963-'64	2.2	1.8	2.2	2.1
All years	2.34	2.07	2.77	2.52
n	388	179	247	178

differences in the separate years all point in the same direction, makes it very probable that the difference in mean fat value of males and females is real.

The fact that males carry more fat than females is in accordance with the observations by KLUYVER (1951, 1957) on the dominance of males over females when feeding at food provided by man. The same relation probably exists in fights over natural food, but observations on this subject are lacking. Moreover, KLUYVER (1957) described the dominance of males over females (and of older birds over yearlings) in the competition over nest-boxes as roosting sites. This possibly results in a better condition of the males, assuming that a nest-box is a more favourable roosting site than natural roosts. But this factor is unlikely to play a role in our material because all birds were caught when roosting in nest-boxes and it is probable that both males and females had roosted in these boxes for a period of some weeks preceding the catch.

3. LOCAL AND REGIONAL DIFFERENCES IN BODY WEIGHT

In the introduction the possibility of variations in weight and wing length in relation to habitat was mentioned as the principal subject of this study. While the differences in wing length due to habitat were small, examination of Figure 5 and Table 9 shows that larger differences occur in the average weight in groups of tits from different habitats. From Table 9 it is clear that the highest mean weights occur in the broadleaved habitats (Oosterhout, Liesbosch, and Meyendell). An exception is formed by the females in Meyendell, which are about as heavy as the females from the pine woods in the Veluwe area, and by the females from the Imbosch, but in the latter case the number of observations is probably too small for a valid conclusion.

The difference in the mean weight of tits from the Hoge Veluwe and

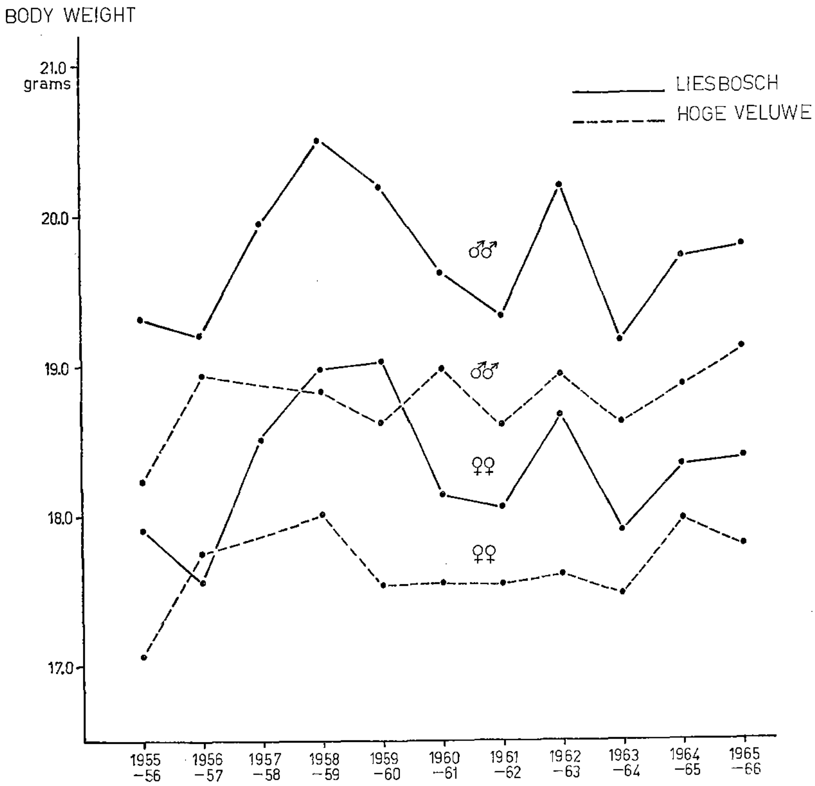

FIGURE 6. Annual fluctuations in the average weight in the two main areas.

Liesbosch is in most years very marked. This can be seen in Figure 6, where the mean weights of males and females over the period of the study are plotted. There is one exception, i.e. the winter of 1956-'57 when a change from the usual procedure, viz. continuation of the weighings in the Liesbosch until three hours after midnight, complicated the picture. When the average for the Liesbosch in this winter is corrected, it increases to about 19.4 grams (♂♂) and 18.1 grams (♀♀), which is higher than the average for the Hoge Veluwe. The difference in the mean weight of tits from the Hoge Veluwe and Liesbosch is in almost all years significant ($P < 0.01$), except in 1956-'57 for the ♀♀ ($P = 0.14$ for the corrected data) and in 1963-'64 for the ♀♀ ($P = 0.07$).

Apart from a difference in mean body weight the tits from the Liesbosch and Hoge Veluwe also differ in the variability of body weight. In the Liesbosch the standard deviation of the weight is 0.96 gm for the males, and 1.00 gm for the females; the corresponding values for the Hoge Veluwe are 0.84 and 0.74 gm. This means that body weight is more variable in the area with the highest mean weight. The same conclusion holds when the coefficients of variation are compared, i.e. the standard deviation expressed as a percentage of the mean weight. We conclude that body weight is more variable in the Liesbosch, both absolutely and relatively. This can be explained by assuming that in the Hoge Veluwe the tits are not able to attain their full range of weight variation because food shortage prevents them from becoming heavier, and starvation possibly eliminates the very light birds.

A further aspect of the study of weight variability is the relation of weight variability to the mean weight of an individual. BALDWIN & KENDEIGH (1938) showed that in the Chipping Sparrow (*Spizella passerina*) an individual varies least in weight when its average weight most nearly agrees with the average of the species. To study this aspect in the Great Tit I selected all individuals of which at least two weight records were available and classified these birds according to their mean weight in the weight classes 16.01-17.00, 17.01-18.00 gm, etc. For the total of all weight records of all individuals belonging to each of these weight classes the mean weight, the standard deviation, and the coefficient of variation were computed. The standard deviation proved to be essentially equal for all weight classes, and the coefficient of variation decreased with increasing mean weight of an individual. Thus, heavy birds vary as much in weight as light birds, in an absolute sense, but in relation to their mean weight they are less variable.

In section III. 2 we showed that the difference in weight between males and females, found by comparing the total weight data, continued to be significant when birds of the same class of age and wing length are compared. Here we will follow the same procedure and compare the weight of birds from the two main habitats classified according to age and wing length (see Table 12). In this table the data from all years have been combined. Among the first-year males the difference is significant in 5 out of 7 cases; in the remaining two cases the Liesbosch group is too small to permit a valid conclusion. Among the older males the difference is significant in all 7 cases, even where the groups contain only a few birds. Among the females the situation is less clear, but here too in all cases where both groups contain at least 10 birds, the Liesbosch birds are considerably heavier than those from the Hoge Veluwe. In only two cases is this difference significant; but in two other cases significance is nearly reached. The difference in weight of birds from the Liesbosch and

Hoge Veluwe is therefore most marked among the male tits, and is moreover more marked in older than in first year birds. The relation between body weight and age will be discussed further in section III. 5.

At least part of the difference in the weights of birds from these two woods can be attributed to a difference in the amount of subcutaneous fat. Table 11 shows that in two out of five years (1959-'60 and 1962-'63) the Liesbosch birds carried considerably more fat than those from the Hoge Veluwe. This difference is significant in these two winters and in the combined data from all five winters. Comparison with Figure 6 shows that in these two winters the difference in body weight in the two habitats was very large, but that in the other three winters the Liesbosch birds were still heavier than those from the Hoge Veluwe. Hence, the larger amount of fat is not the only factor responsible for the higher weight of the birds in the oak wood.

A comparison of the mean body weight in our study areas with data from other authors must necessarily be a very rough one because many factors influence body weight and the effect of these factors on the results of other authors is often unknown. The only conclusion we can draw is that the mean weight of OWEN's tits near Oxford (19.5 gm for the males; OWEN 1954) and the mean weight of KEIL's tits near Frankfurt (18.8 gm for the males; KEIL 1962) do not differ appreciably from the mean weight of the Dutch tits, and that the mean weight found by HAFTORN in Oslo (20.5 gm for the males; HAFTORN 1951) is considerably higher. This agrees well with the conclusions drawn by SNOW (1954) who found a good correlation between body size and winter climate.

4. THE RELATION BETWEEN WING LENGTH AND BODY WEIGHT

In several bird species a correlation of wing length and weight in material from the same population has been established. Examples of this are given by BEER & BOYD (1962, 1963) for the geese *Anser brachyrhynchus* and *Anser albifrons*, and by GRIMM (1954) and LÖHRL & BÖHRINGER (1957) for the House Sparrow (*Passer domesticus*). In this respect wing length is assumed to be a good indicator of body size.

To investigate this problem, the weight data for the male and female tits from the Liesbosch and Hoge Veluwe were divided into groups according to the corresponding wing length, usually in wing length classes of 1 mm width, at the ends of the frequency graphs wider. In this section and section III. 5 data from another winter (1965-'66) have been included to obtain larger samples. The resulting mean weights per wing length class can be seen in Figure 7.

TABLE 12

DIFFERENCE IN WEIGHT OF GREAT TITS FOR THE TWO MAIN AREAS, WITH EQUAL AGE AND WING LENGTH

a. *First-year birds*

Wing length	Males					Females				
	Liesbosch		Hoge Veluwe		P of difference	Liesbosch		Hoge Veluwe		P of difference
	n	x̄	n	x̄		n	x̄	n	x̄	
68-68.5						4	18.24	7	17.25	0.23
69-69.5						1	—	19	17.57	—
70-70.5	5	18.93	20	18.54	0.45	11	18.37	11	17.58	0.06
71-71.5	9	18.58	33	18.58	—	7	18.11	6	18.50	(0.52)
72-72.5	14	19.56	54	18.81	< 0.01	7	18.45	8	17.93	0.23
73-73.5	16	19.49	32	18.83	< 0.01					
74-74.5	15	19.96	25	18.71	< 0.01					
75-75.5	7	20.05	18	19.11	0.03					
76-76.5	3	20.66	6	19.21	0.02					

b. *Second and third-year birds*

Wing length	Males					Females				
	Liesbosch		Hoge Veluwe		P of difference	Liesbosch		Hoge Veluwe		P of difference
	n	x̄	n	x̄		n	x̄	n	x̄	
69-69.5						20	18.94	11	17.56	< 0.01
70-70.5						26	18.06	23	17.57	0.09
71-71.5	3	19.27	6	18.14	0.02	35	18.03	18	17.77	0.32
72-72.5	16	19.45	26	18.65	< 0.01	27	18.34	22	17.59	< 0.01
73-73.5	29	19.53	38	18.57	< 0.01	10	18.59	14	18.05	0.18
74-74.5	35	19.77	59	18.62	< 0.01	8	18.33	7	18.40	(0.87)
75-75.5	47	19.95	52	18.77	< 0.01					
76-76.5	30	20.04	24	18.99	< 0.01					
77-78	9	19.79	20	18.93	< 0.01					

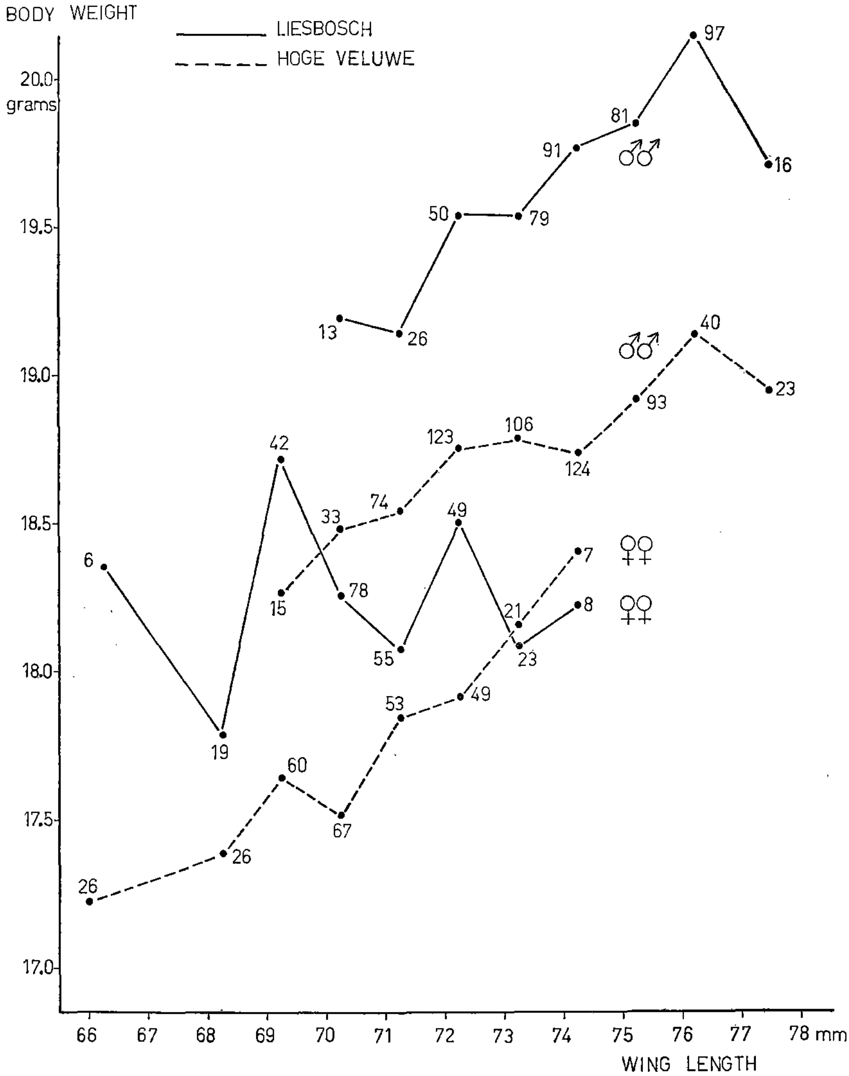

FIGURE 7. Relation of weight and wing length in the two main areas. Numbers beside the points give the sample size.

From this figure it is clear that in three of the four groups of birds there is a distinct positive correlation between weight and wing length. The female tits from the Liesbosch do not show this correlation, but have an irregularly fluctuating weight without an upward trend over the range of wing length. This group forms an exception to the usual pattern since the positive correlation of weight with wing length is also present in the data from Vlieland, Meyendell, and Oranje Nassau's Oord, for both males and females. From the position of the lines in Figure 7 it is clear that the long-winged females in the Liesbosch have a much lower weight than would be expected from the values of the males and females from the Hoge Veluwe and the Liesbosch' males. Proceeding from the conclusion that conditions in the Liesbosch permit a higher body weight than in the Hoge Veluwe (section III. 3) we must restrict this conclusion to the males and the short-winged females. Possibly conditions are not sufficiently favourable to permit a high body weight for the long-winged females. It is reasonable to suppose that the long-winged females, i.e. females with a large body size, need more food to maintain themselves than the short-winged females. The objection that the male tits, which have a still larger body (judged from the wing length), do not encounter the same difficulties in reaching a high body weight, can be met by assuming that the males are dominant over the females in the competition for food. In section III. 2 this possibility has already been mentioned. We point out, however, that this explanation for the low body weights of the long-winged females in the Liesbosch must be regarded as purely suggestive. Another possibility might be the assumption that in the Liesbosch the females' wing length is not a good indicator of the body size, but there are no known reasons why this should be the case.

Further, we investigated the significance of the correlation between wing length and weight for each of the age classes. To this purpose we classified the data from the two main areas according to the age of the birds and applied a rank correlation test (KENDALL) to the data on weight and wing length in each of the age classes. The results, given in Table 13, show that in each of the groups there is a positive correlation between wing length and weight as judged from the plus signs for the r_k value. The Liesbosch females once more form an exception, and we will restrict the discussion to the other groups. The positive correlation is in most cases significant ($P < 0.05$). In two cases (the oldest ♂♂ in the Liesbosch) this level of significance is not reached, but this is probably due to the relatively small sample size. (Addition of the 1965-'66 data to the total of the preceding years resulted in all cases in a decrease in the value of P, so the adding of more data to the total of Table 13 would probably result in a decrease in the value of P below 0.05). The value of r_k fluctuates with the age of the birds, and is minimal in the second-year birds. This means that the increase of body weight with increasing wing length

TABLE 13

SIGNIFICANCE OF THE CORRELATION BETWEEN WING LENGTH AND BODY WEIGHT IN BIRDS OF DIFFERENT AGE CLASSES

Age	Liesbosch						Hoge Veluwe					
	Males			Females			Males			Females		
	n	r_k	P	n	r_k	P	n	r_k	P	n	r_k	P
e	76	+0.349	< 0.001	40	0	1.00	221	+0.171	< 0.001	71	+0.261	0.001
*m*2	153	+0.139	0.01	116	—0.045	0.47	211	+0.148	0.001	102	+0.158	0.02
*m*3	54	+0.160	0.08	41	+0.039	0.72	58	+0.192	0.03	21	+0.348	0.02
*m*4-7	37	+0.186	0.10	30	—0.123	0.43						

NOTE: r_k is the coefficient of rank correlation according to KENDALL.
P is the probability with which the observed correlation can be attributed to chance.

is less steep in this age class than in both younger and older birds. Probably only the difference in the r_k value of *e* and *m*2 is significant; for the older birds the samples are much smaller.

5. VARIATION OF BODY WEIGHT WITH AGE

In many species of birds the yearling birds are lighter in weight during the first summer and autumn than the adults. In the following winter this difference has ceased to exist in some species and continues to exist in others (BALDWIN & KENDEIGH 1938). To the latter group of species belong, for instance, the House Sparrow (*Passer domesticus*, LÖHRL & BÖHRINGER 1957), Rufous-sided Towhee (*Pipilo erythrophthalmus*, DAVIS 1961), Rook (*Corvus frugilegus*, BÄHRMANN 1960), Capercaillie (*Tetrao urogallus*, KOSKIMIES 1958), and several goose species (ELDER 1955, COOCH *et al.* 1960, BEER & BOYD 1962, 1963).

In the Great Tit the nestlings weigh at fledging time about 0.5 to 1.0 grams less than their parents. This difference occurs in all study areas from which nestling weights are available. From the period of fledging until October no weights are available. The following discussion is based on winter data (November to January).

Since the age of many of our tits is known and many of these birds were weighed several times during their life, it is possible to study the weight fluctuations during the life of an individual tit. On the other hand, many factors influence body weight and it is usually impossible to eliminate their effect by weighing the same individual year after year under similar conditions (time of the year, time of the day, temperature, density of the tits, feeding conditions, wing length of the birds). Hence it is more profitable to collect a large number of weights from many different birds and to assume that the factors cited above have a roughly equal effect on the mean weight of each of the groups of birds. This is acceptable because the birds of all age-classes were weighed in the same period of the evening and likewise on the same dates in each winter, therefore under identical conditions. Only the difference in wing length between yearlings and older birds has to be allowed for.

We will consider first the relation between age and weight in the combined data of all winters. Figure 8 gives the mean weight of each of the age groups separately for the whole sample and for that part of the sample consisting of birds of exactly-known age. In the Liesbosch the highest mean weights occur in the third-year birds, both males and females, and the body weight decreases sharply in the fourth year. The figures for Vlieland agree well with this. For the Hoge Veluwe there is no

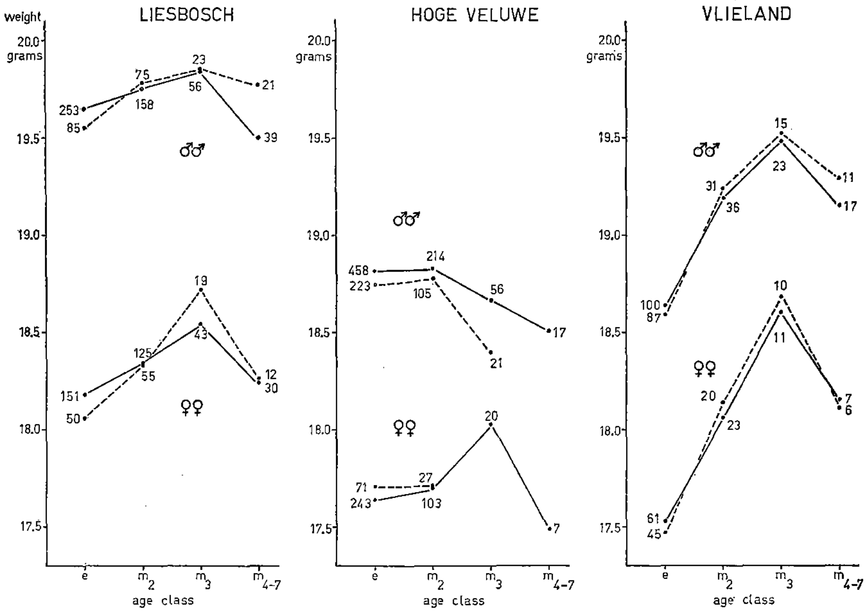

FIGURE 8. Relation of weight and age. Full lines give the whole sample, broken lines birds whose age is exactly known. Numbers beside points give the sample size.

weight change from the first to the second age group, a decrease in the third year among the male tits, and a doubtful (on account of the small sample size) increase among the females. Male and female tits in this area show a similar decrease in body weight in the fourth year. Probably it is usual for a Great Tit to increase in body weight up to its second or third year, and to decrease in its fourth year, possibly as a consequence of old age. The results for the Hoge Veluwe may be explained by assuming that feeding conditions in this wood are less favourable. Apart from a lower mean weight for all tits (cf. section III. 3), this might have some effect on the ability of the tits to increase in weight in the second and third year, and might even advance the weight decrease associated with old age. In this respect mention must be made of the fact that the mean life span of the tits in the Liesbosch is considerably longer than that of the Hoge Veluwe birds.

The broken lines in Figure 8 do not deviate appreciably from the solid lines. The main differences are in the Liesbosch males and females, where the immigrants are somewhat heavier than the yearlings, and in most cases where the samples are relatively small (Liesbosch ♂♂ *m*4 and ♀♀ *m*3, Hoge Veluwe ♂♂ *m*3). Since the differences between immigrants and indigenous birds are small, we will combine the two groups of birds in the following discussion.

From Figure 8 it is clear that the differences in weight due to age are relatively small. It turned out that in the Liesbosch and the Hoge Veluwe these differences are not apparent in each winter, and that in some winters the differences do not correspond with the picture shown in Figure 9, but are actually reversed (*e* heavier than *m* in the Liesbosch in 2 out of 10 winters, *e* lighter than *m* in the Hoge Veluwe in 2 out of 10 winters). In other winters the mean weight of yearlings and older birds was equal, especially in the Hoge Veluwe. In only one case the difference was significant (Liesbosch ♀♀, 1960-'61; $P = 0.006$). However, we must remark that in most winters the samples, especially from the yearlings, were very small. Therefore we cannot expect significant differences in most of the winters.

In section II. 3 we argued that wing length might not be a good indicator of body size when we study variations in the course of the life of the tits. For this reason we refrain from an analysis of the effect of age on body weight in birds of equal wing length.

6. The daily weight cycle

In birds that feed by day there is a weight increase during the day and a weight decrease during the nocturnal period of rest. The extent of the weight fluctuations within one day varies from species to species. Nice (1938) found in some North American passerines values varying from 4.6% to 10.8% of the mean body weight. Moreover, there are other factors that affect the extent of the daily weight fluctuations. Lees (1949) found in the Robin (*Erithacus rubecula*) that the daily weight fluctuations were much smaller in summer than in winter (3% and 6% of the evening weight, computed by me from his data). This difference can be readily understood if we bear in mind that in winter the nights last longer and the temperature is lower, both factors that cause a larger weight decrease. The nocturnal weight decrease has not a constant value during the course of the night, but is largest in the first few hours of the night, during the period of food digestion (cf. Helms & Drury 1960).

When studying the weight decrease during the night we must know something about the length of the nocturnal period of rest. Some data on this point, collected in a garden at Ede, have been published by Kluyver (1950). Since feeding conditions there were probably very different from the more natural conditions in our present study areas, it seemed advisable to collect more data on this point, and especially to

TABLE 14

A. AVERAGE TIME OF RISING IN RELATION TO SUNRISE

Area	December		January		February	
	I	II	I	II	I	II
Garden	—27.8		—25.1		(—21.8)	
Pine wood	—30.1	—24.0	—	—3.2	+0.3	—3.6
Oak wood	—22.1	—19.3	—	—3.5	—5.6	—8.2

B. AVERAGE TIME OF ROOSTING IN RELATION TO SUNSET

Area	December		January		February	
	I	II	I	II	I	II
Garden	+4.8		—1.3		—16.7	
Pine wood	+15.6	+17.3	—	+0.3	— 4.4	—12.8
Oak wood	+16.4	+ 7.9	—	—2.1	—11.0	—18.5

NOTE: + means after sunrise (sunset), — before sunrise (sunset). Bracketed figures are less reliable.

study different habitats. For this purpose we recorded the times of rising and roosting from January to March 1959 and December 1959 to February 1960 in an oak wood (Oosterhout) and a pine wood (Hoge Veluwe). Times of rising and roosting were automatically recorded by a chronograph (actograph), for 7 tits in the pine and 5 in the oak wood. Table 14 summarizes the results and compares them with those of KLUYVER (1950) from 1938-1941. KLUYVER's data (from his Figures 2 and 3) have been grouped as monthly averages, the recent data as half-monthly averages. Table 14 reveals a considerable difference in the rising time when the garden data are compared with those from the two woods. In January and February the birds in the woods rose about 20 minutes later than in the garden. Smaller differences exist in the roosting time: about 10 minutes later in December, a few minutes in January, and about 5 minutes in February. These differences in roosting time can be understood if we assume that the tits are satisfied earlier in the habitat where artificial food is provided. Another factor affecting the times of rising and roosting is the light intensity. This might show considerable differences according to habitat. However, it is improbable that this factor played an important role in the determination of the roosting time, since KLUYVER (1950) demonstrated that the variability in roosting time is not so much affected by weather factors (including changes in light intensity), as by the food requirements of the birds. The time of rising, on the contrary, was apparently strongly affected by weather factors, especially cloudiness. The difference in average time of rising in garden versus woods seems too large to be explained wholly by differences in light intensity, especially as the light intensity in the oak wood, which is without leaves during the winter, probably was not lower than in the garden. Thus, it is not clear why the garden birds rose so much earlier than the birds from the woods.

Differences in time of rising and roosting in oak and pine woods are small and do not exceed 10 minutes. In the evening the birds in the oak wood entered their roosts somewhat earlier (with the exception of December I). This may indicate that feeding conditions in the oak wood are better, permitting the tits to go to their roosts earlier. In the morning the birds in the oak wood rose 5 to 8 minutes later in December than the tits from the pine wood, in January the mean time of rising in the two woods was equal, and in February the oak tits were 5 minutes earlier. It seems probable that the light intensity in the oak wood, which has no leaves in winter and spring, is greater than that in the evergreen pine wood. This might explain the difference found in February, when the oak birds were the earlier risers. The difference in December (and possibly January) indicates once more the need of the tits in the pine wood to exploit the daylight fully for feeding.

We will take as average values for both habitats in the period November to January: 20 minutes before sunrise and 10 minutes after sunset. The mean duration of the period of activity is 8 hours 35 minutes, for the night period 15 hours 25 minutes.

The nocturnal weight decrease can be studied by means of the data from the normal night inspections, usually made between 19.00 and 23.00 hours. All times are expressed in relation to sunset, to facilitate comparison. Figure 9 shows the mean weights of all tits weighed in 1955-1965 in relation to the time of weighing. In general there is a gradual decrease in weight during this part of the night, except in a few cases, mainly where the sample is too small. This applies to the first hour after sunset and to the last point for the Hoge Veluwe ♂♂. Other irregularities may be caused by the variable effect of other factors such as wing length, age, and temperature.

In order to eliminate the effect of these other factors the weight loss of a group of 16 Great Tits (11 ♂♂ and 5 ♀♀) was studied during the night

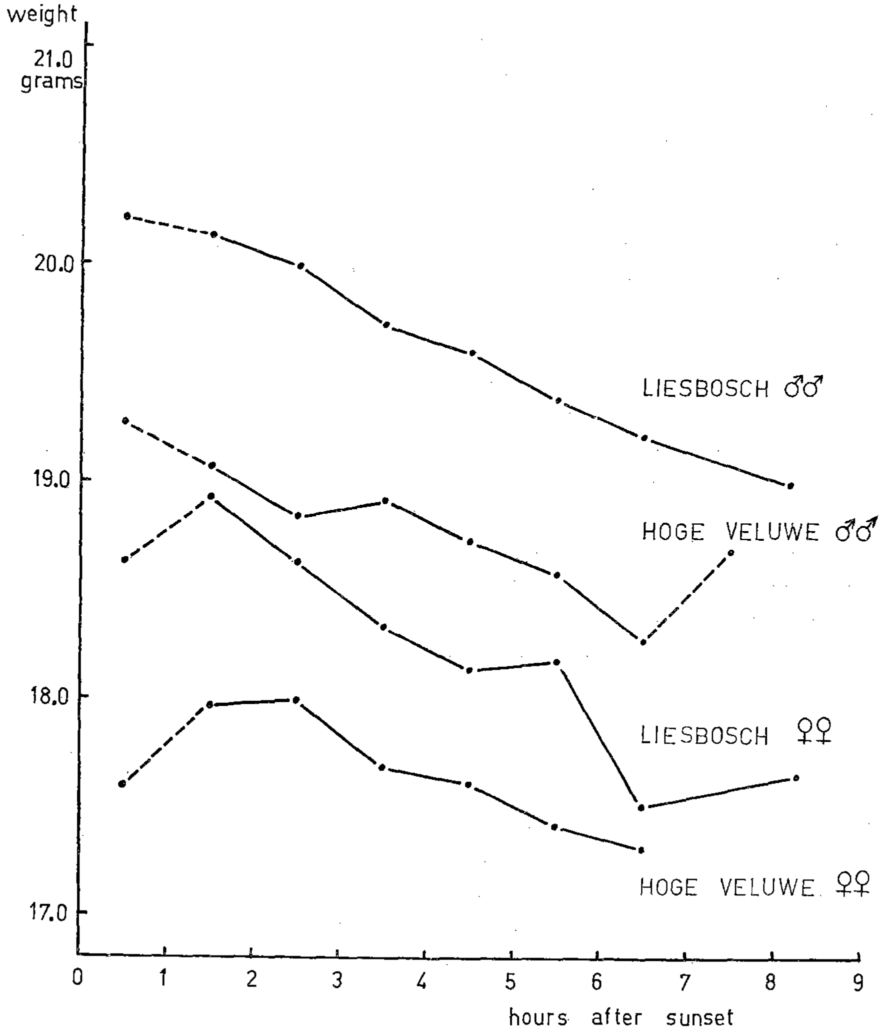

FIGURE 9. Body weight in relation to time of weighing. Dotted lines connect samples smaller than 20.

of 30 to 31 January 1964. These birds were taken from their roosting boxes shortly after sunset, weighed and then transferred to a row of nest-boxes on the wall of the field laboratory at the Hoge Veluwe. In the course of the night they were taken from these boxes and weighed at intervals of two hours. Handling did not disturb them appreciably. The

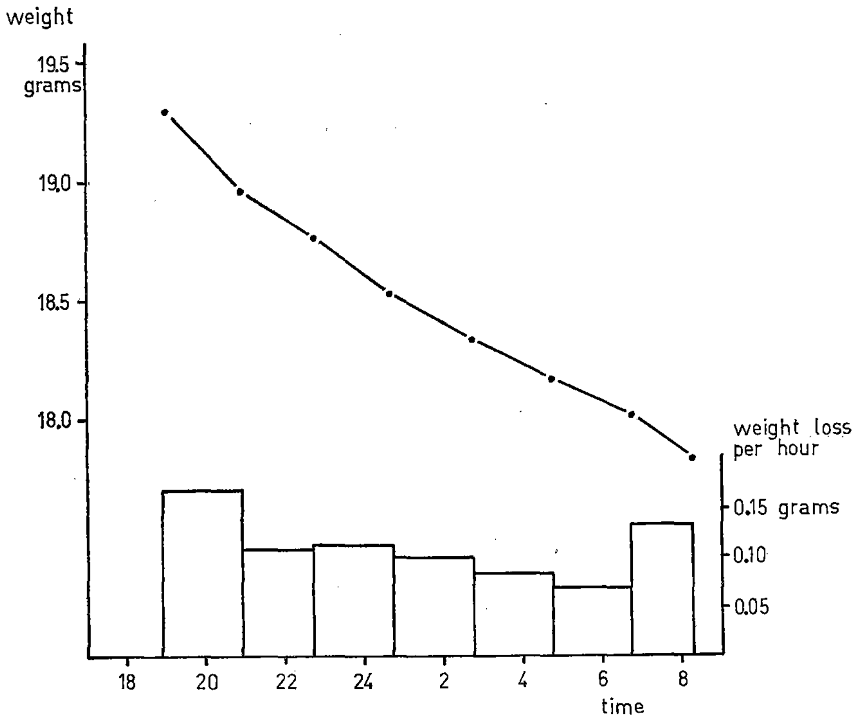

FIGURE 10. Nocturnal weight loss in a group of Great Tits (Hoge Veluwe 30/31-1-1964).

birds stayed in these boxes from 19.00 hours (i.e. about 1 hour and 40 minutes after their usual time of roosting) to 8.20 hours (i.e. about their usual time of rising). In this period of more than 13 hours they lost on the average 1.47 grams in weight (standard deviation 0.25 gm). This weight loss amounted to 7.6% of the weight at the start of the experiment, which is in good agreement with the value found for birds weighed only two times, at sunset and sunrise (see below). Figure 10 shows then weight decrease during this night and the magnitude of the decrease per hour between successive weighings. The weight loss is clearly largest in the first interval (0.167 gm per hour) and decreases in the course of the night, reaching 0.070 gm per hour in the last interval but one. Presumably the larger weight loss in the last interval is caused by some activity of the tits in the boxes at dawn.

Because it seemed interesting to learn more about the nocturnal weight loss and to investigate the factors influencing this weight loss, we weighed large numbers of Great Tits shortly after sunset and shortly before sunrise. These weighings were carried out at the Hoge Veluwe and in the Liesbosch in the winters of 1960-'61 and 1961-'62, from mid-November to early March. The period over which the weight loss was measured was somewhat shorter than the usual tit's night, viz. on the average from 50 minutes after roosting time to 25 minutes before the time of rising. Each tit remained in the box it had chosen for roosting. The only differences from the normal procedure at night were: the entrance hole was partly blocked to prevent escape and a plastic tray was placed in the nest-box to collect the tit's faeces. The dry weight of the faeces produced during the night was determined. The minimal temperature, measured in the wood with a thermometer at nest-box level, corresponded well with temperatures measured by neighbouring weather stations. We therefore used the temperature data provided by these stations (Deelen, 2 km from the Hoge Veluwe, and Gilze-Rijen, 17 km from the Liesbosch) when studying the effect of air temperature on the weight loss and the production of faeces during the night.

Table 15 gives the results of these weighings. The second column shows the composition of the groups of tits; it was impossible to keep the male-female ratio constant. It will be shown later that the results from males and females are nearly identical, which justifies combination of the results of the two sexes. Since the weighings are spread over a three-month period with a variable duration of the night, a correction is required. The mean weight loss over the period between the two weighings (column 5) was therefore converted to the weight loss in a 14-hour night. This corrected weight loss (column 7) was expressed as a percentage of the evening weight (column 8). The mean night temperature was computed as the average of the temperatures measured at 18, 21, 24, 3, and 6 hours.

In Table 15 it is noticeable that the mean nocturnal weight loss of a group of Great Tits is a rather variable quantity. For the Hoge Veluwe the data in column 7 result in a mean of 1.22 gm with a standard deviation of 0.18 gm, for the Liesbosch 1.23 gm and 0.25 gm. Moreover, it is clear that the night temperature affects the nocturnal weight loss. Weight losses exceeding 1.3 grams are only found with temperatures under zero. When the corrected weight loss is plotted against the night temperature (Figure 11) the result is a distinct negative correlation for both woods. In the data from the Hoge Veluwe the correlation appeared to be significant (KEN-

TABLE 15

MEASUREMENTS OF NOCTURNAL WEIGHT LOSS

1 Date	2 Sample size	3 Mean weight at night (gm)	4 Mean weight in morning (gm)	5 Mean weight loss (gm)	6 Mean interval between weighings (hours & minutes)	7 Corrected weight loss (gm)	8 Percentual weight loss	9 Mean dry weight of faeces (gm)	10 Mean night temperature (C)
					A. Hoge Veluwe				
6-12-1960	5♂, 2♀	19.37	18.18	1.19	14.36	1.15	5.9%	0.212	4.4
13-12-1960	8♂, 4♀	18.95	17.73	1.22	14.04	1.22	6.4%	—	—0.2
29-12-1960	5♂, 1♀	19.25	18.22	1.03	14.25	0.99	5.1%	0.191	0.0
5-1-1961	8♂, 2♀	18.93	17.90	1.03	14.19	1.01	5.3%	0.148	2.8
10-1-1961	6♂, 3♀	18.44	17.27	1.17	14.09	1.16	6.3%	0.137	1.6
13-1-1961	8♂, 2♀	19.06	18.00	1.06	14.00	1.06	5.6%	0.148	3.6
14-2-1961	7♂, 3♀	18.48	17.56	0.92	12.07	1.07	5.8%	0.137	7.0
21-2-1961	8♂, 7♀	18.20	17.17	1.03	11.50	1.20	6.6%	0.129	2.0
24-2-1961	6♂, 5♀	18.07	17.22	0.85	11.53	0.99	5.5%	0.094	8.4
15-11-1961	8♂, 1♀	18.56	17.36	1.20	13.43	1.22	6.6%	0.119	—0.4
24-11-1961	10♂, 3♀	18.65	17.43	1.22	13.43	1.24	6.6%	0.124	2.0
6-12-1961	5♂, 2♀	18.79	17.47	1.32	14.20	1.30	6.9%	0.128	0.2
15-12-1961	8♂, 3♀	18.86	17.30	1.56	14.30	1.51	8.0%	0.143	—3.0
18-12-1961	6♂, 3♀	18.99	17 38	1.61	14.12	1.59	8.4%	0.154	—8.2
4-1-1962	6♂, 2♀	18.59	17.17	1.42	14.27	1.38	7.4%	0.182	—1.4
23-1-1962	4♂, 4♀	17.84	16.77	1.07	13.54	1.08	6.1%	0.131	3.8
2-2-1962	3♂, 3♀	17.57	16.07	1.50	14.00	1.50	8.5%	0.114	—0.6
16-2-1962	1♂, 4♀	18.21	17.06	1.15	13.01	1.24	6.8%	0.112	5.0
					B. Liesbosch				
21-12-1960	6♂, 4♀	19.12	17.93	1.19	14.05	1.18	6.2%	0.150	3.0
22-12-1960	3♂, 2♀	19.26	18.27	0.99	14.16	0.97	5.0%	0.157	1.4
23-12-1960	6♂, 5♀	18.53	17.51	1.02	14.03	1.01	5.4%	0.119	1.4
18-1-1961	10♂, 5♀	19.44	18.07	1.37	13.27	1.42	7.3%	0.151	—4.6
19-1-1961	5♂, 6♀	19.05	17.92	1.13	13.34	1.17	6.1%	0.125	1.6
20-1-1961	7♂, 5♀	19.41	18.31	1.10	13.41	1.12	5.8%	0.130	3.0
27-2-1961	2♂, 2♀	18.86	17.96	0.90	11.59	1.05	5.6%	0.115	5.4
28-2-1961	6♂, 5♀	18.28	17.37	0.91	11.20	1.12	6.1%	0.097	5.0
1-3-1961	6♂, 8♀	18.57	17.69	0.88	11.26	1.07	5.8%	0.104	4.8
14-12-1961	13♂, 10♀	19.31	18.11	1.20	13.51	1.21	6.3%	0.168	2.8
30-1-1962	8♂, 4♀	19.94	18.29	1.65	12.52	1.78	8.9%	0.226	—5.8
31-1-1962	8♂, 5♀	20.14	18.54	1.60	13.29	1.66	8.2%	0.219	—0.8

DALL; $P < 0.01$). Essentially the same pattern emerges when the percentual weight loss (column 8) is plotted against temperature. In this case too the results from the Hoge Veluwe were significant ($P < 0.01$). From this we must conclude that the tits lose weight at a faster rate during cold than during mild nights, both absolutely and in relation to their evening weight.

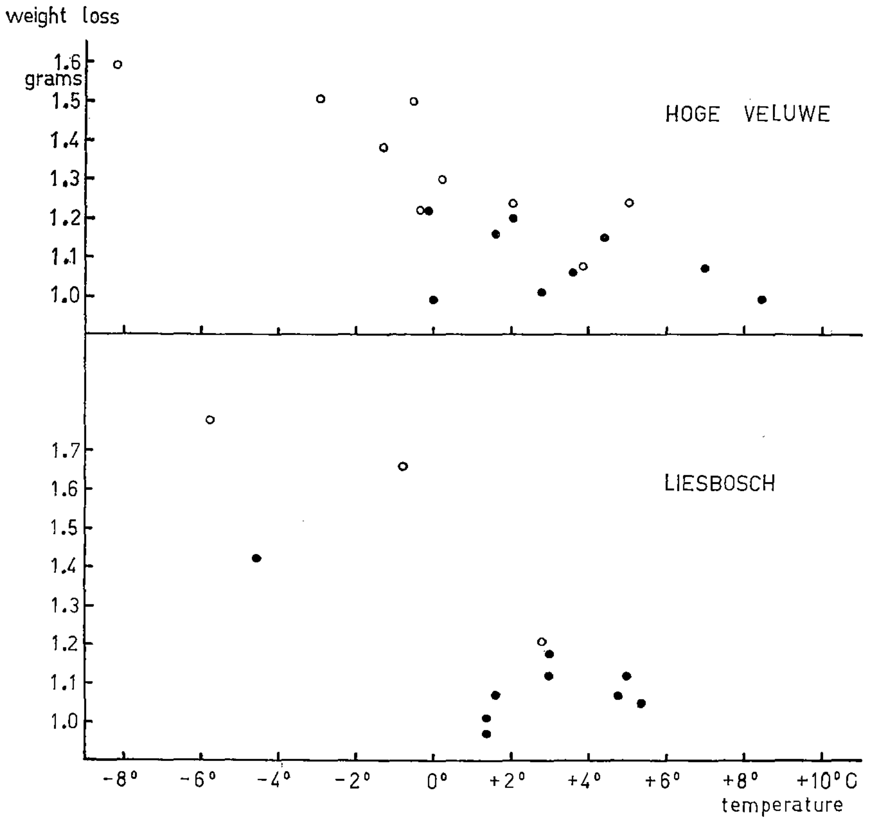

FIGURE 11. Corrected nocturnal weight loss in relation to night temperature. *Dots*: 1960-'61. *Circles*: 1961-'62.

For comparison of the results from the two habitats, the effect of the temperature must be taken into account. Therefore, we divided the data in two groups, one with night temperatures of at least 0° C, and one with temperatures under zero. The resulting mean weight, weight loss, and faeces production are given in Table 16. The sizes of the samples are such that it seems justified to draw the following conclusions:

TABLE 16

SUMMARY OF NOCTURNAL WEIGHT LOSS IN TWO HABITATS

	Temperature 0° C or higher					Temperature below 0° C				
	Sample size	Mean weight at night (gm)	Corrected weight loss (gm)	Percentual weight loss	Dry weight of faeces (gm)	Sample size	Mean weight at night (gm)	Corrected weight loss (gm)	Percentual weight loss	Dry weight of faeces (gm)
♂♂ Hoge Veluwe	73	19.03	1.14	6.0	0.141	39	19.05	1.39	7.3	0.152
♂♂ Liesbosch	54	19.55	1.17	6.0	0.145	26	20.32	1.59	7.8	0.191
♀♀ Hoge Veluwe	38	17.69	1.10	6.2	0.128	16	17.75	1.42	8.0	0.131
♀♀ Liesbosch	47	18.27	1.07	5.9	0.120	14	18.89	1.62	8.6	0.204

1. With temperatures of 0° and higher, differences in weight loss in the two areas are negligible. The production of faeces in the two woods is also nearly equal. Both males and females lose about 6% of their weight in a 14-hour night. The females produce a smaller amount of faeces, but when this is expressed as a percentage of the tit's body weight the difference becomes very small (Hoge Veluwe ♂♂ 0.74%, Liesbosch ♂♂ 0.74%, Hoge Veluwe ♀♀ 0.72%, Liesbosch ♀♀ 0.66%).

2. When the temperature falls below zero, the nocturnal weight loss increases. In the pine wood (Hoge Veluwe) the evening weight did not increase over the value found with higher temperatures. This results in an increase in the percentual weight loss and a decrease in the morning weight (not shown in Table 16). The production of faeces showed a very small increase. These results indicate that the tits in the pine wood are unable to increase their food intake as a response to the lower air temperature and are therefore unable to compensate for the increased nocturnal weight loss.

3. In the oak wood (Liesbosch) the temperatures below the freezing point are accompanied by a considerable increase in the evening weight, as well as in the absolute and the percentual weight loss. The increase in evening weight is so large that in spite of the high nocturnal weight loss the morning weight is still higher than in mild weather. The increase in evening weight is achieved by an increase in food intake, apparent from the large production of faeces. In this wood the tits succeed quite well in maintaining their body weight under unfavourable conditions.

4. With temperatures below the freezing point the females lose more weight overnight than the males, both absolutely and in relation to their evening weight. This difference in weight loss occurs in both habitats, which suggests that the larger weight loss by females is not caused by a higher food intake in the favourable oak wood. Presumable, the insulation of the plumage is less effective in the females.

7. Seasonal variation in body weight

In general, passerines in temperate regions tend to be heavier in midwinter than in any other season, except in migratory species and in female birds during the egglaying period. Several students of Great Tits have published information on this subject, but their results do not agree. Haftorn (1951) and Owen (1954) found that weight was maximal in December and November respectively. In both cases this was considerably earlier than the coldest months (January to February) in which the weight of most passerines usually reaches a peak. On the other hand KLUYVER's (1952) tits, at any rate the males, had their weight maximum in the coldest month, in this case December. OWEN (*loc. cit.*) explained his results by assuming that the tits build up a fat reserve in late autumn or early winter, when presumably there is plenty of food. As discussed earlier (section III. 1) it is not clear what causes the decrease in weight from November to March.

For a valid conclusion about the seasonal variation in body weight we should have a series of observations from autumn to spring, preferably from several winters. The information collected by us comes, however, from many winters and from a rather short period (about a month) within each winter. This period usually fell in December, in some years partly in November or in January. In three winters a number of birds were weighed in February. Most of the observations come from winters without artificial feeding. This is perhaps not entirely true for the Liesbosch, where the birds may obtain some food near houses outside the wood, but in our opinion it is improbable that more than a few of the birds had fed there regularly. (There are no recoveries from these houses). In the Hoge Veluwe it is improbale that artificial food near houses affected the weight of the tits because there are very few houses near the study area. During two winters (1958-'59 and 1959-'60) we provided artificial food in 8 boxes regularly filled with seed throughout the whole winter. During the first winter only one of these was visited frequently, so only a small percentage of the tit population will have profited from this food supply. In 1959-'60 most of the feeders were visited frequently, so we suppose that the artificial feeding influenced the weight and survival of the tits in this winter. The information from 1959-'60 has therefore been omitted for the following presentation.

The data from the remaining winters have been added together and classified according to date of weighing, usually in half months. The resulting graphs, given in Figure 12, show that the fluctuations in body weight in the four groups of birds are essentially similar. A small decrease from November to early December is followed by a regular increase up to late January. During February and March three of the groups show a sharp decrease in weight, as far as can be concluded from the small samples. In general, weight seems to be correlated inversely with the air temperature, which usually reaches a minimum in January.

Study of the seasonal weight fluctuations in relation to age reveals considerable differences in the material from the Hoge Veluwe. Here the increase in weight starts earlier among the adult tits (from 15 November

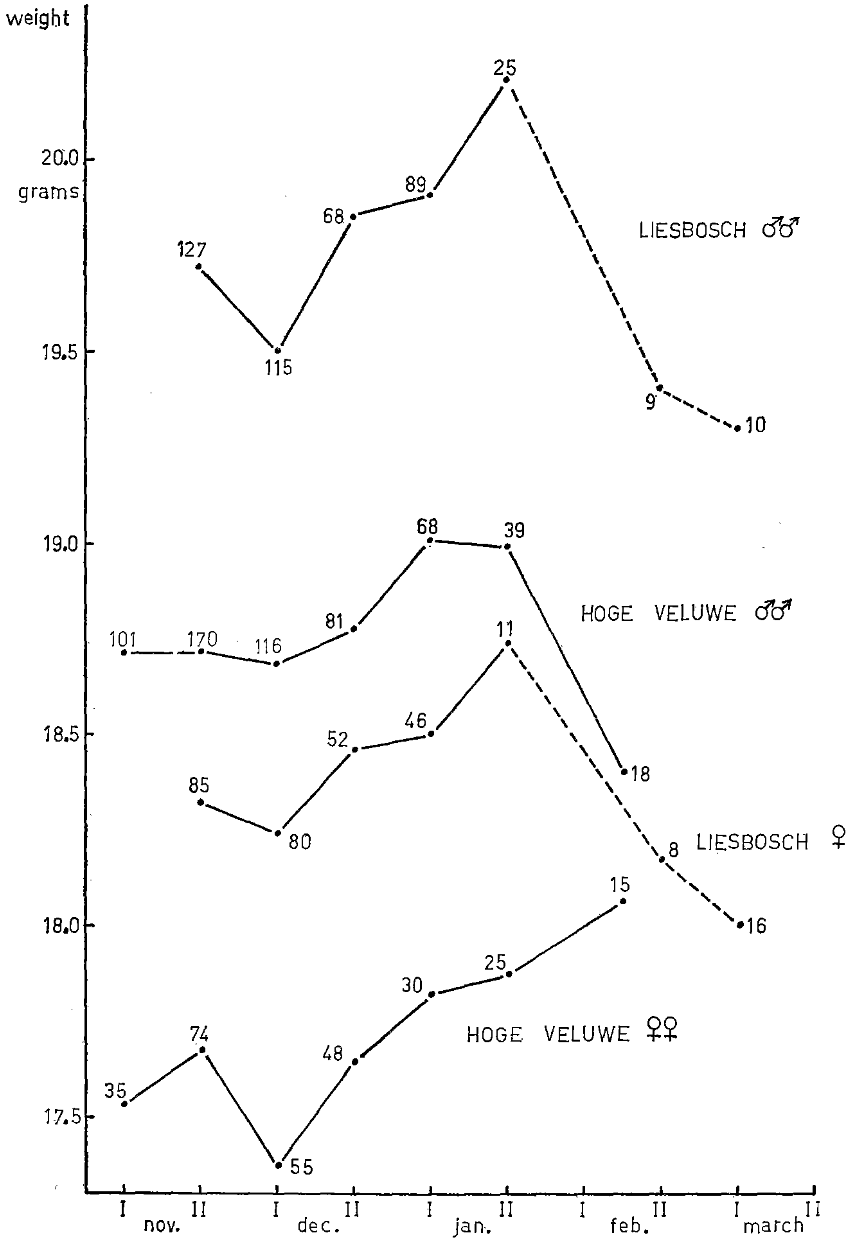

FIGURE 12. Seasonal variation in body weight in the two main areas. Numbers beside the points give the sample size. Samples smaller than 10 are connected by broken lines.

TABLE 17

WEIGHT FLUCTUATIONS IN SPRING 1965 AT THE HOGE VELUWE

Date	Mean weight				Weight change in tits weighed repeatedly	
	Males		Females			
15 Feb	19.76	(13)	18.24	(8)	—0.63	(9)
12 March	19.18	(15)	18.12	(6)	—0.28	(11)
22 March	18.80	(11)	17.50	(10)	—0.06	(6)
2 April	18.78	(8)	17.57	(8)		

NOTE: figures in brackets give the sample size.

in the females, 1 December in the males) than among the yearlings (from 15 December in the females, 1 January in the males). This difference of about one month was not found for the Liesbosch.

In the spring of 1965 several additional night inspections were made in order to collect more information about weight fluctuations in spring. These observations covered the same part of the wood, with the result that most of the tits were weighed several times. From Table 17 it is clear that these observations confirm the impression gained from Figure 12, viz. that the body weight decreases strongly in this part of the year in both male and female tits. This decrease amounted to about 1 gm in a number of birds which were weighed repeatedly. It can be seen that most of the decrease occurs before the middle of March and that the weight is more or less constant in the last days of March. Similar observations in the oak wood at Oosterhout gave as result: a decrease of about 0.5 gm in a group of female tits in the second half of March and a small increase in weight among the males in the same period. Combination of the two sets of data suggests that most of the weight decrease in the males occurs before 15 March, and most of the decrease in the females after this date.

In the winter of 1964-'65 numbers of Great Tits were trapped by day at a fixed spot in the Hoge Veluwe. At first this was done by placing mist nets at the edge of shrubs and trees. Later, from the end of December, the tits were caught in an automatic trap baited with seed. Seed was constantly available and may have contributed considerably to the condition of the tits. Table 18 gives the mean body weights at all trapping days from September to March. The means had to be corrected since captures were made at varying times of the day. The corrected means, given in Table 18, refer to a time of four hours before roosting time. Once more, the highest means are found in January or early February. The few data from late December, not shown in the Table, indicate a high weight in this period. Later (section III. 9) we will see that the air temperature had a great effect on the fluctuations in body weight during the winter.

TABLE 18

MEAN WEIGHT OF GREAT TITS TRAPPED BY DAY (Hoge Veluwe 1964-'65)

date	Males		Females		date	Males		Females	
15 Sept	18.84	(10)	17.28	(5)	5 Jan	19.83	(3)	—	(0)
16 Sept	18.13	(18)	16.46	(8)	15 Jan	19.10	(3)	—	(1)
22 Sept	17.57	(6)	16.69	(3)	21 Jan	19.26	(4)	—	(0)
23 Sept	17.67	(4)	17.29	(5)	2 Feb	19.31	(11)	17.73	(4)
30 Sept	18.80	(4)	—	(2)	9 Feb	18.76	(9)	—	(2)
7 Oct	18.73	(6)	16.93	(6)	17 Feb	18.55	(7)	—	(0)
13 Oct	18.60	(5)	—	(2)	25 Feb	18.60	(13)	17.61	(3)
20 Oct	18.07	(8)	17.34	(4)	17 March	18.24	(21)	17.03	(7)
27 Oct	18.49	(5)	—	(1)	24 March	18.34	(16)	16.94	(9)
5 Nov	19.14	(11)	17.09	(5)					

Observations made in recent years in Oosterhout show that the body weight does not increase until shortly before egg laying. These and other observations on weight fluctuations in summer will be published elsewhere.

8. ANNUAL VARIATION IN BODY WEIGHT

HAFTORN (1951) and OWEN (1954) demonstrated the existence of variations in the body weight of Great Tits from year to year, and argued that these variations were due to differences in air temperture between the winters. This phenomenon has been found in several passerine species.

For a valid comparison of the mean weight in different years it is necessary to allow for the seasonal variation discussed in the preceding section; this because the dates of weighing do not fall in the same period each year. In the early years the observations were done in December and January, from 1959-'60 mainly from mid November to the second half of December. Therefore, we must classify the data per month and compare the annual averages for each month. Table 19 gives the figures from the Hoge Veluwe. From this table it is clear that the differences in weight between years are relatively small. In December the annual means differ by at most 0.5 grams in the males; the somewhat larger differences in the females are unreliable on account of the small size of the samples. In November the annual differences are rather larger, and in some cases they are significant (in 1962-'63 the males were significantly heavier than in the preceding and the following winter; the females were heavier in 1962-'63 than in 1963-'64).

TABLE 19

MEAN WEIGHT OF MALES AND FEMALES IN DIFFERENT MONTHS AND YEARS (Hoge Veluwe)

	Males			Females		
	November	December	January	November	December	January
1955-'56	—	18.48 (20)	18.07 (7)	—	16.87 (13)	17.54 (5)
1956-'57	—	18.92 (35)	—	—	17.71 (19)	—
1957-'58	—	—	19.87 (2)	—	—	18.05 (5)
1958-'59	—	18.61 (16)	19.00 (39)	—	17.75 (11)	17.96 (20)
1959-'60	18.64 (25)	18.58 (31)	—	17.66 (16)	17.43 (23)	—
1960-'61	19.00 (17)	18.76 (21)	19.07 (49)	17.37 (11)	17.47 (11)	17.61 (20)
1961-'62	18.59 (124)	—	—	17.54 (50)	—	—
1962-'63	18.99 (40)	18.79 (15)	—	17.87 (11)	17.31 (9)	—
1963-'64	18.51 (28)	18.67 (59)	—	17.14 (10)	17.56 (30)	—
1964-'65	18.86 (50)	18.79 (31)	—	17.99 (23)	17.89 (10)	—

Among the factors possibly responsible for the differences in weight found above, air temperature is the most obvious. The effect of temperature on body weight will be discussed in section III. 9. Other likely factors are the food supply and the density of the tits in winter. Nothing is known about the winter food of the Great Tit in our study areas. Several authors have found that beechmast is very important as winter food in Great Britain and Sweden, and that the population fluctuations and the emigration of the tits are correlated with the size of the beechmast crop (HARTLEY 1953, GIBB 1954, BETTS 1955, ULFSTRAND 1962, PERRINS 1965). Although there are few beech trees in the Hoge Veluwe, it is perhaps worthwhile to search for a possible correlation of body weight with the beechmast crop, since PERRINS (*loc. cit.*) has shown that the population fluctuations are mainly synchronous over wide areas, including areas without beeches. Information obtained from annual communications of the State Forestry Service (Mededelingen Staatsbosbeheer) shows that moderate to good beechmast crops occurred in 1956, 1958, and 1960, in the remaining years the crop was nil to poor. There are slight indications that the winter weight of the tits varied in parallel with the beechmast crop in the early years of the study, but the size of the beechmast crop is clearly insufficient to explain the significant weight fluctuations in the years 1961-1965. The same applies to the data from the Liesbosch, where the body weight usually fluctuates in parallel with the fluctuations in the Hoge Veluwe (see Fig. 6).

A similar attempt to correlate the fluctuations in body weight with the density of the tits in winter was unseccessful. We conclude that neither the size of the beechmast crop nor the density of the tits has a demonstrable effect on the body weight in winter. In the next section it will become clear that the air temperature is the major factor responsible for the fluctuations in body weight.

9. Body weight and air temperature

In several of the preceding sections the effect of the air temperature on the body weight of tits has been mentioned. The birds appeared to lose more weight on cold than on mild nights, and in the oak wood the evening weight increased considerably with falling temperatures (section III. 6). With respect to the seasonal variation in body weight (section III. 7) the weights were apparently highest in the coldest month, January.

For a closer examination of the effect of air temperature, the mean body weight per observation day was compared with the mean temperature of that day and with the mean temperature of the preceding ten days. All days were used on which at least 10 ♂♂ (or ♀♀) were weighed, from November to January of all the years 1955-1965. For the mean air temperature, the temperatures registered every three hours at the weather stations Deelen (for Hoge Veluwe) and Gilze-Rijen (for Liesbosch) were taken. Because the information from each winter was not sufficiently ample we were forced to combine the data from all winters, and therefore could not distinguish between intra- and interseasonal fluctuations.

The temperature of the observation day, i.e. the mean of the temperatures measured at 9, 12, 15, and 18 hours, appeared to have little effect on the weight in the following night. In the data from the Hoge Veluwe there is no question of any correlation, but in the Liesbosch data weights were higher with low than with high temperatures. This correlation was weak and insignificant in the females, and only just significant in the males ($P = 0.049$, Kendall).

The effect of the air temperature is more clearly demonstrated when the mean temperature of the preceding 10 days is used. Figure 13 gives the resulting scatter diagrams for the Liesbosch. Both diagrams show a good negative correlation between temperature and body weight ($P < 0.01$). Once more the correlation is absent in the data from the Hoge Veluwe. This is in good agreement with the conclusions reached in section III. 6, where the nocturnal weight loss in the two habitats is discussed. Both results indicate that feeding conditions in the Liesbosch are better than in the Hoge Veluwe, where the tits do not succeed in raising their body weight with falling temperatures.

The amount of information available from Meyendell is so extensive that it permits the comparison of a number of dates within each winter.

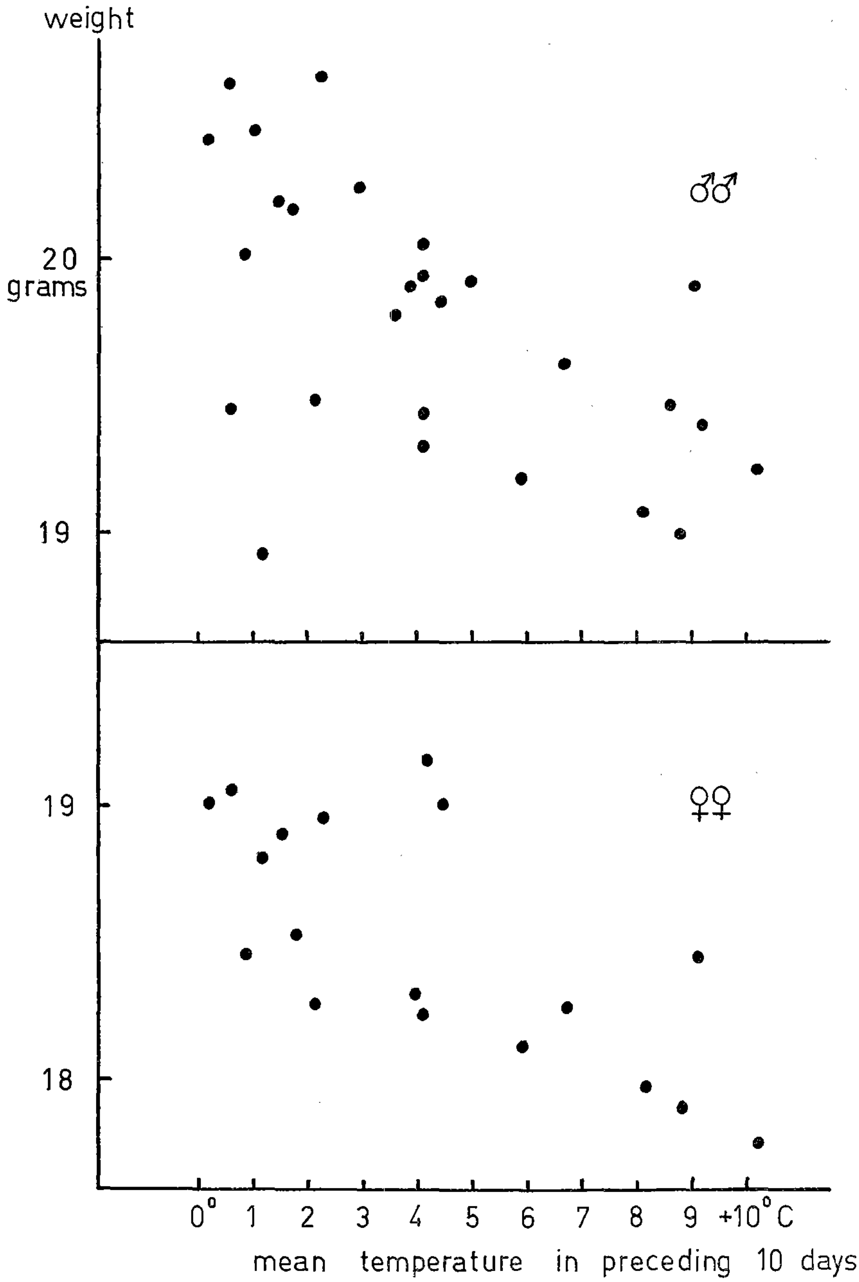

FIGURE 13. Relation of body weight and temperature in the Liesbosch. Each dot shows the mean weight of a group of tits, weighed at a given day, and the mean air temperature in the preceding 10 days. All years combined.

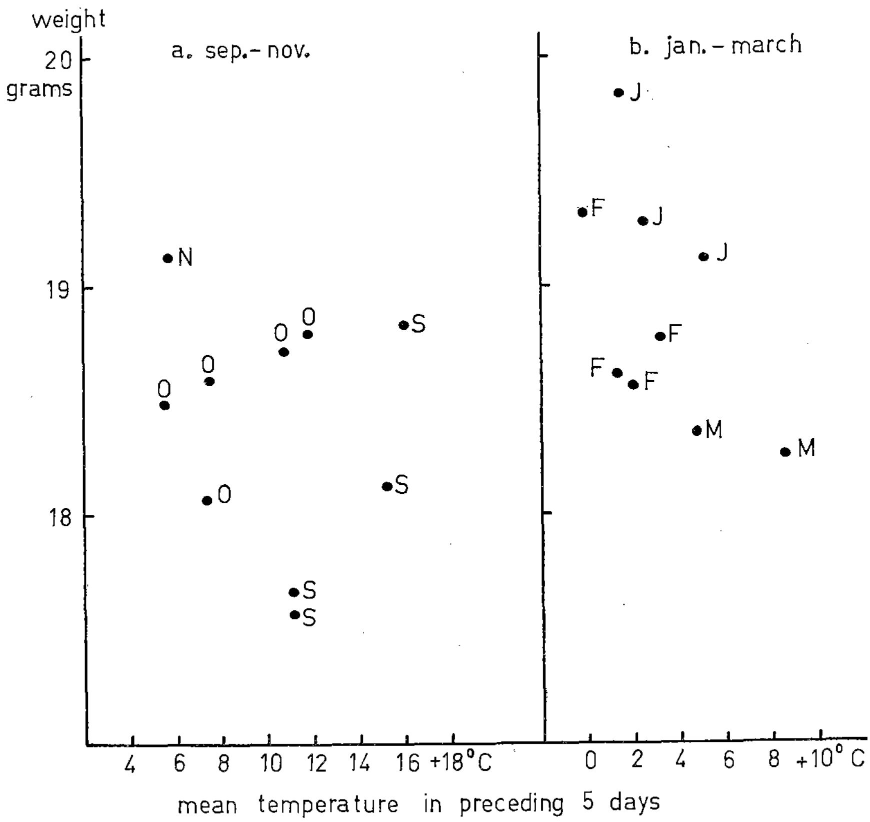

FIGURE 14. Relation of body weight and temperature in birds caught by day in the Hoge Veluwe. S = September, etc. Further explanation see text.

This results in a significant negative correlation between body weight and air temperature in each of the five winters studied (1959-'60 to 1963-'64).

The daytime catches of tits in winter 1964-'65 at the Hoge Veluwe can also be used to study the effect of temperature. In these catches we must distinguish between the period September to November, when the tits were caught in unbaited mist nests, and the period January to March, when food was provided by the observers to attract the tits permanently to the trapping site. During the autumn (Figure 14a) there is clearly no negative correlation between weight and temperature. On the one hand, the body weight seems to increase from September to November, on the other hand weight seems to be positively related to air temperature within each month. After the feeding station had been established the body weight increased considerably (January), but then decreased during

February and March, when temperatures rose. In these three months body weights showed a distinct negative correlation with air temperature. This also holds when the figures for each month are compared separately. Therefore, provision of food by man enabled the tits to react positively to the winter cold by putting on more weight. A similar conclusion was reached in section III. 6, for the noctural weight loss in relation to temperature, in oak and pine woods. Normally, feeding conditions on the Hoge Veluwe are such that a drop in temperature does not result in an increase in body weight, but an artificial improvement in the feeding conditions may change this into the same situation as that normally prevailing in the oak wood.

10. Conclusions

In section III. 3 we concluded that Great Tits living in deciduous woods are heavier in winter than tits from coniferous woods, which suggests that feeding conditions in deciduous woods are more favourable. This statement was confirmed by several conclusions from other parts of the study concerning differences between tits from Liesbosch and Hoge Veluwe. Among these conclusions we may mention: the larger variability of weight in the Liesbosch as compared with Hoge Veluwe (III. 3), the larger amount of fat carried by the Liesbosch birds (III. 3), the differences in the relation of weight to age (III. 5), the need for a slightly longer feeding period in the pine wood (III.6), the adequate response to cold in the oak wood, consisting of an increase in food intake (judged from increased faeces production at night) and resulting in a higher evening weight, whereas in the pine wood evening weights and faeces production did not increase with falling temperatures (III. 6), and lastly the correlation between body weight and air temperature found in the Liesbosch and the result of an improvement in feeding conditions in the Hoge Veluwe mentioned in the preceding section. All these facts indicate that feeding conditions during the winter are much better in oak than in pine woods.

Summary

A study was made of the various factors contributing to variation in wing lenght and body weight in the Great Tit, with special reference to differences due to habitat. Many hundreds of data on weight and wing length were collected in nine areas during the winters of 1955-'56 to 1964-'65. Most of this information was obtained from two areas: the Liesbosch (oak wood) and the Hoge Veluwe (mainly pine wood).

Special attention was given to the reliability of age determination and to the various methods of measuring wing length.

The wing length of the males exceeds that of the females by about 4%. The sex difference in wing length is largest in deciduous woods. In these woods the wings of both male and female tits are somewhat longer than in coniferous woods. This applies to yearling and older birds. Yearlings have shorter wings than older birds. After the first complete moult (i.e. in their second summer) the wing length remains constant. Abrasion of the primaries is very slight during winter, but plays a role during the breeding season. The mean wing length in a population varied strongly from year to year, probably influenced by feeding conditions and possibly by the weather during the moulting season.

Male Great Tits are significantly heavier than females during winter. This holds true when males and females of equal age and wing length are compared. Males have more subcutaneous fat than females. In both sexes the highest mean weights occur in the deciduous habitats. In these habitats, where feeding conditions in winter are presumably better, the variability of body weight is larger than in less favourable habitats. In most cases there is a distinct positive correlation between weight and wing length. This correlation exists in all age classes, but is least pronounced among the second-year birds. In most tit populations body weight increases with age until the second or third winter and then decreases. In the Hoge Veluwe, where feeding conditions are probably worse than in the areas mentioned above, body weight decreases from the first to the fourth winter, presumably representing a gradually worsening condition of the birds.

Observations on the times of rising and roosting show that in oak woods the birds need a slightly shorter period of activity for feeding than in pine woods. The rate of weight loss during the night is not constant but decreases in the course of the night. The nocutrnal weight loss was strongly affected by the air temperature; the tits lose weight at a faster rate in cold than in mild nights. With temperatures below zero the birds in the oak woods increase their evening weight by means of an increase in food intake, and more than compensate for the increased noctural weight loss. The pine wood birds are apparently unable to do this, and consequently lose weight during periods of prolonged cold. Body weight fluctuates seasonally with a maximum in January and a minimum shortly before the start of the breeding season. Annual variation in weight is very small and is not clearly affected by the size of the beechmast crop or the density of the tits. Seasonal and annual fluctuations in body weight are related to air temperature, especially when feeding conditions are good.

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SAMENVATTING

Onderzocht werd welke factoren bijdragen tot de variatie in *gewicht* en *vleugellengte* van de Koolmees. Hierbij werd speciale aandacht geschonken aan verschillen, veroorzaakt door het bewonen van verschillende biotopen. Dit werd bestudeerd aan de hand van vele honderden gegevens, die in de periode van 1955 tot en met 1965 des winters in negen bossen verzameld werden. De

meeste gegevens zijn afkomstig van het *Liesbosch* bij Breda (eikenbos) en het zuidelijk gedeelte van de *Hoge Veluwe* (vooral dennenbos).

Speciale aandacht werd geschonken aan de betrouwbaarheid van de *leeftijdsbepaling*, en aan de verschillende methoden waarmee de *vleugellengte* kan worden gemeten.

Vleugellengte. De vleugellengte van de ♂♂ is ongeveer 4% groter dan die van de ♀♀. Het verschil tussen sexen is het grootste in loofbossen. In deze bossen hebben beide geslachten iets langere vleugels dan in naaldbossen. Dit geldt voor eerstejaars en overjarige mezen. Eerstejaars vogels hebben aanzienlijk kortere vleugels dan overjarige vogels. Na de eerste volledige rui (d.i. in de tweede zomer) blijft de vleugellengte constant. Slijtage van de slagpennen is 's winters zeer gering, maar is in het broedseizoen aanzienlijk. De gemiddelde vleugellengte in een populatie is variabel van jaar tot jaar, waarschijnlijk onder invloed van de voedselvoorraad en mogelijk ook van het weer in de ruitijd.

Gewicht. Mannelijke Koolmezen zijn des winters significant zwaarder dan vrouwelijke. Dit gaat ook op als ♂♂ en ♀♀ van gelijke leeftijd en vleugellengte vergeleken worden. Een deel van dit verschil komt op rekening van een grotere vetvoorraad bij de ♂♂. Beide sexen zijn in loofbossen aanzienlijk zwaarder dan in naaldbossen. In de gunstige biotopen, waar vermoedelijk het meeste voedsel beschikbaar is, is de variabiliteit in het lichaamsgewicht groter dan in de minder gunstige biotopen. In de meeste gevallen bestaat er een duidelijk positief verband tussen vleugellengte en gewicht. Dit verband treedt op bij alle leeftijdsklassen, maar is het minst duidelijk bij de tweedejaars vogels. In de meeste door ons onderzochte populaties neemt het lichaamsgewicht toe met toenemende leeftijd tot aan de tweede of de derde winter, en daalt daarna. In het dennenbos neemt het gewicht af van de eerste tot de vierde winter, wat wijst op een geleidelijk slechter wordende conditie van de vogels.

Waarnemingen over de tijdstippen, waarop de mezen 's morgens en 's avonds hun slaapplaatsen verlaten resp. betrekken, wezen uit dat de vogels in eikenbos kunnen volstaan met een iets kortere periode voor voedselzoeken dan in dennenbos. Het gewichtsverlies des nachts vindt niet plaats met een constante snelheid, maar deze snelheid neemt af in de loop van de nacht. De luchttemperatuur heeft grote invloed op het nachtelijk gewichtsverlies; de mezen verliezen in koude nachten veel meer gewicht dan in warme nachten. Bij temperaturen onder het vriespunt vertonen de vogels uit het eikenbos een hoger avondgewicht (doordat ze overdag meer gegeten hebben) en compenseren hiermee ruimschoots het toegenomen gewichtsverlies des nachts. De vogels uit het dennbos zijn hiertoe blijkbaar niet in staat; zij nemen af in gewicht tijdens langdurige koude perioden. Gewoonlijk fluctueert het gewicht in de loop van de winter, met een top in januari en een dal kort voor het begin van het broedseizoen. De variatie in gewicht van jaar tot jaar is gering, en wordt niet beinvloed door de grootte van de oogst aan beukennoten en door de dichtheid van de mezen. Seizoensfluctuaties en jaarverschillen in gewicht hangen samen met de luchttemperatuur, vooral wanneer er voldoende voedsel beschikbaar is.