Daylength and time allocation in relation to reproductive effort in the Common Treecreeper *Certhia familiaris*

Markku Kuitunen & Jukka Suhonen

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The influence of daylength was studied by seeking answers to the following questions: 1) How does the feeding rate of the Treecreeper relate to the seasonally changing daylength? 2) What are the effects of brood size and nestling demand on the rates of feeding by parents? 3) How do adult Treecreepers allocate their time?

Parents fed the nestlings for 89% of the time between sunrise and sunset and the feeding activity varied significantly with the daylength. The feeding rate showed a clear correlation with nestling age. Brood size did not correlate with the number of visits per hour, but a correlation was found with the number of visits per day. This suggests that adult birds cannot increase the hourly feeding rate, but, as daylength increases, they can increase the number of visits per day and, in consequence, feed a larger brood.

The third question was examined using a time budget study. The foraging time increased with nestling age, reaching 89% of the active time for older nestlings.

The results support the conclusion that daylength has some importance as a determinant of the feeding capacity of Treecreepers, together with such factors as the food supply and ambient temperature.

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Introduction

The reproduction of diurnal birds in temperate areas may be limited not only by the seasonal variation in food resources, but also by the number of daylight hours available for foraging and other activities (Lack 1954, 1966). The clutch size of the Common Treecreeper *Certhia familiaris* (later Treecreeper) first increases as the season progresses and then decreases (Kuitunen 1987). This indicates that it is beneficial to adjust the reproduction to the seasonal variation in the food supply and possibly also to the seasonal change in daylength.

During the springtime, the food supply varies in parallel with the seasonal course of clutch and brood size (Kuitunen 1989). The importance of the seasonal change in daylength is due to the time available for foraging in relation to the food supply. The importance of the foraging time probably varies between species, depending on the food supply or the foraging technique.

The importance of the food supply for avian reproduction has been studied intensively during the last 10 years. Many studies have used experimental manipulation of the food supply (e.g. Perrins 1965, 1970, Kluyver 1970, van Balen 1973, Källander 1974, Högstedt 1981, but see Perrins & Moss 1975) or of brood size (e.g. Högstedt 1980, Bryant & Westerterp 1983, Nur 1984), often together with energy budgets (e.g. Ettinger & King 1980, Turner 1983) and also using the doubtly labelled water technique (e.g. Westerterp & Bryant 1984, Goldstein & Nagy 1985, Williams & Nagy 1985). In most cases the aim has been to find evidence for Lack's hypothesis (1954, 1966) that the most common clutch size is also the most productive. The results have varied (for reviews of the effects of extra food see Davies & Lundberg 1985; for brood manipulation, see Lessells 1986, Arcese & Smith 1988).

There are also time budget studies dealing with the same question (e.g. Hickey & Titman 1983, Lundberg 1985). Few studies have examined the seasonal

Table 1. Data used in analysis of feeding rates. * = Not used in all analyses.

Number of nest	Hatching time	Clutch size	Number of hatchlings	Number of fledglings	Type of brood	Feeding visits per day (Mean)
1.	19.5.1985	5	4	4	First	198
2.	3.6.1985	7	7	0	Renewal	269
3.	27.6.1985	6	5	5	Second	215
4.	25.6.1985	7	6	6	Second	188
5.	15.5.1986	5	5	5	First	263
6.	23.5.1986	5	5	5	First	202
7.	20.6.1986	8	7	7	Second	206
8.	26.5.1987	6	6	0	First	277
9.*	21.6.1987	7	7	7	Renewal	175
10.*	5.7.1987	6	6	6	Second	180

variation in reproductive output in association with the diurnal variation in activity (see however Masman et al. 1988). This could be more important than comparing the average values for the whole breeding period. Daylength and the time available for foraging vary not only seasonally but also geographically. Lundberg (1985) did not find any significant geographical variation in the time budgets of Starlings *Sturnus vulgaris*.

A positive relationship between the seasonal or geographical variation in reproduction and the time used for foraging can be tested by measuring the variation in the diurnal activity of the feeding parents using a time budget analysis.

In this study answers will be sought to three questions:

1) How does the feeding rate of the Treecreeper relate to the seasonally changing daylength?

2) What are the effects of brood size and nestling demand on the feeding rates of parents?

3) How do adult Treecreepers allocate their time?

Assuming that the clutch size of the Treecreeper has evolved in relation to the seasonal change in daylength, we can predict that the total feeding rate should increase with increasing nestling age and brood size. However, the feeding rate measured per hour or per nestling should only increase with nestling age, because brood size changes with daylength (see Kuitunen 1987).

Methods and study area

The field work was carried out in Central Finland near the Konnevesi Research Station (62°37'N, 26°20'E) during 1985–1987. Mixed coniferous (*Picea abies* and *Pinus sylvestris*) forests of Cajander's *Myrtillus* and *Oxalis-Myrtillus* type abound. In 1983, we put up 50 specially designed nest-boxes (see Kuitunen 1985) in the study area. A relatively large study area was chosen (100 km^2) in order to obtain as many breeding Treecreeper pairs as possible.

The total numbers of breeding attempts were 33 (1985), 16 (1986) and 11 (1987) and the number of broods used in the feeding activity study 4, 3 and 3, respectively.

The number of visits to the nest by parent Treecreepers was determined using a photocell device. A light-emitting diode produced a beam, which was broken when a bird entered or left the nest-box. Each interruption of the beam was scored by an automatic recorder. The recorders (n=4) were rebuilt table calculators. They consisted of a clock recording the time in seconds. When the photocell device gave an impulse, the calculator printed the number of seconds on paper. This anabled us to determine the intensity of the feeding activity, and the last and first feeding visits of the day, but it was not possible to separate the sexes.

The feeding activity was measured at 10 nests for 3000 hours. The records represent different months (4 nests in May, 5 in June and 1 nest in July) and different clutch sizes (1 brood of 4, 3 broods of 5, 3 broods of 6 and 3 broods of 7). For details of the nests studied, see Table 1. Only nests with nestlings between 1 and 15 days old were used in the analyses.

Time budgets were made during the same years and in the same study area for which we obtained the feeding activity data. We made observations in 13 territories in 1985 and 4 territories in 1986. We established 14 distinct behavioural categories, which were:

1. Picking up food item
2. Foraging on tree trunk
3. Foraging on branch
4. Foraging on ground
5. Flying from one tree trunk to another
6. Flying to/from the nest
7. Feeding in the nest box
8. Brooding
9. Body maintenance
10. Vocalising (when vocalisations were not connected with a particular activity, e.g. territory defence)
11. Partner interactions
12. Territory defence, interactions with neighbouring Treecreepers
13. Interspecific interactions
14. Resting on the tree trunk

Observations made at 10-second intervals were assigned to the appropriate categories and recorded on a duplicated form covering a maximum of 15 min. On the basis of the categories, Treecreeper behaviour was assigned to one of four groups: 1) Foraging (nos 1–4), 2) Flying (nos 5, 6), 3) Brooding or resting (nos 7, 8 and 14) and 4) Other activities (nos 9–13).

Altogether 207 forms were filled in (188 in 1985 and 19 in 1986). Due to the relatively large (mean = 3.3. ha) home ranges of Treecreepers, it was exceptional to be able to observe one bird for 15 minutes. The average observation period was 5.3 min (SD=3.7).

Samples (n=43) nestling food were collected during the same years in the same study area (unpubl. Suhonen & Kuitunen; for details about the methods see Kuitunen & Törmälä 1983). The weather records were obtained from the Tikkakoski meteorological station, which was about 50 km west of the study area.

Results

Feeding activity in relation to nestling age, nestling size and air temperature

The observed activity pattern of the Treecreeper was diurnal and practically unimodal. The adult birds, presumably the females, came out of the box for first time on average 36.9 minutes (SD=17.4, n=8) after sunrise and activity ceased 92.6 minutes (SD=32.7, n=8) before sunset. The Treecreeper female was observed, without exception, to roost with its nestlings until they were 7–8 days old. After this, the female may still roost with the nestlings but this depends on the individual.

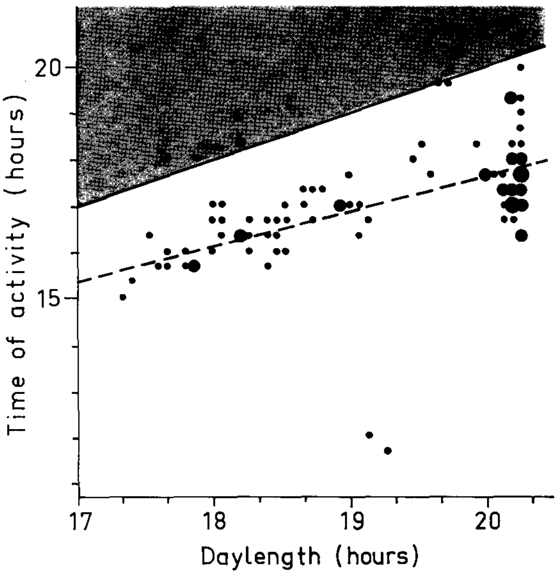

Fig. 1. Activity time (broken line, regression equation: y=0.7x+2.9) of the Common Treecreeper in Central Finland during the breeding period in relation to the daylength (continuous line). The dots show the time of activity during one day. Small dot = one observation, medium dot = two observations and large dot = three observations.

The correlation between the hour of sunrise and the first record in the morning was 0.88 (n=8, $P<0.01$) and between the hour of sunset and the last record 0.47 (n=8, $P>0.10$). The time of activity averaged 89.1% of the period between sunrise and sunset (min 84.5, max 96.5, n=8) and varied with the seasonal change in daylength (r=0.75, n=8, $P<0.05$; Fig. 1).

The average feeding rate was 227 visits per day (SD=36, n=8) and 13.2 visits per hour (SD=1.9, n=10) during the active feeding time. The average interval between two feeding visits was 4.6 minutes (SD=0.7, n=8).

The feeding rate was constant during most of the day, being lower in the early morning and the late evening. Fig. 2 shows the number of visits per hour in broods of different ages. The rate was similar from

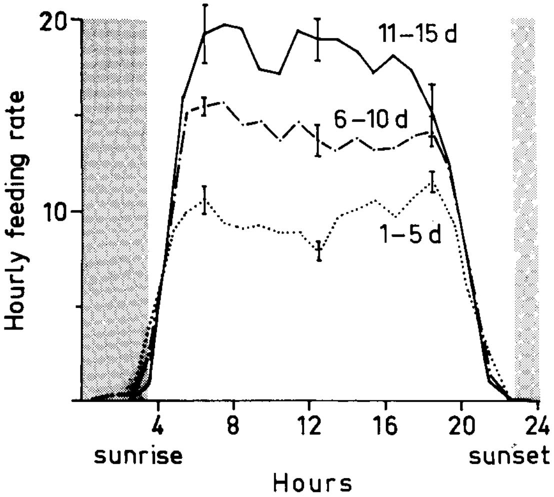

Fig. 2. The hourly feeding rate of Common Treecreepers in three nestling age groups. The vertical lines show the standard errors of the means and the shaded area represents the night time.

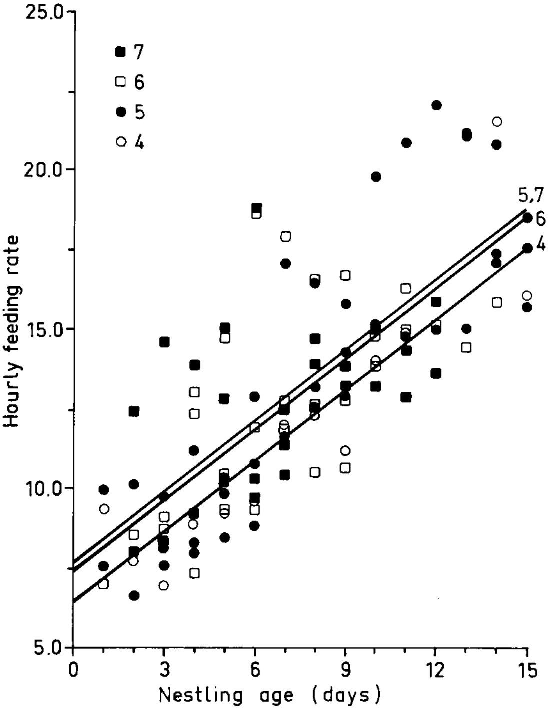

Fig. 3. The hourly feeding rate (Fh) in relation to nestling age (A) and brood size (4–7). The equations for the brood sizes are Fh_4=0.75A+6.38, Fh_5=0.75A+7.6, Fh_6=0.75A+7.4 and Fh_7=0.75A+7.6. The model explained 60% of the variation.

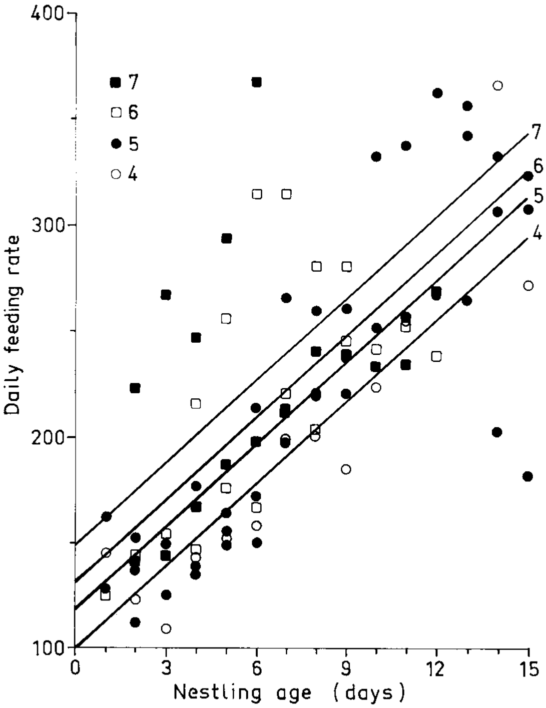

Fig. 4. The daily feeding rate (Fd) in relation to nestling age (A) and brood size (4–7). The equations for the brood sizes are Fd_4=13A+100, Fd_5=13A+119, Fd_6=13A+137 and Fd_7=13A+149. The model explained 57% of the variation.

06.00 to 21.00 (ANOVA, P>0.05; in broods of 1-5 days the time span was from 05.00 to 21.00).

There was a strong positive correlation between nestling age and feeding rate: between nestling age and hourly feeding rate (r=0.98, n=15, P<0.001; Fig. 3), between nestling age and daily feeding rate (r=0.97, n=15, P<0.001; Fig. 4) and between nestling age and hourly feeding rate per nestling (r=0.97, n=15, P<0.001; Fig. 5, Table 2). The proportion of the total daylength used did not increase with the age of the nestlings (Fig. 6).

According to the predictions, the daily feeding rate should increase with brood size as well. The hourly feeding rate did not differ between brood sizes (covariance analysis, age: F=147, df=1, P<0.001; brood size: F=0.9, df=3, P=0.44, n=107 days; Fig. 3), which indicates that the adult birds were working at their maximum capacity. When the same analysis was made for the whole day, the rate was in fact found to

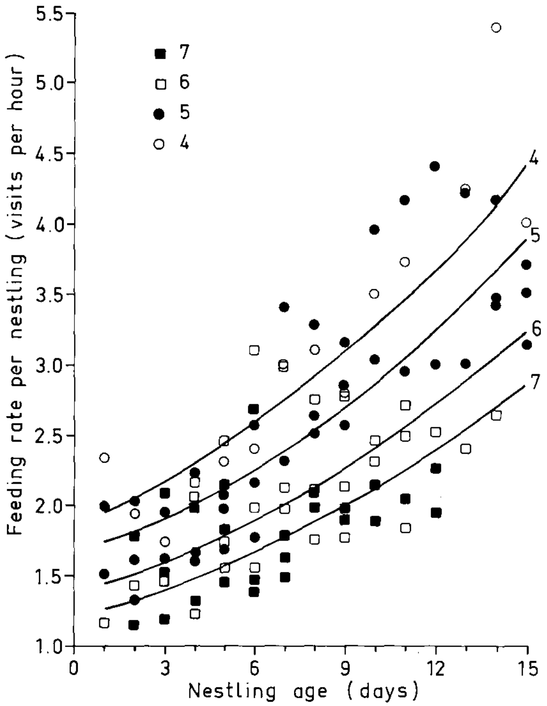

Fig. 5. The daily feeding rate per nestling (Fdn) in relation to nestling age (A) and brood size (4–7). The equations for the brood sizes are $\ln(Fdn4)=0.06A+0.6$, $\ln(Fdn_5)=0.06A+0.5$, $\ln(Fdn_6)=0.06A+0.3$ and $\ln(Fdn_7)=0.06A+0.2$. The model explained 71% of the variation.

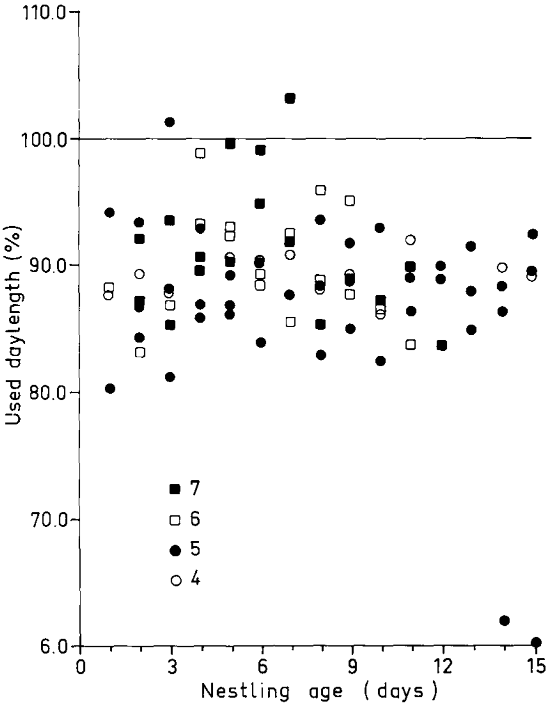

Fig. 6. Proportion of the active time in relation to daylength and nestling age.

increase with brood size (covariance analysis, age: F=100.1, df=1, P<0.001; brood size: F=3.4, df=3, P=0.02, n=88 days; Fig. 4). This suggests that Treecreepers feeding larger broods delivered more food because they used more hours for foraging and feeding during the day, that is, when the day was longer.

However, the daily feeding rate per nestling also differed between the brood size (covariance analysis, age: F=137.5, df=1, P<0.001; brood size: F=6.1, df=3, P=0.001, n=88 days), which indicates that the nestlings in larger broods did not receive as much food as in smaller broods, if the food load is supposed to have been constant.

The daily feeding rate and the daily mean air temperature were negatively, but not significantly, correlated (r=–0.54, n=8, P>0.10; Fig. 7). The variance of the variables in this analysis was noteworthy, however, which indicates that the real causal relation-

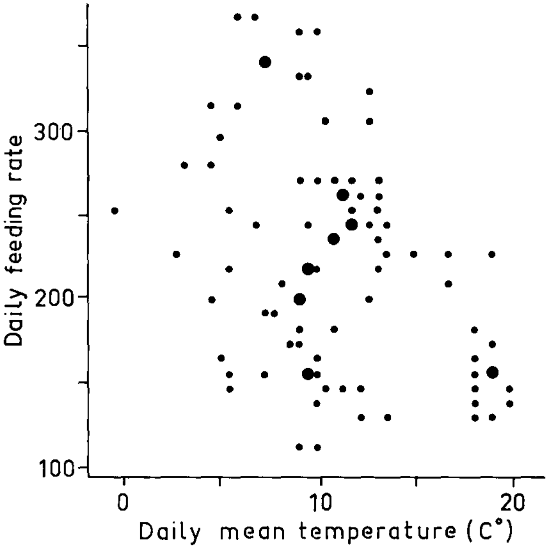

Fig. 7. The daily feeding rate in relation to the mean daily temperature. The small dot represents one case and the large dot two cases.

Table 2. Feeding frequency in relation to brood size and nestling age.

	Brood size											
	4			5			6			7		
Age (Days)	Mean	SD	n	Mean	SD	n	Mean	SD	n	Mean	SD	n
Daily feeding frequency												
1–5	134.4	17.8	5	145.2	17.2	14	174.0	46.4	7	208.8	57.7	8
6–10	193.4	24.3	5	231.2	46.2	13	252.4	50.3	9	243.6	57.2	7
11–15	298.3	60.0	3	296.0	57.4	13	246.0	9.9	2	252.0	24.0	2
Hourly feeding frequency during active time												
1–5	8.4	1.1	5	8.9	1.3	14	10.1	2.5	10	11.6	2.7	9
6–10	11.9	1.6	5	14.0	2.9	13	13.7	2.9	14	13.1	2.5	12
11–15	17.6	3.6	3	18.3	2.7	13	15.4	0.7	5	14.2	1.3	4
Hourly feeding frequency per nestling during active time												
1–5	2.1	0.3	5	1.8	0.3	14	1.7	0.4	10	1.7	0.4	9
6–10	3.0	0.4	5	2.8	0.5	13	2.3	0.5	14	1.9	0.4	12

ship is between feeding rate (f) and a factor covarying with ambient temperature (e.g. phenological development in general, seasonal variation of the food supply or thermoregulation of the nestlings).

The feeding rate and precipitation did not correlate (r=–0.12, n=8, P>0.10) and precipitation probably decreases the feeding rate only occasionally.

Time budget of the parents

On average, the adult Treecreepers used 54% of their active daytime period for foraging or carrying food to the nestlings (Table 3). When the nestlings were 11–15 days old, the total time used for foraging and flying filled 89% of their active time. The proportion spent on other activities and rest or brooding was small. These results together with those for feeding activity imply that the adult birds feed the nestlings intensively and increases their foraging and feeding time with nestling age. However, larger brood sizes were not associated with higher proportions of foraging time (Table 4). Nor was there a notable variation in foraging activity between the three brood size classes for old (11–15 days) nestlings (Table 5), which agrees well with the pattern for hourly feeding rates.

Food load

The food received by the nestlings depends on both the feeding rate and the size of the food load (see e.g. Moreno 1987). The mean load size in material from Konnevesi was 24.2 mg (dry biomass, SD=14.9, n=43). The load size did not correlate with feeding date (r=–0.16, n=43, P=0.30) or with the age of the nestlings (r=0.06, n=43, P=0.69). Nor did the load size vary between brood sizes (ANOVA, F=1.2, $df_1=2$, $df_2=40$, P = 0.33).

Discussion

Response to the change in daylength

There are rather few studies which deal with time allocation in relation to the abundance of resources, or to constraints due to conditions during the breeding season. The response to the change in daylength has been studied by, for examples Calder (1975), Lundberg (1985) and Masman et al. (1988). They concluded that the change in daylength did not play a major role in the species studied. Observations on parental Starlings suggest a threshold in the time that can be devoted to energetically costly flight, rather than a shortage of absolute time (Drent & Daan

Table 3. The time budgets (in %) of breeding Common Treecreepers in relation to nestling age. Numbers of observations made at 10-s intervals given in brackets.

	1–5 days	6–10 days	11–15 days	Total
Foraging	27.2 (889)	48.5 (627)	74.8 (1471)	45.7 (2987)
Flying	4.0 (132)	10.0 (129)	13.8 (271)	8.1 (532)
In the nest box	68.1 (2231)	39.7 (513)	9.8 (192)	44.9 (2936)
Other activities	0.7 (22)	1.9 (24)	1.7 (33)	1.2 (79)
Total	100.0 (3274)	100.0 (1293)	100.0 (1967)	100.0 (6534)

Table 4. The time budgets (in %) of breeding Common Treecreepers in relation to brood size. Numbers of observations made at 10-s intervals given in brackets.

	Brood size			
	4	5	6	Total
Foraging	50.4 (892)	39.5 (1116)	50.4 (979)	45.7 (2987)
Flying	9.0 (160)	7.8 (219)	7.9 (153)	8.1 (532)
In the nest box	39.4 (697)	51.5 (1453)	40.5 (786)	44.9 (2936)
Other activities	1.1 (20)	1.2 (35)	1.2 (24)	1.2 (79)
Total	100.0 (1769)	100.0 (2823)	100.0 (1942)	100.0 (6534)

Table 5. The time budgets (in %) of breeding Common Treecreepers in relation to brood size, when the nestlings are 11–15 days old. Numbers of observations made at 10-s intervals given in brackets.

	Brood size			
	4	5	6	Total
Foraging	74.6 (349)	72.4 (609)	78.0 (513)	74.8 (1471)
Flying	12.8 (60)	15.5 (130)	12.3 (81)	13.8 (271)
In the nest box	11.3 (53)	9.0 (76)	9.6 (63)	9.8 (192)
Other activities	1.3 (6)	3.1 (26)	0.2 (1)	1.7 (33)
Total	100.0 (468)	100.0 (841)	100.0 (658)	100.0 (1967)

1980). The difficulties in determining the real importance of the change in daylength are partly due to the fact that the environmental conditions have to be predictable enough for natural selection to operate (see also Drent and Daan 1980). Most of the avian species studied probably do not live in environments that are sufficiently predictable to change their behaviour or produce observable variation in their reproductive strategy in relation to the ambient conditions.

Treecreeper parents change their behaviour in parallel with the seasonal change in daylength during the breeding season, benefiting from the prolonged daylight by increasing their foraging. In dusky spruce forests, visually foraging Treecreepers naturally wake up after the sun has risen and go to rest before the sun sets, but without a clear correlation with the sunset. The habitat used by the Treecreeper in the study area is mature coniferous forest, which represents a sufficiently predictable environment compared with that of the frequently studied gleaning passerines. The food used by the Treecreeper parents for the nestlings consists mostly (70%) of predatory spiders (Kuitunen & Törmälä 1983), which are also present in the food supply in the same proportions (Kuitunen 1988). This kind of food varies less between years (two- or threefold, e.g. Huhta 1965, Huhta et al. 1967, Huhta & Koskenniemi 1975) than the caterpillars (even more than tenfold, e.g. Perrins 1965) consumed by gleaning passerines (e.g. Gibb & Betts 1963).

Effect of nestling age and brood size

The feeding rates and nestling age were strongly positively correlated, which implies an increase in the energy demand of the nestlings. Brood size was positively correlated with the daily, but not with the hourly feeding rates. Adult Treecreepers probably cannot increase their feeding rate much on short-term basis, but can supply more food when the daylength allows more hours for foraging and feeding. In most studies the feeding rate per hour and brood size have been positively correlated (e.g. Klomp 1970, Moreno 1987). According to the present study, however, the nestlings in larger broods do not seem to receive as much food as in smaller broods. Nor do Treecreepers increase the food load for older nestlings or larger broods. However, the larger broods are laid in the middle of the breeding period, and by the time when the nestlings of these broods are older, the day is long, the food supply is maximal and the ambient temperature is at its highest. Since the daily feeding rate and the daily air temperature are correlated, the energy demand of the nestlings in larger broods will probably be satisfied in spite of the lower delivery rate of the food. Nestlings in larger broods do not need as much food as nestlings in smaller broods, because their thermoregulation does not require as much energy later in the summer as that of the nestlings in smaller broods during the springtime.

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Selostus: **Päivän pituus ja pesivän puukiipijän ajankäyttö suhteessa lisääntymispanokseen**

Päivän pituuden vaikutusta puukiipijän lisääntymiseen tutkittiin Konneveden tutkimusaseman ympäristössä kymmenellä pesällä vuosina 1985–1987. Erityisesti selvitettiin (1) kuinka puukiipijän ruokinta-aktiivisuus vaihtelee suhteessa vuodenaikaiseen päivänpituuden vaihteluun, (2) mikä on poikuekoon ja poikasten iän vaikutus aikuisten lintujen ruokintakäyttäytymiseen ja (3) kuinka aikuiset puukiipijät käyttävät aikansa pesimäkaudella?

Emolintujen ruokinta-aktiivisuutta tutkittiin automaattisten, pöytälaskimista rakennettujen laskureiden avulla. Pöntön aukolle sijoitettu valokenno antoi sykäyksen laskurille emolinnun katkaistessa valokennon infrapunasäteen. Aikabudjetin laskenta toteutettiin tarkkailemalla pesiviä emolintuja ja merkitsemällä lomakkeelle kymmenen sekunnin välein lintujen käyttäytymisen laatu.

Aikuiset linnut olivat liikkeellä, ruokkivat tai lämmittivät poikasiaan 89% auringon nousun ja auringon laskun välisestä ajasta. Liikkeelläoloaika vaihteli merkitsevästi päivänpituuden mukaan. Mitä vanhempia poikaset olivat sitä enemmän emot niitä ruokkivat. Poikuekoon kasvaessa ei ruokintatiheys kasvanut tuntia kohden, mutta vuorokauden kokonaisruokintamäärä kasvoi, koska emolinnuilla oli käytettävissään pidempi päivä samaan aikaan, kun poikuekoko oli suuri.

Aikuisten lintujen aikabudjetti kertoo, että linnut käyttävät saalistukseen sitä enemmän aikaa mitä vanhempia poikaset ovat. Saalistukseen käytetty aika ei kuitenkaan kasvanut poikuekoon kasvaessa. Enimmillään puukiipijäemot käyttivät 89% liikkeelläoloajastaan saalistukseen, lentelyyn puiden runkojen välillä sekä ravinnon kuljetukseen pesälle ja lentämiseen pesältä pois.

Tulokset antavat aihetta olettaa, että emot voivat lisätä ruokintatehokkuuttaan käyttämällä pidempää päivää hyväkseen. Puukiipijä munii pesimäkauden alussa pienempiä pesyeitä kuin pesimäkauden keskivaiheilla. Kesäkuun puolivälissä, jolloin puukiipijän isot poikueet ovat lähdössä pesistä, on puukiipijälle tarjolla pitkän päivän lisäksi myös eniten ravintoa. Samaan aikaan on myös lämpötila korkea, jolloin poikasten lämmönsäätely ei kuluta yhtä runsaasti energiaa kuin aiemmin keväällä. On hankalaa erottaa toisistaan näiden tekijöiden vaikutuksia. Ravinto on kuitenkin tärkein tekijä, lämpötilan kasvu vähentää energian tarvetta ja pitkä päivä auttaa lisääntymismenestystä erityisesti huonoissa sääolosuhteissa.

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