

## Incubation, hatching, and clutch desertion of the Treecreeper *Certhia familiaris* in south-western Sweden

ANDERS ENEMAR

---

### Abstract

Breeding data were collected on a Treecreeper population nesting in artificial nest sites, erected in deciduous forests in south-western Sweden. From 1982 through 1994, 74 incubation periods were estimated by measuring the time from laying of the last egg to either the hatching of that egg or the appearance of the last hatchling. The mean period was  $15.7 \pm 1.44$  (SD) days, showing a negative relation to laying date from about 17 days for clutches laid in early April to about 14 days in late June, as well as to the mean ambient temperature of the egg-laying period and the first five days of incubation. Mean hatching asynchrony was

$1.0 \pm 0.37$  days ( $n=38$ ). Approximately 90% of the eggs surviving until hatching produced viable chicks. A third of the losses were perished hatchlings, the rest unhatched eggs. Out of 443 clutches with at least one egg, 13% were abandoned without signs of robbing or other destruction. Part of the desertions occurred in connection with heavy rain soaking the nests. – The concept of incubation period is discussed.

*Anders Enemar, Department of Zoology, University of Göteborg, Medicinarg. 18, S-413 90 Göteborg, Sweden.*

---

Received 8 March 1995, Accepted 2 June 1995, Editor: H. Smith.

### Introduction

The Treecreeper *Certhia familiaris* is a year-round resident inhabiting coniferous as well as deciduous forests. Its breeding ecology has been studied in coniferous forests in Finland (Kuitunen 1989) but is otherwise poorly known. To document its breeding ecology in deciduous forests, a long-term study has been performed in south-western Sweden from 1982 to present.

In south-western Sweden the species is facultatively double-brooded. Its breeding season begins in early April and may extend into late July, which is a very long period compared to that of other resident passerines in the area except the Wren *Troglodytes troglodytes*. The current studies are carried out with the final aim to understand what determines the choice between single- and double-brooded breeding strategies. To this aim seasonal trends in reproductive performance are investigated.

Information on the timing of breeding and clutch size have been published previously (Enemar 1992). This paper presents data on the length of the incubation period, hatching asynchrony, hatching success and clutch desertion, together with a brief and crit-

ical review of how the concept of the incubation period has been defined and put into practice in the field.

### Methods

The present study, initiated in 1982, has been carried out in the deciduous woods of the Gunnebo recreation grounds, located about 10 km south-east of Göteborg in south-western Sweden ( $57^{\circ}39'N$ ;  $12^{\circ}4'E$ ). The study area and the special breeding devices for the Treecreeper used (300 nest pockets) have been presented previously together with an account of the routines of the field work (Enemar 1992).

The incubation period was estimated for a large number of clutches by counting the days elapsing from the laying of the last egg to the hatching of the last young, i.e. the technique indicated by Evans (1891), later described in full by Heinroth (1922), and further evaluated by Swanberg (1950). In accordance with Nice (1954), only clutches where all eggs hatched were considered. The date of the ap-

pearance of the last egg was often calculated assuming that the Treecreeper lays one egg a day, which was repeatedly confirmed in this study. The hatching of the last laid egg was presumed to have occurred, on average, half a day prior to the morning when the hatching was first observed, provided that the nest, with still at least one egg unhatched, had been inspected the preceding morning.

Most occupied nest pockets were in 1994 inspected daily before noon during the egg laying period to mark the eggs according to their laying order and, later, to record the hatching days of the individual eggs. This procedure allowed the incubation time of the last egg laid to be accurately established even in clutches which tended to hatch synchronously. In such cases, the last egg laid is not necessarily the last egg to hatch, which may lead to an overestimation of the incubation period defined according to Heinroth and Swanberg (von Haartman 1956).

The onset of incubation and the developmental asynchrony were in 1994 investigated by transillumination and photographing the eggs during the first few days of incubation (Enemar & Arheimer 1989). The time interval between the youngest and oldest embryos of a clutch was estimated by comparing their appearance on the photographs (swelling of the yolk sphere, size of the embryo, extension of the extra-embryonic membranes, cf. Fig. 1).

The hatching asynchrony was measured in 1993 and 1994 by inspecting the nests every morning of the last few days of the incubation period. It was calculated as follows. In case the whole clutch appeared as hatched on the same morning, the eggs may have hatched either synchronously since the preceding inspection (minimum hatching asynchrony=0 days), or in a sequence from immediately after the inspection of the unhatched clutch the preceding morning to just before the visit the following morning (maximum hatching asynchrony=1 day). The mean of these values (0.5 days) is considered to indicate, on average, the degree of the hatching spread. The minimum and maximum values were calculated in a corresponding way when the appearance of the hatchlings was distributed over two or three mornings.

The daily mean temperatures of the breeding seasons were obtained from the meteorological station of Säve airport, about 15 km to the north of the study area (SMHI 1982–1994). These mean temperatures may differ somewhat from those of the study area. On the other hand, the major temperature fluctuations, which are of importance in the present context, are certainly more or less the same. This

became evident when the data from Säve were compared with those of other weather stations around the study area (Landvetter and Göteborg). Data on precipitation were also obtained from Säve.

The statistical tests used are Student's t-test, Pearson correlation and analysis of covariance following Bonnier & Tedin (1940).

## Results

The incubation periods were recorded for 74 clutches, a third of which were based on clutches with marked eggs. Majority of the periods were estimated in 1993 (20) and 1994 (25), the rest in the seasons of 1982 through 1992. The data refer to clutches with laying starts from April 10 to June 19.

The average incubation period was  $15.7 \pm 1.44$

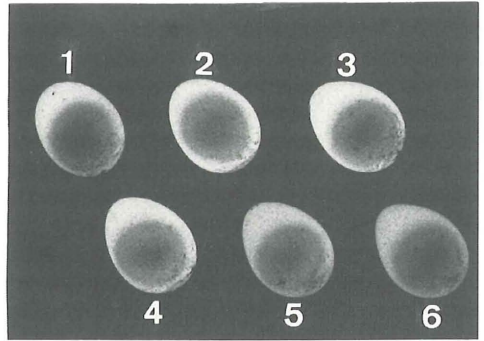
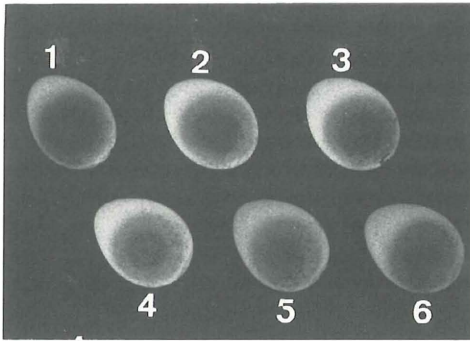
Fig. 1. Photographs of the transilluminated eggs of an asynchronous clutch (A, first egg 30 April, mean temperature of laying period  $+9.6^\circ\text{C}$ ) and a synchronous clutch (B, 28 April,  $+8.4^\circ\text{C}$ ) about 24, 48, 72, and 96 h after the appearance of the last egg. Numbers indicate laying order. The developmental asynchrony is clearly visible in clutch A after 72 h, ranging from a large embryo (dark spot at the lower margin) and coarse blood vessels in egg No.1 to merely a swollen yolk globe without visible embryonic structures in egg No.6. At the same time, all eggs of clutch B are only in the yolk swelling stage, showing embryos and blood vessels first after another 24 h of incubation. The developmental asynchrony is estimated at slightly more than 1 day for clutch A, and less than 0.5 day for B. This is in agreement with the hatching spreads recorded later on in the field. The photographs show that the difference between the two clutches with regard to the developmental progress of the sixth egg is insignificant, the A-egg having a slight developmental lead. This means that full incubation started very soon after the laying of the last egg in clutch B. The recorded incubation periods were between 15 and 16 days for both clutches.

*Foton av de genomlysta äggen av en asynkron (A, värpstart 30 april, medeltemperatur för värpperioden  $+9,6^\circ\text{C}$ ) och en synkron kull (B, 28 april,  $+8,4^\circ\text{C}$ ) ca 24, 48, 72 och 96 timmar efter sista äggets värpning. Siffrorna anger värpföljden. Spridningen i utvecklingsstadierna mellan äggen i kull A framgår klart efter 72 timmar, med synligt embryo (mörka fläcken vid äggets nedre kant) och tydliga blodådror i ägg 1, medan ägg 6 ännu visar endast uppsvälld gula utan synligt embryo. Vid samma tidpunkt har kullen B inte hunnit längre än till uppsvällda gulor över lag. Spridningen i utvecklingen mellan ägg 1 och 6 bedöms vara drygt 1 dygn för A och mindre än 0,5 dygn för B. Detta stämmer med den i fält senare konstaterade kläckningsspridningen. Fotona visar vidare att skillnaden mellan de båda kullarnas 6:e ägg är obetydlig med litet försprång för A-ägget. Detta betyder att full ruvning kom igång i kull B mycket snabbt efter sista äggets värpning. Den konstaterade ruvningstiden blev för båda kullarna mellan 15 och 16 dygn.*

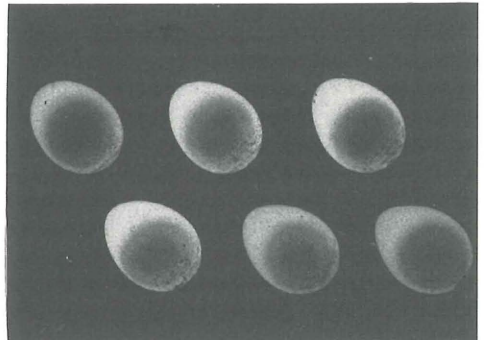
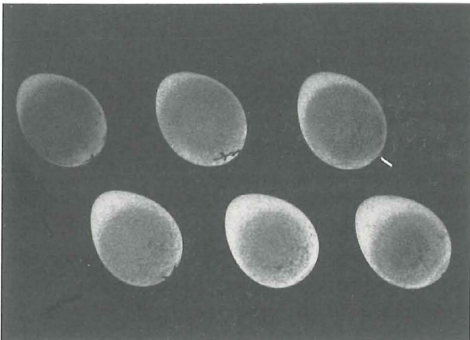
A

B

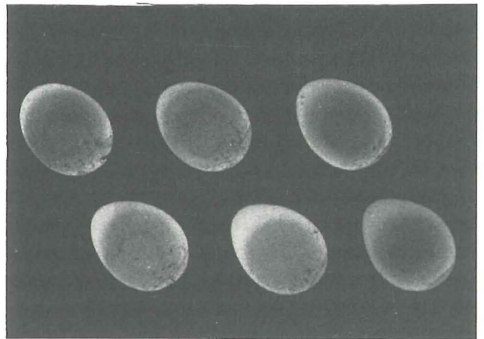
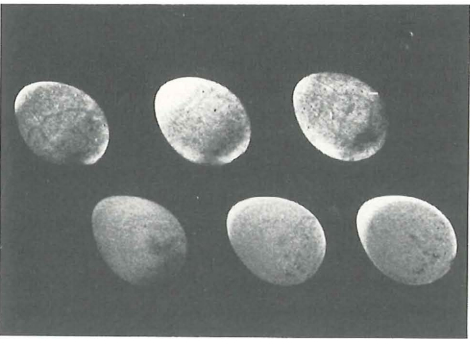
24 h



48 h



72 h



96 h

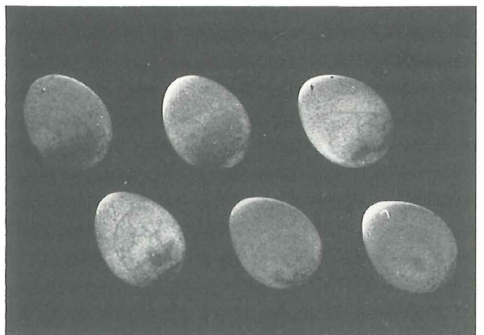
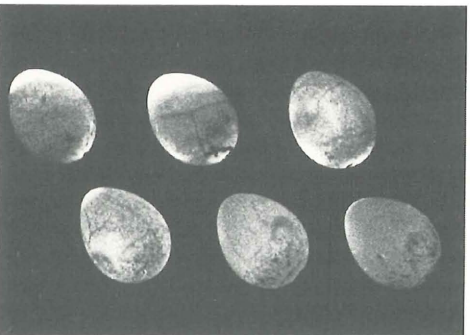


Table 1. Number of clutches distributed according to the incubation time of the last egg laid and month of laying start. The mean incubation periods ( $\pm$ SD) were calculated presuming that the eggs hatched, on average, in the middle of the indicated 24-hour periods. Measurements were based on marked eggs (25 clutches) or were carried out according to the Heinroth-Swanberg method (49 clutches).

*Antal kullar grupperade enligt det sist lagda äggets ruvningstid och månaden för värpstarten. Medelvärdena för ruvningstiden har uträknats under förutsättningen att äggen i genomsnitt kläckts vid de angivna dygnsintervallens mitt.*

Month <i>Månad</i>	Day interval of hatching <i>Kläckningsdygn</i>							Mean incubation period <i>Medelruvningstid</i>
	13< >14	14< >15	15< >16	16< >17	17< >18	18< >19	19< >20	
April	–	7	9	3	5	5	1	16.3 $\pm$ 1.56
May/ <i>maj</i>	4	9	14	3	6	–	–	15.4 $\pm$ 1.22
June/ <i>juni</i>	2	3	2	1	–	–	–	14.8 $\pm$ 1.04
Total	6	19	25	7	11	5	1	15.7 $\pm$ 1.44

(SD) days (Table 1). The estimated 74 incubation periods showed a negative and significant regression on time (Fig. 2), indicating that they decreased from about 17 days for clutches started in early April to about 14 days for those incubated in late June.

The eggs of 38 clutches hatched within a period of about 24 hours, the mean time interval between the first and last egg being  $1.0 \pm 0.37$  days (Table 2). The examination of transilluminated eggs from the first few days of incubation revealed a developmental

asynchrony of the same magnitude ( $0.8 \pm 0.44$  days,  $n=15$ ). As expected, the developmental ( $x$ ) and hatching ( $y$ ) asynchrony covaried significantly and positively for 11 clutches where both measurements were carried out ( $r=0.89$ ,  $df=9$ ,  $p<0.001$ ).

Approximately 90 per cent of the eggs surviving until hatching time produced viable chicks (Table 3). About one third of the failures consisted of perished hatchlings, the rest being unhatched eggs. Part of these eggs contained visible embryos of different ages.

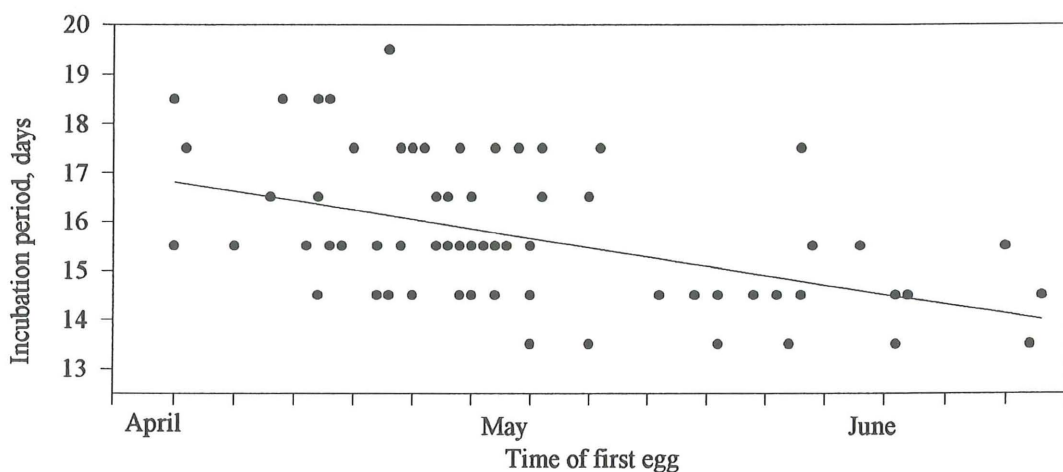


Fig. 2. The relation between the incubation period and the laying date. The negative relationship is significant:  $y=17.0-0.04x$ ,  $r=-0.46$ ,  $df=72$ ,  $p<0.001$  (1 April = 1, 5-day periods are indicated on the x-axis, four dots represent two observations each, three dots three observations).

*Sambandet mellan ruvningsperiodens längd och datum för värpningens start. Medelminskningen under säsongen visas av linjen, vars lutning är statistiskt säkerställd.*

Table 2. The hatching spread (days) as determined by watching the clutches during the last few days of the incubation period.

*Kläckningsspridningen i dagar, bestämd genom bevakning av äggkullarna under ruvningens slutskede.*

Year År	Number of clutches <i>Antal kullar</i>	Time of first egg <i>Datum för första ägg</i>	Mean±SD <i>Medelvärde ±SD</i>
1993	18	14/4–4/6	1.1±0.44
1994	20	13/4–13/6	0.9±0.24
Total	38	13/4–13/6	1.0±0.37

Difference *Skillnad* 1993/94:  $t=2.25$ ,  $p<0.05$

No less than 57 out of 443 clutches with at least one egg were abandoned for reasons unknown in 1982 through 1994, i.e. 13%. There were no signs of robbing or other interferences in these cases.

## Analyses and discussions

### *Length of incubation period*

In the Treecreeper, the incubation is carried out by the female birds only. The recorded incubation periods varied from 13.5 to 19.5 days (Table 1), declining significantly from the beginning to the end of the breeding season. The reason for this "calendar effect" is assumed to be the rise of the environmental temperature with the progress of the season. Thus, the relation between the temperature and the length of the incubation period has been investigated, using the mean temperatures of two different periods of the breeding time: first, the egg-laying period together with the first five days following the laying of the last egg and, second, the seven days preceding the hatching of the last egg laid. The data from 1994 and from the years 1982 through 1993

have been tested separately due to the slightly different methods used to measure the length of the incubation period (see Methods, Table 4). Some additional data characterizing the environmental temperature of the study periods are included in Table 4. The reason is that the effect of the temperature may be dependent upon its general level and variation between the tested breedings. Of course, no significant relation is expected when the temperature remains stable or above what is critical for the breeding females.

The ambient temperature around the completion of laying and the start of incubation is probably the most important factor affecting the length of the incubation period (Fig. 3). Both sets of data agree in this (Table 4), implying that the period is reduced by one day, on average, when the temperature mean increases between two and four degrees. A possible effect of the temperature during the last week of incubation is less conspicuous. No correlation is found for 1994. However, the data from 1982 through 1993 show a negative and significant correlation, possibly due to the wide temperature fluctuations compared to 1994 (cf. Table 4). On the other hand, the temperature means of the early and late periods are expected to be positively correlated since the end of the early period and the beginning of the late period are separated by only a few days (mean 3.7, range 0–7). The correlation is in fact significant ( $r=+0.52$ ,  $df=47$ ,  $p<0.001$ ). This seems to imply that much of the recorded inverse relation between the temperature of the late period and the incubation length reflects that which has been established in the early period.

The temperature means of the late periods in 1994 are correlated neither to the length of the incubation periods (Table 4), nor to the means of the early periods ( $r=-0.07$ ,  $df=23$ ,  $p<0.8$ ). This strongly indicates that the early period is generally the most important one in affecting the behaviour of the

Table 3. Hatching success. *Kläckningsframgången*. A=Number of clutches *Antal kullar*, B=Number of eggs *Antal ägg*, C=Number of surviving hatchlings *Antal överlevande nykläckta*, D=100C/B, E=Number of perished hatchlings *Antal omkomna nykläckta*, F=100E/B, G=Number of unhatched eggs *Antal okläckta ägg*, H=100G/B. Bold figures denote percentages. *Procentalen markeras med fetstil.*

Year/År	A	B	C	D	E	F	G	H
1991	18	98	86	<b>88</b>	3	<b>3</b>	9	<b>9</b>
1993	30	168	155	<b>92</b>	5	<b>3</b>	8	<b>5</b>
1994	28	146	127	<b>87</b>	3	<b>2</b>	16	<b>11</b>
Total	76	412	368	<b>89</b>	11	<b>3</b>	33	<b>8</b>

Table 4. The relation between the incubation period and the mean temperature during both the egg laying period, including the first five days after the last egg was laid (EARLY PERIOD), and the seven days before the hatching of the last egg (LATE PERIOD), together with data showing the temperature conditions during the period studied. The slope (b) of the regression line and the correlation coefficient (r) is given together with the probability value (p).

*Sambandet mellan ruvningstidens längd och medeltemperaturen under dels äggläggningstiden och de fem första dagarna efter sista äggets värpning (TIDIG PERIOD), dels de sju dagarna före sist lagda äggets kläckning (SEN PERIOD), tillsammans med data som visar temperaturförhållandena under de studerade perioderna. Värdet på b anger sambandet mellan ruvtid och temperatur (-0.45 betyder att ruvtiden minskar 0,45 dagar då medeltemperaturen för perioden ökar med 1°C).*

	Method of estimating incubation period	
	<i>Metod för mätning av ruvtid</i>	
	Last egg marked <i>Sista ägget märkt</i> 1994	According to <i>Enligt</i> Heinroth/Swanberg 1982–1993
<b>EARLY PERIOD TIDIG PERIOD:</b>		
Number of clutches <i>Antal kullar</i>	25	49
Mean temperature ( $\pm$ SD) <i>Medeltemp.</i>	+10.3 $\pm$ 1.55	+10.6 $\pm$ 3.70
CV <i>Variationskoefficient</i>	15%	35%
Temperature range <i>Temp.omfång</i>	+5.3 to +12.5	+3.5 to +17.3
b	-0.45	0.24
r <i>Korrelationskoefficient</i>	-0.63	-0.55
p <i>Sannolikhetsvärde</i>	<0.001	<0.01
<b>LATE PERIOD SEN PERIOD:</b>		
Number of clutches	25	49
Mean temperature	+12.6 $\pm$ 1.70	+12.0 $\pm$ 3.05
CV	14%	25%
Temperature range	+8.8 to +15.9	+3.3 to +18.7
b	+0.05	-0.23
r	0.08	-0.45
p	<0.8 n.s.	<0.01

parent birds. It is certainly a strenuous period for the female bird, whose energy-demanding task to produce eggs may make her sensitive to falling temperatures with concomitant increasing feeding difficulties. This might postpone the onset of the likewise energy-demanding full and continuous incubation (Mertens 1980). Taken together, this results in a prolongation of the incubation period.

Reported incubation periods for the Treecreeper, usually based on small samples, are 13–14 days (Schönfeld 1983), 14 days (Longstaff 1929), 14–16 days (Swanberg 1982), and 15 days (Evans 1891, Ross 1931, Steinfatt 1939, Bäsecke 1957, Löhrl 1979, Davis 1979). Durango (1963) observed longer incubation periods for the first clutches (15 to slightly more than 16 days) caused by "lower air temperature and longer foraging trips" than for the second clutches (14 days), although he did not give

the number of studied nests. All incubation periods are within the range recorded in this study. The Nest Record Scheme of the British Isles presents a mean of 14.5 $\pm$ 1.4 days (range 12–19) for 44 clutches (Flegg 1973), which is approximately one day shorter than in this study ( $t=4.46$ ,  $p<0.001$ ). Unfortunately, the significance of this difference is uncertain, as no information was given as to how the incubation periods had been calculated from the nest card data.

Examples of an inverse relation between incubation period and air temperature for two passerine species are given by Kendeigh (1952) and Walkinshaw (1952). A similar relation between the duration of the incubation period and the laying date has been shown for some other small passerine species (e.g. Seel 1968, von Haartman 1969, Winkel 1970, Slagsvold 1986, Smith 1993). All this is in accordance

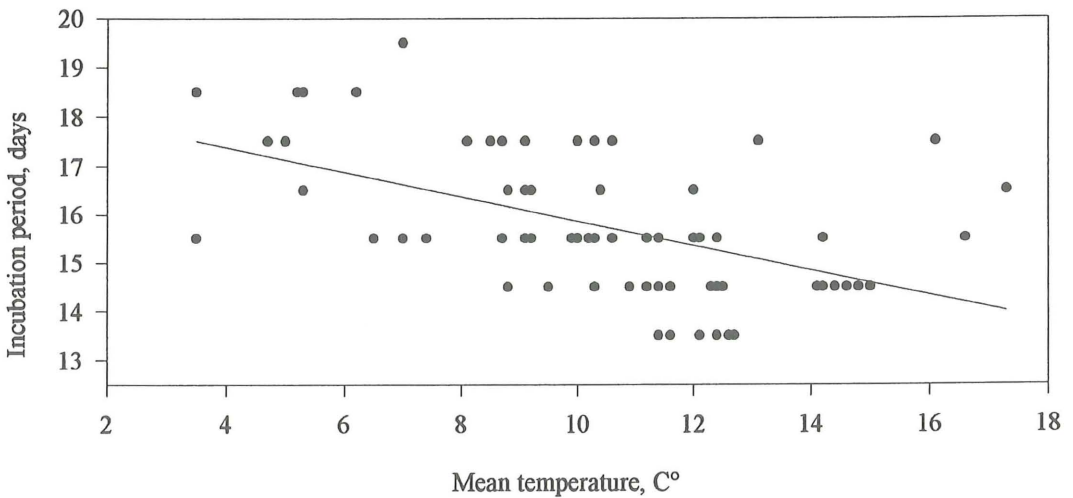


Fig. 3. The relation between the incubation period and the mean ambient temperature of the period from the laying of the first egg through the fifth day after the last egg. The negative relationship is significant:  $y=18.4-0.25x$ ,  $r=-0.55$ ,  $df=72$ ,  $p<0.001$ . (Ten dots in the diagram represent two observations each.)

*Diagram som visar hur ruvningsperiodens längd minskar då temperaturen i omgivningen ökar. Temperaturen är ett medelvärde för tiden från första äggets värpning till och med femte dagen efter sista ägget. Linjen visar medelsambandet, vilket är statistiskt säkert.*

with Huggins' (1941) demonstration that there is a positive correlation between air temperature and average egg temperature during incubation.

#### *The hatching asynchrony*

The hatching spread depends primarily on the amount of heat the first eggs laid receive before the appearance of the last one. In this study, full incubation intensity was in most cases attained after the completion of the clutch. However, the first eggs have usually been slightly incubated by the laying female, giving them a developmental lead of up to 24 hours, as documented by the photographs of the transilluminated clutches (Fig. 1). A hatching spread of about 1.5 days has been recorded for three clutches, all with first eggs layed in May or June and two of them with 7 eggs. However, so far the number of investigated clutches with 4 and 7 eggs is too small to establish the relationship between the hatching spread and clutch size.

Like the incubation period, the hatching asynchrony was affected by the mean ambient temperature during laying and the first five incubation days (Fig. 4). The higher the temperature, the more incubation during the laying period, resulting in a prolonged hatching spread.

The Treecreeper is said to start effective incubation on completion of the clutch or a few days later (Steinfatt 1939, Bäsecke 1957, Durango 1963, Davis 1979, Swanberg 1982). This is also stated in many handbooks (e.g. Groebbels 1937, Witherby et al. 1943, Harrison 1975). However, Ptushenko & Inozemtsev (1968) report that incubation begins with the laying of the penultimate egg. There are also single observations of a clear hatching spread in the literature (e.g. Lövenskiöld 1930, Ross 1931). It is possible that the Treecreeper behaves as the small passerine species in general, i.e. it starts incubation successively before the last egg is laid (Clark & Wilson 1981, Magrath 1990) if not prevented by proximate constraints such as cold weather and food scarcity (Slagsvold 1986, Slagsvold & Lifjeld 1989, Enemar & Arheimer 1989, Nilsson 1993). Whatever the driving selective forces resulting in asynchronous hatching are (cf. reviews by e.g. Magrath (1990), Nilsson (1993)), it is difficult to see why the Treecreeper should be an exception in this context. The many reported instances of delayed incubation start could be explained by the habit of the Treecreeper to begin egg-laying very early in the spring compared to the resident small passerine species in the area, i.e. at a time when constraining conditions such as low temperatures usually prevail.

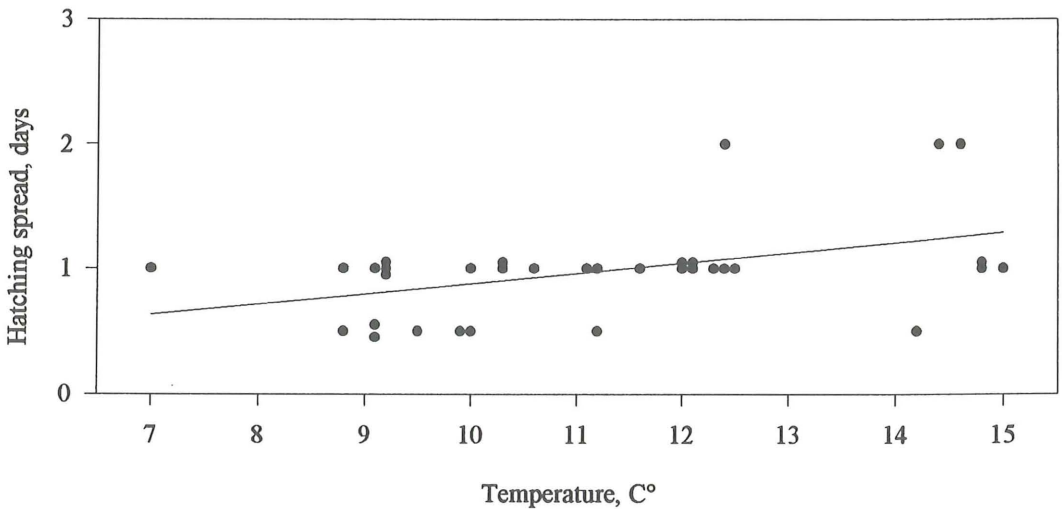


Fig. 4. The relation between the hatching spread and the mean ambient temperature of the period from the appearance of the first egg through the fifth day after the last egg has been laid. The positive relationship is significant:  $y=0.07+0.08x$ ,  $r=0.44$ ,  $df=32$ ,  $p<0.01$ .

Diagram som visar hur kläckningsspridningen i dygn ökar då medeltemperaturen i omgivningen stiger under perioden från första äggets värpning till och med femte dagen efter sista ägget. Medelökningen visas av linjen vars lutning är statistiskt säker.

### The hatching success

Approximately nine out of ten fully incubated eggs hatched and produced viable hatchlings (Table 3). Kuitunen (1987) reports the same outcome of successful breedings in his study area in Finland. In Britain, the number of fledglings per egg was 0.85 to 0.93 for successful nests (Flegg 1973), i.e. the same production of viable hatchlings as in the present study. This level of hatching success seems to be generally valid for avian eggs (Koenig 1982).

In my study area, only 3% of the hatchlings died during or soon after the hatching process. Most of the losses were unhatched eggs (approx. 8%, Table 3), apparently due to the death of the embryos at varying developmental stages within the egg. According to the photos of the transilluminated clutches, all 109 inspected eggs started the developmental processes, as indicated by the swelling of the yolk sphere. Obviously, the frequency of unfertilized eggs has been negligible.

### Clutch desertion

The Treecreepers may postpone the start of incubation several days after completion of the clutch (Bäsecke 1957, Swanberg 1982), as suggested above, due to the impact of constraining environmental factors, such as cold weather. These postponements

could probably in some cases lead to clutch desertion. In fact, it has quite often happened that incomplete or complete clutches have been abandoned in nests which have shown no signs of robbing or other interferences. The desertion rate in my study area was 13%, which is close to the 12% of 369 breeding attempts in nest-boxes, recorded by Kuitunen & Aleknonis (1992) in Finland. Obviously, these desertions are a regular phenomenon in the breeding biology of the Treecreeper.

It is possible that the inspections of the nest pockets and the flushing of the females from the nests could have caused some desertions. However, no clutches were abandoned in 1994, despite the fact that the nests were then inspected more often than previously in connection with photographing the transilluminated eggs (cf. Methods). Therefore the "human factor" seems to have been negligible.

A negative, although insignificant ( $p<0.2$ ), correlation was found between the temperature and the frequency of clutch desertions. However, many abandoned nests containing cold and wet eggs had been soaked in connection with heavy rainfall. In fact, a positive and significant correlation was found between the frequency of clutch desertions and the amount of precipitation during the month (April or May) when the incubation was terminated (Fig. 5).



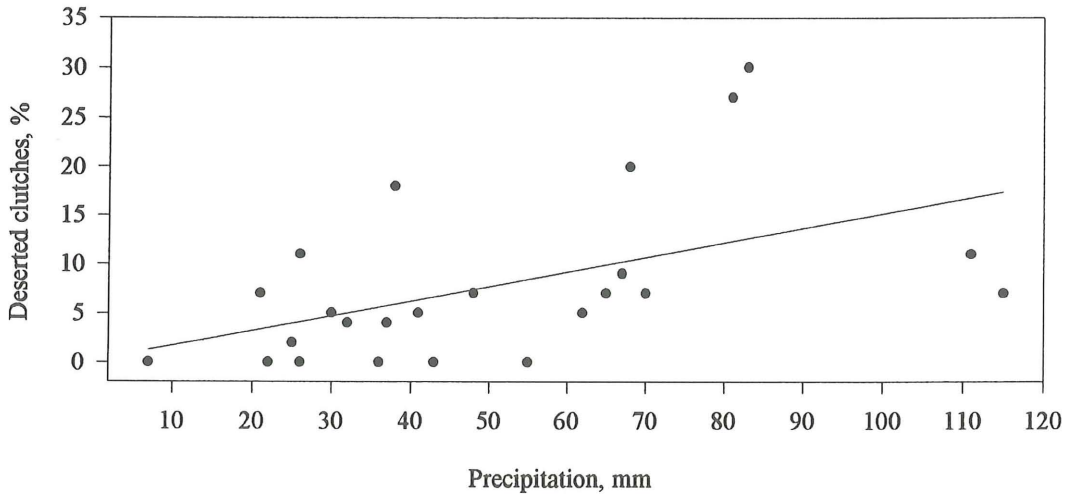


Fig. 5. The relation between the proportion of deserted clutches and the amount of rain during the month of desertion (April or May). The positive relationship is significant:  $y=0.24+0.15x$ ,  $r=0.50$ ,  $df=22$ ,  $p<0.02$ .

*Diagram som visar hur antalet övergivna äggkullar, uttryckt i procent av totala antalet häckningar, ökar med stigande regnmängd under den månad, april eller maj, då övergivningen skedde. Sambandet, som visas av linjen, är statistiskt säkerställt.*

This explains only part of the nest desertions, because many abandoned nests were dry and many parent birds returned to their soaked nests to incubate.

The clutch desertion rate was only approximately 4% for nests placed in natural cavities in Lithuania (Kuitunen & Aleknonis 1992). A higher desertion rate for nests in natural sites was found by Davis (1979), apparently often caused by heavy rain. It is possible that the nest pockets of this study, and perhaps also the nest boxes used by Kuitunen (1985), are rather effective in accumulating water that easily enters the artificial nest cavities along the tree trunks during rainfall, with an increased desertion rate as a consequence.

#### Concluding remarks

The "incubation period" – a concept hard to define and handle?

As indicated above, the concept of incubation period has since long been lively debated, concerning not only how to measure the length of the period in the field but also how to define this period. As for the last-mentioned problem, Swanberg (1950) agrees with and quotes Heinroth's (1922) rule: "By incubation period is understood the time which with regular, uninterrupted incubation of a newly laid egg

elapses until the young has left the egg" (Swanberg's translation). The problem is how to discern and establish in the field what should be regarded as "regular" and "uninterrupted", or, following Drent's (1975) rule, as "regular attention of the parent as typical of undisturbed incubation".

How many of the incubation periods of the Treecreeper, listed in Table 1, should be considered valid according to the "rules" above? It is not an easy task to decide this, which was pointed out already by Evans (1891). He recommended that the incubation period be measured from laying of the last egg to the hatching of the same, marked egg (or of the last young), but he saw difficulties in the fact that incubation may often start either before or some time after the completion of the clutch, facts that have often been recognized as serious complications (cf. e.g. Ryves 1946). Evans therefore concluded that "by means of an incubator all these difficulties are overcome". Although we know a great deal about the physiology and requirements of the egg under development (e.g. Drent 1975, Deeming & Ferguson 1991), it is not easy to imitate the environment of the *naturally* incubated egg (Huggins 1941). Therefore, artificial incubation is not considered satisfactory in this context.

Despite all discussions and reviews dealing with incubation problems during the last few decades, it

has obviously been impossible to arrive at consensus views with regard to concepts and practices. For example, it has recently been stated that "incubation time" should be defined as the period from the last egg laid to the *first* egg hatched when the individual eggs of the clutch cannot be identified (Ehrlich et al. 1994).

It is necessary to arrive at general agreements on how to treat the concept of the incubation period and how to estimate the latter in the field, in order to make meaningful interspecific as well as intraspecific comparisons possible. More precise estimations are now badly needed. For example, as for the small passerines, the numerous references to recorded incubation periods given in today's handbooks do not say much more than what was stated already in the extensive and classical investigations made by Evans (1891), who concluded that "13 to 14 days is a very common period", and by Heinroth (1922), who found that the period lasts mostly between 12 and 14 days.

First a terminological distinction is needed. The nesting time of a breeding pair has traditionally been divided into the nest-building, laying, incubation, and nestling periods. The incubation period starts when laying is completed and lasts until hatching is finished irrespective of its relation to the incubation period according to the above-mentioned rules by Heinroth and Drent. Obviously "incubation period" is an ambiguous term. I here use the term *incubation period* to denote the time elapsing from laying of the last egg to its hatching, because it most often corresponds to the equally designated period of the nesting time. (As mentioned above, small deviations may be caused by some of the synchronously hatched clutches.) I suggest that the term *incubation time* be reserved for the period of incubation which follows when the incubation behaviour of the parent bird is "typical", "regular", "uninterrupted", and "undisturbed", i.e. conforms with the rules mentioned above.

Needless to say, the length of the incubation period mainly depends on two factors: first, the egg through its developmental properties which decide the *minimum developmental time* of the egg, and second, the parent bird through its incubation performance (attentiveness) (cf. Moreau 1946). The latter adds a component of behavioural ecology to the incubation period. Therefore, the incubation period is and has to be accepted as a dynamic phenomenon. In the following, the three kinds of periods of development and incubation will be commented on separately.

### The minimum developmental time

The physiological properties of the egg provide the starting-point, i.e. the minimum developmental time, which is the time elapsing between laying and hatching when the egg is incubated continuously under optimal conditions as regards temperature, humidity, and egg turning (cf. Drent 1975). Inherited physiological differences between the eggs of a clutch are certainly small, probably less than 1% of the standard deviation of the length of incubation time (Ricklefs 1993). This minimum developmental time can be estimated, at least approximately, by artificial incubation. Only few wild species have been investigated using this technique. Heinroth (1922) concludes that the artificially incubated eggs sometimes show a six to twelve hours shorter incubation period, never a longer one, compared to the eggs of undisturbed breedings in the field. The very short incubation periods of ten days estimated in the field later on are certainly faulty (Nice 1953).

Access to the minimum developmental times of different species would open up new possibilities of comparing the incubation periods by using an index, expressed as the quotient between the incubation period and the minimum developmental time. This means that species, which differ in the minimum developmental time of their eggs, could possibly be compared in a fruitful way. This philosophy was introduced by Ricklefs (1993), who used a differently derived "incubation period index" when comparing various taxa.

### The incubation period

This period is what was estimated in the field for the Treecreepers of this study (see Methods). It is probably adaptive to keep the incubation periods as short as possible because the impact of various nest mortality factors is thereby reduced (Clark & Wilson 1981). Ideally, the incubation period should equal the minimum developmental time. This seldom, if ever, happens due to various necessary pauses which may more or less prolong the period. Provided that the incubation leads to normal hatching, all kinds of pauses and interruptions, short or day-long, as well as postponements of the start of full incubation, should be accepted as natural features of the incubation period, with the exception of those caused by humans and other artificial factors.

The varying attentiveness of the parent birds is the main cause of the sometimes wide variation of incubation periods. In contrast to the developmental

time, the incubation period is a dynamic concept of immediate ecological import. It provides a measure of how fit the individual parent bird is to master prevailing internal (own physiological) and external (environmental) constraints. Thus, even wide fluctuations in the incubation periods are informative, although they are sometimes considered problematic by students of breeding biology. The incubation period, as defined here, is a straightforward concept easily manageable in the field.

#### The incubation time

This term denotes the time elapsing from laying the last egg to its hatching when the undisturbed parent bird performs a regular and typical incubation behaviour (cf. the quotations from Heinroth and from Drent above). Such incubation may occur under favourable conditions when the incubating bird can keep the foraging breaks short enough to avoid that the egg temperature falls below the level where the embryonic development ceases. The passerines in general seem to be adapted to adjust their incubation rhythm accordingly (Haftorn 1988). The length of the incubation time will probably most often land somewhere between the minimum developmental time and the incubation period. Its variation is restricted compared to that of the incubation period, because it is expected to be affected mainly by the hereditary variation in the incubation behaviour between the individual birds. This is the "normal incubation period" according to Nice (1954), although she accepted that "it may vary a day or more according to season, weather and attentiveness of the sitting bird". The question then arises: how much of *more* should be accepted? Obviously the incubation time is a rather elusive concept.

It follows from the above that the incubation time is not easily estimated. It might be represented, approximately, by the shortest ones in a series of recorded incubation periods.

#### The Treecreeper as incubator

The Treecreeper belongs to the typical resident species which regularly spends the whole of the harsh wintertime in the study area. It is therefore assumed to be a rather "tough" bird, which is able to start laying early, in fact two weeks earlier, on average, than the nestbox-breeding tits in the same area (Enemar 1992). On the other hand, the species is apparently not tough enough to be entirely unaffected by the weather situation, which can be harsh, not

least during April when most Treecreepers start breeding. They are far from always able to take up full incubation immediately after laying the last egg, and they sometimes give up the breeding process to start anew later on. The early clutches are often found lying ice-cold in the nests during daytime of the first few days of the incubation period. All this must be considered a normal behaviour as a consequence of the early breeding start, the adaptive value probably being to secure time for replacement or genuine second clutches. Thus, as shown above, it is characteristic of the Treecreeper that the incubation period is prolonged in early spring and that it then decreases with the progress of the protracted breeding season of the species.

Despite the sometimes constraining situation, the Treecreeper warms the eggs enough during laying to bring about a hatching spread of one day, on average. This partial hatching asynchrony (Ricklefs 1993) is by some students considered as synchronous. The incubation behaviour during the laying period can differ markedly between females also when followed by equal incubation periods (Fig. 1).

The incubation time of the Treecreeper, as well as the minimum developmental time, is not known. The information given in Fig. 2 indicates that the former lasts for about 13.5 days, which has, so far, only happened for clutches laid in May or June.

#### Acknowledgements

I am grateful to Lars-Göran Lindgren for help in the field work in 1994 and to Björn Arvidsson for help to get the diagrams out of the computer. Financial support to this study was received from Margareta Sparre's Foundation (Margareta Sparres fond för bevarande av Gunnebos natur och kultur).

#### References

- Bäsecke, K. 1957. Zur Brutbiologie des Waldbaumläufers. *Vogelwelt* 78:190-192.
- Bonnier, G. & Tedin, O. 1940. *Biologisk variationsanalys*. Stockholm.
- Clark, A.B. & Wilson, D.S. 1981. Avian breeding adaptations: hatching asynchrony, brood reduction, and nest failure. *Q. Rev. Biol.* 56:253-277.
- Davis, C.M. 1979. A nesting study of the Brown Creeper. *Living Bird* 17:237-263.
- Deeming, D.C. & Ferguson, M.W.J. (eds.) 1991. *Egg incubation: its effects on embryonic development in birds and reptiles*. Cambridge Univ. Press, Cambridge.
- Drent, R. 1975. Incubation. Pp 333-420 in *Avian Biology*. Vol. 5. (Farner, D.S., King, J.R. & Parkes, K.C. eds). Academic Press, London.

- Durango, S. 1963. Trädskryparen, *Certhia familiaris* LINNÉ. Pp. 1677–1685 in *Våra Fåglar i Norden*, 2 uppl. (Curry-Lindahl, K. ed.). Natur & Kultur, Stockholm.
- Ehrlich, P.R., Dobkin, D.S., Wheye, D. & Pimm, S.L. 1994. *The Birdwatcher's Handbook*. Oxford University Press, Oxford.
- Enemar, A. 1992. Laying and clutch size of the Treecreeper *Certhia familiaris* in south-western Sweden. *Ornis Svecica* 2:93–102.
- Enemar, A. & Arheimer, O. 1989. Developmental asynchrony and onset of incubation among passerine birds in a mountain birch forest of Swedish Lapland. *Ornis Fenn.* 66:32–40.
- Evans, W. 1891. On the periods occupied by birds in the incubation of their eggs. *Ibis* 1891:52–93.
- Flegg, J.J.M. 1973. A study of Treecreepers. *Brit. Birds* 20:287–302.
- Groebbels, F. 1937. *Der Vogel* II. Berlin.
- Haartman, L. von 1956. Der Einfluss der Temperatur auf den Brutrhythmus experimentell nachgewiesen. *Ornis Fenn.* 33:100–107.
- Haartman, L. von 1969. The nesting habits of Finnish birds. I. Passeriformes. *Comm. Biologicae* 32:1–187.
- Haftorn, S. 1988. Incubating female passerines do not let the egg temperature fall below the "physiological zero temperature" during their absences from the nest. *Ornis Scand.* 19:97–110.
- Harrison, C. 1975. *A Field Guide to the Nests, Eggs and Nestlings of European Birds*. Collins, London.
- Heinroth, O. 1922. Die Beziehungen zwischen Vogelgewicht, Eigewicht, Gelegegewicht und Brutdauer. *J. Orn.* 70:172–285.
- Huggins, R.A. 1941. Egg temperatures of wild birds under natural conditions. *Ecology* 22:148–157.
- Kendeigh, S.C. 1952. Parental care and its evolution in birds. *Illinois Biological Monographs* 23: Nos. 1–3. Urbana.
- Koenig, W.D. 1982. Ecological and social factors affecting hatchability of eggs. *Auk* 99:526–236.
- Kuitunen, M. 1985. Is the common treecreeper (*Certhia familiaris* L.) more widespread in Hungary than has been previously believed? *Aquila* 92:255–261.
- Kuitunen, M. 1987. Seasonal and geographical variation in the clutch size of the Common Treecreeper *Certhia familiaris*. *Ornis Fenn.* 64:125–136.
- Kuitunen, M. 1989. *Food, space and time constraints on the reproduction in the Common Treecreeper* (*Certhia familiaris* L.). Ph. D. Thesis, University of Jyväskylä, Finland.
- Kuitunen, M. & Aleknonis, A. 1992. Nest predation and breeding success in Common Treecreepers nesting in boxes and natural cavities. *Ornis Fenn.* 69:7–12.
- Löhr, H. 1979. Zur Brutbiologie einer Population des Waldbaumläufers *Certhia familiaris*. *Ökologie der Vögel* 1:127–132.
- Longstaff, T.G. 1929. Incubation- and fledging-periods of Treecreeper. *Brit. Birds* 23:93.
- Lövenskiöld, H.L. 1930. Ornithologiske optegnelser gjennem 59 år av Thomas Jensen. *Norsk Ornithologisk Tidsskrift* III:115.
- Magrath, R.D. 1990. Hatching asynchrony in altricial birds. *Biol. Rev.* 65:587–620.
- Mertens, J.A.L. 1980. The energy requirements for incubation in great tits and other bird species. *Ardea* 68:185–192.
- Moreau, R.E. 1946. The recording of incubation and fledging periods. *Brit. Birds* 39:66–70.
- Nice, M.M. 1953. The question of ten-day incubation periods. *Wilson Bull.* 65:81–93.
- Nice, M.M. 1954. Problems of incubation periods in North American birds. *Condor* 56:173–197.
- Nilsson, J.-Å. 1993. Energetic constraints on hatching asynchrony. *Am. Nat.* 141:158–166.
- Ptushenko, E.S. & Inozemtsev, A.A. 1968. (In Russian.) Cited after Cramp, S. & Perrins, C.M. (eds.) 1993. *The Birds of the Western Palearctic* Vol. VII: p. 568. Oxford University Press, Oxford.
- Ricklefs, R.E. 1993. Sibling competition, hatching asynchrony, incubation period, and lifespan in altricial birds. Pp. 199–276 in *Current Ornithology* 11 (Power, D.M. ed.). Plenum Press, New York.
- Ross, W.M. 1931. Incubation- and fledging-periods of treecreeper. *Brit. Birds* 25:102.
- Ryves, B.H. 1946. Some criticism on the recording of incubation- periods of birds. *Brit. Birds* 39:49–51.
- Schönfeld, M. 1983. Beiträge zur Ökologie und zum intraspezifischen Verhalten der Baumläufer *Certhia familiaris* und *C. brachydactyla* in Eichen-Hainbuchen-Lindenwäldern unter dem Aspekt der erhöhten Siedlungsdichte durch eingebrachte Nisthöhlen. *Hercynia N.F.* 20: 290–311.
- Seel, D.C. 1968. Clutch-size, incubation and hatching success in the house sparrow and tree sparrow *Passer* spp. at Oxford. *Ibis* 110: 270–282.
- Slagsvold, T. 1986. Asynchronous versus synchronous hatching in birds: experiments with the pied flycatcher. *J. Anim. Ecol.* 55: 1115–1134.
- Slagsvold, T. & Lifjeld, J.T. 1989. Constraints on hatching asynchrony and egg size in pied flycatchers. *J. Anim. Ecol.* 58: 837–849.
- Smith, H.G. 1993. Seasonal decline in clutch size of the Marsh Tit (*Parus palustris*) in relation to date-specific survival of offspring. *Auk* 110:889–899.
- SMHI 1982–1994. *Väder och vatten*.
- Steinfatt, O. 1939. Das Brutleben des Waldbaumläufers, *Certhia f. familiaris*. *Mitteilungen des Vereins sächsischer Ornithologen* 6:1–18.
- Swanberg, P.O. 1950. On the concept of "incubation period". *Vår Fågelvärld* 9:63–80.
- Swanberg, P.O. 1982. A simple artificial nest site for Treecreeper *Certhia familiaris*. *Vår Fågelvärld* 41:23–24. (In Swedish with English summary.)
- Walkinshaw, L.H. 1952. Chipping sparrow notes. *Bird Banding* 23:101–108.
- Winkel, W. 1970. Experimentelle Untersuchungen zur Brutbiologie von Kohl- und Blaumeise (*Parus major* und *P. caeruleus*). *J. Orn.* 111:154–174.
- Witherby, H.F., Jourdain, F.C.R., Ticehurst, N.F. & Tucker, B.W. 1943. *The Handbook of British Birds*. Witherby, London.

## Sammanfattning

*Trädkryparens Certhia familiaris ruvning och kläckning samt övergivning av kullar i sydvästra Sverige*

### *Inledning och metod*

De sedan 1982 pågående trädkryparstudierna i Gunnebos fritidsområde, ca 10 km sydöst om Göteborg, presenterades i en tidigare uppsats vad gäller fältarbetets rutiner och de konstgjorda boplatserna (300 häckningsfickor) (Enemar 1952). Där redogjordes för trädkryparens äggläggning och kullstorlek. Under säsongerna 1993 och 1994 ägnades ruvningen och kläckningen särskild uppmärksamhet.

Ruvningstiden mättes från sista äggets värpning till sista äggets kläckning. De bebodda häckningsfickorna inspekterades varje morgon eller förmiddag under kläckningstiden. Den sista ungen antogs i genomsnitt ha kläckts ett halvt dygn före den morgon då alla äggen befanns vara kläckta, allt under förutsättning att boet inspekterats föregående morgon och att då något eller några ägg fortfarande var okläckta. Dagen för sista äggets värpning bestämdes ofta utgående från att trädkryparen lägger ett ägg varje morgon.

Ibland kläcks alla äggen i kullen ungefär samtidigt och då kan det hända att det sist lagda ägget inte kläcks sist. Det betyder att ruvningstidens längd i sådana fall kan något överskattas. För att undvika detta fel, besöktes bona säsongen 1994 dagligen under äggläggningstiden för numrering av äggen i värpföljd. Det sist lagda äggets kläckning kunde därmed bevakas med säkerhet. Dessutom var det av vikt för studiet av ruvningens igångsättande att värporordningen för alla äggen i kullen var känd.

Samma år undersöktes i vad mån trädkryparen börjar ruva äggen innan sista ägget värpts. Detta klarades genom att under ruvningens första dagar genomlysas och fotograferas varje kull med numrerade ägg. Har ruvningen börjat under äggläggningen, får de först lagda äggen ett försprång i utvecklingen (asynkron utveckling), i annat fall utvecklas äggen i takt (synkron utveckling). Detta kan avläsas på fotona av de genomlysta äggen, vilket visas och förklaras i Fig. 1. Börjar ruvningen under äggläggningen kommer de först värpta äggen att kläckas före det sist värpta. Storleken av denna kläcknings-spridning undersöktes genom kontroll av bona varje morgon under slutskedet av ruvningsperioden.

### *Resultat*

Ruvningstiden kunde under åren bestämmas för 74

kullar, varav en tredjedel med numrerade ägg. Resultatet visas i Tabell 1. Medelruvtiden blev  $15,7 \pm 1,44$  dygn. Av tabellen framgår att ruvningstiden var längre för kullar som värpts i april jämfört med dem med värpstart i maj och juni. Som framgår av Fig. 2, ligger ruvningstiden för kullar värpta tidigt i april runt 17 dygn för att sedan minska till ca 14 dygn för kullar som ruvas sent i juni.

Kläckningsspridningen studerades för 38 kullar och redovisas i Tabell 2. Normalt är tidsavståndet runt ett dygn mellan första och sista äggets kläckning. För endast tre kullar växte avståndet till ca 1,5 dygn.

För de kullar som "överlevde" till kläckningstid resulterade ca 90% av äggen i vitala ungar (Tabell 3). En tredjedel av den 10-procentiga förlusten bestod av ungar som dog i samband med kläckningen, resten var rötägg. Inte mindre än 57 av 443 kullar (13%) övergavs utan synbar anledning.

### *Analys och diskussion*

#### Ruvningstidens längd

Ruvningstiden varierade mellan 13,5 och 19,5 dygn med de högsta värdena i början och de lägsta i slutet av häckningssäsongen, ett förhållande som temperaturen kunde misstänkas vara orsaken till. Därför undersöktes sambandet temperatur/ruvning för inledningsskedet och för slutskedet av ruvningen var för sig (Tabell 4). För inledningsskedet kunde ett klart samband visas (Fig. 3): ju högre temperatur under äggläggningen och de fem första ruvningsdagarna, desto kortare ruvningstid. För temperaturen under ruvningens slutperiod var sambandet oklarare (Tabell 4). Förmodligen är det temperaturen under häckningens inledning som påverkar ruvningstidens längd mest. Det inses lätt att äggläggningstiden är ansträngande och tär hårt på honan och gör det än mer om det är kallt, eftersom det då är svårare att finna tillräckligt med föda. När värptiden är över och om kylan fortsätter orkar inte honan omedelbart komma igång med effektiv ruvning, eftersom denna också är en energikrävande process. Mycken tid går åt till födosök. Varje fördröjning i ruvningens inledningsskede innebär en förlängning av ruvningsperioden, bestämd med den metod som beskrivits ovan.

#### Kläckningsspridningen

Effektiv ruvning kommer som regel igång först efter det att äggläggningen avslutats. Dock kan äggen värmas tillräckligt mycket under värpperioden för att de först lagda äggen skall få ett klart försprång i

utvecklingen. Ett sådant försprång avslöjades lätt med hjälp av genomlysning av kullen under de första dagarna av ruvningen (Fig. 1). För trädkryparen håller sig denna utvecklings-spridning mellan äggen runt ett dygn i genomsnitt, vilket innebär att äggens kläckning sedan fördelas under loppet av samma tidsperiod (asynkron kläckning). Denna kläcknings-spridning är temperaturberoende (Fig. 4). Ju högre temperatur, desto mer ruvning under ägg-läggningen med efterföljande större kläcknings-spridning. Under kärva förhållanden blir ruvningen minimal under ägg-läggningstiden och alla äggen kommer att kläckas ungefär samtidigt (synkron kläckning).

#### Kläckningsframgången

Andelen kläckta ägg, 90%, ligger i nivå med vad som allmänt gäller för tättingar. Större delen av förlusterna utgjordes av "rötägg", vilka ofta visade sig innehålla embryoner på olika utvecklingsstadier. Ibland såg ägginnehållet helt färskt ut, alltså utan synliga utvecklingsstadier. Sådana ägg kunde därför misstänkas vara obefruktade. I samband med genomlysningen av äggkullarna, sammanlagt 109 ägg, kunde däremot konstateras att alla ägg startade utvecklingen, även om denna i vissa fall inte kom längre än till att gulan svälldes upp. Andelen obefruktade ägg är uppenbarligen försvinnande liten bland de studerade trädkryparna.

#### Övergivningen av bon

Den relativt stora andelen övergivna bon med äggkullar och ibland även små ungar är förbryllande. Det ligger nära till hands att misstänka, att detta skulle vara en följd av att de ruvande honorna i samband med inspektionerna tvingas lämna boet för att ägg eller ungar skall kunna räknas. Detta motsägs av att inte ett enda bo övergavs under 1994, trots att dessa störningar då var talrikare än tidigare beroende på de täta besöken i samband med genomlysningen av äggkullarna. Vädret spelar säkerligen viss roll, i synnerhet häftiga regnperioder, vilka ofta kombineras med temperatursänkning. De övergivna bona är inte sällan genomblöta. Regnvattnet rinner längs

trädstammen lätt in i häckningsfickorna. Det finns också ett positivt samband mellan andelen övergivna kullar och den totala regnmängden för den månad då kullen övergavs (Fig. 5).

#### Trädkryparen som ruvare

Trädkryparen tillhör de genuina stannfåglarna. Den finns kvar i fältarbetsområdet hela vintern. Trädkryparen kan därför förmodas vara en härdig fågel, vilket kunde vara orsaken till att den kan börja häcka tidigt på våren, i själva verket i genomsnitt två veckor före de holkhäckande mesarna i samma område. Men den är trots allt inte okänslig för väderlekssituationen som ju kan vara kärv, i synnerhet i början av häckningsperioden i första halvan av april. Detta framgår bl.a. av den tidigare nämnda svårigheten att då börja effektiv ruvning omedelbart efter det att sista ägget värpts. Inte sällan får den färdigvärpta kullen ligga iskall under dagtid en eller flera dagar, vilket ibland felaktigt orsakat anteckningen "Övergivet?" i protokollet. Detta innebär en förlängning av den riskabla botiden, i synnerhet för de tidiga häckningarna, alltså en klar nackdel. Varför då inte senarelägga häckningen? Svaret bör vara att det trots allt genomsnittligt lönar sig att satsa på tidig häckning. Fördelen torde ligga i att därmed tillvaratas möjligheten att hinna med en andra-kull under säsongen. Lyckas båda kullarna, blir förökningsframgången utomordentlig. Skulle första kullen misslyckas, finns gott om tid till nya häckningsförsök. Det ligger alltså en försäkring i att börja häcka tidigt, även om det kan kosta på. Det kan noteras att andra-kullar förekommer årligen bland de studerade trädkryparna, visserligen i växlande omfattning men alltid långt oftare än hos mesarna i samma område.

Även om vädret kan ställa till besvär i ruvningen, har trädkryparen ofta nog tillräcklig kapacitet att börja ruva så smått redan under ägg-läggningen även i början av säsongen och alltså skapa olikåldriga ungvullar. Vilken eller vilka fördelar som är förknippade med sådana kullar jämfört med de likåldriga, därom tvistar ännu de lärde.