Wilson Bull., 101(2), 1989, pp. 217–235

SEASONAL AND DIURNAL BODY WEIGHT VARIATIONS IN TITMICE, BASED ON ANALYSES OF INDIVIDUAL BIRDS

SVEIN HAFTORN[1]

ABSTRACT.—The main aim of this study was to test different graphical models showing possible patterns of seasonal and diurnal body weight cycles in passerines as proposed by Lehikoinen (1987). About 13,300 weight records of five different European tit species (Great Tit *Parus major,* Blue Tit *P. caeruleus,* Coal Tit *P. ater,* Marsh Tit *P. palustris,* Willow Tit *P. montanus*) were collected in the period from August 1987 to April 1988 at two study areas in central Norway (61°40′ and 63°15′N). To get sufficient weight data at desirable times of the day (in the early morning, at noon, and in the evening), an electronic balance was used as a bird table. The data collected allowed an analysis of the weight cycles for individual birds. Most birds, regardless of species, followed the "winter fattening strategy," i.e., both the morning weight, noon weight, and evening weight increased during autumn, reached a midwinter peak (usually in December), and then declined. One dominant Great Tit male deviated from this pattern and decreased in weight from September onwards, apparently for reasons other than starvation or competition with other birds. This trend may be related to its high-ranking status in the social hierarchy. It is argued that the weight variations in titmice are controlled by the photoperiod and air temperature, with photoperiod as the prime factor.

For quite some time it has been known that the body weight of many birds living in the northern temperate zone increases during the autumn, reaches a peak in midwinter and declines as springtime approaches. This trend applies, for example, to titmice (e.g., Haftorn 1951, 1976, 1982; Kluyver 1952; Owen 1954; Lawrence 1958; van Balen 1967). It is generally agreed that these variations in weight mainly are due to changes in fat content (Lawrence 1958, Chaplin 1974, Lehikoinen 1986; see also King 1972). Superimposed on this seasonal variation in body weight there is a marked diurnal variation. The birds build up a fat reservoir during the day for use during the coming night.

In some recent studies Lehikoinen (1986, 1987) has put forward four graphical models to illustrate the possible relationship between the seasonal and the daily variation in body weight (Fig. 1). According to model a, the birds only compensate for the nightly weight loss. Consequently, the morning weight decreases in winter, while the evening weight remains stable. If, however, the bird overcompensates, other possibilities exist. In model b, the bird makes only a partial compensation for the expected weight loss during the following night. The amplitude of the daily weight

---

[1] Dept. Zoology, the Museum, Univ. Trondheim, N-7004 Trondheim, Norway.

cycle increases, but the morning weight still falls. In model c, there is a full compensation for the expected weight loss, and consequently the morning weight remains stable. In all three models there is a daily stable point in body weight, either in the evening (a), on average (b), or in the morning (c).

Models a and b seem to be unrealistic because the safety margins are smallest in midwinter, just when the environmental conditions presumably are severest. Model c, on the other hand, seems to be biologically relevant. If, however, the bird overcompensates excessively, both the daily minimum, the average, and the maximum weight will increase in winter (model d). As Lehikoinen (1987) points out, true winter fattening can be achieved only through model d. In practice it is not easy to distinguish between models c and d. Lehikoinen (1987) emphasizes that an analysis based on weight records made at random times during the day can easily give an impression of true winter fattening, although the bird might be following model c, which assumes that the morning weight is stable. Both models assume an increase in the average winter weight. So, by simply looking at weight curves that show daily average weights, it is impossible to discern which of the two models the bird follows.

Birds whose weight pattern fits model d are considered by Lehikoinen (1987) to have adopted the "winter fattening strategy." This strategy presumably improves the survival chances for birds faced with unstable or unpredictable food resources in winter. On the other hand, the condition for adopting model c, the "constant morning weight strategy," is secure access to food throughout the winter.

Up to now, weight data for titmice have been obtained by catching the birds in traps or nets. In this way it is very difficult to get enough records at desirable times of the day, and in practice it is impossible to record weight curves for individual birds. Researchers have therefore been compelled to pool the data for several individuals and deal with the problem on a population level. Nevertheless, by using regression analyses Lehikoinen (1987) was able to establish substantial support in favor of model d, i.e., that both the morning and the evening weights increase in winter.

However, a safer way of testing the weight models would be to avoid estimated weight data and instead to weigh the birds at the correct times of day. These would include weighing the same birds in the early morning, just after roosting time, and then once again in the evening, just before the end of the daily activity period. To obtain enough data of this kind, it is hopeless to rely on usual methods of catching birds. Birds become shy after having been handled a few times. Furthermore, frequent handling disturbs them and may lead to an abnormal weight development. So it is necessary to find an alternative method of obtaining weight data for

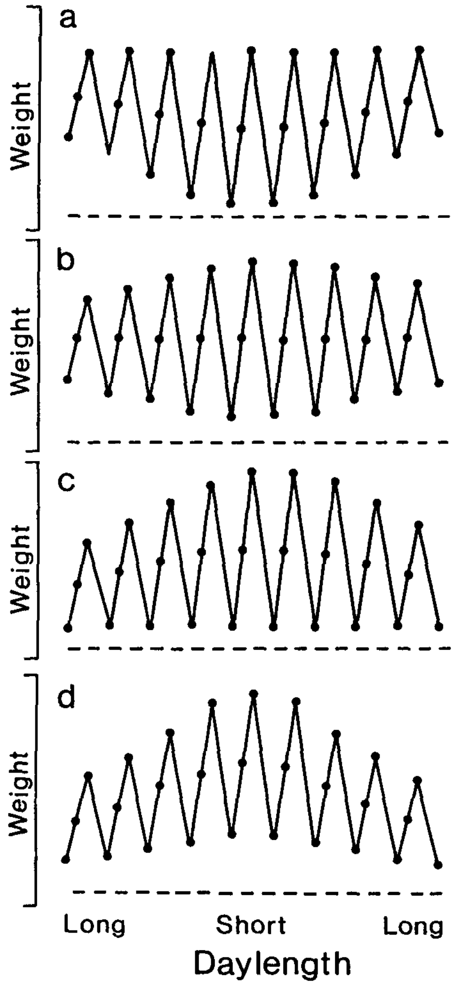


FIG. 1. Four graphical models showing the possible relationship between seasonal and diurnal variations in body weight. Horizontal broken line symbolizes an assumed constant minimum weight level which the birds just can tolerate. The daily weight amplitude is considered to be a direct function of night length, while air temperature is assumed constant. Further explanation in the text. (After Lehikoinen 1987).

free-living birds. Fortunately, such a method is readily obtainable. One can simply use an electronic balance as a bird table.

The main aim of this paper is to test the graphical models proposed by Lehikoinen (1987) and to look for possible interspecific differences.

STUDY AREAS, MATERIALS AND METHODS

I collected data regularly throughout the winter at two different sites in central Norway, in a conifer-dominated forest at Klaebu (63°15'N) near Trondheim at about 160 m above sea level, and in the birch region at Venabu (61°40'N) at about 900 m above sea level. Altogether 13,291 weight records were collected from August 1987 to April 1988 inclusive, for the following five species of titmice, the Great Tit (*Parus major*), the Blue Tit (*P. caeruleus*), the Marsh Tit (*P. palustris*), the Willow Tit (*P. montanus*), and the Coal Tit (*P. ater*) (Table 1). These are all common resident birds in Scandinavia. The Coal Tit is definitely the smallest, weighing only about 9–10 g, and the Great Tit the biggest, weighing about 17–21 g. All five species were present at Klaebu. At Venabu only the Willow Tit was recorded.

The electronic balance used for recording the body weights was a battery operated Sartorius model with an accuracy of 0.1 g. This was placed in a windshield, a box with one side open, outside the observer's house or hut. I could thus sit behind the window and read the data from a distance of a few meters. To attract the birds, a piece of solidified fat embedded with sunflower seeds was placed on the balance. All visiting birds were individually colorbanded. I used a flashlight to see the birds and the balance properly in the poor morning and evening light during the winter. Only birds which remained on the balance until it had stabilized were recorded.

I obtained weights at both study areas during the first and the last hour of the birds' daily activity period. At Venabu, I also collected weight data during one hour around noon (12:00 h ± 30 min). Only the weights of birds which regularly visited the balance are used in the present paper.

When calculating daily weight gain and nightly loss, respectively, I used principally the records made the first and the last 20 min of the daily activity period. Because of the geographical latitude of the study areas, in midwinter the birds had only 6–7 h at their disposal for foraging.

The climate during the winter 1987–88 was unusually mild, with little snow in the Klaebu study area. The average temperature of the coldest month (February) was −3.4°C and never fell below −20°C. At Venabu the temperature was somewhat lower, with a mean of −7 to −8°C for the coldest months (during my periods of stay in December–March), but even here only a few really cold spells occurred, with temperatures down to about −20°C. On the other hand, there were heavy snow falls, 1–2 m deep, at Venabu.

RESULTS AND DISCUSSION

In the present paper I deal with the birds individually and have in no cases pooled the data for different birds.

Seasonal weight variation.—The weight of most of the birds I studied, regardless of species, increased gradually toward a midwinter peak in December. As seen in Figs. 2–4 the winter increase does not apply only to the mean daily weight, a result in line with earlier findings (e.g., Haftorn 1951, 1976, 1982; Kluyver 1952; Lawrence 1958; van Balen 1967; Lehikoinen 1980), but also to the morning and evening weights, as well as to the noon weight (Fig. 2A–C). This pattern is consistent with Lehikoinen's (1987) model d, or "the winter fattening strategy." On the other hand, I found no clear evidence that any birds adopted the "constant morning weight strategy," although in some cases the morning weight was

TABLE 1
NUMBER OF BODY WEIGHT RECORDS FROM AUGUST 1987 TO APRIL 1988, INCLUSIVE

	Klaebu	Venabu	Total
Great Tit	2309 (16)[a]	—	2309 (16)
Blue Tit	356 (5)	—	356 (5)
Coal Tit	875 (4)	—	875 (4)
Marsh Tit	2648 (6)	—	2648 (6)
Willow Tit	3860 (16)	3243 (14)	7103 (30)
Total	—	—	13,291 (61)

[a] Number of different individuals is in parentheses.

relatively stable (Figs. 2D and 4A, C). This concerns especially one female Willow Tit, the morning weight of which showed no significant variation from November to April inclusive (analysis of variance, $P = 0.13$), but unfortunately, weight data from the period before November are completely lacking for this particular bird (Fig. 2D).

The degree of winter fattening can be illustrated by the difference found between the relatively low autumn weight and the winter peak weight. On the whole, the tits in this study increased their body weight by 2–8% from September–October to December. The question then arises as to whether any interspecific differences exist in the degree of winter fattening. According to Lehikoinen (1987), tits which store food increase their winter weight less than those which do not store. The tentative explanation is that food-storing tits have predictable food resources and are, therefore, less dependent on body fat deposition.

Fig. 5, however, lends no immediate support to this hypothesis. None of the Great Tits, a species which does not store food at all, increased their weight proportionally more than did the Marsh Tits or the Willow Tits, both of which are known to be food storers (Haftorn 1944, 1956b; Löhrl 1955; Cowie et al. 1981). Of course, it may be claimed that even the Great Tits had a predictable food resource in the present study, because they were being artificially fed. It is doubtful, however, that such an arbitrary situation would have completely masked a strategy which presumably is inherited.

Whatever the interspecific relationship is, Fig. 5 shows another striking feature, namely the great variation between individuals of the same species. In fact, one male Great Tit did not put on weight at all during the period from September to April, but gradually lost weight throughout the winter (Fig. 4D). Does this mean that the bird suffered from a lack of food or from competition with other birds? Certainly not, this specific male Great

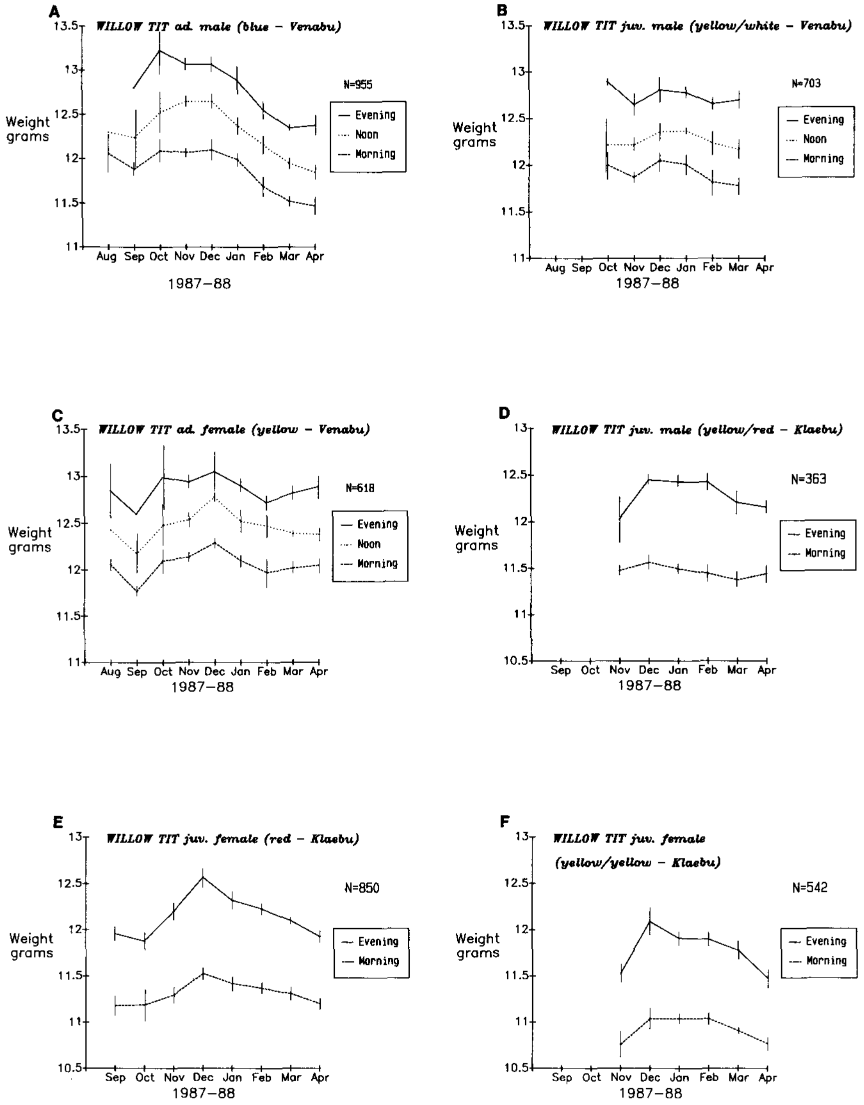


FIG. 2. Seasonal body weight variation (mean ±2 SE) of six Willow Tits. N = number of weight records.

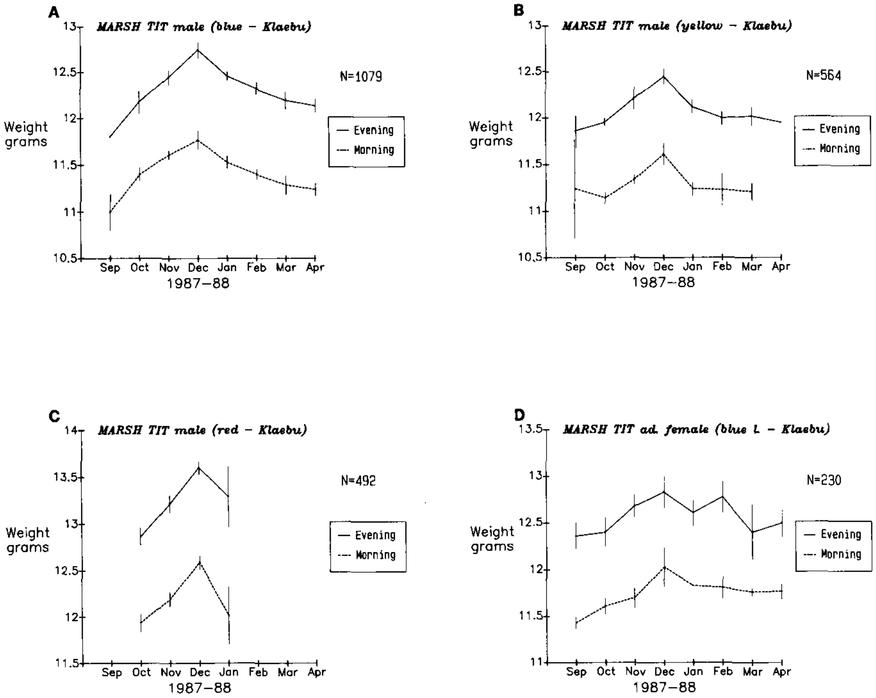


FIG. 3. Seasonal body weight variation (mean ±2 SE) of four Marsh Tits. N = number of weight records.

Tit was, in fact, the dominant bird and chased all other birds from the table and always had free access to the food supply.

Two things can be learned from Fig. 4D. First, this particular male Great Tit does not fit any of the models proposed by Lehikoinen (1987). Second, the weight-change pattern of such odd birds would have remained totally undetected if all the data had been pooled and dealt with at a population level.

Diurnal weight variation.—I found the diurnal weight cycle to be of a considerably higher magnitude than the winter fattening cycle. The daily variation has been expressed as the difference between the evening and morning weights as a percentage of the morning weight. Whereas the degree of winter fattening by the tits usually amounted to only 2–8% of their autumn weight, and for some individuals was even negative, the daily weight increase was about 7–12% of the morning weight. Interestingly enough, some differences between species were noted in this respect

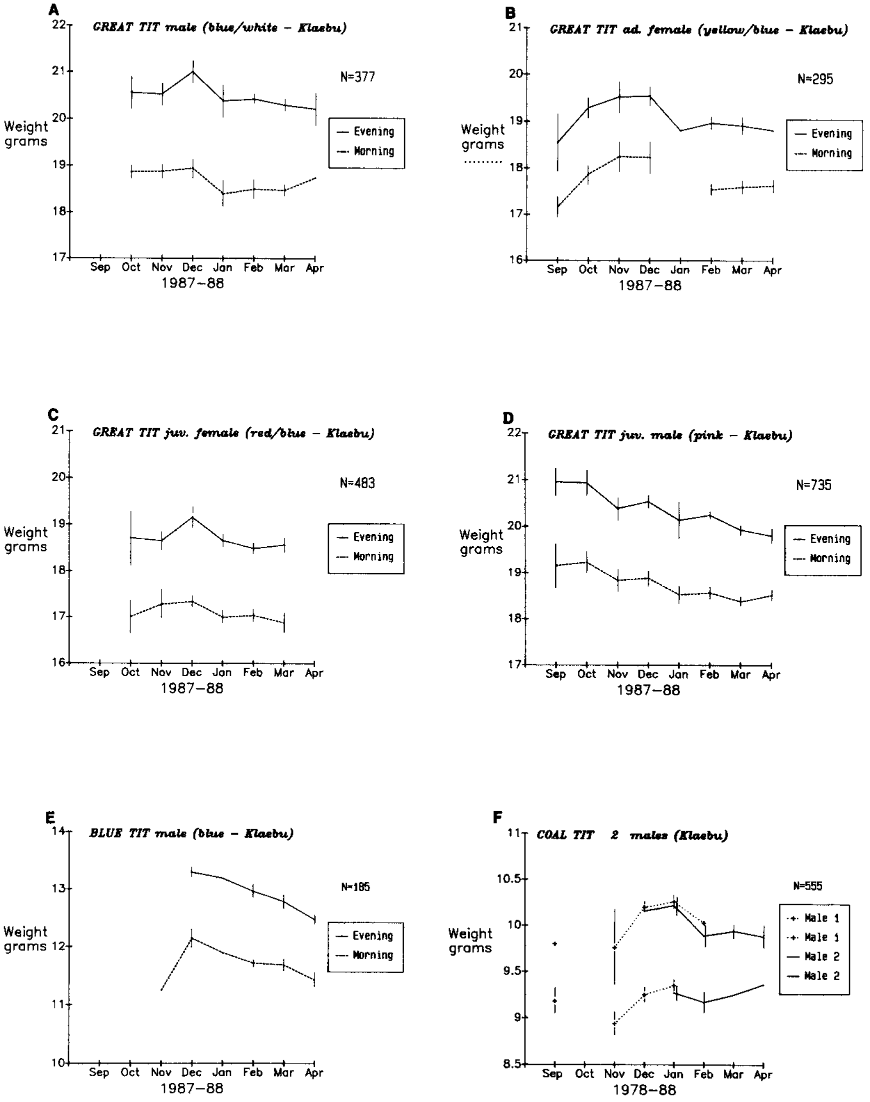
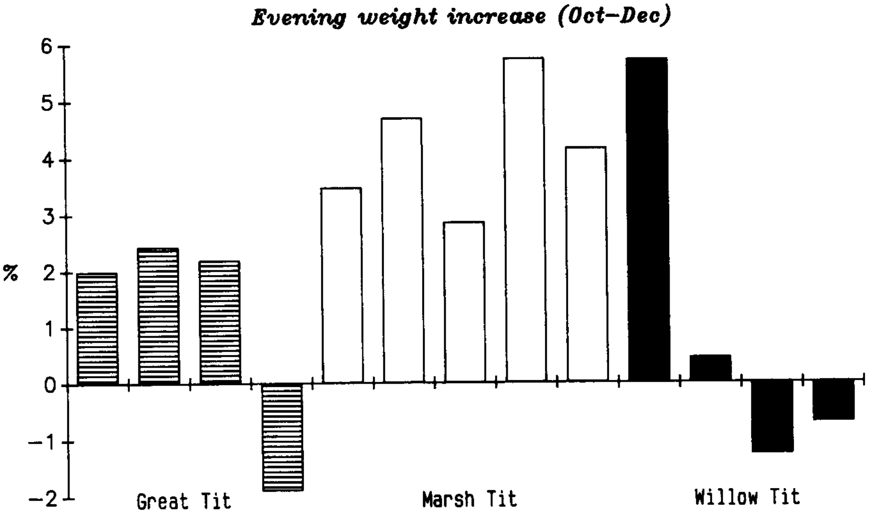


FIG. 4. Seasonal body weight variation (mean ±2 SE) of four Great Tits, one Blue Tit, and two Coal Tits. N = number of weight records.



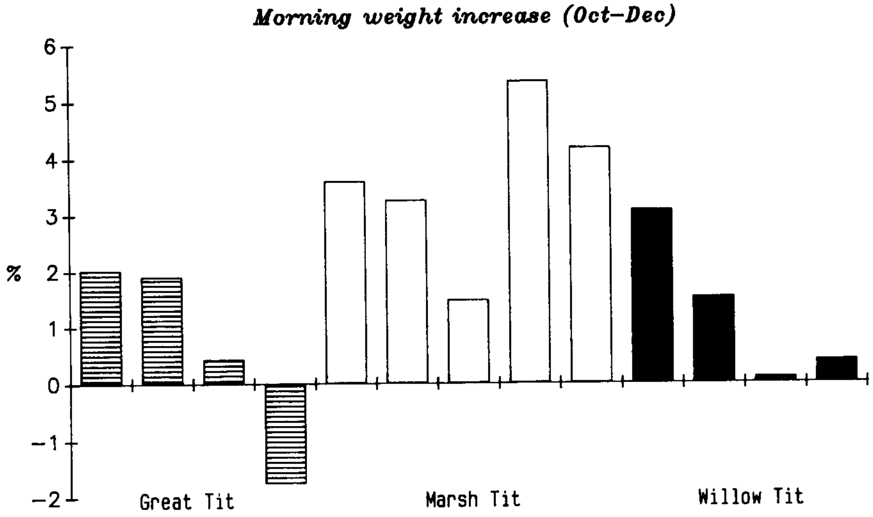


FIG. 5. Increase of the morning and evening body weights, respectively, of four Great Tits, five Marsh Tits, and four Willow Tits, from October on to the weight peak in December (expressed in percentages).

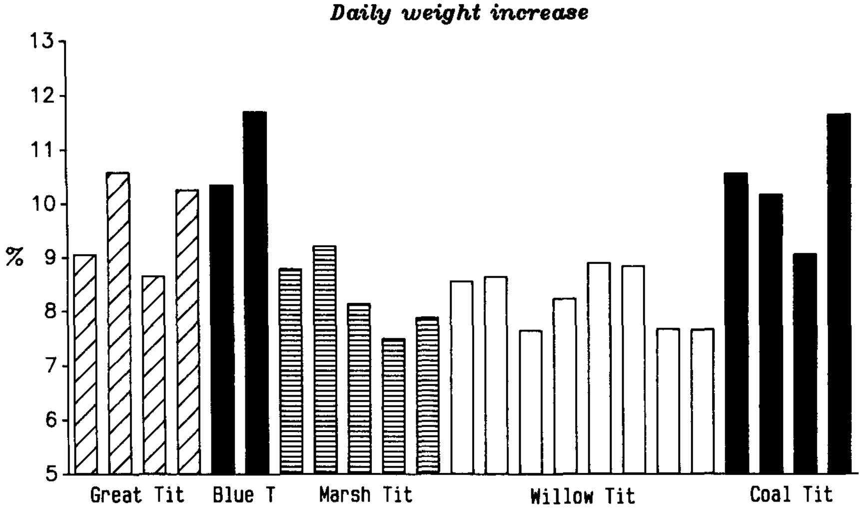


FIG. 6. Mean daily amplitude in body weight during the winter of four Great Tits, two Blue Tits, five Marsh Tits, eight Willow Tits, and four Coal Tits, as expressed in percentage of the morning weight (=minimum weight).

(Fig. 6). The Great Tit, Blue Tit, and Coal Tit all showed a proportionately greater diurnal amplitude in body weight than the Marsh Tit and the Willow Tit, viz. 9–12% and 7–8%, respectively. The difference between the two groups is statistically significant (Mann-Whitney *U*-test, $P < 0.001$).

It is noteworthy that the Coal Tit and the Great Tit, which are the smallest and the largest, respectively, of the present species both belong to the group showing the greatest weight variation. If this trio, the Great Tit, Blue Tit, and Coal Tit need relatively more energy than the Marsh Tit and the Willow Tit, as indicated by the present data, this would possibly have a negative impact on their winter survival rates. It may not be a mere coincidence that the former species lay relatively larger clutches and are fairly regular double-brooders, in contrast to the Marsh Tit and the Willow Tit. Another feature which characterizes the two groups is the degree of sedentariness. The Marsh Tit and the Willow Tit are known to be much more sedentary than the others. On the other hand, representatives of food-storing species are found in both groups, since in addition to the Marsh Tit and Willow Tit, the Coal Tit also regularly stores food (Haftorn 1956a).

As the days get shorter and the nights longer during the early winter,

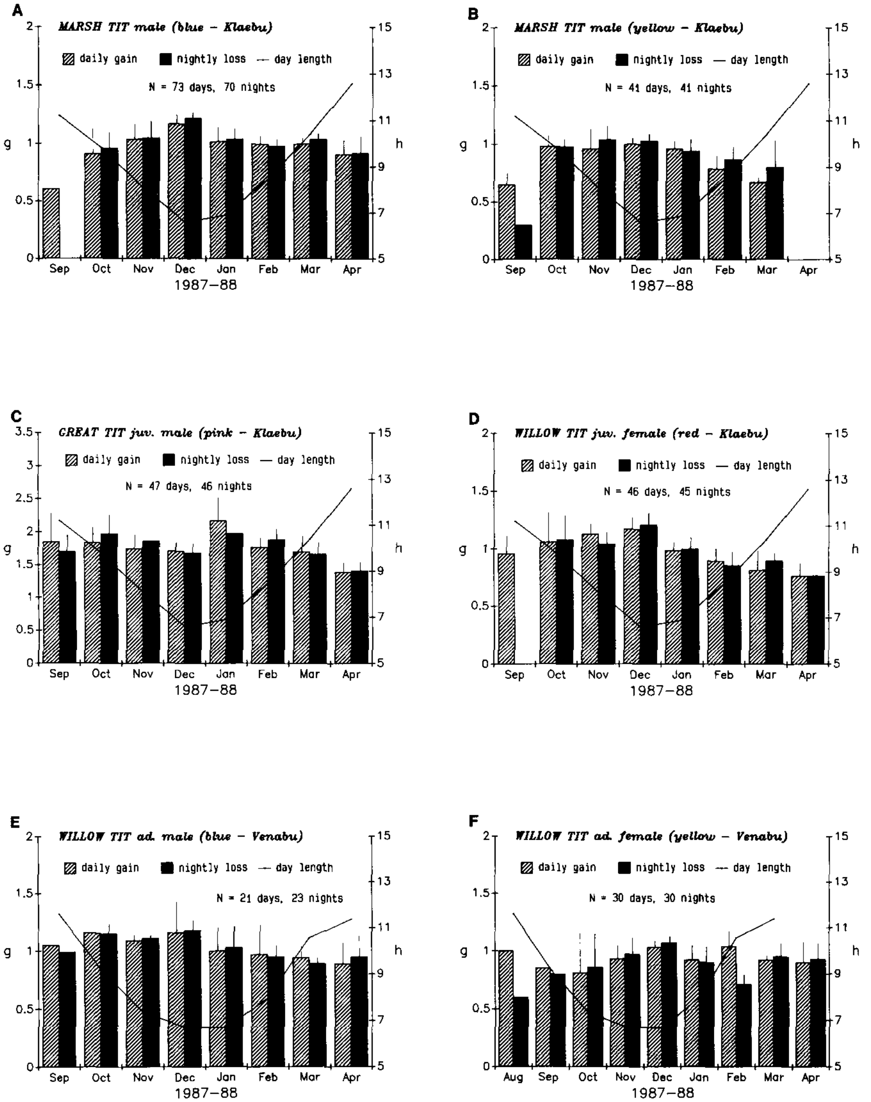


FIG. 7. Mean (±2 SE) daily gain and nightly loss, respectively, of the body weight of two Marsh Tits, one Great Tit, and three Willow Tits. Day length is the duration of the tits' activity period (monthly means).

TABLE 2

PEARSON CORRELATION COEFFICIENTS FOR THE RELATIONSHIP BETWEEN DAILY/NIGHTLY CHANGES IN BODY WEIGHT AND DURATION OF DAILY ACTIVITY (DAY LENGTH), ROOSTING TIME (NIGHT LENGTH), AND AIR TEMPERATURE

			Daily weight gain in relation to			Nightly weight loss in relation to		Rate of daily weight gain in relation to		Rate of nightly weight loss in relation to		
			Nightly weight loss	Day length	Temp.	Night length	Temp.	Day length	Temp.	Night length	Temp.	Location
Great Tit	juv	♂	0.55***	−0.37**	−0.11	0.34*	0.09	−0.88***	−0.27	−0.42**	0.25	Klaebu
			(34)[a]	(48)	(48)	(45)	(46)	(48)	(48)	(45)	(45)	
		♂	0.60***	−0.07	−0.26	0.26	−0.53**	−0.66***	−0.09	−0.37	−0.56 **	Klaebu
			(19)	(27)	(27)	(21)	(23)	(27)	(27)	(21)	(21)	
	ad	♀	0.72	0.03	0.19	0.14	0.06	−0.27	0.17	−0.12	0.14	Klaebu
			(6)	(12)	(12)	(13)	(12)	(12)	(12)	(13)	(12)	
	juv	♀	0.74***	−0.39*	0.02	0.41*	0.15	−0.74***	0.11	0.08	0.07	Klaebu
			(31)	(40)	(40)	(33)	(35)	(40)	(40)	(33)	(33)	
Blue Tit		♂	0.85***	−0.24	−0.49*	0.12	−0.28	−0.78***	−0.42	−0.51**	−0.08	Klaebu
			(13)	(24)	(24)	(25)	(25)	(24)	(24)	(25)	(25)	
Coal Tit		♂	0.80	−0.53	0.26	0.47	−0.16	−0.81**	0.41	0.19	−0.37	Klaebu
			(6)	(12)	(12)	(13)	(13)	(12)	(12)	(13)	(13)	
		♂	0.38	−0.34	−0.25	0.36	0.20	−0.57*	−0.24	0.16	0.22	Klaebu
			(14)	(16)	(16)	(14)	(15)	(16)	(16)	(14)	(14)	
Marsh Tit		♂	0.44***	−0.33**	−0.08	0.30*	−0.16	−0.82***	−0.20	−0.45***	0.00	Klaebu
			(62)	(72)	(73)	(67)	(68)	(72)	(72)	(67)	(66)	
		♂	0.59**	−0.40*	−0.43*	0.34	−0.49*	−0.83***	−0.61**	−0.10	−0.23	Klaebu
			(20)	(24)	(22)	(22)	(22)	(24)	(24)	(22)	(21)	
		♂	0.58***	−0.38*	−0.16	0.44**	−0.16	−0.77***	−0.36	−0.06	0.06	Klaebu
			(29)	(41)	(41)	(40)	(39)	(41)	(41)	(40)	(39)	
	ad	♀	0.56*	0.06	0.33	−0.05	0.30	−0.45	0.05	−0.50*	0.49	Klaebu
			(14)	(19)	(19)	(17)	(16)	(19)	(19)	(17)	(16)	
		♀?	0.77*	−0.01	0.10	0.00	−0.24	−0.43	0.01	−0.27	−0.12	Klaebu
			(8)	(10)	(10)	(9)	(8)	(10)	(10)	(9)	(8)	

TABLE 2
CONTINUED

			Daily weight gain in relation to			Nightly weight loss in relation to		Rate of daily weight gain in relation to		Rate of nightly weight loss in relation to		
			Nightly weight loss	Day length	Temp.	Night length	Temp.	Day length	Temp.	Night length	Temp.	Location
Willow Tit	juv	♂	0.47*	−0.04	0.16	0.06	−0.11	−0.64***	0.15	−0.43*	−0.08	Klaebu
			(19)	(28)	(28)	(22)	(22)	(28)	(28)	(22)	(22)	
	juv	♀	0.54***	−0.44***	0.08	0.30*	0.37**	−0.81***	−0.12	−0.29	0.47***	Klaebu
			(39)	(55)	(55)	(49)	(49)	(55)	(55)	(49)	(48)	
	juv	♀	0.63*	−0.09	0.30	0.39	0.30	−0.54**	0.26	0.01	0.25	Klaebu
			(15)	(25)	(25)	(18)	(20)	(25)	(25)	(18)	(18)	
	ad	♂	0.75**	−0.34	0.10	0.40	0.38	−0.81***	−0.10	−0.50*	0.48*	Venabu
			(14)	(21)	(20)	(23)	(23)	(21)	(20)	(23)	(23)	
	juv	♂	0.51*	0.20	0.19	−0.27	0.25	−0.45*	−0.02	−0.61**	0.21	Venabu
			(18)	(22)	(22)	(23)	(24)	(22)	(22)	(23)	(23)	
	ad	♀	0.78***	−0.17	−0.23	0.33	−0.14	−0.81***	−0.28	−0.32	−0.15	Venabu
			(25)	(30)	(30)	(30)	(29)	(30)	(30)	(30)	(29)	
	juv	♀	0.81**	0.43	0.05	−0.37	0.21	−0.61*	0.70*	−0.72*	−0.15	Venabu
			(10)	(11)	(12)	(10)	(11)	(11)	(11)	(10)	(10)	

[a] Number of records is in parentheses.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

at the same time as the air temperature falls, the birds theoretically need more energy to survive the night. The present data clearly confirm such a trend. Thus, the daily weight gain tends to increase as the winter proceeds and is, on the whole, greatest in midwinter, coincident with the shortest days and longest nights (Fig. 7). All the significant correlation coefficients for the relationship between daily weight gain and day length were negative in the present study, regardless of species (Table 2). Consistent with this trend, the correlation between the nightly weight loss and night length were positive (Table 2).

For those birds that survived the winter, there must have been a close relationship between weight gain during the day and the weight loss during night. This is confirmed by the data shown in Fig. 7 and Table 2.

An increase in the food requirement at the same time as the days are becoming gradually shorter must necessarily influence the feeding rate to a great extent. In fact, the feeding rate, expressed as the weight gain per hour, was about twice as high in the middle of the winter with the day length at its shortest, as it was in the autumn and the spring (Fig. 8, see also Table 2).

The rate of nightly weight loss, on the other hand, turned out to be fairly stable throughout the winter (Fig. 8). A closer look, however, does show a significant tendency in many birds for the rate of weight loss to vary inversely with night length (Table 2). This means that the birds used less energy per hour during the long nights in the middle of the winter than either before or after the solstice. How the birds managed to do that is unknown, but at least in the Willow Tit nocturnal hypothermia may play an important role (Reinertsen and Haftorn 1983). All the species in the present study showed this inverse relationship except the Coal Tit, but the data for this species were too few to be conclusive.

Factors regulating the body weight.—Winter fattening in titmice and other passerines is considered to be regulated by changes in air temperature and photoperiod (e.g., Evans 1969, Newton 1969, O'Connor 1973, King 1972, Haftorn 1976, Lehikoinen 1987). For tits at least, the photoperiod would seem to be the prime proximate factor, whereas the air temperature has only a moderate effect. Typically the birds gain in weight until the winter solstice. Up to this time body weight is inversely correlated with both day length and air temperature. From December onwards, however, the winter weight usually declines despite the continued fall in mean temperature.

I have previously suggested that this trend might be due to starvation (Haftorn 1951, 1976). But even if the tits have unlimited access to food, as when being fed artificially, many birds nevertheless start losing weight

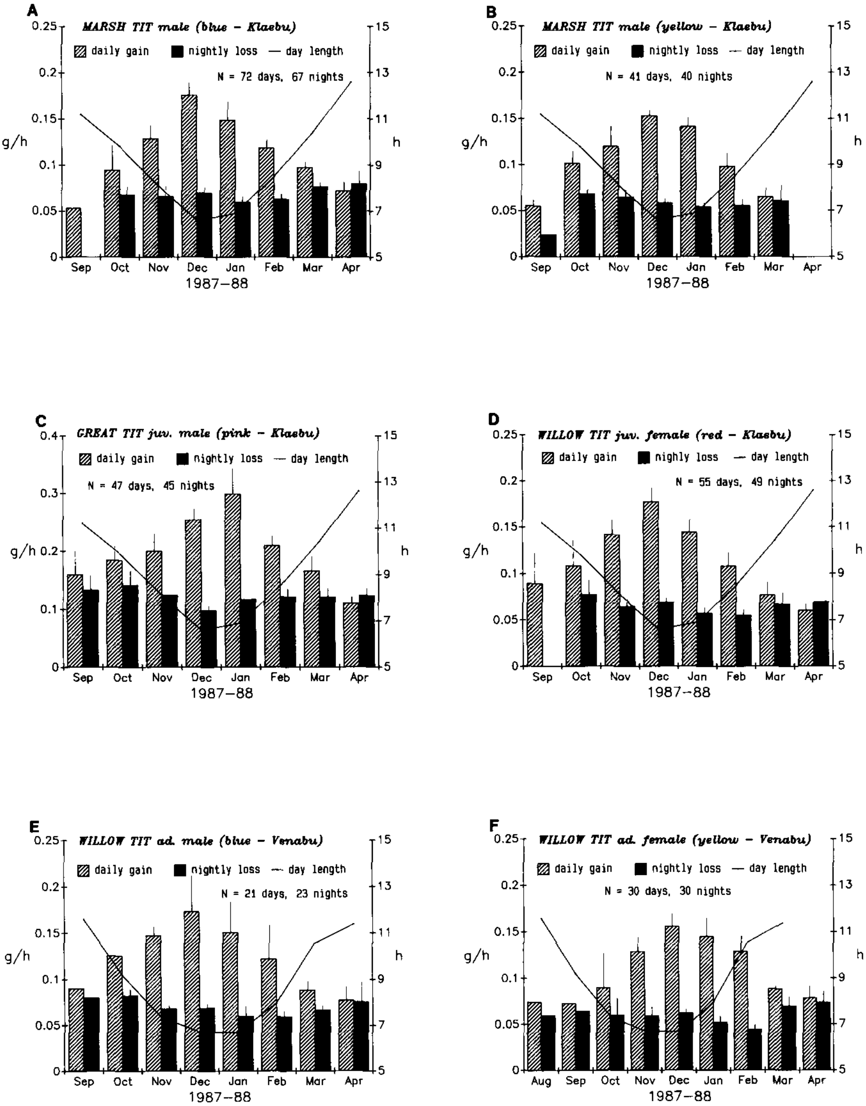


FIG. 8. Monthly means (+2 SE) of the rate of daily body weight gain and nightly loss, respectively, for the same individuals as in Fig. 7. Day length is the duration of the tits' activity period (monthly means).

TABLE 3

STEPWISE REGRESSION ANALYSES OF EVENING BODY WEIGHT IN RELATION TO PHOTOPERIOD (IN TERMS OF DURATION OF THE TITS' DAILY ACTIVITY) AND AIR TEMPERATURE (MEAN DAYTIME TEMPERATURE)

			Independent factors					
			Photoperiod	Air temp.	Multiple *R*	Standardized R^2	N	Location
Great Tit	juv	♂	−0.48	0.39	0.50***	0.22	63	Klaebu
		♂	−0.37	ns	0.37*	0.12	47	Klaebu
	ad	♀	−0.62	ns	0.62***	0.36	29	Klaebu
	juv	♀	−0.42	ns	0.42**	0.16	43	Klaebu
Blue Tit	ad	♂	−0.68	ns	0.68***	0.45	39	Klaebu
Coal Tit	ad	♂	−0.47	−0.41	0.70**	0.44	20	Klaebu
		♂	−0.60	ns	0.60***	0.34	36	Klaebu
Marsh Tit		♂	−0.68	ns	0.68***	0.45	75	Klaebu
		♂	−0.83	ns	0.83***	0.67	28	Klaebu
		♂	−0.64	ns	0.64***	0.40	56	Klaebu
	ad	♀	−0.53	ns	0.53**	0.26	29	Klaebu
		♀?	−0.71	ns	0.71***	0.48	20	Klaebu
Willow Tit	juv	♂	−0.53	ns	0.53***	0.26	41	Klaebu
	juv	♀	−0.78	ns	0.78***	0.60	67	Klaebu
	juv	♀	−0.55	ns	0.55***	0.29	38	Klaebu
	ad	♂	−0.71	0.35	0.75***	0.52	23	Venabu
	juv	♂	ns	0.54	0.54**	0.26	24	Venabu
	juv	♂	−0.57	ns	0.57**	0.29	21	Venabu

* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.
ns = not significant.

from December onwards. Such a development indicates that the regulatory effect of the photoperiod is relatively stronger than that of air temperature. This view is supported by the results of stepwise regression analyses on body weight with photoperiod and air temperature as independent factors. In only four out of 18 individuals studied did the air temperature enter the equation as a significant factor, whereas the photoperiod was included in all cases but one (Table 3). This finding is consistent with the results of previous analyses of the influence of air temperature on the body weight of the Great Tit (Haftorn 1976).

In December, the tits in central Norway utilize the short days effectively by foraging intensively from before sunrise to after sunset. As the days become longer from January onwards, the birds do not follow up by extending their daily activity correspondingly, as would be expected if they were underfed. Instead they cease foraging and go to roost progressively earlier in relation to the time of sunset. Already during the latter

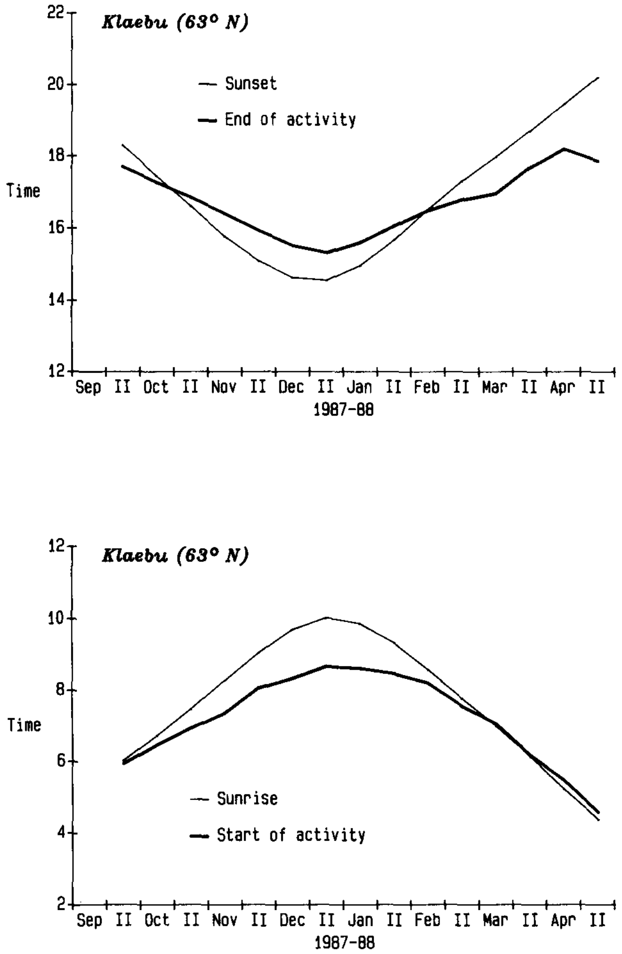


FIG. 9. Start and end of the tits' activity period in relation to sunrise and sunset, respectively. Data from the study area at Klaebu (63°15′N).

part of February, they cease their daily activity before sunset (Fig. 9). In other words, despite the fact that January–February represents the coldest period of the year, they do not seize the chance to build up as great a fat store as they had before, even when there is a food surplus. Apparently they need less energy during the latter part of the winter, possibly because the nights are shorter.

The above statement does not mean, however, that the influence of temperature on body weight is considered to be unimportant. In previous studies of two different Norwegian populations of Great Tits, at Oslo and Drammen, respectively, I found that the mean winter weight varied inversely with the mean winter temperature (Haftorn 1951, 1976). Other workers, too, have found clear effects of temperature on the body weight of Great Tits (van Balen 1967, Lehikoinen 1987).

The relationship between body weight and temperature is not a straightforward one, however. Although the winter temperature was lower at Venabu than at Klaebu, the Willow Tits at Venabu did not show a higher degree of winter fattening, at least not one that was detectable at the individual level.

Concluding remarks.—To sum up, regardless of species, most individuals in the present study, although not all, gained in weight during the winter, and this applied to both the morning and the evening weights. In other words, they followed the "winter fattening strategy." Although the morning weight of a few birds tended to be relatively stable (Figs. 2D and 4A, C), no convincing examples of the "constant morning weight strategy" were found. The usual pattern was that the changes in morning weight parallelled those in evening weight, whether or not the particular bird actually gained or lost weight. It should be added that the noon weights followed exactly the same trend (Fig. 2A–C). At noon, birds had gained about half the daily weight increase.

No clear interspecific differences in the winter fattening patterns were observed. On the whole, the gain in weight from September to the winter peak was moderate in both study areas, usually being between 2 and 8%, for both the morning and the evening weights. The diurnal variation in weight observed in the present study was considerably greater than the degree of winter fattening, namely about 7–12%. Furthermore, it is noteworthy that the most sedentary of the titmice, the Marsh Tit and the Willow Tit, showed significantly less diurnal variation in weight than the other three species.

The winter weight of one male Great Tit did not increase at all, but declined from October onwards, apparently for some reasons other than starvation or competition with other birds. This trend may be related to its high-ranking status in the social hierarchy, a hypothesis which should be tested by further observations.

ACKNOWLEDGMENTS

I thank Toril Berg and Ingeborg Harder for technical assistance, and P. A. Tallantire for improving the English.

LITERATURE CITED

Chaplin, S B. 1974. Daily energetics of the Black-capped Chickadee, *Parus atricapillus,* in winter. J. Comp. Physiol. 89:321–330.

COWIE, R. J., J. R. KREBS, AND D. F. SHERRY. 1981. Food storing by Marsh Tits. Anim. Behav. 29:1252–1259.

EVANS, P. R. 1969. Winter fat deposition and overnight survival of Yellow Buntings (*Emberiza citrinella* L.). J. Anim. Ecol. 38:415–423.

HAFTORN, S. 1944. Food-storing in titmice. Naturen 68:58–63. (In Norwegian.)

———. 1951. An investigation on weight-variations in the Great Tit, *Parus m. major* L. Fauna (Olso) 4:83–91. (In Norwegian.)

———. 1956a. Contribution to the food biology of tits, especially about storing of surplus food. Park II. The Coal-Tit (*Parus a. ater* L.). Kgl. Norske Vidensk. Selsk. Skr. 1956 Nr 2. 1–51.

———. 1956b. Contribution to the food biology of tits, especially about storing of surplus food. Part III. The Willow-Tit (*Parus atricapillus* L.). Kgl. Norske Vidensk. Selsk. Skr. 1956 Nr 3. 1–79.

———. 1976. Variation in body weight, wing length and tail length in the Great Tit *Parus major.* Norw. J. Zool. 24:241–271.

———. 1982. Variation in body measurements of the Willow Tit *Parus montanus,* together with a method for sexing live birds and data on the degree of shrinkage in size after skinning. Fauna Norv. Ser. C, Cinclus 5:16–26.

KING, J. R. 1972. Adaptive periodic fat storage by birds. Proc. XV Int. Orn. Congr.:200–217.

KLUYVER, H. N. 1952. Notes on body weight and time of breeding in the Great Tit, *Parus m. major* L. Ardea 40:123–141.

LAWRENCE, L. K. 1958. On regional movements and body weight of Black-capped Chickadees in winter. Auk 75:415–443.

LEHIKOINEN, E. 1980. Patterns of weight variation in some passerine birds wintering in the north-temperate zone—a preliminary report. Pp. 44–57 *in* Animal adaptations to winter conditions (V. E. Sokolov, ed.). (In Russian, mimeograph in English).

———. 1986. Winter ecology of passerines: significance of weight and size. Rep. Dept. Biol. Univ. Turku 14.

———. 1987. Seasonality of daily weight cycle in wintering passerines and its consequences. Ornis Scand. 18:216–226.

LÖHRL, H. 1955. Welche Meisenarten verstecken Futter? Vogelwelt 76:210–212.

NEWTON, I. 1969. Winter fattening in the Bullfinch. Physiol. Zool. 42:96–107.

O'CONNOR, R. J. 1973. Patterns of weight change in the House Sparrow, *Passer domesticus* (L.). Pp. 111–125 *in* Productivity, population dynamics and systematics of granivorous birds (S. C. Kendeigh and J. Pinowski, eds.). PWN—Polish Scientific Publishers. Warszawa, Poland.

OWEN, D. F. 1954. The winter weights of titmice. Ibis 96:299–309.

REINERTSEN, R. E. AND S. HAFTORN. 1983. Nocturnal hypothermia and metabolism in the Willow Tit *Parus montanus* at 63°N. J. Comp. Physiol. 151:109–118.

VAN BALEN, J. H. 1967. The significance of variations in body weight and wing length in the Great Tit, *Parus major.* Ardea 55:1–59.