Daily Routines of the Great Tit, Parus m. major L.

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Daily routines of the Great Tit, *Parus m. major* L.

by

H. N. KLUIJVER

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Introduction.

The aim of the observations described in this paper was to gather information about the time which is occupied daily by various important activities in the life of the bird, such as roosting, feeding, brooding etc. Information was also wanted concerning the time at which these various activities start and finish.

It is clear that these activities are influenced by both internal and external factors, and further that they are closely related to each other. The beginning and termination of sleep are for instance related to the rising and setting of the sun, and also to cloudiness, wind-speed, rainfall and the hunger of the bird. Similar consideration apply to the time taken daily in the search for food, in brooding, in singing and in other activities. It was our aim to trace out these various interrelationships in order to achieve a further understanding of the daily routines. Only those activities on which systematic observations were carried out are treated in this paper.

I am greatly indebted to J. A. EYGENRAAM, O. BRIEDÉ and F. DROST who yielded their observations for this study, to Dr. N. TINBERGEN and Dr. L. TINBERGEN, for valuable criticism and to G. VAN ROSSEM and Dr. D. LACK for help in translating it into English.

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The observations were carried out in 5 different localities, viz. by J. A. EYGENRAAM at Ede, by O. BRIEDÉ at Blaricum (N.H.), by F. DROST at Meppel and by the author at Bennekom and Wageningen. Special nest-boxes with two entrances were used by BRIEDÉ, DROST and the author. These entrances are constructed in such a way that the bird which uses the box is compelled to enter through one opening and to leave through the other, while in so doing it touches a contact so that an electric circuit is closed. In this way it is possible to record every entry and exit of the bird from the box. A detailed description of the principles of this apparatus has already been published by KLUIJVER (1933). The accuracy of the record was considerably improved by using the chronograph made by FUESS. Differences in time of only 10 seconds could then be read easily.

The observations with this apparatus were started at Bennekom in 1936, but owing to technical imperfections it was not possible to obtain a complete series of observations in that year. We were more successful in 1937, 1939 and 1944 (in the last two years at Wageningen). BRIEDÉ's observations were carried out during 1940, 1941, and 1942, those of DROST in 1947.

The routine life of the Great Tit during the reproductive period is here analysed on the basis of the 1937 records, which give a complete picture of the entrances and exits of the same (ringed) couple during the raising of two successive broods. The records at other nests are less complete, but they fully confirm the picture of the daily routine given below for the pair studied in 1937.

EYGENRAAM made his observations at Ede during 1938, 1939, 1940 and 1941. He particularly studied a roosting place used each night during the winter, and recorded the times at which a bird entered its nestbox to roost each evening and left it again next morning. At the same time, he noted details of the weather conditions, viz. temperature, cloudiness, wind-speed and rainfall.

In tracing the influence of weather conditions on the behaviour of the birds at Bennekom and Wageningen we used, besides our own notes, the records of the Physical Laboratory of the Agricultural High School at Wageningen.

PART 1. TIMES OF RISING AND RETIRING FOR THE DAY

The beginning and end of the day's activities are, in a diurnal species, mainly controlled by the light intensity. During the summer the birds have a long working day, whereas in winter they start later and finish earlier. There is no doubt that light is a very important factor, and birds are very sensitive to small changes in the light intensity. This is evident for instance from the fact that there is a fixed order in which the different species of song-birds start to sing in the half-light of the early

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morning in spring. It has even been thought that there is a fixed „Weckhelligkeit" (waking-light) for each species of bird. This, however, is too simple an explanation, for the light-intensity at which the birds start and finish their diurnal activity is somewhat different at different seasons of the year, and even varies a little under different conditions at the same season.

In order to study the influence on the bird's diurnal rhythm of different factors, such as weather, or the physiological condition of the bird, it is best to trace how far these cause deviations from the average of the above-mentioned seasonal waking light. The waking light can be measured with a photometer, and SCHWAN (1921-1922) has studied in this way the influence of air temperature, relative humidity, wind speed and other factors on the time of commencement of the early morning song in passerine birds. In the present study, accurate light-measurements were not made, but the beginning and end of the daily activity have been compared with the time of sunrise and sunset. In some cases details were added of the degree of the cloudiness.

From its nature, the above method is rough, and it allows of reliable conclusions only when the differences to be investigated are marked ones. It must also be born in mind that the duration of twilight is dependent on the angle at which the trajectory of the sun cuts the horizon, an angle which, apart from the variation with latitude, varies also with the season of the year. The number of minutes of official twilight, i.e. from sunset until the sun is 6° below the horizon, and from the latter time in the morning until sunrise, varies in the Netherlands as follows:

1st	January	47.4 min.	1st	July	55.2 min.
„	February	42.9 „	„	August	47.4 „
„	March	39.4 „	„	September	41.0 „
„	April	39.8 „	„	October	39.0 „
„	May	44.9 „	„	November	41.3 „
„	June	53.2 „	„	December	46.2 „

The Great Tit is a diurnal bird. It usually rises in the morning shortly before sunrise and retires to roost at sunset. During the winter (November-March), the Great Tit sleeps in a natural cavity in a tree or in a nest-box (never more than one in a cavity). During the summer the bird does not as a rule use a cavity, but selects a sheltered place against a tree-trunk or among the foliage. The males change from their sleeping cavities to the summer roosting places during March or April, but the females still continue to sleep in their cavities, and they take up summer roosting places only after their young have flown from the nest. The young, once they have left the nesting cavity, never return there. At first they sleep together, but later they select solitary perches among the foliage. Like many young song-birds, they retire to roost rather earlier than the

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adult birds. During the autumn the Great Tits return to their winter roosting places, some of them doing so already in August, but many others not until November.

As the breeding behaviour of the birds so greatly affects their diurnal activity, the reproductive period and the rest of the year will be treated separately in what follows.

§ 1. The reproductive period.

There is a great difference in the daily routines of the male and the female in this period, connected with the marked division of their labour during the reproductive period. During laying and incubation, the general behaviour of the female, including her times of rising and retiring, is greatly affected by these functions. In contrast, the breeding season does not demand a full day's work from the male until after the young have hatched and they require feeding regularly.

The nestbox records provide a complete series of observations concerning the behaviour of the female. The male sleeps outside the box, and therefore we have only incidental observations with regard to the time at which he retires for the night. For the male's time of rising, however, we can use records of the beginning of the early morning song.

The female's time of rising.

During the whole period of reproduction, the female uses the nestcavity for sleeping. Indeed she already does so during nest-building, and even before this, and usually the cavity in which she sleeps during March and April later becomes the nestcavity.

As will be seen later, the female in general rises rather later than the male. By singing (mostly the so-called "saw-sharpening") near the nestcavity, the male calls the female out. Often it takes him a considerable time before she appears. In April 1943, I noted down the interval which passed between the first singing of a certain male and the emergence of his female: April 7th: 18 min; April 9th: 26 min; April 12th: 14 min; April 14th: 17 min; April 16th: 45 min. On the last mentioned date, the female laid her first egg. Long before the female appears, she answers the male from the sleeping cavity with a soft whining sound. On the above-mentioned dates I heard this call 13, 8, 5, 2 and 20 minutes respectively before she emerged. From this it is evident that the female is already awake some time before she leaves the sleeping cavity.

The times at which the female leaves the nestbox for the first time, and enters it for the last time, each day are shown in Fig. 1 B. During the laying period, and during the incubation of the first clutch, she usually leaves the nestbox shortly after sunrise, at the latest 30 minutes after sunrise. During this period she only two days started her activity

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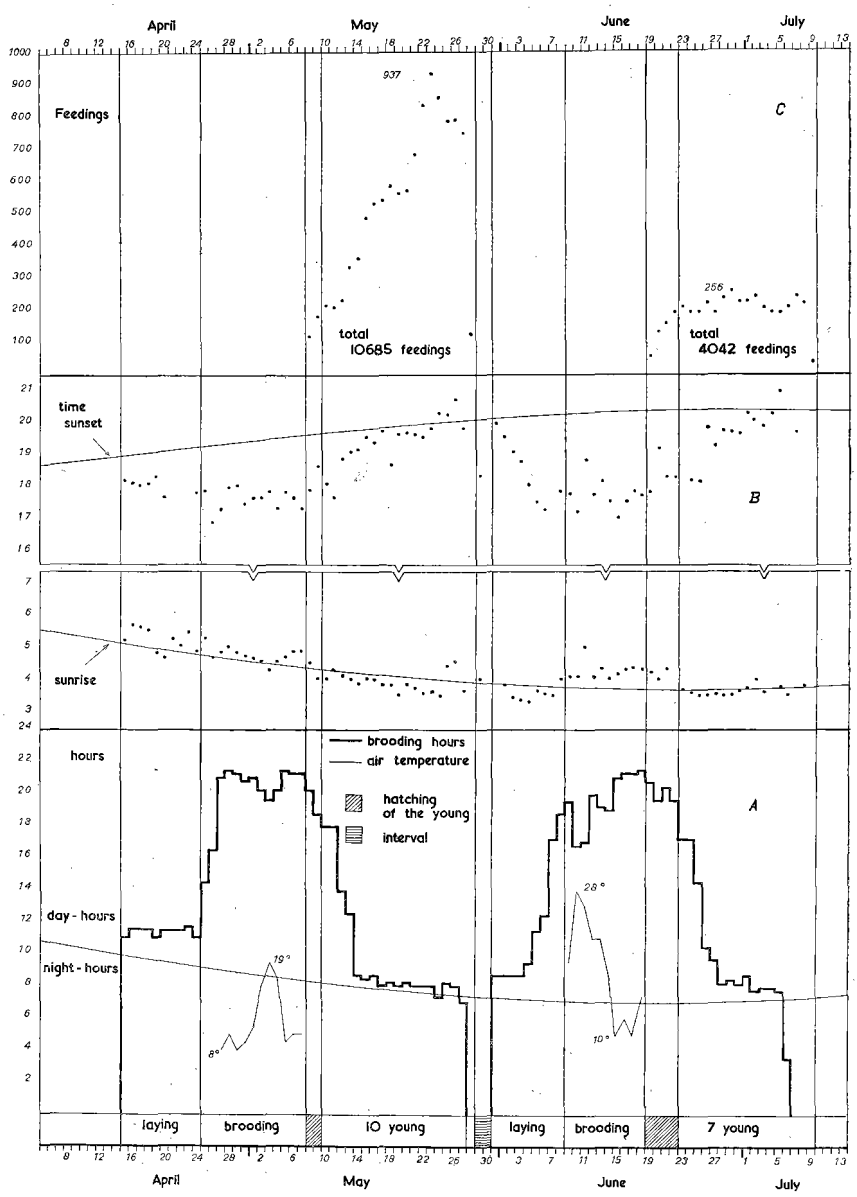

Fig. 1. Daily routines of pair Bennekom 1937.
A: incubation of female; B: times of rising and retiring of female;
C: number of feeding visits to young.

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as much as 5-10 minutes before sunrise, and on the average she rose 20 minutes after sunrise, which is very late — about 45 minutes later after sunrise than her average time of rising during the winter months. During the laying-period, this late rising is certainly connected with the fact that the female lays an egg each morning just before leaving the nest, while during the incubation period, it is connected with the brooding-impulse.

As soon as the young have hatched, the female becomes active at an earlier hour. Instead of rising after sunrise, she now rises on an average 6 minutes before sunrise. (Two inexplicable cases in which she became active very late have been left out of account). Compared with the male, the female is still a late-riser (31 minutes later than the male on an average). The need for warming the nestlings during the cool spring and summer nights is possibly responsible for her relatively late start in search of food (about sunrise). Evidently, the female has to compromise between her task of collecting food, which makes early rising necessary, and her task of brooding, which requires late rising.

For the second brood, matters are rather different. During laying, the female rises relatively much earlier in relation to sunrise than she does in the same period for the first brood. Presumably this is related to the fact that she is still feeding the young of the first brood during the laying of the second clutch.

The female's interest in the young of the first brood gradually wanes, and as a result her time of rising gradually gets later, until it is again after sunrise. During the incubation period of the second brood, the female rises as late, relative to sunrise, as she did during the incubation period of the first brood. She rises rather earlier again when feeding the young.

The graph shows the existence of rather large daily variations in the female's time of rising; while she is feeding the young, this time fluctuates between 30 minutes before and 44 minutes after sunrise. I have not been able to account for these variation. There was no apparent correlation with climatic factors (cloudiness, rain etc.).

The female's time of retiring to roost.

Fig. 1 B shows that, as regards the female's time of rising, there is no difference between the laying and the incubation periods. There is, however, a difference between these two periods in regard to her time of retiring to roost.

At the beginning of the laying period the female retires early, but later in the laying period her time of retiring gets earlier, and this tendency is continued into the incubation period. This is the more striking because the days are drawing out continually during this time, hence

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the difference between her roosting time during laying and during incubation is very great in relation to the time of sunset. During the laying period, the female retires to roost on the average 64 minutes before sunset, but during the incubation period, on the average 100 minutes before sunset. This difference is clearly correlated with the development of the brooding impulse, as is also the case for her late rising in the morning during the same period. Indeed, the beginning of the brooding impulse is already perceptible during the laying period, because her average time of retiring to roost then, which is 1 hour before sunset, is very early in comparison with her roosting time at other periods of the year. After the young have hatched, the female gradually changes to a later time of retiring, at first shortly before sunset and eventually after sunset.

During the laying period of the second brood, the female's time of going to roost gradually becomes earlier again, until it takes place 2½ hours before sunset. This change occurs gradually, not suddenly, probably because in the first part of the new laying period, she is still feeding the fledged young of the first brood (see parallel comment on time of rising during this period). Gradually the female gives up the feeding of the first-brood young entirely to the male, but she may still be feeding them a little even when incubating the second clutch.

Throughout the incubation period of the second brood, the female retires for the night relatively early. Her late time of rising during this period has already been mentioned. As a result, although it is now the middle of June, with a much larger daylength than in April, the female is active during the day for only the same number of hours as in April.

After the second brood have hatched, there follows another period of prolonged activity, completely in accordance with that observed for the first brood. The regularity in the time of waking and retiring is no doubt connected with the need for food of the female and her young. The time when the Great Tit has the longest working day, both absolutely and relatively (i.e. in relation to sunrise and sunset), occurs during the time when the nestlings are just full-grown. At that time, the food requirements of the family are at their maximum. With the first brood, the parents are active literally from sunrise to sunset. With the second brood, they are rather less busy, because the number of young in the brood is smaller and the day is also longer. This is noticeable both in the relatively later start, and especially in the relatively earler termination, of the day's activity.

The male's time of rising.

As already remarked, the male wakens the female during the reproductive period by singing near her sleeping cavity. Hence he always

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rises earlier than she does. We have no observations on the time which he leaves his roosting place during this period. We have, however, a number of data on the time at which he begins to sing. It is not certain that the first singing takes place immediately after he has left the roosting place. Indeed, I have one observation on this point. On 16th April 1937, the male of a pair arrived at the sleeping cavity of his female at 4.20 a.m. He called a few times softly "tsjing tsjing". After that, he remained quiet until 4.30 a.m., and only then started the "saw-sharpening". This observation shows that the male may leave his roosting place as much as 10 minutes before he first sings.

We collected comparatively few data on the time of first singing of the male during the reproductive period. I have therefore added some observations from Hulshorst which Dr. L. TINBERGEN has allowed me to publish, and also SCHWAN's (1921-22) data from Halle. Altogether this makes a total of 60 observations for the reproductive period (16th April-May 20th). In these data, no allowance can be made for the influence of the stage of the breeding cycle on the male's time of rising. As already noted, such an influence is clear in the case of the female. SCHWAN did not assess the time of first singing in relation to sunrise. Instead, he recorded the actual light intensity at the moment when song was first heard. This is a superior criterion, as it allows for the influence of cloudiness. SCHWAN in general concluded from his figures that the birds start their morning song at a lower light intensity during the period of pairing than before and after that period. Thus his Great Tits started their song in March with an average light-intensity of + 75 lux (= meter — candle), but in the first twenty days of April (the laying period of the Great Tit) with a light intensity of + 3 lux. This is a large difference. SCHWAN also concluded that, during the incubation period, the male starts singing later than during the laying period, but I have failed to prove this from his data in the case of the Great Tit. On only some days in May did the male start singing at a higher light-intensity, and there were many other days on which singing started already at 1.5 lux.

The male starts his morning song before sunrise, the number of minutes being given in fig. 2. Whereas during the winter no Great Tit (male or female) ever left its roosting place more than 40 minutes before sunrise, during March, April and May the first song starts appreciably earlier than this. As already mentioned, the males often did not start their singing immediately after leaving the roosting place. Hence for the males, the difference between the waking time in summer and winter is a little greater than would appear from the graph. As already mentioned on p. 104, the females rise later, not earlier, in relation to the time of sunrise when breeding. Hence during the laying period, the male is active at a very early hour, while the female makes her appearance very

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late. As the male continues singing until the females appears, his early morning song lasts longest during this period.

In the period between April 7th and May 20th, the singing of the male started on the average 37 minutes before sunrise (standard deviation + 1.1). At this time of day, the sun is still 5° below the horizon. The

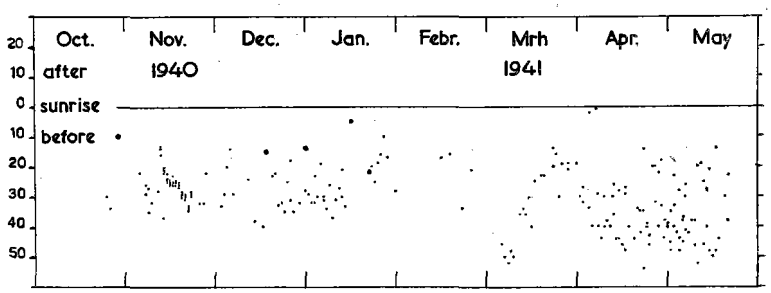

Fig. 2. Time of rising, plotted with sunrise as a baseline. Heavy dots indicate rainfall at the time of rising. The observations between October and February were carried out by EYGENRAAM at Ede and record the time at which several males and females left their sleeping cavities. The observations between March and May were carried out at Halle (SCHWAN), Hulshorst (L. TINBERGEN) and Bennekom (KLUIJVER) and record the first morning song of the males in minutes before sunrise.

earliest record of song was 54 minutes before sunrise. These figures will be compared below with those for the beginning of the bird's activity during the winter.

The male's time of retiring to roost.

We have little data on the time at which the male retires to roost, indeed there are only 10 observations, made during one fortnight just before the reproductive period started. Then, a male entered his sleeping cavity on the average 20 minutes before sunset. His female entered hers about 22 minutes earlier than the male. On the day on which the female laid her first egg (April 18th), the male abandoned his sleeping cavity, and thereafter slept in an unknown place. From May till July the males never sleep in cavities, and all that can be said about the male's time of retiring to roost, during laying and incubation, is that he remains out for longer than the female, who retires very early in this period. When there are young in the nest, the male continues feeding them until the female settles on the nest for the night. It is not known how long after this the male remains active, but probably only a very short time.

§ 2. Autumn and winter.

During the autumn and winter, there is much less difference between the behaviour of male and female. The female, however, who in some

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parts of the reproductive period was active for one hour less each day than the male, still has on the average a rather shorter day. The difference, however, is reduced to about 12-15 minutes. Not infrequently, male and female pass the day together during the winter. In such cases the male comes early in the morning and waits for the female at the sleeping cavity. In the Blue Tit and Marsh Tit, this behaviour is more pronounced, but it is not at all exceptional in the Great Tit. In winter, however, the male Great Tit does not sing near her sleeping cavity as he usually does in spring. During the winter, the female emerges in the morning 1 or 2 minutes after the male. In the evening, the male also retires to roost later than the female and then the difference in their times is somewhat greater.

Time of rising.

The observations on the time of rising (nearly all made by EYGENRAAM) have been summarised in fig. 2, in which sunrise has been taken as a base-line. It may be noted that during the winter (from the end of October to February) the birds always start their activity before sunrise. It is also noteworthy that, during the short days of December, the birds do not rise earlier in relation to sunrise than they do in November and January. During these three winter months, the time of rising is on the average 26 minutes before sunrise. In December the sun is at that time 3¼° below the horizon, whereas on about May 1st the male starts singing when the sun is still 5° below the horizon (see page 107). It might be asked whether the relatively late rising in December results merely from the fact that the weather is cloudier in December than in May, and whether the light intensity at which the Great Tit start its morning activity is similar in both months. This, however, is not the case, because even on bright days during December the Great Tit did not appear until on the average 34 minutes before sunrise, whereas in April and May the males often started singing 50 minutes before sunrise (and they may have left their sleeping quarters 10 minutes before starting to sing). Thus during the short days of December, the Great Tit starts its morning activity at a considerably higher light intensity than during the breeding season.

The time at which the birds rise during December (26 minutes before sunrise on the average) is very variable, the extreme figures being 14 and 40 minutes before sunrise respectively. This variability might be due either to external factors (especially the degree of cloudiness, also other weather factors) or to the internal state of the bird, such as how hungry it is for food. In the early morning, however, the birds do not in general seem to feel hungry. This may be inferred from the fact that they sing especially in the early morning. Further, as already mentioned, they do not rise relatively earlier in the short December days than they

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do in January and November, nor do they rise relatively earlier in winter than they do in spring.

Great Tits which pass the arctic winter under extreme conditions (short daylength and low temperature) commence their day's activities relatively earlier in December that they do during the months which provide better conditions of existence. Thus in lat. 67° N, FRANZ (1943) found that they became active nearly 2 hours before sunrise in December, whereas in February they became active only about 15 minutes before sunrise. The significance of this observation will be apparent later.

In our rather mild Dutch winters, the Great Tit continues its sleep relatively later into the morning than those observed by FRANZ, so it may certainly be inferred that the Dutch birds are not starving. It is interesting that, despite the large differences in the time of rising on successive days, (those shown in fig. 2 nearly always refer to the same individual), there is only a small difference in the time of rising of different individuals on the same day. In November 1941, EYGENRAAM recorded the time of first appearance of three individuals. They always appeared within 3 minutes of each other (in irregular order).

The difference between the times of rising on successive days is not therefore a chance result of consistent differences in the times of rising of different individuals. It must therefore be due to external factors. In this connection the influence of rainfall or snow is clear. The Great Tit hesitates to come out when it is raining or snowing. Sometimes one can see the bird peeping out of its hole for a minute but then drawing back again, and it may not leave for another ten minutes or so. Sometimes also, a bird may remain for some minutes undecided in the entrance, but on other days they did not do this. The days on which it rained during the observations have been marked with a heavy dot in fig. 2. From this it is clearly seen that the birds emerged relatively late on all the rainy days.

During his observations, EYGENRAAM also recorded the air-temperature, the degree of cloudiness and the wind-speed. This was done at the moment when the bird first emerged. The temperature was recorded in degrees centigrade, the cloudiness was assessed on a four-fold scale, viz. bright (1), slightly cloudy (2), heavily clouded (3), completely overcast (4), and the wind speed was estimated according to a similar four-fold scale, viz. calm or soft breeze (1), moderate wind (2), strong wind (3), storm (4). The influence of the above three factors can be studied by plotting them against waking-time, the latter being recorded in relation to sunrise. The results are shown in table 1, from which it is clear that all these factors have some influence, though none of them have as great an influence as rainfall.

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TABLE 1

Correlation coefficients between waking time of Great Tit (in relation to sunrise) and the degree of cloudiness, temperature and wind speed at the time.

Correlation of waking time with cloudiness	r_{ab}	= —0.58
,, ,, ,, ,, ,, temperature	r_{ac}	= —0.47
,, ,, ,, ,, ,, wind speed	r_{ad}	= —0.44
,, ,, cloudiness with temperature	r_{bc}	= +0.43
,, ,, ,, ,, wind speed	r_{bd}	= +0.04
,, ,, temperature with wind speed	r_{cd}	= +0.14

In the above table the negative correlation coefficients mean that the first appearance of the Great Tit in the morning is delayed by heavy cloud, by strong wind and by high temperature. The correlation coefficients are not high, but are significant ($n = 51$). Of course, heavy cloud decreases the light intensity, and so delays the bird's emergence for this reason alone.

As those days on which rain fell were omitted from the calculation, the correlation between waking time and cloudiness was really higher than $r_{ab} = -0.58$. A more exact method of recording cloudiness might also have given a higher correlation coefficient. During the winter, a high temperature often goes together with a cloudy sky, as expressed by the positive correlation coefficient $r_{bc} = +0.43$. Hence, the negative correlation between waking time and temperature ($r_{ac} = -0.47$) is partly due to the influence of cloudiness. When the latter consideration is eliminated, by calculating the partial correlation coefficient for the relation: waking time-temperature, this amounts to $r_{ab.c} = -0.30$, which is just high enough to be statistically significant. Nevertheless the influence of temperature does not seem to be very important; and it may be added that the period between December 1940 and January 1941 was particularly favourable for such observations, as fluctuations in temperature were large (between + 5° and —9° C).

While as seen above, cold prompts the birds to emerge earlier, SCHWAN on the contrary found that a high temperature resulted in an earlier start of the beginning of song. This apparent contradiction between his results and mine is due to the fact that the temperatures at which SCHWAN made his observations were between 0° and 16° C. Within that range of temperatures, and at that time of year, song is stimulated by high temperatures. But below 0° there is no song, and under these conditions a low temperature stimulates earlier rising. Probably the latter is related to the feeling of discomfort which the roosting bird experiences under such circumstances.

The coefficient of the combined correlation between waking time, cloudiness, temperature and wind speed amounts to 0.74. This is not high, and shows that, in addition to these factors and to rain, there must

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be yet other factors which have an important influence on the time at which the Great Tit starts its activity in the morning. Bearing in mind, however, the primitive meteorological measurements employed, the results are not at all unsatisfactory.

Retiring to roost.

As we already pointed out, during the breeding season the male is active for rather longer each day than the female. The difference is probably not great, but it cannot be measured accurately as we have no data on the time at which the male retires to roost during this period. For the rest of the year, however, we have a few data on this point. In observations made on seven evenings in December 1940, the male retired to roost on an average 12 minutes later than the female, and in 21 observations during March 1939 on an average 11 minutes later than the female. Similar differences between the sexes have been found in the case of other songbirds, the literature on this subject being reviewed by NICE (1943).

The observations concerning the time of retiring to roost are summarised in fig. 3 (upper part for a male and lower part for a female Great Tit). When fig. 3 is compared with the waking times in fig. 2, two differences immediately leap to the eye. Firstly, the birds retire for the night at a much higher light intensity than at which they rise in the morning. Thus, in general they retire to roost before sunset, and only during December slightly after sunset, whereas they first appear in the morning on the average 26 minutes before sunrise.

Secondly, the relation between the time of retiring to roost and the time of sunset changes markedly with the season of the year, whereas the relation between time of rising and sunrise does not change much with the season, as already mentioned. Thus in August, the birds go to their roosting places one hour before sunset, but during the course of the autumn their time of retiring gets gradually later (relative to the time of sunset), so that in November it is only about 5 minues before sunset and in December 5 minutes after sunset. After December, there is a gradual change in the reverse direction, until the birds retire about 10 minutes before sunset. When this point is reached, however, there is no further change until the beginning of April. Then, when the reproductive period begins, a quite different set of factors come into play.

There can be no doubt that this seasonal change in the time of going to roost (relative to sunset) is correlated with the length of time available during the day for collecting food. Not only is the winter day shorter, but there is a greater need of energy during cold weather, and food is also scarcer then than in the summer. This last point is clearly shown by the fact that the birds retire to roost later in the day at the end of March and the beginning of April than they do at the end of August and the be-

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ginning of September, although the day length at these two periods of the year is about the same. Presumably, the birds are compelled to be active for a longer time each day in March than in September because food is shorter in March than September.

EYGENRAAM, appreciating fully the above situation, tried to determine by experiment whether a correlation existed between the time of retiring

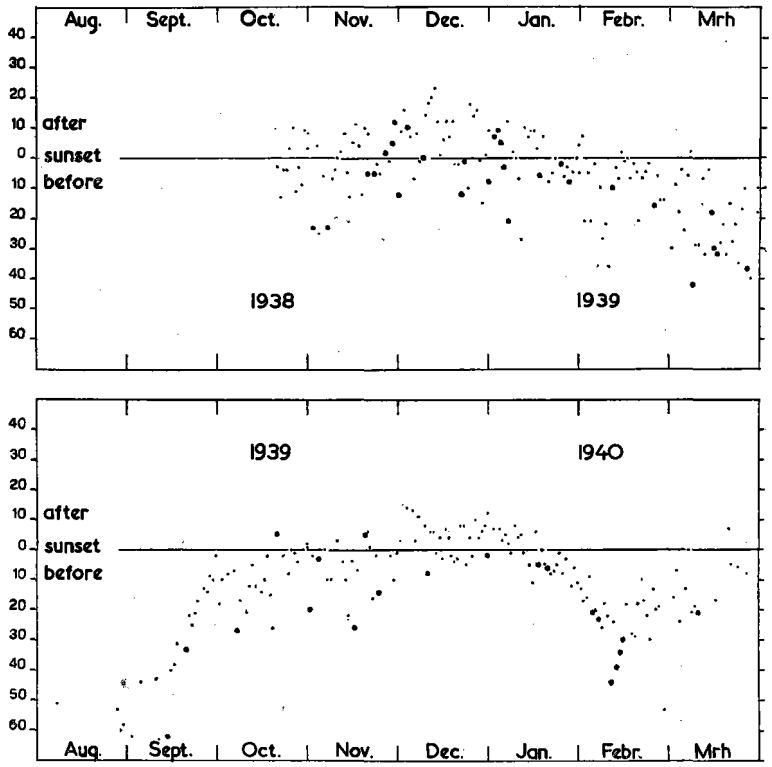

Fig. 3. Time (in minutes) of retiring to roost, plotted with sunset as a base line. Heavy dots indicate rainfall at the moment of retiring to roost.

to roost and the state of hunger of the bird. He used to feed his Great Tits daily with peanuts. Between January 12th and February 20th 1940, he provided alternately much, or little, or no food for them, and he recorded each day the time at which the same individual went to roost. To make a clear comparison possible, those days were eliminated in which the weather might have had a disturbing influence. Only the data obtained on cloudy days were used in the comparison which follows.

During the eleven days on which food was provided all day long, the bird went to roost at, on the average, 15 minutes before sunset (standard deviation 2.7). During the eleven days on which little or no food was

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provided, the bird went to roost at, on the average, only 2 minutes before sunset (standard deviation 2.7) i.e. on the days on which the bird was fed by EYGENRAAM, it retired for the night an average of 13 minutes earlier than on the other days. The standard deviation of this difference is 3.8, which is smaller than $^1/_3$ of the difference involved, hence the latter is statistically significant. The experiment therefore demonstrates that the nutritional condition of the bird has a marked effect on the time at which it retires for the night. On the other hand, as already noted, the time of rising in the morning is (in Holland) influenced much less or not at all by the nutritional condition of the bird.

On page 110 it was seen that differences in the time of rising on successive mornings are mainly due to differences in the weather. Has the weather a similar influence on the roosting time in the evening? The days on which it was raining or snowing at the moment when the bird retired to roost are denoted in fig. 3 with heavy dots. This shows clearly that weather has some influence. On many of the occasions on which the bird retired to roost very early in the evening, it was raining at the time. On the other hand it was not raining on any of the occasions when the bird retired to roost very late. The influence of rainfall is, however, much smaller than in the case of the time of rising in the morning.

Owing to the marked seasonal variation in the time of retiring (relative to sunset) the influence of cloudiness, temperature and wind-speed can be analysed only for short periods at a time, in which the influence of the seasonal trend can be neglected. The months of November, December and March have been selected for this purpose, as set out in table 2.

TABLE 2

Correlation coefficients between roosting time of Great Tit (in relation to sunset) and the degree of cloudiness, wind speed and temperature at the time.

	n	cloudiness	wind speed	temperature
November	36	—0.34	—0.04	+0.07
December	36	—0.28	—0.02	+0.19
March	36	—0.43	—0.42	—0.26

The correlation coefficients in table 2 are much smaller than those concerned with the time of rising in the morning (in table 1). There is no evidence that the temperature influences the time of retiring. Heavy cloud has a slight tendency to cause earlier retiring. Strong wind has a similar effect in March, but the correlation coefficients for November and December are not significant. Hence weather conditions appear to have little influence on the time of retiring. This is confirmed by the fact that there are great and variable differences between the time of retiring of different individuals on the same day. For instance, during March 1939, EYGENRAAM studied a pair in which, as usual, the female

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always retired to roost before the male, but whereas on some days the male retired only 3 minutes after the female, on other days he was much later, even up to 40 minutes after her.

In his observations during the winter in the far north (67° N), FRANZ (l.c.) found that during December the Great Tit, like all the other diurnal species wintering there, was active for about 5 hours of the day. This means a period of activity extending from 2 hours before sunrise until 2 hours after sunset. He notes: "Diese Gleichheit der Aktivitätsdauer zeigt schon, dass sie durch Beleuchtungsverhältnisse erzwungen ist; länger ist die Nahrung einfach nicht zu erkennen. Wie dunkel es tatsächlich war, lässt sich ohne photo-elektrisches Messgerät kaum angeben". As, however, the light intensity at twilight is simply determined by the position of the sun below the horizon, we can in fact calculate the figure concerned (for normal clear weather). According to data for which I am indebted to Dr. J. J. M. REESINCK, in December at 67° N, te sun is 7° below the horizon 2 hours after sunset. The light intensity is then about 1 lux in the open on a clear evening. When there is snow, which is always the case in the arctic in December, the light intensity is, of course, rather higher. In the Netherlands in December, the Great Tit retires for the night at, on the average, 5 minutes after sunset, when the light intensity in the open is about 243 lux, a much higher intensity than that at which the species retires for the night in lat. 67° N. The latest at which we ever saw a Dutch Great Tit still active was 25 minutes after sunset (on 25th November, when the light intensity would be about 16 lux). In May, however, the early morning song of the male starts on the average 37 minutes before sunrise (see page 107). The sun is then nearly 6° below the horizon, and the light intensity is about 1 lux. Likewise SCHWAN found that at Halle the Great Tits started singing at about 1½ lux. Hence the light intensity at which the Great Tit becomes active and retires in the arctic winter is approximately the same as that at which the males in our latitude start their early morning singing in spring, and it is much lower than the light intensity at which our Great Tits retire for the night.

PART 2. TIME SPENT ON AND OFF THE EGGS

In all the nests of the Great Tits which we had under observation, incubation was carried out exclusively by the female. Indeed the male was almost never found alone in the nest cavity. In fig. 1 A are shown the data obtained with an automatic recording apparatus set up at two nests in 1937. In addition to a nearly complete record of the movements of the old birds, the time of the laying of the eggs and of the hatching and flying of the young are also known accurately for these nests.

The recording apparatus was already set up in March, and on April 1st

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the pair started to make their nest. However, nest-building was not accurately recorded, as some adjustments still had to be made to the apparatus. The latter were completed by the time that the first egg was laid on April 15th, and the apparatus continued to function well from then until the second brood left the nest on July 9th.

§ 3. The laying period.

In fig. 1 A is recorded the number of hours spent by the female in brooding the eggs during each 24-hour day. (The 24-hour day is taken from midnight one day to midnight the next, and so includes parts of two nights and the full daytime in between.) The number of hours spent in brooding is shown on the graph by the length of the vertical columns. The curved (nearly horizontal) line separates the night hours (= sun below horizon) from the daytime hours (= sun above horizon).

During the laying period, the number of hours spent on the eggs was always somewhat greater than the number of night hours, because the female remained on the nest during the whole of each night and was also there during very short periods of the daytime. During the laying period of the first brood, however, the female visited the nest only occasionally during the daytime, for purposes of building, and she then usually left again within one minute. The nest was slowly completed during the laying period. The eggs were not brooded by day during this time.

The female's behaviour was very different during the laying period of the second brood. During the first four days the eggs were not brooded by day. Already on the 5th day, however, the female sat on the eggs for one hour during the daytime, and before the clutch was completed, she was brooding for 8 hours during the day.

Observation showed that 9 out of the 10 young of the first brood hatched within 24 hours, and the tenth within another 24 hours. Most probably this last nestling hatched only shortly after the others. In the second brood, however, the last nestling hatched at least 72 hours after the first. The much longer period over which hatching was spread is no doubt related to the fact that, with the second brood, incubation started before some of he eggs had been laid. As a result, the young of this brood were of different ages. This striking phenomenon is not peculiar to the pair under observation, but is a general fact. We already knew from the observations on the young in many other nesting boxes that there were often one or two "late-comers" in second broods. These late-comers are pushed away by the older young during feeding, so that they do not get their proper share of food. As a result, their backwardness in development increases with time, and often such young die before the others leave the nest.

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NIETHAMMER (1937) states that, in the Great Tit, incubation starts before the last egg is laid, with the laying of the second egg before the last, or even of the fifth egg before the last. In general, this statement is incorrect. The time at which incubation starts is not a specific character, it is not even constant for a particular individual. It changes according to the circumstances.

Probably, the earlier start of incubation in the second brood is related to the fact that the brood-patch has already been formed. During the night, the female sits continuously on the nest, even during the laying period. Thus, during the laying period of the first brood the eggs are covered by the female for 11 to 11½ of each 24 hours. Clearly, therefore, the female has already sat on the first egg for more than $9 \times 11 =$ 99 hours, before the last egg is laid. For the second egg the corresponding figure is more than $8 \times 11 = 88$ hours, etc. How under these circumstances is it possible that all the eggs nevertheless hatch within 24 hours of each other?

The answer seems to be that the female is merely sitting on the eggs without incubating them, i.e. that the eggs do not reach the temperature necessary for development to start. On this point we have only some incidental observations. To some of the nesting boxes a thermometer was fixed by means of a perforated cork through a hole in the bottom of the box. The thermometer was placed with the mercury between the eggs, and the scale could be read by the observer outside the box without disturbing the sitting bird. By this means, it was learnt that the normal temperature of the eggs during the incubation period fluctuates between 36.2° C and 39.3° C. In the short periods for which the female left the eggs, the temperature fell somewhat, e.g. to 33.5° C or 32.3° C, but not lower. (These temperatures are considerably higher than those which were established by GIBB (1950) in a Great Tit's nest near Oxford.)

It is interesting to compare the above figures with the temperature reached by the eggs at night during the laying period. The following observations concern another clutch:

April	28th	19.30 h.	3	eggs	temp.	31.2° C.
,,	30th	20.30 h.	4	,,	,,	33.6° C.
May	3rd	23.00 h.	7	,,	,,	33.2° C.

At the time when the above observations were made, the temperature in a neighbouring empty box was 8.6° C on April 30th, and 14.6° C on May 3rd. Thus at night during the laying period, the temperature of the eggs was far above the external temperature, but the eggs did not reach the temperature normal during incubation. Clearly, therefore, during the laying period the warmth from the bird's body does not heat the eggs so much as it does during the incubation period.

STRESEMANN (1927/'34) states that, if the normal speed of development of hens' eggs is reckoned as 1 at 38° C, then at 35° C it is

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0.80, at 34° C it is 0.65 (and at 24° C it is zero). During the laying period, the average night temperature of the Great Tit's eggs is 33° C Hence development might be expected to proceed during the night at about half the speed of that during the incubation period. For the first egg of the clutch, the total nightly brooding amounted to about 90 hours before the penultimate egg was laid. Hence the first egg might have been expected to hatch $0.50 \times 90 = 45$ hours earlier than the penultimate egg. (The penultimate, not the last, egg was selected for this comparison as the time of hatching of the last egg was not accurately known). In fact, the penultimate egg hatched less than 24 hours after the first. Thus there is a discrepancy from the calculated figure of more than 20 hours. Considering, however, the inaccurate method of determining the average night temperature of the eggs during the laying period, this difference is not altogether surprising. Further, it is not impossible that the index of development for small eggs such as those of the Great Tit is lower with a reduced temperature than it is in the case of hens' eggs, i.e. it might be below 0.50 at 33° C.

That less warmth is conveyed to the eggs by the body of the bird during the laying period than during incubation may be connected with the way in which the brooding bird arranges her feathers. It is also possible that the brood-patch is not yet fully developed at this time, i.e. that the feathers have not yet come away, or that the supply of blood to the brood-patch is insufficient. In the case of the Great Tit moreover, there is another possibility. It is known that the Great Tit covers its eggs with nest-material during the laying period, and it is possible that the female does not remove this cover when she enters the nest for the night. Indeed, there is some indication that this is in fact the case. Observations made in the early morning, immediately after the female had left the nest for the first time, showed on several occasions that the eggs were covered with a thin layer of flattened nest material, on top of which the last egg had been laid, and was uncovered. This last egg is very often covered up by the bird during the course of the day, and for this purpose she collects some new nest material. The thin cover on top of the other eggs is then removed.

However, observations at other nests showed that there were other females which did not leave a cover on top of the eggs at night during the laying period, but sat on the uncovered eggs. There are, of course, many other species of song-birds which sit on the eggs at night during the laying period but certainly do not cover their eggs. Nevertheless, their eggs usually hatch within 24 hours of each other, or only slightly longer. Hence the main factor involved in the absence of incubation during the laying period must be the fact that the brood-patch is as yet incompletely developed.

The young of the second brood of the Great Tit hatch over several days

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because not only does the female brood these eggs by day during the laying period, but her brood-patch has already developed.

§ 4. The incubation period.

During the hours of daylight, the female Great Tit never sits continuously on the eggs for a long period, but leaves the nest repeatedly for a few minutes at a time, in order to feed and preen herself. The number of such periods off the nest varies between 12 and 29 per day. With the first brood, the average length of the periods spent on the eggs was 27.6 minutes, and of the periods off the eggs was 7.9 minutes. For the second brood, these values were 26.2 and 10.9 minutes respectively. The length of each period on the eggs is extremely variable. Sometimes the female sits for only a few minutes and then leaves her eggs again as a result of disturbance or of a call by the male. With no such outside disturbance, the periods of brooding are longer. The longest recorded was

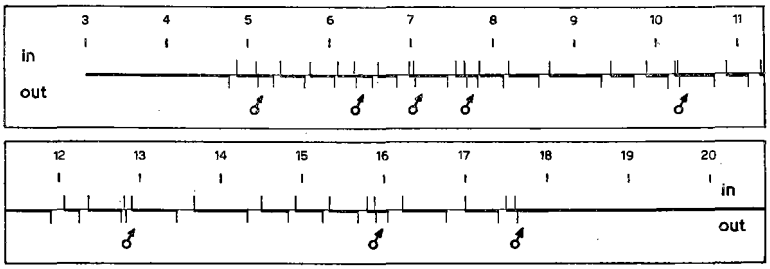

Fig. 4. A sample record of one day's activity during the incubation period. ——— = female on the eggs, ——— = female off the eggs. Arrivals at and departures from the nest, that are not marked with the sign ♂ concern the ♀. Date: 30 April 1937, 7th day of incubation.

68 minutes, but periods of more than 50 minutes do not occur often. The periods off the nest are of more uniform length than the brooding periods. However, both are strongly influenced by the air temperature, as will be discussed below. A day in the life of an incubating female Great Tit is shown diagrammatically in fig. 4.

From fig. 1 A, it is seen that, on the day that the 10th egg of the first brood was laid, the female did not, as yet, sit on the eggs during the day. As on the preceding days of the laying period, she left the nest about fifteen minutes after sunrise, and returned only two hours before sunset. On the next day, however, she sat on the eggs for 5 hours during the day-time (i.e. between sunrise and sunset), and on the following day for 7 hours. Only on the third day after the clutch was completed, did the female attain her full brooding time of 11½ hours during daylight. Her total period on the eggs then amounted to 21 hours out of the 24. (The maximum figure recorded for this brood was 21½ hours out of 24).

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With the second brood, as already recorded, the female started brooding during the day after the laying of the 5th egg, but in this case also, the number of hours of brooding during the daytime increased gradually, and the full period was attained only after the last egg had been laid. The change from no brooding at all during daylight up to full brooding, which took 3 days in the first brood, took 5 days in the second brood. The small number of hours spent in brooding during the first days is mainly the result of the female not brooding during the mornings. In table 3, the number of minutes that the female spent in brooding during the first 5 days is shown separately for the morning (05-11 h.) and afternoon (11-17 h.). After the first 5 days, there was no difference between the length of her morning and afternoon spells of brooding. From table 3 it is seen that, in the case of the first clutch, no brooding occurred during the mornings on the first days. In the second clutch, a little brooding took place during the mornings, but much less than in the afternoons.

TABEL 3

Time spent in brooding (in minutes) before and after 11 a.m. each day.

Brooding-day	1937	1st clutch		1937	2nd clutch		1939	1st clutch	
		05-11 hours	11-17 hours		05-11 hours	11-17 hours		05-11 hours	11-17 hours
1	Apr. 25	0	178	June 5	14	60	Apr. 27	0	52
2	26	0	277	6	51	73	28	56	143
3	27	269	279	7	196	149	29	84	275
4	28	280	300	8	250	189	30	251	326
5	29	297	295	9	250	240	May 1	258	319
average of the other days		276	247		273	270		273	263

These findings may be summarised as follows:

(1) During the first few days of incubation, the total time spent on the eggs by day is less than later on.

(2) In particular, there is less brooding during the morning than in the afternoons.

(3) In the first clutch, full brooding activity is not reached until 3 days after the laying of the last egg.

(4) In the second clutch, full brooding activity is reached as soon as the clutch is complete.

In the above summary, (1) and (2) are explicable through the female's great need for food during the period when she is producing eggs, while (3) and (4) are perhaps related to a difference in the quantity of avail-

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able food at the times of the year when the first and second clutches respectively are laid.

The normal incubation period of the Great Tit can be determined only from the last egg, because only this egg is brooded regularly from the beginning. In the first clutch, the last nestling hatched 15 days after the laying of the last egg, and in the second clutch 14 days afterwards. The extra day required in the incubation of the first clutch can be attributed to the smaller number of hours which the female spent in brooding these eggs on the first days after they had been laid. The difference may also be related to the lower air temperature prevailing during the incubation period of the first clutch.

The possible influence of the air temperature on the brooding attentiveness of the female was studied with the help of the automatic recorder. The average day temperature during the incubation period of the first and second clutches is included in fig. 1 A, calculated from the average of three observations made during the day, at 08, 14, and 18 o'clock respectively. (The air temperature at night is of no significance in this investigation, as the female always remains on the eggs during the night.) From these data, it is seen at once that the variations in the air temperature generally correspond with those in the number of hours spent in brooding. That is to say, the female stays longer on the eggs on cold than on warm days. The small number of hours spent in brooding on 10th and 11th June is particularly striking. These two days were characterized by a tropical temperature, with averages of 28° C and 26° C respectively. The correlation coefficient between air temperature and the time spent in brooding amounted to —0.86 for the first brood and —0.92 for the second brood.

Postulating a linear regression, calculation shows that an increase of one degree Centigrade in the air temperature causes a decrease of 8 minutes in the brooding time per day in the case of the first brood, and a decrease of 15 minutes per day in the case of the second brood. For the nest at Wageningen in 1939, the correlation coefficient between air temperature and brooding time amounted to —0.81 (regression 15 minutes per 1° C), and for the nest at Laren in 1942 (studied by BRIEDÉ) of —0.84 (regression 10 minutes per 1° C). Hence at all the nests studied, the influence of the air temperature on brooding time was unmistakable, though the quantitative relation between the two was rather different at different nests.

As the time spent in brooding at night shows only very small fluctuations, the above mentioned correlation is due wholly to variations in the number or length of the brooding periods during the day. The latter, of course, are correlated with the average length of the times spent off the nest. In fig. 5 is shown the influence of the air temperature on the average length of the periods spent on, and those spent off, the nest each

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day. The correlation between the air temperature and the length of the periods spent off the nest is higher than that between the air temperature and the average length of the brooding periods, the correlation coefficients being + 0.88 and —0.67 respectively. The reason for this might be discoverable if the air temperature inside the nesting box had been accurately recorded.

Fig. 5 also shows that the influence of the air temperature is greater

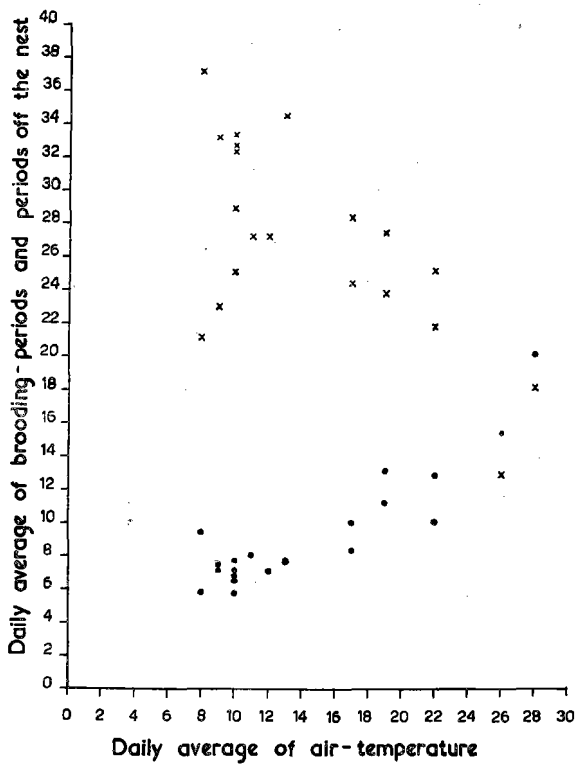

Fig. 5. Correlation between air-temperature each day and average length of (a) brooding periods (×) and (b) periods off the nest (•) each day. Periods are recorded in minutes, temperatures in degrees Centigrade. Only the daylight hours are considered.

at the higher temperatures. This, incidentally, provides an explanation of why, in the 1937 pair, the regression was higher in the case of the second brood (15 minutes per 1° C) than in the first brood (8 minutes per 1° C), for the average day-temperature was higher in the case of the second brood (18° C) than in the first (11° C).

The incubating female must herself gather the food needed for her own sustenance, for the food which the male brings to her 10 to 20 times a

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day is quite insufficient. The female at Bennekom in 1937 usually left her eggs for 2½ hours per day. As the available quantity of insect food is probably larger in the middle of June than in April, the female could probably allow herself more time for brooding during June than April. As already seen, however, the brooding period was shorter in June than April. Probably even in April, 2½ hours is often more than sufficient time in which to collect the daily ration. (Of course this depends on the quantity of food available within the feeding range of the pair.) BRIEDÉ observed a brood at Laren in 1942 in which the female left the eggs for only 2 hours per day on some days.

During the first few days after the young have hatched, the female remains on the nest during most of the day. The length of time which she spends in brooding decreases gradually as the young grow older. In graph 1 A, it is seen that, in both first and second broods, the female completely stopped brooding during the day-time on the 6th day after the last nestling had hatched. In the first brood, she remained on the nest during the night until the young left the nest. In the second brood, she remained on the nest at night until two days before the young left.

PART 3. FEEDING

§ 5. The feeding of the female by the male.

LACK (1940), summarising the literature on courtship feeding in birds, stated that, in the Paridae, this habit was recorded only during incubation. This, however, is not correct. We observed several cases of courtship feeding before the incubation period had started, also many during it. It is likely that courtship feeding is easier to observe during the incubation period than before it, because during incubation it is performed near the nesting cavity, whereas before this time it may take place anywhere in the territory.

During the incubation period, courtship feeding takes the following form: the male approaches the nesting cavity with food in his beak. He announces his arrival with the well known saw-sharpening call, which in this case, however, is much softer than usual. The brooding female answers the call with a soft whining sound — the same sound which she makes when the male wakes her up in the morning with his singing (see p. 102).

BRIEDÉ and the author observed some cases in which the male arrived at the nest with food just after the female had left. When his call notes remained unanswered, he disappeared quietly with the food. When the female answers, one of two things may happen. Either the female remains in the nesting box and the male enters, delivers the food and leaves the nesting box immediately afterwards, or the female comes out and

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then takes the food from the male. After that, she either enters the box again or remains outside to collect food for herself for some time.

BRIEDÉ observed a pair in which the male at first delivered the food to the female inside the nesting box, but later in the incubation period the female used to come out to receive it, returning to her eggs immediately afterwards. In the case of a pair at Bennekom in 1937, the male always brought food to the female inside the nesting box. The number of such feeding visits varied, in the case of the first brood being between 4 and 24 (average 12) per day, and in the case of the second brood between 2 and 19 (average 8) per day. In the case of a brood at Laren studied by BRIEDÉ, the number of feeds varied between 11 and 23 (average 15) per day.

Courtship feeding can be observed at any hour of the day, but is most frequent in the morning, with a second but smaller peak between 2 and 4 p.m. In the case of the two 1937 broods, these peaks of activity were more clearly marked in the first than the second brood.

TABLE 4

Number of times that the brooding female was fed by the male on the nest. Note that the number of days on which observations were made was different at each nest.

Hour	Bennekom 1937 24 Apr.-5 May (14 days of observation)	Bennekom 1937 7-16 June (10 days of observation)	Laren 1941 17-24 May (6 days of observation)
3- 4			
4- 5	6	1	
5- 6	22	5	
6- 7	26	5	14
7- 8	17	3	17
8- 9	9	6	4
9-10	12	5	3
10-11	10	7	4
11-12	8	2	6
12-13	9	3	6
13-14	6	3	4
14-15	13	3	5
15-16	12	5	1
16-17	5	3	8
17-18	8	1	4
18-19	2	1	3
19-20	0	0	0

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The number of times that the female is fed by the male each day is comparatively low. For her sustenance, the female must obviously depend mainly on what she collects for herself during her periods off the eggs. As far as I can judge LACK (1940) was right in supposing that the function of courtship feeding is not the provision of food for the brooding female, but rather a behaviour-bond keeping the pair together.

§ 6. The feeding of the nestlings.

On the day that the young hatch, the male Great Tit immediately starts collecting food for them. The female, on the other hand, takes up this behaviour only gradually, and on the first two days she frequently enters the nesting box without bringing food. Only on the third or fourth day after the young have hatched, does the female bring food regularly. As a result, the number of visits to the nest shown by an automatic recorder (as in fig. 1 C) is somewhat higher than the number of times on which food is brought. I would estimate that the real number of feeds per day amounts to only 80 % of the number of visits made by the parents on the first day after the young have hatched, to 95 % on the second day, and thereafter to 100 %.

The behaviour of the parents on the first days after the young have hatched shows that they are not yet "accustomed" to feeding them. Thus when male and female arrive at the nest simultaneously, the female begs the male for food, and during the first days often eats this food herself, though later on she normally passes it on to the young. On the first and second days, also, the female sometimes arrives at the nest without food, then looks for something in the immediate surroundings of the nest, and enters with it. This gives the impression that she has suddenly remembered that there are young to be fed.

The automatic recording of the number of feeding visits will be discussed below. The recorder does not of course, distinguish between the visits of male and female, so that the share of the two sexes has to be determined by direct observation. The results of the latter are shown in table 5. (Where the data for one day are insufficient to calculate a reliable percentage, they have been combined with those of the following day.)

At Bennekom the share of the male in feeding the young decreased from about 90 % on the first days to 40-50 % on the last days of the nestling period. The observations of EYGENRAAM at Ede showed that at this nest the share of the female on the first days was relatively much larger than it was at Bennekom (see table 5). As a result, the total number of feeds received by the Ede nestlings on the first days was nearly twice as great as at the Bennekom nest. This was achieved at the cost of less brooding of the young. Clearly, there are large individual dif-

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TABLE 5

Share of the sexes in feeding the young.

Age of nestlings	Nest at Bennekom		Share of male (as % age)	Nest at Ede		Share of male (as % age)
	Number of feeds by			Number of feeds by		
	male	female		male	female	
0	26	1	96	14	11	59
1	35	6	85	8	4	
2	21	3	86	39	11	78
3	3	1		66	47	58
4	12	11	61	37	29	56
5	7	1				
6				25	30	45
7				43	52	45
8	11	10	52	45	67	40
9	16	11	59	72	82	46
10				79	113	41
11				20	29	46
12				10	6	
13	9	13	41	61	67	48
14				45	46	49
15	1	6	44			
16	15	14		54	66	45
17				49	37	57
18				18	30	37
19	36	43	46	5	9	
20	6	11	35			
21				17	18	49
22				4	4	

ferences in this matter, differences which do not seem to be injurious to the development of the young.

The number of visits to the nest each day is shown in fig. 1 C. In the first broods, this amounted to 120 on the first day and it increased successively to a maximum of 937 on the 16th day. Then it decreased gradually to 750 per day. On the day that the nestlings left the nest (between 6.45 and 7.20 a.m.), they had already received 137 feeds. The total number of feeds for the whole period was 10 685, or 1068 per nestling. I attribute the decrease in the number of feeds during the last days in the nest to the fact that the male and female were then already preparing for a second brood. The parents continually stayed near each other at these times, and on several occasions I observed their courtship in the neighbourhood of the nesting box in which the young still remained.

In the second brood, there were 52 feeds on the first day. With some irregularities, the number increased to a maximum of 256 on the 11th

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day. After that, it decreased somewhat again. On the day before that on which the nestlings left, there were 222 feeds. On the day that the young left (between 7.25 and 7.35 a.m.), they received 48 feeds. The total number of feeds for the whole period was 4042, or 577 per nestling.

Sometimes, the male completely stops feeding the young a few days before they leave the nest. This seems commoner in second broods (16 cases out of 139) than in first broods (21 cases out of 305). Occasionally, also, the female has stopped feeding the young towards the end of the nestling period, but this was observed only 5 times in a total of 444 broods. It was not always possible to determine whether in such cases the defaulting parent was still alive, but this was certainly true in the case of some of the males involved (e.g. the male mentioned on p. 130). Some of those males which did not feed their young during the last days in the nest nevertheless looked after them after they had left the nest.

The daily number of feeds per day at all nests fitted with automatic recorders is set out in table 6.

MOREAU (1944) found that for several species of tropical birds the total number of feeds per day is greater in broods with many young than it is in broods with rather fewer young, though the increase in the feeding rate is not proportional to the number of nestlings. Thus each nestling is fed more frequently in a small than in a large brood. GIBB (1950) observed visiting frequency of the Great Tit in 1948 and 1949 near Oxford. He confirmed that the greater number of nestlings in a brood the more frequent are the visits to the nest. But this increase was not proportional to brood size and one member of a less numerous brood therefore received more visits than does one member of a more numerous brood.

We did not find this relationship. For the 8 nests at which a recording apparatus was set up, we calculated the average number of feeds per young per day during the second half of the nestling period, i.e. for the 10 days during which the young grew from 7 to 16 days old. The results are shown in the last line of table 6, the first figure giving the average number of feeds per day received by each brood, and the figure in brackets the average number of feeds per day received by an individual nestling in each brood. There is not the slightest indication of a negative correlation between the number of nestlings and the number of feeds per nestling. To the author's opinion the feeding frequency, provided that it is within the working capabilities of the adults (which in general seem quite adequate), is chiefly determined by the "begging activity" of the young. As this "begging activity" is stimulated by the hunger of the nestlings, the number of feeds per nestling is inversely proportionate to the size of the prey brought. It seems unprobable that the number of feeds was in any case limited by the working capabilities of the parents. GIBB (l.c.) stated, however, that nestlings of the smaller brood sizes were on

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TABLE 6

Number of feeding visits per day. The date on which the observations were started at each nest is put below the year. Bk = Bennekom, Wag. = Wageningen, Blar. = Blaricum. The average number of feeds per day per brood and (in brackets) per nestling, from the 7th until the 16th day inclusive is shown in the last lines of the table.

Age of nestlings	Bk 1936 17 VI	Bk 1937 8 V	Bk 1937 19 VI	Wag. 1939 12 V	Laren 1941 25 V	Laren 1941 18 VI	Blar. 1942 25 V	Meppel 1947 27 VI
	8 young	10 young	7 young	9 young	6 young	6 young	9 young	9 young
0		120	52	172		47	145	118
1		167	132	269	233		200	124
2		213	156	288		148	238	131
3		206	190	272	322	149	259	127
4		228	206	319	500		381	104
5		332	196	422	567	152	392	134
6		357	196	390		218	410	154
7	208	491	221	358		204	377	161
8	221	532	192	411	544	246	428	228
9	262	549	233	476	548	216	381	270
10	259	568	256	430	438	232	403	267
11	234	557	224	378		291	402	197
12	249	573	225	453		295	458	228
13	268	677	244	467	395	239	478	213
14	259	843	201	415		262	630	241
15	260	937	196	441	544	243	926	229
16	206	856	194	405	456	293	935	239
17	222	786	210	415	289	220	990	
18	209	788	248	530		226		201
19	207	750	222	86				28
20	220	137	48					
21	48							
7-16	243 (30)	658 (66)	219 (31)	423 (47)	487 (81)	252 (42)	542 (60)	227 (25)

an average slightly heavier than those of the larger-sized ones. This was in accordance with his observation, that members of the former broods receive more feeding visits than those of the latter broods.

We have already called attention to the fact that, in the pair studied in 1937, the nestlings were fed more frequently in the case of the first brood in May than in the case of the second brood in June and July. From the calculation on page 126, it is clear that this difference is not due solely to the smaller number of nestlings in the second than the first brood; for the total number of feeds during 20 days amounted in the case of the

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first brood to 1068 per young, and in the case of the second brood to 577 per young. This difference is the more striking when it is considered that the daylight (and hence the potential working day) lasts longer at the time of the second brood in June-July, than at the time of the first brood in May. What, then, is the cause of the above difference in feeding? It lies in the fact that the size of the insects brought to the young is not so large in May as it is in June and July. This size-difference struck me while I was making observations through field-glasses of the adults bringing food to the nest, and the first impression was fully confirmed subsequently, both by a detailed series of observations through field-glasses, and by food samples taken with the "collar method" (KLUIJVER 1933). This investigation was carried out with the broods at Bennekom in 1937. The birds in question collected most of the food for their young in a pine-wood (*Pinus silvestris*), and the results are given below:

1. In general, the adult bird brings only one organism at each visit. On only one occasion did we observe two little caterpillars brought simultaneously.

2. There is no clear correlation between the age of the nestlings and the weight of the prey organisms brought to it. But the Great Tit very often divides the contents of one large prey organism among several of the young by squeezing it out (PROMPTOW and LUKINA 1938).

3. The average weight of a prey organism brought to the nestlings of the first brood (10th-27th May) was 45-50 mg.

254 preys organisms were identified as follows: 115 larvae of *Evetria* spp.; 42 green caterpillars (mainly larvae of *Panolis griseovariegata*); 38 miscellaneous insects, e.g. *Bibio* (Diptera), Coleoptera, and larvae and pupae of Lepidoptera; 45 spiders (Arachnida); and sand on 14 occasions. The weight of an *Evetria* larva was 40 mg, while the other prey organisms averaged somewhat heavier. The weight of a *Panolis* larva was about 60 mg at that time of the year. From the 8th day onwards, the parents started to collect beakfulls of yellow sand from a place near the nest where a man had been digging. They often did this several times in succession after each other. Apart from the insects listed above, I also observed some instances in which small fragments of white bread and sunflower seeds were fed to the young. (The nest was situated near a human dwelling.) Large prey organisms are "prepared" before they are fed to the young. Thus BRIEDÉ once observed a Great Tit which arrived at the nest with a large caterpillar. Before the bird entered the nest, it decapitated the caterpillar. This makes it possible for it to divide the contents of the caterpillar among the nestlings. The nestling whose turn comes last gets the nearly empty skin of the caterpillar.

4. The average weight of a prey organism brought to the nestlings of the second brood (23rd June-9th July) was about 240 mg. 52 prey organisms were identified as follows: 13 larvae of *Panolis griseovariegata*;

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1 larva of *Euproctis chrysorrhoea*; 1 larva of *Lophopterix camelina*; 32 miscellaneous lepidopterous larvae and 1 imago; 1 larva of *Cimbex fagi*; 1 sawfly larva (Hymenoptera, Tenthredinidae); 2 spiders (Arachnida); sand on one occasion. The heaviest prey organism brought to the nest weighed 580 mg.

Between 4th and 7th July, at some second-brood nests in a pinewood intersected by an avenue of Beech trees (*Fagus sylvatica*), the following prey organisms were collected by means of the collar method: 39 larvae of *Panolis griseovariegata,* 38 larvae of *Lophopterix camelina*; 12 larvae of *Cimbex fagi*; 4 larvae of *Euproctis chrysorrhoea*; 7 Noctuid imagines; 14 unidentified lepidopterous larvae; 14 unidentified lepidopterous pupae; 2 larvae and 1 image of *Lophyrus pini*; 4 unidentified insects; 1 spider; sand on one occasion. Before large moths were fed to the young, their wings were removed by the parent bird.

As already noted, the average weight of a prey organism brought to the first brood was 45-50 mg. For the second brood, it was 240 mg. Allowing for the total number of feeds received by each brood, it is easily calculated that, during the 20 days of the nestling period, the 10 nestlings of the first brood received a total of 640 grams of food, or 64 grams per nestling, while the 7 young of the second brood received a total of 973 grams, or 139 grams per nestling. From this, it is clear that the young of the second brood enjoyed an abundance of food. The difference is still more striking when it is considered that the percentage of roughage (ectoskeleton) of the small insects brought as food in May is higher than that of the larger prey organisms brought in June and July.

An important difference in feeding frequency can sometimes be observed among broods hatching at the same time but in different places. In a site where prey organisms of large size are available, the feeding frequency is reduced, and conversely the presence of prey organisms of small size causes an increase in the feeding frequency. A particularly interesting example of this was observed by BRIEDÉ in an oakwood suffering from a plague of *Tortrix viridana* at Blaricum in 1942. The automatic recording of the feeding visits here are set out in table 6, 7th column. The food which was brought to the nest was studied with the help of field-glasses for half an hour each morning. Up to and including the 14th day after the young hatched, BRIEDÉ observed 240 instances in which a caterpillar of *Tortrix viridana* was fed to the young, and only 5 cases in which unrecognisable insects were brought. On the 14th day, a change occurred: The caterpillars suddenly started to pupate. Everywhere they were seen suspending themselves, and by the next day most of them had disappeared. The Great Tits brought the pupae much less frequently than the caterpillars. Moreover, the nestlings did not seem to like the pupae much, and a large number were found in the nest after the young had flown. The parent birds now collected other, and on the

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average much smaller, kinds of prey. The immediate result was a sharp rise in the feeding frequency (see table 6).

A remarkable series of observations was made by EYGENRAAM during May 1940. The brood in question hatched on 9th May. On that day, the male brought food 5 times, and the female twice, which is quite normal. For the next 11 days, the observer could not study the nest owing to the German drive into Holland. On 20th May, the pair were still there, and were feeding the 10 nestlings in a normal way. From 23rd May, however, the behaviour of the male suddenly changed. He completely gave up feeding the young, and restricted himself to flying up and down with the female, behaving in the way that a male generally does when the female is building a nest. Further, he courted her, and chased intruders from the territory. It was clear that he was ready to start a second brood. The insects which he now and then offered to the female, she passed on to the young. The female regularly fed the young 50-60 times per hour, on 24th May 73 times in the hour, and on 25th May as much as 83 times during one hour's watch. The food consisted partly of peanuts, which the female obtained in large quantities from a human source, but natural insect food was brought up to 40 times per hour. Apparently, her thus carrying out single handed the work normally shared between both parents imposed a severe strain upon her. Her plumage was in very poor condition, this being especially striking in comparison with the sleek plumage of the male. Eventually, she even lost her tail!

It was also noteworthy that the above female scarcely carried away the faeces of the young. For the most part, she ate them. The latter was once observed as she sat in the nest opening. While in song-birds the faeces of young nestlings are usually eaten by the parents, those of the older nestlings at a later stage are always carried away. The eating of the faeces of such older young was perhaps a sign that the above female was hungry.

Of the 10 nestlings present on 23rd May, only 5 flew on 31st May. The others must have died. It is not certain that this was the result of food shortage, as the female's feeding rate did not greatly differ from that of both parents combined under normal conditions. In this case, however, a great part of the food (peanuts) was obtained unusually easily. L. TINBERGEN (in litt.) mentions the case of a female Great Tit which had a high feeding frequency but did not select prey of sufficiently large size, with the result that, in total, she did not bring enough food, and many of her young died. Likewise in the case studied by EYGENRAAM, much of the food (especially the peanuts) may have been unsuitable for the young.

At EYGENRAAM's nest, a few days after the young had flown, the female started building a new nest. This was on 3rd June, and the first egg of a new clutch of 9 appeared on 5th June. When the young of this

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second brood hatched, the male fed them throughout the nestling period in a perfectly normal manner.

PALMGREN (1944) has published detailed observations on the fluctuations during the day in the migration-activity (Zugunruhe) of birds. He ascribes great importance to a certain fixed internal rhythm in the bird. It is also well known that the intensity of the singing of birds shows a peak in the morning and a decrease during the afternoon. A similar

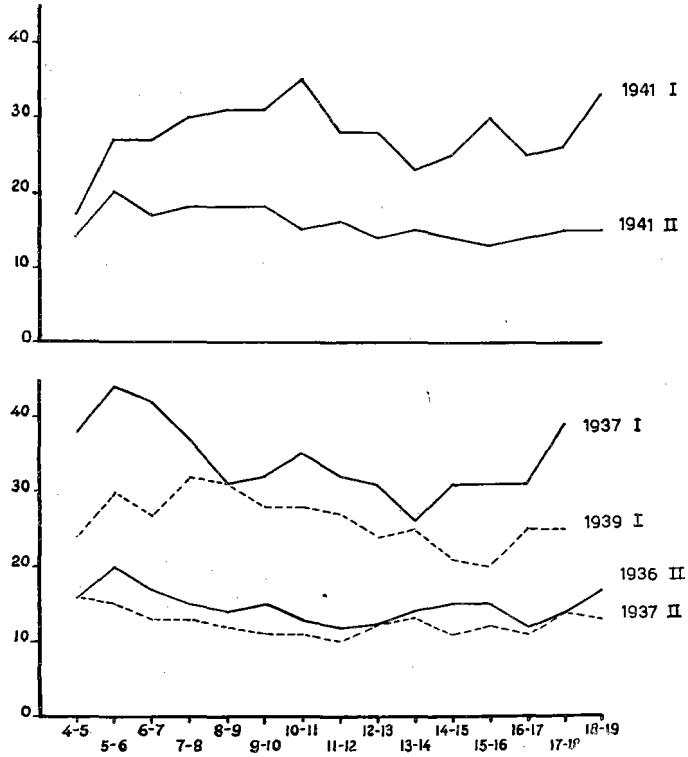

Fig. 6. Daily rhythm in the feeding-activity. Average number of feedings per hour in some broods, mentioned in table 6. I = first brood; II = second brood.

rhythm certainly plays an important part in the feeding activity of the Great Tit. In all the pairs studied, the maximum activity clearly occurred in the morning, before 12 o'clock. This was followed by a definite minimum in the afternoon, and there was a second maximum during the evening, which, however, was always smaller than the morning peak (fig. 6). A remarkable feature of fig. 6 is that in all cases the minimum feeding frequency is about 60 % of that of the morning maximum. Whether there is great or only a little activity in the morning, the decline in the afternoon is always to about 60 % of it. This suggests that tiredness

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on the part of the adults is not a major cause of the afternoon decline in their activity.

The feeding frequency is not influenced solely by the feeding impulse of the parents, but also by the intensity of the begging behaviour of the nestlings. Hence a decline in the feeding frequency during the afternoon might be due to the nestlings being temporarily satiated, and therefore begging for food less violently. However, another observation points against this idea. As noted on p. 129, the young of the second brood in 1937 received about double the quantity of food received by the young of the first brood. If the temporary satiety of the young was an important factor in producing the afternoon decline in feeding frequency, one would have expected this decline to be greater in the case of the second than of the first brood. This, however, is not so. (The relation of the satiety of the young to the feeding frequency is a problem which could easily be tested further by simple experiments.)

The afternoon minimum also coincides approximately with the warmest time of the day. Nevertheless I do not think that the rising air-temperature is reponsible for the decline. As already remarked, the afternoon decline in the feeding frequency is proportionally the same in the case of both the first and the second broods. As the afternoon temperature maximum is higher during the time of the second brood in June-July than of the first brood in May, a greater decline would have been expected during the time of the second than the first brood if the influence of temperature had been important.

As neither the air temperature, nor the tiredness of the adults, nor the satiety of the young provides a satisfactory explanation of the afternoon decline in the feeding frequency, I conclude with PALMGREN (l.c.) that great importance must be attributed to the bird's autonomic rhythm. That is not to say, however, that an internal rhythm rigidly controls the details of the bird's activities. This can be seen from a study of fig. 6. Some pairs start to work at full capacity immediately after first rising in the morning. In other pairs the peak of activity comes between 7 and 8 a.m., and in yet others between 10 and 11 a.m. Likewise, neither the afternoon minimum nor the evening peak occurs at exactly the same time in all pairs. Moreover, although it might appear from fig. 6 that the afternoon minimum of each pair is very clear-cut, this is not really so. If a comparison is made of the frequency curves for the same brood on successive days, the time of the minimum is found to be rather different on different days. Thus for brood I in 1937, the minimum came on the average between 13 and 14 o'clock, but on two days it came between 11 and 12 (a.m.), on two days between 12 and 13 o'clock, on 6 days between 13 and 14 o'clock, and on 2 days between 14 and 15 o'clock, while there were 8 days which showed no clear minimum. These variations may be caused partly by the fact that the minima of activity of the two parents

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did not necessarily coincide. The possibility might also be suggested of a gradual shift in the time of the minimum during the nestling period. Such, however, was not found; the variations were erratic. Heavy rainfall, for instance, has a strong depressing influence on the number of feeds, and if the birds have taken shelter during a shower (e.g. in the nesting cavity), their feeding rate is accelerated in the period immediately following. If, however, they have got wet, this increase occurs only after they have had an opportunity to dry themselves somewhat, and to smooth out their plumage.

SUMMARY

Times of rising and retiring for the day.

a. *The reproductive period.*

During the whole period of reproduction the female sleeps in the nest cavity, the male sleeps outside. He starts his daily activity earlier than the female and calls her out by song. During the laying and the brooding period the female rises on an average 20 minutes after sunrise; as soon as the young have hatched she rises 6 minutes before sunrise.

In April and May the male starts singing on an average 37 minutes before sunrise.

The female retires very early to roost, viz. 64 minutes before sunrise during the laying period and 100 minutes before sunrise during the brooding period. After the young have hatched the moment of last activity of the female gradually moves to sunset.

b. *Summer, autumn and winter.*

During November, December and January the beginning of the activity starts on an average 26 minutes before sunrise, the extremes being 14 and 40 minutes before sunrise. This variability is due to differences in windspeed, temperature and cloudiness. The male rises ± 2 minutes earlier than the female, he remains active 12 minutes longer than she does.

In August the birds go to roost an hour before sunset, in winter ± at sunset, only in December slightly after it. These differences are connected with day-length and food requirements. Weather conditions are of little influence on the time of retiring.

Time spent on and off the eggs.

a. *The laying period.*

In the first brood no brooding takes place during the day time. The female only visits the nest now and then for nest building. She abandons it, however, usually within a minute. Brooding begins after the last egg is laid.

In the second brood the female sits on the eggs on the 5th day for an

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hour during the daytime. Before the clutch is completed she broods 8 hours during the day. The fact that in the second brood the young hatch over a longer period is related with this early start of brooding.

During the night the female sits continually on the nest and the eggs reach a temperature of ± 33° C, besides 36°-39° C during the incubation period.

b. *The incubation period.*

The female exclusively broods the eggs. During the day time the length of the periods which a female spent on the eggs amounted to an average of 27.6 minutes, the length of the intervals was 7.9 minutes. In the second brood these periods were respectively 26.2 minutes and 10.9 minutes. The longest period of perpetual brooding was 68 minutes. The number of interchanges diverged between 12 and 29 per day. During the first days of the incubation period the female gradually changed from no brooding at all to full capacity. The low number of brooding hours during the first days is mainly the result of no brooding in the morning.

The brooding attentiveness of the female decreases if air temperature rises.

Feeding.

During the incubation the male feeds the female in or out the nesting hole. The number of feedings per day is relatively low. On the day of hatching of the young the male immediately starts with the food supply. The female takes up this task only gradually.

In the first brood of a pair the number of feedings increased successively from 120 on the first day to 937 on the 16th day (10 young). The total number of feedings amounted to 10685 (1068 per nestling). In the second brood of the same pair the parents started with 52 feedings on the first day and the number increased to a maximum of 256 on the 11th day (7 young). The total number of feedings amounted to 4042 (577 per nestling). The difference in number of feedings is connected with the fact that insects are larger in June and July than in May.

Nestlings of other broods received different numbers of feedings (see table 6).

Feeding activity of the parents is greater in the morning than in the afternoon. The afternoon minimum is usually found on the level of 60 % of the morning maximum.

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Overzicht van de broedkolonies van de Blauwe Reiger, *Ardea cinerea* L., in Nederland in 1949

Mededeling van de Afdeling Natuurbescherming en Landschap van het Staatsbosbeheer

door

SJ. BRAAKSMA EN DR. M. F. MÖRZER BRUYNS
met medewerking van
G. A. BROUWER

(Met 2 kaarten en plaat III)

Inleiding.

Sinds 1900 is tot driemaal toe een onderzoek ingesteld naar de verspreiding van de Blauwe Reiger in Nederland, waarbij het aantal nesten van de verschillende kolonies zoveel mogelijk geteld werd. Deze onderzoekingen hadden plaats in 1908/1909, 1925/1926 en 1935/1937. Sindsdien vond geen landelijk georganiseerd onderzoek meer plaats en werd alleen een aantal losse mededelingen over de sterkte van diverse kolonies bekend.

Het is om verschillende redenen van belang op de hoogte te blijven van de fluctuaties van de getalssterkte van deze vogelsoort, die zo kenmerkend is voor ons Nederlandse landschap.

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