Reprint from

PROCEEDINGS OF THE FIFTH NORDIC ORNITHOLOGICAL CONGRESS, 1985

Ingvar Lennerstedt:

Feeding rhythm in three passerines under subarctic conditions in Lapland.

Feeding rhythm in three passerines under subarctic conditions in Lapland

Matningsrytm hos tre tättingar under subarktiska betingelser i Lappland

Ingvar Lennerstedt

Lennerstedt, I. 1987, Feeding rhythm in three passerines under subarctic conditions in Lapland. — Acta Reg. Soc. Litt. Gothoburgensis. Zoologica 14: 109-117.

Ficedula hypoleuca rested for 4-6 hours around midnight. The nest visit frequency was related to the number of nestlings and, in one case, to the type of food brought to the nestlings. *Turdus iliacus* rested before midnight, usually 2-4 hours, but the rest period was sometimes longer or shorter. Two pairs with 5 nestlings in 1983 had shorter night rests than two pairs with 6 nestlings in 1985, probably because there was less food available in 1983. Two clutches in 1985 were raised to the abnormal number of 7 nestlings, and the parents responded by raising their nest visit frequency and shortening the rest length, one night both parents were active all night. *Luscinia svecica* rested after midnight, usually 2-4 hours, but the rest was shortened or abandoned in stressful situations. The availability of food in the habitat during different hours of the day, and the demand for food from the nestlings were factors that affected the diurnal rhythm of activity in adult *T. iliacus* and *L. svecica*.

Svartvit flugsnappare vilade 4-6 timmar omkring midnatt. Frekvensen bobesök var beroende av antalet ungar och typen av föda som ungarna fick. Rödvingetrasten vilade före midnatt, vanligen 2-4 timmar, men viloperioden var ibland längre eller kortare än så. Två par med fem ungar 1983 hade kortare nattvila än två par med 6 ungar 1985, förmodligen beroende på sämre tillgång på föda 1983. I två kullar 1985 ökades antalet ungar till 7, ett abnormt antal, och föräldrarna svarade med att öka frekvensen bobesök och minska nattvilans längd, båda paren föräldrar var en natt aktiva hela natten. Blåhaken vilade 2-4 timmar efter midnatt, men i ansträngda situationer förkortade den nattvilan eller tog ingen vila alls. Tillgängligheten på föda under dygnets olika timmar och ungarnas krav på föda var faktorer som påverkade dygnsrytmen hos de gamla rödvingetrastarna och blåhakarna.

Ingvar Lennerstedt, Småskolevägen 1, S-223 67 Lund, Sweden

Introduction

In the continuous daylight of the subarctic summer, birds can be active all night, but they usually have rest periods like birds further south where the nights are dark. Peiponen (1970) discussed the diurnal rhythm of subarctic passerine birds feeding nestlings and divided the species into three groups according to the time of rest: (1) species with rest principally before midnight, (2) species with rest symmetrically around midnight, and (3) species with rest principally after midnight. Earlier studies in the subalpine birch forest at Ammarnäs (65 °N) have shown that Redwing *Turdus iliacus* and Reed Bunting *Emberiza schoeniclus* rest before midnight, Willow Warbler *Phylloscopus trochilus* and Pied Flycatcher *Ficedula hypoleuca* around midnight (Lennerstedt 1969, 1973, Arheimer 1978, 1982). In the present study, I give additional data for Pied Flycatcher, Redwing, and Bluethroat.

Methods

The study was carried out 1982-1985 in the subalpine birch forest between the river Tjul-

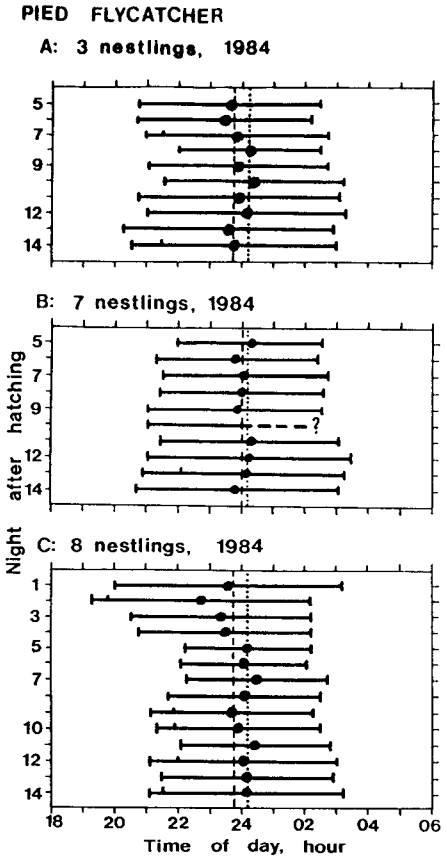


Fig. 1. Night rest in three pairs of Pied Flycatcher.

ån and the mountains Gaissats and Valle, 6 km to the west of Ammarnäs (65°58N, 16°13E). The bird's visits to the nest were recorded by a mirco switch connected to an automatically recording apparatus. The Pied Flytcatchers bred in nest boxes and the switch was put up at the inner side of the entrance hole. The Redwings were recorded by the device used by Arheimer (1978), a copper thread formed round the edge of the nest and connected to a switch. The Bluethroats were recorded when they pressed a pin attached to a switch at the entrance way to the nest with other ways to reach the nest blocked by sticks in the ground. I visited the nests twice every day and checked the functioning of the device.

The recording apparatus was specifically built for this study. It was placed in a small hut a few hundred meters from the nests. The apparatus has 20 channels, each with a needle rasping a line on a paper with a thin wax layer. The paper was driven by a clockwork motor at 2 mm per minute. Each needle has a left and right position. When a bird pressed a switch, an electrical circuit was closed and the needle moved from one side to the other. Thus, two close events could b detected, up to three events within 5 seconds. The voltage was delivered by a 12 volt car storage battery.

The Pied Flycatchers and Bluethroats were observed from a tent and their behaviour compared with the records. Most recorc were easy to interprete. Sometimes, there were many records within a very short period of time, the meaning of which was obscure. Then I counted two nest visits, one for the male and one for the female. The adult birds should have reasonable length of time to get new food for the nestlings before a new nest visit was counted. Sometimes, there was only one record. Then the female might have arrived at the nest, fed the nestlings, and laid down brooding them. To avoid this being regarded as one nest visit. I counted each "to" and "from" the nest in one hour and divided the figure by two. The nest visit frequencies discussed below are thus interpreted frequencies.

The start and end of night rest were easy to identify. In the evening the number of nest visits decreased and then ended at a distinc time. The night rest was sometimes disrupted by a few records. The female might have left the nest to preen herself or to do something else not connected with feeding. As a definition, the night rest started when there wer more than 15 minutes between the end of regular activity and single records. The end of night rest was determined using the same principle.

Results and discussion

Pied Flycatcher

Three pairs of Pied Flycatcher were studied in 1984. Pair A had 3 nestlings, pair B had 7

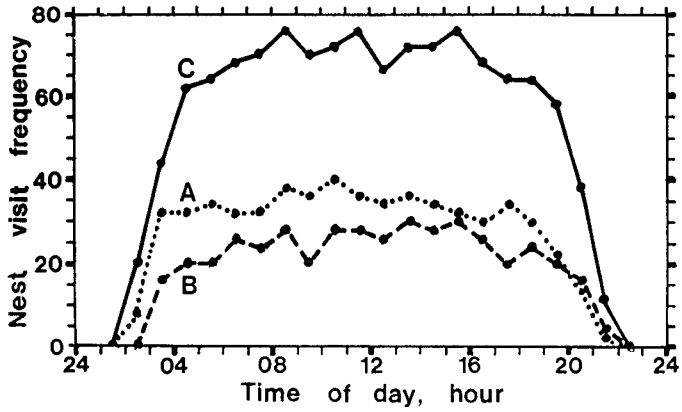


Fig. 2. Average nest visit frequency for days 5-14 in three pairs of Pied Flycatcher. A, 3 nestlings. B, 7 nestlings. C, 8 nestlings.

nestlings, and pair C had 8 nestlings. The 7- and 8-clutches were natural but exceptionally large, the average clutch size in 1984 in the Ammarnäs nest box areas was about 6,3 (E. Nyholm, pers. comm.). These large clutches were the result of a warm weather period in late May, favourable for insect activity, and an abundance of *Epirrita* larvae, already available during the laying period.

The length of night rest in the three pairs is shown in Fig. 1.

The activity of pair C with 8 nestlings was recorded from the hatching to the fourteenth day after hatching at which point the young left the nest. The first and second rest were the longest, and the fifth and sixth the shortest, 7 and 4 hours respectively. The twelfth to fourteenth night rests were 5-6 hours. The newly hatched nestlings had yolk sacs to complete the food brought by the parents. Thus the nestlings' need for food was comparatively low over the first few days, and the female obviously spent much time brooding the nestlings. The most intense period of growth occurred in the middle of the nestling period.

The nests of pair A and pair B were followed from the fifth day. Pair B with 7 nestlings had longer night rest than pair C with 8 nestlings. Pair A with 3 nestlings took the longest rest. The average length of rest for the nights 5-14 was calculated for the three pairs (Tab. 1).

The midpoint of the night rest in the three pairs was around midnight and it was almost the same for all three clutches.

There were interesting differences among the three pairs in the frequency of nest visits. Fig. 2 shows the average values for days 4-14. Pair C with 8 nestlings had, on average, more

Table 1. Average night rest and nest visit frequency during days 5-14 in three clutches of Pied Flycatcher breeding in 1984.

Pair	Clutch size	Night rest				Mean no. of nest visits per hour
		Start time	Midpoint time	End time	Length h m	
A	3	21 00	23 30	2 50	5 50	32
B	7	21 15	00 00	2 50	5 35	28
C	8	21 45	23 50	2 30	4 45	66

than 60 nest visits/hour, whereas pair B with 7 nestlings made only about 30. Pair A with 3 nestlings only had, on average, 5-10 visits per hour more than pair B. These figures were checked over several hours by direct observations from a tent.

The great differences in nest visit frequency between pair B and pair C was not explained by the extra demand of one more nestling in the clutch of eight of pair C. Rather, the parents brought different kinds of food to the nestlings. The 8-clutch parents perpetually brought small amounts of food in each visit to the box, hardly visible from the tent some 10 meters away. The 7-clutch parents showed a quite different strategy. In each visit they brought a large quantity of food to the nestlings. The bill was filled up and *Epirrita* larvae and adult moths were clearly visible. The 8-clutch parents might have taken a lot of prey in the air, whereas the 7-clutch parents might have picked prey from leaves, bark or ground (cf. Lennerstedt 1983).

Fig. 2 also shows the nest visit frequency during different hours of the day. There were differences in the number of nest visits from hour to hour, also in the same hour from day to day. But there were no recognizable patterns in the variation. On average, the frequency of nest visit for each pair was fairly constant during the day, and there was no peak of activity in any part of the day.

Twenty years ago, in 1965, I carried out a similar study of breeding Pied Flycatcher at Ammarnäs (Lennerstedt 1969). Then the length of night rest during the nestling period was 4-4.5 hours. The night rest during the first part of the nestling period was around midnight, but as the nestlings grew older, some pairs displaced the night rest towards the latter part of the night. This did not occur in the three pairs studied in 1984.

In 1965, the nest visit frequency was about the same during the active hours of the day, a pattern similar to that in 1984. The parents with 3 nestlings in 1965 had the lowest frequency and the parents with 6 the highest. In 1965, the differences between the clutches were explained merely by the number of nestlings the parents had to feed.

Summary:
- The night rest of Pied Flycatcher was around midnight but might be displaced towards the latter part of the night.
- The night rest was shortest for the pairs with large clutches and longest in those with small clutches.
- The nest visit frequency in 1984 varied considerably between the pairs and was related to the kind of food brought to the nestlings.
- In 1965, two pairs with large clutches hac higher frequencies than one pair with a small clutch, and the frequency was correlated to the clutch size.
- The frequency of nest visits was on average at the same level throughout the d with no peak of activity in any particular part of the day.

Redwing

The breeding biology of Redwing in the subarctic conditions at Ammarnäs has been studied by Arheimer (1978), and the biology in mixed woods in southern Finland (62 °N) by Tyrväinen (1969). My study comprises six pairs. Pairs A-B bred in 1983 and pairs C-F in 1985. Pairs E and F were given an extra nestling each and the brood size experimentally raised to seven. The purpose was to find out how the adult birds behaved in a stressful situation.

To start with the normal breedings in 1985, pair C had six nestlings, which they succeeded in raising. Their night rest lasted for 3-4 hours (Fig. 3) and the midpoint was a little after 21.00 h. There were only minor variations in the time of rest from night to night. The twelfth night rest lasted for more than 7 hours, but then the parents had already diminished the frequency of nest visits, a normal behaviour in Redwings (Tyrväinen 1969).

Pair D also had 6 nestlings in 1985 and their activity was recorded over days 6-13. The behaviour of these birds was comparable to that of pair C. On average they started the night rest at 19.10 h and ended it at 23.20 h. The night rest of pairs C and D coincided with the average values given by Arheimer (1978).

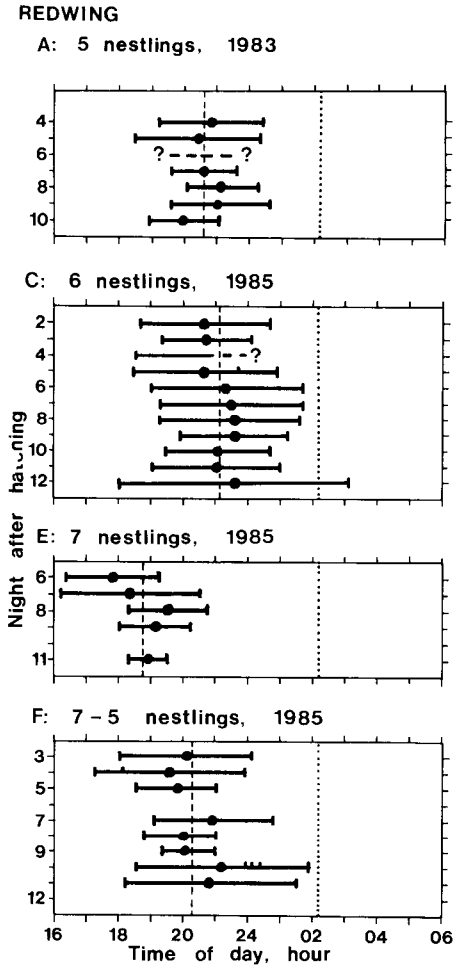


Fig. 3. Night rest in four pairs of Redwings.

In 1983, pair A had 5 nestlings. The night rest usually lasted for 2-3 hours, and only one rest extended to 4 hours. The night rest of pair A was, therefore, shorter than that of pair C, even though pair A had one nestling less than pairs C and D.

In 1983, pair B also had 5 nestlings and the activity was recorded over days 10-12. The tenth night rest lasted for two hours, at 20.15-22.00 h, with one short break. The eleventh rest was only 45 minutes, at 21.15--22.20 h. The twelfth and last rest extended to three hours, but then some nestlings had probably left the nest.

Although pairs A and B both had 5 nestlings in 1983 they had a noticeably shorter night rest than pairs C and D with 6 nestlings in 1985. The most simple reasons for this difference is that the Redwings had less food available in 1983 than in 1985. Redwings take food exclusively on the ground, principally worms, large insects and *Epirrita* larvae, the latter when descended on ground (Arheimer 1978). In 1985 the *Epirrita* larvae were abundant and probably an important food resource, but not so in 1983.

Pair E bred in 1985 and had originally 6 nestlings. On the sixth day, I added an extra nestling of similar size as the rest of the brood into the nest. The sixth and seventh night rest had normal length, 3-4 hours. During the eighth and ninth nights, the rest was shortened to 2.5 hours. On the tenth night there was continuous activity throughout the night, 5-15 nest visits during each of the normal rest hours compared to 15-25 nest visits during the day hours. All the seven nestlings fledged and left the nest on the twelfth day.

I did not weigh the nestlings as they would then probably have left the nest prematurely, and therefore I did not know whether or not they were undernourished.

Pair F was given an extra nestling on the third day. During the two nights following the increase of brood size, the night rest lasted for more than 4 hours, a normal rest length comparable with pairs C and D. On the fifth night, however, the rest was shortened to 2.5 hours, and during the sixth night there was no rest at all. The adult birds made 6 nest visits in each of the two hours between 19.00 and 21.00 h, when they normally rested. The 6 nest visits can be compared with 10-15 visits per hour in the day. During the seventh day, one nestling disappeared. I did not see how, but probably it died and was then removed by the parents. Predation is improbable, as predation usually results in disappearance of several nestlings, not just one of them. The night rest after the disappearance of one nestling lasted for almost four hours, a restoration of the original length. On the eighth day, an extra nestling of the same size as those in the nest was added. The two following night rests were

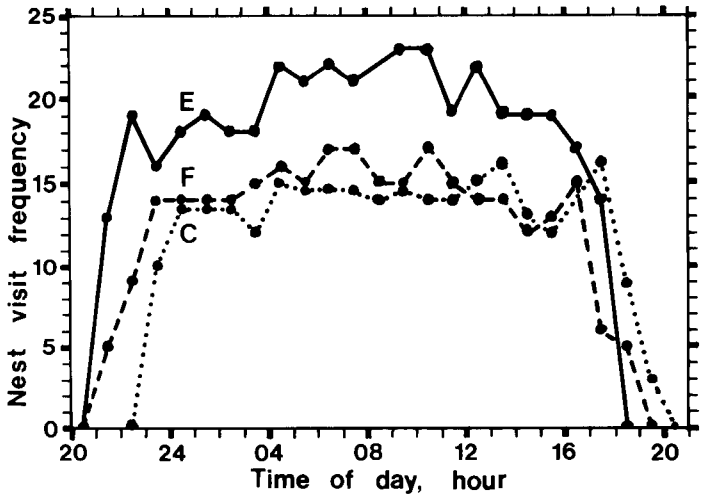


Fig. 4. Average nest visit frequency for days 6-13 in three pairs of Redwings. C, 6 nestlings. E, 7 nestlings. F. 7-5 nestlings.

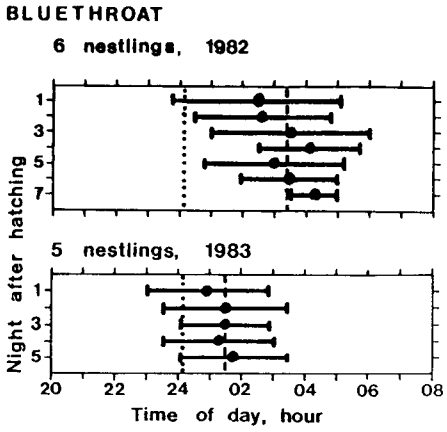
shortened to 1-2 hours, an immediate response to the extra burden. On the tenth day, the two smallest, original nestlings disappeared, and the clutch was reduced to 5. The tenth and eleventh night rests were lengthened to more than 5 hours. On the twelfth day the five nestlings left the nest. Hence, pair E shortened and lengthened the night rest in relation to the number of nestlings.

The time of night rest in the two pairs E and F given additional young varied considerably from night to night. This was clear when the midpoint of the rest was examined. There were also great differences between the two pairs. Pair E had very early night rests, two rests starting by 16.10 and 16.20 h. The average night rest of pair E was about 1.5 hours earlier than that of pair F, and more than 2 hours earlier than that of pairs C and D. Pair E had already started the activity of the next "day" when some other Redwings were just about to end the activity of their "day before".

The average nest visit frequencies of the three pairs C, E and F, all breeding in 1985, are shown in Fig. 4. The frequencies of pairs A and B breeding 1983 are not shown as the food conditions that year differed and the records of pair B were unreliable for several hours. The frequencies shown in Fig. 4 were calculated as daily means for days 6 to 11. Frequencies were lower at the beginning and the end of the day and during some hours in different days, but, on average there was no peak of activity in any particular part of the day. Parent birds fed nestlings with the same intensity throughout the day.

Pairs E and F were given an extra burden with the addition of an extra nestling to feed, raising their clutches to seven. Both pair then had a higher nest visit frequency than pair C with 6 nestlings. These three nests support the idea that the more nestlings the pairs have, the higher is the nest visit frequency.

Pair E succeeded in raising 7 nestlings and had a higher nest visit frequency than pair F that did not succeed in raising 7 nestlings. As shown in the study of Pied Flycatcher, described above, the nest visit frequency may not be proportional simply to the amount of food brought to the nestlings. Therefore, the higher nest visit frequency of pair E is not adequate to explain their greater breeding success. Both nests were on the ground, but the nest of pair E lay close to a stream with wet luxurious vegetation, and that of pair F



ig. 5. Night rest in two pairs of Bluethroats.

on a dry slope some 70 meters from the stream. The Redwings at Ammarnäs take food on the ground, mostly worms but also large insects and *Epirrita* larvae (Arheimer 1978). If pair E and F sought food in the vicinity of the nest, pair E would probably had better access to food. Pair F had to fly up and down the slope, a vertical difference of some 10 meters, to feed in the wet habitat. This difference in nest position might be one reason for the higher nest visit frequency and more successful breeding of pair E.

Summary:

- The night rest was always before midnight. The lenght varied from 2 to 5 hours. The midpoint was about 20.00h, but there were substantial differences between the pairs.
- The nest visit frequency was related to the number of nestlings.
- The nest visit frequency was at the same level throughout the day, no peak of activity at any part of the day.
- When birds were burdened by an extra nestling, they shortened the night rest or they were active all the night but at a lower frequency than daytime. The midpoint of night rest varied from night to night more in the pairs given additional young than in the other.
- One pair with an extra nestling succeeded in rearing 7 nestlings, whereas the other did not. The successful pair had a higher nest visit frequency and probably a more favourable nest position in relation to food resources. Food that year was obviously abundant.
- The length of night rest and frequency of nest visits differed between pairs breeding in 1983 and 1985, probably dependent on different food conditions the two years.

Bluethroat

Two pairs of Bluthroats were studied and the night rests are shown in Fig. 5. Pair A bred in 1982 and had 6 nestlings. The first night rest was long, lasting for 4-5 hours, whereas the following rests were shorter. The seventh rest was only 1.5 hours. On the eighth day all nestlings disappeared, probably due to predation by Weasel being observed in the habitat. The start of night rest varied considerably, from 23.40h on the first night to 00.30h on the seventh night. The end of the rest was more precise, most nights at about 05.00h, but one nights as late as 06.00h. Thus, the position of the midpoint varied by almost two hours.

Pair B bred in 1983 and had 5 nestlings, which disappeared on the sixth day. The night rest lasted for 3-4 hours. There was less variation in the time of night rest in pair B than in pair A, and the midpoint lay about two hours earlier.

In 1968 and 1969, I studied three pairs of Bluethroats at Ammarnäs in a similar way (Lennerstedt 1973). Then the midpoint of night rest lay between 01.00 and 02.00h, and there were variations in the start and the end of the rest comparable to those noted in 1982 and 1983. An extra nestling was added to one of the 1968 nests making a total of 7 nestlings. During the tenth to twelfth nights, the parents were active all night. The records during these night hours were made in the same manner as those in the day, so the night activity in 1968 was probably involved with feeding.

Timing of the night rest in relation to the activity of prey insects

When feeding nestlings, the Redwings at Ammarnäs had a night rest that lay before midnight. This was also found by Arheimer (1978). The same diurnal feeding rhythm

occurred in other parts of Swedish and Finnish Lapland as observed by Swanberg (1951), Brown (1963), and Peiponen (1970). Arheimer noted that the average time for night rest was from 19.45 to 23.00h. But variations between the pairs were great. Pair E in my study started the rest on some nights as early as 16.10h and ended it by 19.30h. The Redwing food at Ammarnäs consists principally of worms but also large insects and *Epirrita* larvae when available on ground (Arheimer 1978). As worms are more active or more easy to find in the humid night hours, the Redwings responded to this by being active at night. This raises the question, how do Redwings find out that they should stop activity early in the afternoon in order to be active at night. A possible explanation is that it is normal behaviour for Redwings to be active all the night, and birds find out the best time to search for food. If this is so, the great variation in time for night rest between pairs might be understood.

Concerning the nest visit frequency in the Redwings, Arheimer (1978) concluded that pairs with clutch sizes 4, 5 and 6 had, on average, the same length of night rest. The same conclusion may be drawn from my study if the two pairs with 5 nestlings in 1983 are compared with the four pairs with 6 or 7 nestlings in 1985 (Fig. 3). But the food conditions the two years were different, at least with respect to the *Epirrita* larvae. From the pairs of Redwing I have studied it seems more reasonable to conclude that Redwings may shorten the length of night rest and raise the nest visit frequency as a response to an increased demand for food from the nestlings. But, of course, there is a ceiling for how many nestlings a pair may raise, and the ceiling may vary from year to year.

The Bluethroats at Ammarnäs had a night rest in the morning hours (Arheimer 1982). Consistent observations were made by Peakall (1965) at 68 °N in Sweden and by Peiponen (1970) at 69 °N in Finland. When the Bluethroats, studied by me, had large clutches or were given an extra nestling, they shortened their night rest or, in one case, were active all the night. The Bluethroats fed their nestlings with insects, often large insects such as crane-flies, that they obviously caught on or close to the ground. The activity of the insects probably followed changes in the air temperature, which means that they were more active before midnight than after midnight, since the lowest air temperatures occurred about sunrise. Thus, the Bluethroats varied the timing and length of the night rest in a way comparable to that of the Redwings though the night rest was in the early morning hours.

The Pied Flycatchers at Ammarnäs generally have the night rest symmetrically divided by midnight although in 1968 there was a minor tendency to displace the night rest towards the morning hours. In northern Finland at 69 °N, Hannila and Järvinen (198? found that Pied Flycatchers rested during the morning. At that latitude, the nights are even lighter than at Ammarnäs and the Pied Flycatchers probably took advantage of the higher insect activity before midnight.

Birds have an internal rhythm, a biological clock, that controls daily activity and night rest. The internal rhythm is synchronized to the environment by external zeitgebers, the most important of which is the changes between light and dark (Aschoff 1969, Daan & Aschoff 1975, Brinkley 1982). Krüll (1976a, 1976b) found in the high arctic of Spetsbergen, that in the absence of dark night hours the colour changes of the sun and probably the position of the sun in relation to landmarks might function as zeitgebers. The behaviour of the Redwings and Bluethroats at Ammarnäs showed that the availability food in the habitat and the nestlings' demand for food were factors that affected the activity rhythm. From my study it is impossible to state whether these factors are zeitgebers for the internal rhythm or factors tha mask the internal rhythm entrained by lig (Aschoff et al. 1982).

References

Arheimer, O. 1978. Födoval och matningsprestation hos rödvingetrast *Turdus iliacus* i subalpin ängsbjörkskog vid Ammarnäs i svenska Lappland. — Anser, Suppl. 3:31-46.

Arheimer, O. 1982. Blåhakens *Luscinia svecica* häckningsbiologi i fjällbjörkskog vid Ammarnäs. — Vår Fågelvärld 41:249-260.

Aschoff, J. 1969. Phasenlage der Tagesperiodik in Abhängigkeit von Jahreszeit und Breitengrad. — Oecologia 3:125-265.

Aschoff, J., Daan, S. & Honma, K.-I. 1982. Zeigebers, entrainment, and masking: some unsettled questions. — Pp. 13-24 in Aschoff, J., Daan, S., and Groos, G. (eds.): Vertebrate circadian systems. Springer Verlag, Berlin.

Brinkley, S. 1982. Circadian organization in mammals and birds (yearly review). — Photochem. Photobiol. 35:887-890.

Brown, R.G.B. 1963. The behaviour of Willow Warbler *Phylloscopus trochilus* in continuous daylight. — Ibis 105:63-75.

Daan, S. & Aschoff, J. 1975. Circadian rhythms of locomotor activity in captive birds and mammals: their variation with season and latitude. — Oecologia 18:269-316.

Hannila, J. & Järvinen, O. 1987. Feeding activity of hole-nesting passerines during the nestling period in northern Lapland. — Acta Reg. Soc. Sci. Litt. Gothoburgensis. Zoologica 14: 102-108.

Krüll, F. 1976a. The position of the sun as a possible zeitgeber for arctic animals. — Oecologia 24:141-148.

Krüll, F. 1976b. Zeitgebers for animals in the continuous daylight of high arctic summer. — Oecologia 24:149-157.

Lennerstedt, I, 1969. Night rest and nest-visit frequency at five nests of pied flycatchers, *Ficedula hypoleuca* (Pall.), in Swedish Lapland. — Arkiv för Zoologi 22:279-287.

Lennerstedt, I. 1973. Night rest during nestling period in four passerine species under subarctic summer conditions. — Ornis Scand. 4:17-23.

Lennerstedt, I. 1983. Födoområden hos lövsångare *Phylloscopus trochilus* och svartvit flugsnappare *Ficedula hypoleuca* i fjällbjörkskog. — Vår Fågelvärld 42:11-20.

Peakall, D.B. 1956. Some notes on the Red-spotted Bluethroat. — Brit. Birds 49:135-139.

Peiponen, V.A. 1970. Animal activity patterns under subarctic summer conditions. — In: Ecology of the subarctic regions. Proceedings of the Helsinki Symposium UNESCO 1970, pp. 281-287.

Swanberg, P.O. 1951. Till kännedom om vissa fåglar i Lappland, II. — Fauna och Flora 46:111-136.

Tyrväinen, H. 1969. The breeding biology of the redwing (*Turdus iliacus* L.). — Ann. Zool. Fennici 6:1-46.