

The egg size variation of the Treecreeper *Certhia familiaris* in south-western Sweden

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Abstract

Egg measurements were in 1994–1996 collected on a Treecreeper population nesting in artificial nest sites erected in deciduous forests in south-western Sweden. The mean egg volume was 1.21 ± 0.091 (SD) cm^3 ($n=533$) and the mean weight was 1.26 ± 0.100 g ($n=133$). The mean volume decreased as the clutch size increased from 1.26 ± 0.091 cm^3 (4-egg clutch) to 1.16 ± 0.079 cm^3 (7-egg clutch). Within clutches, the volume showed on average an 8% increase from first to last laid egg, and the size and laying order coincided for about 50% of the eggs on each separate day in the laying sequence. The egg sizes of neighbouring clutches with laying start on the same day tended to vary in parallel from first to last egg, indicating

a constraining influence of environmental origin on egg formation. The size of an egg was positively correlated with the ambient temperature of the first two or three days before laying. This relation was less clear during periods of falling temperature, probably because the temperature influence was counteracted by the tendency of the female to successively increase egg investments in the laying sequence. The consequences and adaptive value of this trait are discussed.

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Introduction

The problems related to egg-size variation have been observed since long (Lack 1968) and its functional significance is still only partly understood, especially in passerine birds. Both proximate (Slagsvold et al. 1984) and ultimate (Järvinen & Ylimaunu 1986) factors have been used to explain the size variations. Many findings, such as the positive relationship between egg size and offspring fitness within clutches, are still controversial (Williams 1994). This applies also to the observation that the egg size sometimes increases towards the end of laying, as well as to the interpretation that the larger last-layed eggs reduce the competition between the siblings when hatching is asynchronous (references, see below). Of course there are many factors causing egg size variation (cf. e.g. Nilsson & Svensson 1993a), one of which is the often mentioned constraints of environmental origin (e.g. temperature, food availability) (e.g. Slagsvold & Lifjeld 1989, Järvinen 1991). However, feeding experiments have so far given varying information regarding the importance of food availability for the size of the eggs (Arcese

& Smith 1988, Carlson 1989, Arnold 1992, Magrath 1992a, Nilsson & Svensson 1993a, Föger & Pegoraro 1996). No doubt, more research is needed before we can establish to what extent known proximate and ultimate factors govern the egg formation process. The egg size variation still remains a rich area for investigation (Perrins 1996).

The aim of this study was to establish the size and size variation of the eggs in a Treecreeper *Certhia familiaris* population, with special regard to (1) the possible occurrence of general trends in the intra-clutch variation patterns and (2) the relation between the ambient temperature and egg sizes.

Study area and methods

The field work was carried out in the deciduous woods of the Gunnebo recreation grounds near Göteborg, in the south-western part of Sweden ($57^{\circ}39'N$; $12^{\circ}4'E$). The qualities of the study area have been described by Enemar (1992). The investigated population breeds in artificial nest pockets. The occupied pockets were in 1994–1996 inspected

daily during the laying period to mark the eggs according to their laying order. The clutches were transilluminated and photographed the day after the appearance of the last egg (Enemar & Arheimer 1989, cf. also Mänd et al. 1986). The measurements were taken on slightly enlarged prints of the eggs to the nearest 0.05 mm using a sliding caliper. The volumes were calculated according to Hoyt (1979) and scaled down to their actual values. The correction factor was derived from 23 eggs which were measured before photographing.

The eggs laid in 1996 were also weighed with a 5-g Pesola balance, sheltered from the wind in a transparent acrylic cylinder. The egg weights were estimated with a precision of about 0.01 g within the marked 0.05-g intervals. The readings were made with the aid of a magnifying glass and adjusted in relation to the sometimes wide variations in the ambient temperature. Special tests revealed that the balance showed an average weight decrease of 0.03 g at about +3°C compared to at about +18°C. The weight of the egg-holder (tare), always read before the introduction of the egg, indicated the magnitude of the necessary adjustment.

The daily mean temperatures of the breeding season were obtained from the meteorological station at Säve airport, about 15 km to the north of the study area (SMHI 1994–1996). These values were in 1996 compared with the temperature means in the study area, calculated from day-time measurements made from 07h a.m. to 07h p.m. The two temperature means were closely correlated ($r=0.98$, $n=62$, $p<<0.001$).

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

Results

The shape of the Treecreeper eggs may show some observable deviations from the normal oval appearance (cf. Harrison 1975). Most conspicuous are those approaching an elliptical shape with nearby equally-rounded ends. No less than 31 such eggs were identified, distributed in 24 of 95 examined clutches. The laying order was known for 21 of these eggs and 11 of them were the first-layed ones in the clutch (Figure 1). The volume of these eggs will be somewhat underestimated when Hoyt's formula is used and will, therefore, bias the pattern of the intra-clutch egg size variation. On the contrary, the calculated volumes of the eggs with the narrow ends more pointed than normal (pyriform eggs, Figure 1) will

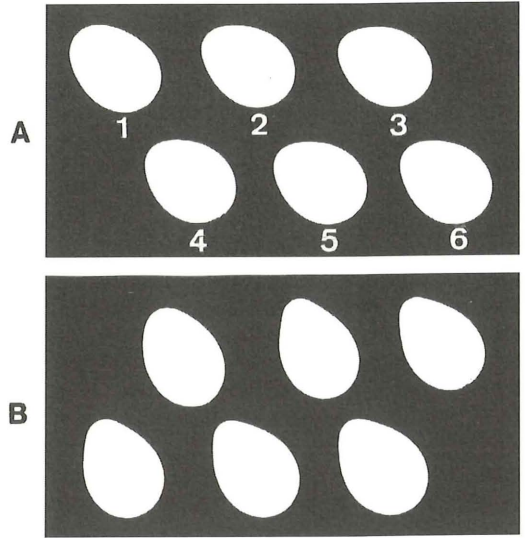


Figure 1. Photographs of two transilluminated clutches, showing the profiles of the eggs. Numbers indicate laying order. A. Clutch with first-layed egg with the pointed end broad and rounded compared to the other ones of normal appearance. B. Clutch with most eggs showing a narrow end more pointed (pyriform) than normal.

Foto av genomlysta kullar som visar äggens profil. Siffrorna anger värföljden. A. Kull med det först lagda ägget tydligt trubbigt jämfört med de övriga normala äggen. B. Kull med ägg spetsigare än normalt, med antydning till päronform.

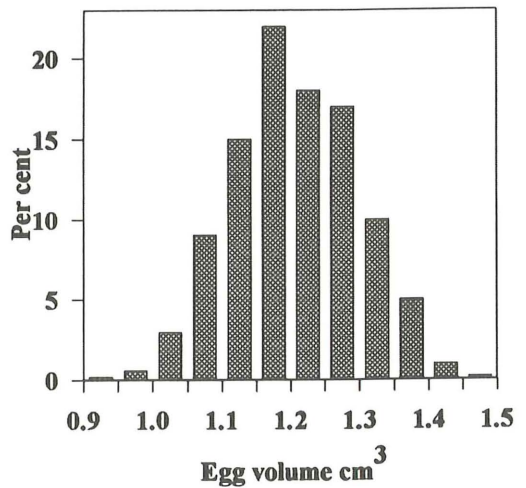


Figure 2. Percentage distribution of 533 Treecreeper eggs across size classes. Class breadth = 0.05 cm³.

Den procentuella fördelningen av 533 trädkryparägg på storleksklasser. Klassbredd = 0,05 cm³.

Table 1. Egg measurements (mm, mean of clutches) from the seasons of 1995 and 1996. n = number of clutches. Äggmåttén från säsongerna 1995 och 1996 (mm, medelvärden för kullarna). n = antal kullar. C.V. = variationskoefficienten.

Year År	n	Length <i>Längd</i>			Breadth <i>Bredd</i>		
		Mean \pm S.D. <i>Medelvärde</i>	C.V. %	Range <i>Utbredning</i>	Mean \pm S.D. <i>Medelvärde</i>	C.V. %	Range <i>Utbredning</i>
1995	45	16.0 \pm 0.56	3.5	15.0–17.0	12.2 \pm 0.32	2.6	11.5–12.7
1996	30	15.9 \pm 0.49	3.1	14.7–16.6	12.2 \pm 0.28	2.3	11.7–12.7

Table 2. Egg sizes (cm³, mean \pm S.D.) of the Treecreeper for different clutch sizes and years. Number of eggs within parentheses.

Trädskryparens äggstorlekar, medelvärden för olika kullstorlekar och år. Antal ägg inom parentes.

Clutch size <i>Kullstorlek</i>	1994	1995	1996	1994–1996
4	1.19 \pm 0.068 (4)	1.27 \pm 0.097 (20)	1.26 \pm 0.057 (4)	1.26 \pm 0.091 (28)
5	1.25 \pm 0.067 (45)	1.21 \pm 0.103 (70)	1.24 \pm 0.084 (30)	1.23 \pm 0.091 (145)
6	1.18 \pm 0.071 (72)	1.21 \pm 0.092 (137)	1.20 \pm 0.090 (124)	1.20 \pm 0.087 (333)
7	–	1.15 \pm 0.086 (13)	1.16 \pm 0.075 (14)	1.16 \pm 0.079 (27)

be overestimated. No measures were taken to compensate for the effect of these rather few extreme variants.

The measurements of the eggs are presented in Table 1. The sample from 1994 has been excluded because the clutches from the last half of that season were not investigated. According to the CV-values, the mean egg length of the clutches is more variable than the breadth. The two parameters are, however, significantly correlated ($r=0.24$, $n=75$, $p<0.05$).

A sample of 133 eggs were weighed in 1996. As expected, the weights are strongly correlated with the calculated volumes of the same eggs ($r=0.90$, $p<<0.001$). The mean egg weight \pm SD of the sample is 1.26 ± 0.100 g, and the mean density 1.05 ± 0.040 g/cm³. The density variation is considerable, partly due to errors following the calculation of the volumes of eggs with deviating shape, ranging from 0.87 g/cm³ (a pyriform egg) to 1.20 g/cm³ (egg with both ends broad and rounded).

The distribution across size classes of the calculated volumes of 533 eggs is presented in Figure 2, resulting in a mean egg volume of 1.21 ± 0.091 (SD) cm³. The egg volumes of the total sample, divided on clutch sizes and years, are given in Table 2. Obviously, the mean volume decreases as the clutch size increases ($r = -0.28$, $n=96$, $p<0.01$). This reduction amounts, on average, to about three per cent following each addition of one egg to the clutch size.

The mean egg volumes, expressed as percentages of the clutch means for the purpose of eliminating the female-related variation, increase with the laying order of the egg within the clutch (Table 3). Exceptions from this "rule" are regularly found when examining the clutches one by one (Table 4). The laying order and size order nevertheless coincide for around 50% of the eggs on each day in the laying sequence. The b-values of the linear regressions of egg size upon laying sequence are 2.2 and 1.6% for the 5- and 6-clutches of Table 3, with

Table 3. The mean egg volume (as a percentage of the clutch mean) in the laying sequence of the investigated 5- and 6-egg clutches.

Äggets medelstorlek i procent av medelvärdet för kullen i värpföljden för undersökta 5- och 6-kullar. n = antal ägg.

Clutch-size Kullstorlek		Laying order Värpordning					
		1	2	3	4	5	6
5	%	96	97	99	104	104	
	SD	4.4	2.1	3.1	2.7	3.0	
	n	16	16	14	13	21	
6	%	96	98	99	102	103	104
	SD	3.8	2.7	2.3	2.9	3.1	3.7
	n	28	27	32	37	43	48

Table 4. Percentage distribution of the eggs of the different laying orders according to their size position in the clutch, where the smallest egg is indicated by the figure 1.

Den procentuella fördelning av de olika äggen i värpföljden enligt deras storleksposition i kullen, där 1 betyder det minsta ägget osv.

Laying order Värpordning	Size order within the clutch Storleksordning inom kullen						Number of eggs Äggantal
	1	2	3	4	5	6	
5-clutches 5-kullar:							
1	57	31	6	0	6		16
2	22	57	14	7	0		16
3	22	8	62	0	8		14
4	0	8	0	54	38		13
5	0	0	19	33	48		21
6-clutches 6-kullar:							
1	50	20	13	7	7	3	28
2	14	48	10	14	4	10	27
3	12	12	43	18	15	0	32
4	9	6	9	51	14	11	37
5	5	7	10	10	46	22	43
6	4	4	2	20	15	55	48

$r=0.72$ ($p<0.001$, $n=80$) and 0.64 ($p<0.001$, $n=215$), respectively. Accordingly, the calculated volumes of the first laid eggs are, on average, the smallest ones in the clutch. This might be a consequence of the tendency of the first egg to appear with the narrow ends rounded, leading to underestimated volumes, as mentioned above. The weights of the 133 eggs from 1996 were used to test this, because weight as

a size parameter is estimated independently of the egg shape. In this sample the mean weight of the first egg is significantly smaller than the mean of each of the three last laid eggs in 5-clutches ($n=7$) as well as in the 6-clutches ($n=13$) (p varying from <0.02 to <0.001 , t -tests). The b -values of the regression equations are 2.3 and 1.1 %, respectively, with r -values of 0.79 ($p<0.001$, $n=35$) and 0.43 ($p<0.001$, $n=78$).

Analyses and discussions

The egg measurements

Rosenius (1926) presented the measurements of 117 Treecreeper eggs from Sweden with a mean length of 16.19 (range 15 – 18) mm and a mean breadth of 12.11 (11.5 – 13.2) mm. These often cited measurements agree fairly well with those of my sample (412 eggs, Table 1) even if the eggs he has studied tend to be a little longer. This difference, whether statistically significant or not, is not very enlightening since the two samples may not be comparable concerning i.a. environmental conditions and frequency of different clutch sizes. Egg measurements of the same subspecies from populations outside Sweden are given by Jourdain in Witherby (1943), Makatsch (1976) and Schönwetter (1984). They are based on samples too small to admit reliable comparisons between regionally separated populations.

Information on the weight of fresh Treecreeper eggs is scanty. Makatsch (1976) reports 1.27 g (sample size unknown) which is close to the mean weight of the eggs of this study. Weight and volume are strongly correlated also in other small passerines, as in *Ficedula hypoleuca* (Järvinen & Väisänen 1983, Potti 1993), *Parus major* (Järvinen & Pyl 1989), *Sturnus vulgaris* (Ricklefs 1984) and *Xanthocephalus xanthocephalus* (Arnold 1992), with *r*-values varying from 0.84 to 0.95, i.e. of the same magnitude as in the Treecreeper.

The density of the egg is not expected to vary much between the small passerines. The value of the Treecreeper egg (1.05 ± 0.040 (SD) g/cm³) is close to the slightly larger eggs of *Troglodytes aedon* (first egg 1.05 ± 0.068 , last egg 1.03 ± 0.025) (Kendeigh et al. 1956), *Hirundo rustica* (1.0518 ± 0.0025) and *Sayornis phoebe* (1.0505 ± 0.0026) (Manning 1979). According to the formula, derived by Paganelli et al. (1974), the weight of the Treecreeper egg should correspond to a density of 1.04 g/cm³. These comparisons indicate that my weighings in the field and the standardised calculations of the egg volumes have not introduced a systematic deviation from the true values.

The positive correlation between the egg length and breadth in the Treecreeper is shared with the eggs of other passerine species, including the fact that breadth varies less than length (Ojanen et al. 1978 with references, Bancroft 1984, Järvinen & Pyl 1989, Järvinen & Väisänen 1983, Potti 1993). The egg breadth is limited by the diameter of the oviduct whereas the length is more free to vary, e.g. to increase when the egg volume enlarges as a

response to environmental or other stimuli (Järvinen & Väisänen 1983).

The egg-size/clutch-size relation

According to Table 2, there is a small but significant tendency of the size of the Treecreeper eggs to decrease when the clutch size increases. This relation is clear as far as the most common clutch sizes of 5 and 6 are concerned whereas the number of 4- and 7-clutches is still too small to provide useful information. It is, however, difficult to find corresponding examples from other passerine species. Briskie & Sealy (1990) report a significant negative relationship in *Empidonax minimus*. Potti (1993) found a weaker one in *Ficedula hypoleuca*, and Cichon (1997) had heavier eggs in 6-egg than in 7-egg clutches in *Ficedula albicollis* in one of two investigated seasons. Jones (1973) established the same trend in a British *Parus major* population, as did Horak et al. (1995) in two of the populations they investigated. However, other authors have reported no consistent trend at all in this species (Winkel 1970, Järvinen & Pyl 1989, Järvinen 1991). On the other hand, a positive correlation has been found in *Parus major* (Ojanen et al. 1978) as well as in *Sturnus vulgaris* (Ojanen et al. 1978, Margis 1992) although Greig-Smith et al. (1988) reported a negative correlation in the latter species. Moreover, no consistent, or only minor, correlation between egg size and clutch size has been observed, as in e.g. *Parus caeruleus* (Winkel 1970, Nilsson & Svensson 1993a), *Turdus philomelos* (Pikula 1971), *Ficedula hypoleuca* (Ojanen et al. 1978, Järvinen 1991), *Parus cinctus* (Järvinen 1991), *Phoenicurus phoenicurus* (Ojanen et al. 1978, Järvinen 1991), *Delichon urbica* (Bryant 1975), *Spinus tristis* (Holcomb 1969), *Quiscalus quiscula* (Howe 1976), *Corvus corone cornix* (Rofstad & Sandvik 1985), *Tachycineta bicolor* (Zack 1982, Wiggins 1990) and *Tyrannus tyrannus* (Murphy 1983). Obviously the observations sometimes vary between authors investigating the same species.

The general impression is that an adjustment (trade-off) between clutch size and egg size is not an important mechanism in the reproductive biology of passerine birds, not even in the Treecreeper. In this species, each addition of one egg to the clutch size is followed by a decrease in mean egg volume of only about 3%. This corresponds to about 15% of an egg, when a clutch of 5 eggs is compared with a 6-egg one, or slightly more than half an egg when the 4- and 7-egg clutches are compared. The eco-physiological

significance of these savings are not immediately apparent. Perhaps it is negligible, which is indicated by the fact that the difference in mean egg size may sometimes fail to occur, which holds true for the clutches of 5 and 6 eggs of the Treecreeper in 1995 (Table 2). On the other hand, according to Ekman & Johansson-Allende (1990), a trade-off between egg size and number is possible especially when the laying female produces the eggs mainly from a daily energy surplus and not from endogenous reserves. However, we do not know much about to what extent the small passerines are building up such reserves before the laying period (cf. e.g. Drent & Daan 1980, Ojanen 1983b, Krentz & Ankney 1995, Houston et al. 1995).

The intra-clutch egg size variation

The Treecreeper belongs to the passerine species, showing an increase in egg size in the laying sequence (Tables 3 and 4). This is true for at least the two most common clutch sizes. The difference is fairly small, amounting to an increase of about 8% from the first to the last laid egg. Eggs of each laying order are distributed on most size orders although the laying and size orders coincide for about half the number of the eggs. There are no doubt many reasons for these deviations, i.a. the variation in ambient conditions (cf. below).

The pattern of the intra-clutch variation in egg size among passerine birds is far from uniform. Contradictory reports relating to the same species are also found. An average size increase from the first to the last egg, as shown in the Treecreeper, has been established in rather few passerines. An outstanding example is *Regulus regulus* with an almost continuous weight increase totalling about 20% in four clutches of ten to twelve eggs (Haftorn 1986), followed by *Troglodytes aedon* with a corresponding increase of 10 to 13% in clutches of 5 and 6 eggs (Kendeigh et al. 1956) and *Empidonax minimus* with 6.5% in 4-egg clutches (Briskie & Sealy 1990). Among other investigated resident species, only *Parus montanus* shows a moderate increase (Ekman & Johansson-Allende 1990) whereas no clear trends are found in other tits such as *Parus major* (Winkel 1970, Ojanen et al. 1981) and *P. caeruleus* (Nilsson & Svensson 1993a). Moreover, a more or less continuous egg size increase in the laying sequence has been established in *Ficedula hypoleuca* (Ojanen et al. 1981, Ojanen 1983a, Slagsvold et al. 1984, Yli-maunu & Järvinen 1987, Slagsvold & Lifjeld 1989), *Ficedula albicollis* (Chicon 1997), *Quiscalus quis-*

cula (Howe 1976), *Turdus merula* (early clutches, Rydén 1978; Magrath 1992a,b), *Luscinia luscinia* (Pryl 1980), *Tachycineta bicolor* (Wiggins 1990), *Tyrannus tyrannus* (Murphy 1983) and *Sturnus vulgaris* (Margis 1992, in contradiction to Ricklefs (1984)). Earlier information on other species, including those with the size increase mainly confined to the last-laid egg, is found in the reviews by Ojanen et al. (1981) and Slagsvold et al. (1984).

The fact that the egg size often increases with laying order in many passerines calls for a search for its ultimate adaptive value. A common interpretation is that the larger last eggs prolong the survival of the last hatched young when hatching is asynchronous (e.g. Howe 1976, Rydén 1978, Slagsvold et al. 1984, Wiggins 1990). This justifies the hypothesis of a brood-survival strategy, especially when food is scarce (Schifferli 1973). As asynchronous hatching is common in the Treecreeper (Enemar 1995), this interpretation seems to fit.

Other researchers regard the trend as simply a direct effect of the environmentally-induced proximate constraints on the female during the egg-laying period, in combination with the increasing trend, on average, of the ambient temperature (and food availability) during the breeding period (Järvinen & Yli-maunu 1986, Slagsvold & Lifjeld 1989, Ekman & Johansson-Allende 1990, Magrath 1992b, Nilsson & Svensson 1993a) (but see the feeding experiments referred to in the Introduction). In compliance with this view, the successive increase in egg size should be less clear or disappear in the Treecreeper when harsh weather and low ambient temperatures prevail during breeding. As will be demonstrated below, this is in fact the case (Table 5). Moreover, the hatching pattern turns synchronous under such harsh conditions (Enemar 1995).

The conclusion is that it is necessary to consider both the ultimate and proximate causes when interpreting possible adaptive values of the intraclutch variation pattern in the Treecreeper. This requires a close analysis of the relation between egg size and environmental conditions, as presented in the following.

General environmental influence on egg size

The Treecreeper is a resident bird which normally spends the winter within its breeding area. It starts nesting early and therefore sometimes meets harsh weather with low environmental temperature and periods of heavy rain (or snow). Such conditions may force the bird to postpone the incubation start

Table 5. Correlations (*r*-values) between the egg volumes, actual and corrected (corrected = the intra-clutch sequence-dependent increase in egg size eliminated, see text!), and the mean temperature of different days before laying. Day_e = day before the appearance of an egg; b_e = volume change (slope of regression, cm³/egg) from first to last egg, mean of clutches; b_t = temperature change (°C/day) of different Day_es, mean of the laying period of clutches.

Sambandet (r-värden) mellan äggvolymerna (verkliga och korrigerade) och medeltemperaturen olika dagar före äggets värpning. Day_e = dag före ett äggs värpning; b_e = volymändringen (cm³/ägg) från första till sista ägg, medelvärde för kullarna; b_t = temperaturändringen (°C/dag) för olika Day_e, medelvärde för kullarnas värpperioder.

Clutch size <i>Kullstorlek</i>		6		5		
No. of clutches <i>Antal kullar</i>		9		5		
Number of eggs <i>Antal ägg</i>		53		25		
First egg <i>Första ägg</i>		22–28 April		27 May–4 June		
Egg volume <i>Äggvolym</i>		Actual <i>Verklig</i>	Corrected <i>Korrigerad</i>	Actual <i>Verklig</i>	Corrected <i>Korrigerad</i>	
b _e		0.008	-0.013	0.034	0.006	
Day _e	b _t	r	r	b _t	r	r
1	-0.29	0.30*	0.49***	0.47	0.53**	0.49*
2	-0.60	0.11	0.38**	0.60	0.56**	0.62***
3	-0.70	-0.04	0.23	0.11	0.49*	0.50*
5	-0.76	-0.33*	-0.05	0.41	0.11	0.04
7	0.30	-0.14	-0.26	0.72	0.68***	0.46*
9	1.20	-0.10	-0.51***	0.45	0.68***	0.63***

*, **, *** = $p < 0.05, 0.01, 0.001$, respectively.

after laying, to prolong the incubation period (Enemar 1995), and even to desert eggs or young nestlings (Davis 1979, Kuitunen & Aleknonis 1992, Enemar 1995). A case in point is the cold and rainy season prevailing in my study area in 1996, when all 19 first nests with eggs or small young were abandoned in the middle of May.

The sensitivity of the Treecreeper to the varying ambient temperature presumably affects the formation of its eggs, being reflected in the variation of the egg sizes. If so, the eggs of females who start laying simultaneously are expected to show a variation pattern in parallel from the first to the last egg. There are six such female pairs, with eggs of known laying order, where the pair members have nested in the same part of the study area. The changes in egg sizes in the laying sequence are shown in Figure 3. Out of the 29 possible comparisons, the direction of the change in egg size within pairs conforms in no less than 25 cases. This indicates that the environmental

conditions have a considerable influence on the egg formation in the Treecreeper.

The co-ordinating environmental factor that first comes to mind is the temperature. Decreasing temperature may constrain the egg formation partly directly, as proportionally more energy is spent on the body maintenance of the female and partly indirectly, as the prey may become less available. The last-mentioned effect might, however, be of minor importance in the Treecreeper because its hunting efficiency is probably less dependent on the mobility of the prey selected by this species (Kuitunen 1989).

Correlations between egg size and ambient temperature

The influence of the ambient temperature on the egg size has not been easily established in the Treecreeper. Even if the temperature increases during the long

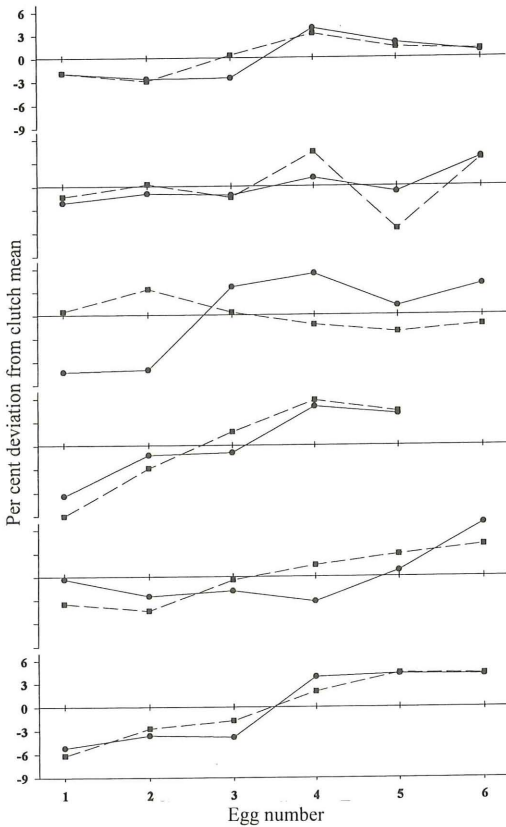


Figure 3. The size of the eggs, expressed as percentage deviation from the clutch mean, in the laying sequence of six pairs of neighbouring females. The paired females started laying simultaneously.

Äggens storlek, angiven som procentuell avvikelse från medelstorleken för kullen, i värpordning för sex par honor, som inom paren häckade nära varandra och lade första ägget samma dag.

laying season, only a weak though statistically insignificant seasonal enlargement of egg size appeared in the three investigated years. The result is the same when the calculations are based on the mean egg size of the clutches (which means that the intra-clutch variation is eliminated). Moreover, the mean egg size of clutches laid in April in 1995 and 1996 (1.20 ± 0.076 (SD) cm^3 , $n=29$) does not differ from that of clutches produced in May and early June ($1.22 \pm 0.077 \text{ cm}^3$, $n=29$) ($t=1.07$, $p<0.3$).

On the other hand, the correlation between the clutch means of the 5- and 6-clutches from April (with 1994 included) and the mean temperature of

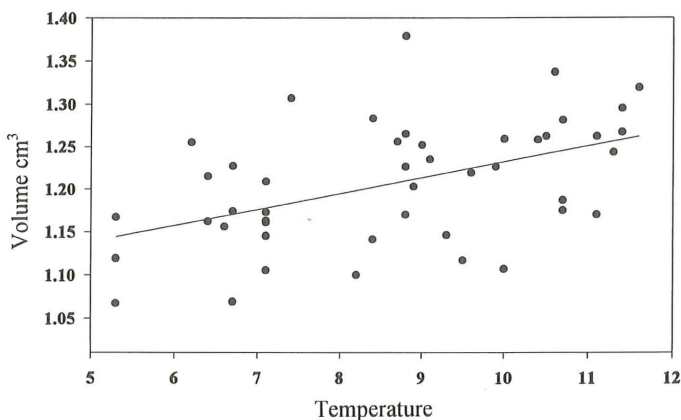
the corresponding laying periods (counted from the day before the appearance of the first egg to the day before the last one) is highly significant ($n=46$, $r=0.49$, $p<0.001$, Figure 4). The result is the same when the two clutch sizes are tested separately, although significant only for the 6-clutches (5-clutches: $b=0.018$, $r=0.41$, $n=16$, $p<0.2$; 6-clutches: $b=0.015$, $r=0.42$, $n=30$, $p<0.02$). There is, however, no corresponding relation between the means of the late clutches laid in the last half of May or early June and the ambient temperature ($n=33$, $r=0.22$, $p<0.3$). The reason could be that the temperature is more critical or constraining during the investigated laying periods in April ($8.7 \pm 1.86^\circ\text{C}$, range $5.3\text{--}11.6^\circ\text{C}$) than during those in May or June ($11.2 \pm 2.17^\circ\text{C}$, $7.9\text{--}15.1^\circ\text{C}$).

Many factors other than the ambient temperature may influence the variation in egg size, such as age, quality and size of the female, laying time, habitat quality, food abundance, clutch size and position in the laying sequence, to mention the most important ones. Ekman & Johansson-Allende (1990) demonstrated a positive correlation between egg weight (first clutches) and temperature in two early breeding species, *Parus cristatus* and *P. atricapillus*. They used variables normalized for variation between clutches in egg mass and laying date (ambient temperature) by expressing the weight as the deviation from the clutch mean, and the temperature as the deviation of the mean of the four days of egg formation from the mean of all egg formation periods. They received r -values of 0.53 and 0.37 ($p<0.05$), respectively.

The same analysis using the Treecreeper eggs laid in April 1996 (first clutches) unveils a highly significant *negative* correlation ($n=78$, $r=-0.47$, $p<0.001$), i.e. a decreasing temperature is followed by the formation of larger eggs. This result seems absurd, indeed, and arouses the suspicion that the tendency of the eggs to increase in size in the laying sequence (Table 3) is upheld to some degree even in periods of falling temperature. To test this, the effect of the size increasing trend of the eggs within clutches was arbitrarily eliminated by using the information in Table 3, i.e. the volume of egg Nos. 1 to 5 is divided in turn by the factors 0.96, 0.97, 0.99, 1.04, and 1.04 in the 5-egg clutches, and by the factors 0.96, 0.98, 0.99, 1.02, 1.03, and 1.04 in the 6-egg clutches. The corrected egg sizes appeared positively, although still insignificantly, correlated with the temperature ($n=66$, $r=0.02$, $p<0.2$). (The eggs from 7-egg clutches were excluded due to lack of adequate correction factors.)

Figure 4. The relation between the mean egg volumes of 46 5- and 6-egg clutches with first egg laid in April (1994–1996) and mean temperature of the egg formation period, counted from the day before the first egg to the day before the last egg. The equation of the regression line is $y=1.05+0.019x$, $r=0.485$, $n=46$, $p<0.001$.

Sambandet mellan äggets medelvolum i 46 5- och 6-kullar, med första ägg lagt i april (1994–1996), och medeltemperaturen för äggens tillväxtperiod, räknad från dagen före första ägg till dagen före sista ägg.



The final correlation tests were made in order to identify the period before laying which is most important for egg formation. The results are presented in Table 5. To reduce the influence by other factors than the ambient temperature on egg size, the two clutch sizes were analysed separately, sampled from two restricted and separated periods (6-egg clutches from April, 5-egg clutches from late May/early June), in the same year (1996) and in the same deciduous forest area. The absolute values were used, which means that the interclutch female-dependent variations were included since they may partly reflect also the temperature fluctuations. Moreover, the direction of change in egg size in the laying sequence has been calculated for each clutch and the mean values of b_c (the inclinations of the regression equations) is presented in Table 5. The corresponding mean values (b_i) are given for the temperature change during each clutch production period as measured and calculated for each sequence of first days, second days and so on before the laying. Table 5 shows that the 6-egg clutches were laid during periods of falling temperature. The variation in the egg volumes of the actual (uncorrected) clutches with an insignificant increasing egg size trend is correlated with the temperature of only the first day before laying ($p<0.05$), whereas the corrected volumes covary highly significantly with the temperature of the first two days before laying ($p<0.01-0.001$). This indicates that the impact of the ambient temperature on egg formation will be counteracted during periods of falling temperature due to the female's tendency to increase her investments successively. The 5-clutches were laid during periods of increasing temperature when both the actual and

corrected egg sizes increase in the laying sequence. As expected, both volume parameters are positively correlated with the ambient temperature. This covariation is significant during the first three days before the appearance of the egg, i.e. within the period of about four days when the preovulatory egg cell grows rapidly, as established in other investigated passerines (Ojanen 1983a,b, Kremetz & Ankeny 1986, Perrins 1996). The significant covariation seven and nine days before laying, i.e. before the follicle growth period, might be mere coincidental. This assumption is supported by the 6-egg clutches, which do not show a corresponding positive covariation. After all, the information in Table 5 strongly indicates that the formation of the Treecreeper egg is somehow affected by the daily mean ambient temperature and that this influence is restricted to the last two to three days preceding laying. This relation between the variation of temperature and egg size has been documented also in some other mainly resident passerine species. In *Parus major* a slight correlation exists mainly during day 5 and day 6 before laying (Ojanen et al. 1981, Järvinen & Pyl 1989) and there seems to be a difference between eggs in the laying sequence concerning the prelaying day of best correlation. Noordwijk (1984) demonstrated an effect during the last three days of the prelaying period restricted to temperatures below $+10^{\circ}\text{C}$ (but see Nager (1990)). The ambient temperature affects the egg size in a similar way in *Parus cristatus* and *P. montanus* (Ekman & Johansson-Allende 1990), *Regulus regulus* (Haftorn 1986) as well as in *Turdus merula*, where the correlation increases with the successive eggs in the laying sequence (Magrath 1992a). A slight correlation has

been observed also in the tropical migrant *Ficedula hypoleuca* (Järvinen & Ylimaunu 1986, Järvinen 1991) whereas no relation was found in *Hirundo rustica* (Möller 1994, Banbura & Zielinski 1995). Quite exceptional is *Empidonax minimus* with eggs that correlate negatively with the mean temperature from four to six days prior to laying (Briskie & Sealy 1990).

Although the information on the correlation between egg size and ambient temperature in passerines is still rather scanty and partly contradictory, perhaps some trends could be discerned. The temperature impact seems to be best manifested at low temperatures, as indicated by Noordwijk (1984) and by the fact that the information emanates mainly from early breeding resident species. The covariation is most often obvious during the last two to three days of the egg formation period, which seems reasonable because the growth rate is always at its peak during the last day before laying. The Treecreeper eggs are in accord with this description.

As shown in this study, the increasing trend of the intra-clutch egg size may interfere with, if not completely hide, the relation between egg size and ambient temperature. In fact, the correlation tests could be quite misleading without taking this tendency into consideration. The increasing trend might in some cases explain the fact that the proportion of egg size variation ascribed to temperature change is very small (Ojanen et al. 1981). Anyhow, the “interplay” between the variation patterns of egg size and ambient temperature offers some cues to be used when looking for the ultimate value of the intraclutch variation of egg size in the Treecreeper.

Is the intra-clutch egg size increasing trend adaptive?

The ultimate value of the increasing egg size within a clutch has been analysed mainly in relation to different breeding “strategies”, most often with focus on the size of the last laid egg. Opinions differ, to say the least. The variations around the clutch mean are small and they might be explained solely by the proximate constraints on the female (references above). Stoleson & Beissinger (1995) conclude, based on their recent review of the hatching asynchrony problem and referring to Pierotti & Bellrose (1986), that “there is little evidence to support or refute the idea of an adaptive role for increasing egg size within a clutch”.

It has been documented that the larger eggs in a clutch are more advantageous, giving rise to heavier and more fit chicks (e.g. Schifferli 1973, Howe

1976, Bryant 1978, Briskie & Sealy 1990, Perrins 1996). There are, however, conflicting information on the corresponding quality differences between eggs of different sizes. Even if the energy content is strongly correlated to egg weight in some species (Ojanen 1983a,b, Muma & Ankney 1987), no or only poor correlation has been found between the sizes of yolk and egg (Bryant 1978, Ricklefs 1984). The weight “surplus” of the larger eggs is mainly due to inclusion of more water (Bryant 1978, Ojanen 1983a) or more albumen and water (Ricklefs 1984). Moreover, the intra-clutch size variation is limited, as shown above, and Williams (1994), in his critical review, emphasized the paucity of data which unequivocally support the view that egg size and offspring fitness are positively related, particularly in altricial species. With all this in view, it seems well-advised to look for possible ultimate values, not only in the size-related variation in the different qualities of the egg as such, but also in the habit and capacity of the Treecreeper female to successively increase her egg investments in the laying sequence.

The Treecreeper is an early breeder, which supports the widely held view that it is adaptive for an insectivorous passerine to start egg production early (Perrins 1970). Moreover, starting as early as possible means for the Treecreeper i.a. securing time to rear a genuine second brood; however, it is also a riskful undertaking. Harsh weather with low temperatures often appears in early spring constraining the egg formation process, as shown above. The point is that, once the female has started to lay, in order to be maximally successful she has to continue 1) to produce eggs of the size and quality required to give rise to viable hatchlings and 2) to do this without gaps in the laying sequence (cf. also von Haartman (1990)). Table 5 shows that, despite the fact that the 6-egg clutches in April 1996 were produced during a period of declining temperature (mean daily decrease 1.3°C), the volumes of the eggs were, on average, kept at a constant level. Moreover, there were no gaps in the laying sequences. Gaps should be avoided because they prolong the nesting period leading to increased risk of egg predation (Clark & Wilson 1981). (Laying gaps are on the whole comparatively rare in my Treecreeper population. Out of 57 clutches, where the laying day was known for all eggs, only two had a one-day gap between the first two eggs, a low value (4%) compared with 16 to 37% as established in other hole-nesting species (Schmidt & Hamann 1983, Nilsson & Svensson 1993b).)

In other words, the Treecreeper female is assumed

to have escaped the detrimental effect of the low and falling temperature (too small eggs, frequent laying gaps) thanks to the fact that she is programmed to increase her egg investments successively during the laying period, i.e. the very trait which under normal and favourable conditions results in increasing egg size. This interpretation is in accordance with the “environmental variance” hypothesis, proposed by Magrath (1992a), namely that “species-specific patterns of egg-mass variation within clutches could have evolved to minimize the effect of energetic constraints on egg viability”. Magrath also argues that “the tendency to lay relatively large eggs later in the clutch might be selected for in order to counter the effects of an increasing risk of unfavourable conditions”. This is obviously a prime adaptation for the Treecreeper which starts breeding very early in the spring (Enemar 1992), i.e. when the weather development is more unpredictable than later on.

It is important to note that the energetic surplus available under favourable conditions is by the female invested not only in successive egg enlargement but also in an earlier incubation start with subsequent asynchronous hatching, as shown in the Treecreeper (Enemar 1995). This habit affects the brood rearing conditions considerably and, if disadvantageous, should be selected against, thus undermining the capacity of successful egg formation under harsh conditions. There are, however, no indications of such opposing selection pressures. The increased risk of brood reduction due to competition between the different-sized siblings in the newly hatched brood is probably counteracted by the enlarged size of the last laid eggs (Clark & Wilson 1981). Other consequences of the asynchronous hatching have been considered adaptive according to a plethora of interpretations of varying quality (cf. reviews by Slagsvold & Lifjeld 1989, Magrath 1990, Stoleson & Beissinger 1995). The mere fact that asynchronous hatching is so common among passerines indicates that it is adaptive. In any case, according to the analyses by Stoleson & Beissinger (1995), based on modelling, an onset of incubation around the middle of laying a 5-egg clutch produced the greatest fledging success. Therefore, and to sum up, I propose the hypothesis that the capacity of the Treecreeper female to increase her egg investments in the laying sequence is a hereditary character which is selected for not only under constraining (Magrath 1992a) but also under favourable breeding conditions.

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Sammanfattning

Äggens storlek och storleksvariation hos trädkryparen *Certhia familiaris* i sydvästra Sverige

Det förhållandet att fågeläggen varierar i storlek mellan likstora arter och ofta även inom en och samma kull har ägnats en betydande uppmärksam-

het i den ornitologiska forskningen under senare decennier. Resultaten har varit delvis motstridiga, vilket gäller t.ex. variationsmönstret inom kullen eller storlekens beroende av omgivningens temperatur och tillgången på föda. Detta har i sin tur givit upphov till mångskiftande tolkningar rörande orsakerna till och anpassningsvärdet (“nyttan”) av storleksvariationen hos äggen.

Av denna anledning har variationen i äggens storlek beaktats i den forskning över trädkryparens biologi, som bedrivs i Gunnebo fritidsområde med angränsade terräng, ca 10 km sydöst om Göteborg. Arbetet med trädkryparna påbörjades 1982 och härmed presenteras den tredje rapporten. Studieområdets natur och fältarbetets rutiner liksom de konstgjorda, för trädkryparen särskilt anpassade boplatserna har presenterats tidigare (Enemar 1992). Först utreddes värptider och kullstorlekar (Enemar 1992) varpå studierna under ett par säsonger ägnades åt ruvningen (Enemar 1995). Säsongen 1994 lades mätning av äggen in i fältarbetsprogrammet.

Metoder

De färdiga bona besöktes dagligen för märkning av äggen enligt värpordningen med en liten siffra på äggets tjockända. De fullvärpta kullarna fotograferades under genomlysning. Äggens längd och bredd mättes med skjutmått på de framkallade fotografierna (Figur 1) och volymerna räknades ut med hjälp av en formel. Våren 1996 vägdes de nyvärpta äggen i samband med märkningen. Då användes en fjädervåg, monterad i en plastcylinder som skydd mot störande vind. Vid jämförelse visade det sig att äggens variation i volym och vikt följde varandra mycket väl, vilket är att vänta om mätningarna i fält genomförs med tillräcklig precision.

Resultat

Trädkryparäggen uppvisar viss variation i formen. Det förekommer att något av äggen är trubbigt i båda ändarna, vilket är något vanligare för det först värpta ägget än för de övriga (Figur 1A). Enstaka kullar uppvisar ägg som är spetsigare än normalt, ibland med antydning till päronform (Figur 1B).

Äggens längd och bredd redovisas för två säsonger i Tabell 1. Den uträknade medelvolymen för alla 533 ägg är 1,21 cm³. Hur äggen är fördelade på olika storleksklasser visas i Figur 2. Medelvikten för 133 ägg är 1,26 g. När kullstorleken ökar minskar äggen i storlek från ett medelvärde av 1,26 cm³ i kullar med 4 ägg till 1,16 cm³ i kullar med 7 ägg (Tabell 2).

Inom kullen ökar storleken med i medeltal 8% från första till sista ägg (Tabell 3). Ökningen är alltså ganska obetydlig och endast för ungefär halva antalet ägg stämmer nummerordningen i värpföljden med platsen i den ordningsföljd som baseras på storleken (Tabell 4).

Analys och diskussion

De ovannämnda resultaten rörande variationen i äggstorleken mellan kullar med olika äggantal och inom kullarna var inte lätta att fastställa. Det beror självfallet på att äggstorleken påverkas av en lång rad faktorer, såsom honans egenskaper (storlek m m), revirets kvalitet, vädrets växlingar, tidpunkt på säsongen, osv. Om omgivningen med dess variationer i temperatur, nederbörd och födotillgänglighet har betydelse för honans förmåga att producera sina ägg, borde de honor, som häckar nära varandra och börjar värpa samma dag, uppvisa viss samstämmighet i äggens storleksändring från dag till dag. Detta kunde undersökas för sex par honor och resultatet visas i Figur 3. Som synes överensstämmer ändringen (ökning eller minskning) i 25 av de möjliga 29 jämförelserna. Detta talar starkt för att produktionen av äggen påverkas av växlingarna i olika tillstånd i omgivningen.

Det omgivningstillstånd som först faller i tanken är temperaturen. Då det är kallt går mer energi (föda) åt för att hålla honan vid liv, och då blir det mindre "över" till äggen, som alltså borde minska i storlek. Vidare kan låg temperatur tänkas försvåra födosöket vilket skulle ha samma effekt. Om detta stämmer skulle alltså ett samband råda mellan ändringarna i dygnsmedeltemperaturen och äggens storlek. Detta visade sig också vara fallet för de 46 kullar som började värpas i april under förutsättning att äggets medelstorlek i kullen jämförs med medeltemperaturen för kullens värpperiod (Figur 4). Medelägget ökar från ca 1,15 cm³ vid +5°C till ca 1,25 cm³ vid +12°C. För de 33 kullar som värptes i slutet av maj

och början av juni gäller ej detta samband. Förmodligen beror denna skillnad på att den lägre temperaturen i april oftare ligger i ett område, som verkar hämmande på äggproduktionen, än vad fallet är senare under säsongen.

Det faktum att äggets medelstorlek i kullarna samvarierar med omgivningstemperaturen borde betyda att också det enskilda äggets storlek uppvisar samma temperaturberoende. Detta var dock knepigare att avslöja, bl a beroende på den störning som orsakas av honans ovan nämnda böjelse att öka äggstorleken under värpperioden, vilket alltså motverkar att äggen minskar då temperaturen faller. Om denna effekt "räknas bort", får man ett positivt samband mellan äggstorlek och temperatur, vilket visas i Tabell 5. Den analys som ligger bakom tabellens tillkomst ger också till resultat att det är temperaturen de två till tre dagarna före äggets värpning, som har störst inverkan. Detta är väntat eftersom det är just under den perioden, som ägget tillväxer snabbast.

Avslutningsvis diskuteras problemet vilket anpassningsvärde eller "nytta", som ligger i att äggen blir större under värpningens gång. Det görs sannolikt att denna tendens är av värde för häckningens framgång både under kyliga och normalt varma förhållanden. Detta borde gälla inte minst för trädkryparen, som tillhör våra mycket tidiga häckare på våren (äggläggningen börjar två till tre veckor före talgoxen och blåmesen i samma område). Det innebär en risk för att vädret kärvar till sig under äggläggningen, som då kan hållas igång med livsdugligt stora ägg tack vare att honan är programmerad att fortlöpande öka insatsen i ägg. Under normala förhållanden, då denna "reserv" inte behövs för att hålla äggstorleken över den funktionsdugliga miniminivån, blir alltså äggen successivt större, vilket också anses vara en fördel för häckningsframgången – men hur detta i detalj skall förstås, därom tvistar ännu de lärde.