First, second and replacement broods in the breeding biology of a Treecreeper *Certhia familiaris* population

Förstakullar, andrakullar och omläggningskullar i häckningsbiologin hos en population trädkrypare Certhia familiaris

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Abstract

The breeding behaviour of a Treecreeper population that bred in nest pockets and in which all females were colour-ringed was followed over ten seasons. On average, 50% of the first breeding attempts in spring failed. Between half and two thirds of the successful females were double-brooded. The remaining females were single-brooded. These two breeding categories were identical in terms of initial clutch size and egg volume. The double-brooded females invested less in their second than their first clutch. Most of the females that failed laid replacement clutches of similar size as in the first attempt but with larger eggs. A replacement brood where young successfully fledged was never followed by a second breeding attempt. The average distance between the first and the repeat nest was the same for double-brooded and replacement-breeding females. The egg volumes of the first and the repeat clutches were strongly correlated. The double-brooded pairs were the most common breeding category and reared 50% of the population's total output of fledged broods, while the single-brooded and replacement breeding pairs each fledged ca. 25%. The adaptive values of the three breeding categories are compared.

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Introduction

Many passerine bird species rear more than one brood per breeding season. In cases where they lay two or more clutches after having successfully fledged a first brood, they are said to be double or multi-brooded, respectively. If there is only one clutch, they remain single-brooded. Clutches laid to compensate for failed breeding attempts are often called replacement clutches or broods. The occurrence of multi-broodedness among birds has been analysed in relation to e.g. the quality of the parent birds, reproductive timing, seasonal pattern of clutch size variation, food abundance, migratory behaviour and regional location (e.g. Klomp 1970, Drent & Daan 1980, Crick et al. 1993, Svensson 1995, Verboven & Verhulst 1996, Farnsworth & Simons 2001, Dhondt et al. 2002, Weggler 2006, Siefferman & Hill 2008). The subject of this study, the Treecreeper *Certhia familiaris*, is a resident and insectivorous small passerine that starts breeding in early spring. These characteristics suggest that the Treecreeper should be more or less frequently double-brooded and exhibit an intra-seasonal clutch size variation with a mid-season peak, and earlier studies have confirmed this (Kuitunen 1987, Enemar 1992, Crick et al. 1993).

The aim of the present study is to describe the breeding course of a Treecreeper population with regard to the frequency and significance of the different categories of reared broods. This requires a comparison between the first, second and replacement broods, primarily with regard to the frequency, number and size of eggs, timing of laying and length of distance from the nest site of the first brood to that of the second or replacement broods. Unfortunately, reliable data on fledging success are not available for the later part of the breeding seasons. Nor has the abundance of food in the habitats been investigated. As replacement clutches have been identified in the present study females that lay these clutches are designated "replacement-breeding" and comprise the failed presumptive single and double-brooded females. The replacement-

breeding pairs constitute an important part of the studied breeding population.

Methods

The data of the present study were collected between 1995 and 2005, i.e. ten seasons excluding the 2004 season, in a study area of about 2.5 km^2, mainly located in the Gunnebo recreation grounds near Göteborg (57° 39′ N; 12° 4′ E). The area is mainly covered by deciduous broad-leaved forests and contains 200 nest-boxes for Treecreepers, so-called nest pockets. They were made of pieces of roofing felt and attached to the tree trunks with a mean distance of 75 m between them (Enemar 1992). A piece of aluminium sheet was attached to the occupied nest pockets to prevent the Great Spotted Woodpeckers *Dendrocopos major* from penetrating the pocket wall to rob the nest. The density of pockets was sufficiently high to permit the Treecreeper pairs to easily find another pocket for the repeat nests. The pockets were inspected at various intervals depending on the demands of the season's research program, but always frequently enough to establish the number and character of the clutches.

Most breeding females were caught and colour-ringed when incubating complete clutches. They were forced to leave the nest-pocket and captured in a plastic bag at the opening, after which they were provided with unique combinations of one metal and three coloured rings for identification of individuals and confirmation of second or replacement broods.

The length of the breeding season of the double-brooded and replacement-breeding Treecreepers was counted from the start of laying the first clutch to the fledging of the repeat brood. The distance between the two nest-pockets used by the re-nesting females was measured on maps with a scale of 1:10,000.

The daily mean temperatures were obtained from Säve airport (SMHI 1995–2005), about 15 km to the north of the study area. These temperatures are closely correlated to those of the study area (r = 0.98; Enemar 1997). The mean ambient temperature during laying of a clutch was calculated using the mean daily temperatures during the period from one day before the first laid egg to the day before the last egg.

The egg lengths and breadths were measured to the nearest 0.05 mm on enlarged prints of photographed clutches using a sliding calliper (Enemar 1997, 1999). The volumes were calculated in ac-

cordance with Hoyt (1979). The measurements by Enemar (1997) were used when allowing for the effect of the varying clutch size on egg volumes. In order to control for the effect of ambient temperature variation, the previously established correlation between the temperature and the egg volumes of the first clutches in April was applied (r = 0.49, b = 0.19) (Enemar 1997). This relation is almost the same for the repeat clutches laid in May and early June (r = 0.34, b = 0.11, calculated for this study).

The statistical methods used were the Chi square test, G-test, Mann-Whitney U-test, correlation and regression, two-sample t-test, t-test for matched pairs and one-way ANOVA, mainly in accordance with Fowler & Cohen (no printing year). The variability is given as standard deviation.

Results

The total number of laid first clutches and the frequency of second and replacement clutches can be found in Table 1. The frequency of replacement clutches (71% of the females that failed in their first brood) significantly exceeds that of second clutches (51% of the females that had a successful first brood) (G_{adj}=5.12, p< 0.05). As no second clutches were laid in 1996 due to the fact that all first broods failed, that year should be excluded from the comparative test, which increases the frequency of the replacement clutches to 76% and the difference between the two repeat clutch categories by five percentage units (G_{adj}=7.07, p< 0.01). However, no less than 43 out of the 118 first clutches were laid by females that stayed in or returned to the study area for one to three seasons after surviving the winter. Including each female only once in the analysis (to avoid pseudoreplication) reduces the number of studied females to 75. Their breeding behaviour was only considered in the season during which they were ringed. They produced 42 successful and 33 failed first broods. Despite this reduction in sample size (not applied to the remaining analyses in the present study), the frequency of laid replacement clutches (79%) still significantly outnumbers that of the second clutches (57%) (G_{adj}=3.91, p< 0.05). The conclusion is that failed breeders produced replacement clutches at a higher rate than successful first breeders produced second clutches.

The annual figures for the three breeding categories are presented in Table 1. The number of second and replacement clutches represents the number of double-brooded and replacement-breeding Treecreepers, respectively. The number of single-

Table 1. Number and frequency of the different categories of clutches among 118 Treecreeper pairs that started laying their first clutches in the nest pockets within three weeks after the appearance of the season's first egg. The percentage values of the second and replacement clutches indicate the shares of successful and failed first clutches, respectively.
Antal och procentuella andelar av de olika slagen av kullar hos 118 trädkryparpar som började värpa förstakullen inom tre veckor efter säsongens första ägg. Procenttalen för andrakullarna och omläggningarna är beräknade på antalet lyckade resp. förlorade förstakullar.

| | First clutches *Förstakullar* | | | | Repeat clutches *Förnyade kullar* | | |
Year *År*	Number laid *Antal värpta*	Successful *Lyckade*	Failed *Förlorade*	Second clutches *Andra- kullar*	Replace- ment *Omlägg- ningar*	None * *Inga*	Unkn- own** *Okända*
1995	16	7 (44%)	9 (56%)	5 (71%)	8 (89%)	2 (29%)	1
1996	13	0 (0%)	13 (100%)	0 (0%)	7 (53%)	0 (0%)	6
1997	12	5 (42%)	7 (58%)	5 (100%)	6 (86%)	0 (0%)	1
1998	11	7 (64%)	4 (36%)	5 (71%)	4 (100%)	2 (29%)	0
1999	15	10 (67%)	5 (33%)	4 (40%)	4 (80%)	6 (60%)	1
2000	11	8 (73%)	3 (27%)	4 (50%)	2 (67%)	4 (50%)	1
2001	11	5 (45%)	6 (55%)	2 (40%)	4 (67%)	3 (60%)	2
2002	4	2 (50%)	2 (50%)	0 (0%)	2 (100%)	2 (100%)	0
2003	11	4 (36%)	7 (64%)	1 (25%)	4 (57%)	3 (75%)	3
2005	14	11 (79%)	3 (21%)	4 (36%)	1 (33%)	7 (64%)	2
Totals	118	59 (50%)	59 (50%)	30 (51%)	42 (71%)	29 (49%)	17

*) The figures also represent the number and frequency of single-brooded pairs.
   Siffrorna anger även antal och procentuell andel enkullhonor.
**) The figures represent the number of females that disappeared after the failed first brood.
   Siffrorna anger antal försvunna honor efter misslyckad förstakull.

brooded pairs is presented in the second last column of Table 1 ("None").

The time schedule of the double-brooded and replacement-brooded females is presented in Table 2. The laying of the replacement clutches started about two weeks before the second clutches, thus there is a significant difference between the median dates (Mann-Whitney, U=29, p < 0.05). It took about two days less to fledge the second broods compared to the replacement broods, also a significant difference ($F_{1,28}$ = 8.39, p < 0.01). The double-brooded females needed about one week longer to fledge two broods than the replacement-brooded females to fledge one, a small yet significant difference (Mann-Whitney, U = 26, p < 0.05). The median date (relative value counted from the first egg of the season) of the laying start of 25 single-brooded females tended to be one day later than that of 31 double-brooded females (t=1.69, 0.2>p>0.1). The tendency was the same although increased to two days as regards the fledging dates of 28 single-brooded females and 30 double-brooded females (t=1.91, 0.10>p>0.05). According to data from six breeding seasons (Table 2), the mean nesting periods of a total of 15 successful double-brooded females are 37.8 days and 34.5 days for the first and second brood, respectively, a significant difference of 3.3 ± 2.5 days (matched pairs t = 5.077, df=14, p<0.001). The mean temperature during the nesting periods of the two brood categories increased significantly from 10.4±1.3 °C to 14.0±1.1 °C ($F_{1,29}$ = 6.32, p<0.05). The durations of the first nesting periods are not correlated with temperature means, whereas those of the second broods indicate a negative relationship (r^2 = 0.22, df = 13, 0.1> p>0.05).

The females moved a mean distance of 146±90 m (n=32) and 166±110 m (n=40) to lay their second and replacement clutches, respectively. The difference between the means is not statistically significant (t = 0.849, df = 70, 0.4>p>0.3).

The variation in clutch size during the progress of the breeding season is presented in Table 3. The laying season starts and ends with small clutches belonging to the first and second broods, with peak size in the middle of the season mainly consisting of replacement clutches. The 36 females that fledged a first brood (mean clutch 5.51±0.56) laid second clutches with fewer eggs (5.22±0.72),

Table 2. Time schedule of the breeding process of 30 female Treecreepers that laid either second or replacement clutches. The failed first clutches were deserted mainly due to trapping and colour ringing, heavy rain, or robbing. The figures in brackets below the median dates indicate the earliest and latest first-eggs. The interval between broods is counted from the fledging or desertion day of the first clutch to the day on which the laying of the repeat clutch was started.

Häckningens tidsförlopp för 30 trädkryparhonor som värpte antingen en andrakull eller en ersättningskull. De misslyckade förstakullarna övergavs som följd av fångst och ringmärkning, ymnigt regnande eller borövning. Siffrorna inom parentes under varje mediandatum anger datum för det tidigaste och senaste första-ägget. Antal dagar mellan kullarna räknas från förstakullens utflygning till nästa kulls värpstart.

	First brood *Första kullen*				Repeat brood *Nästa kull*		
	Number of females	Median date of 1st egg	No. of days from 1st egg to fledging or nest desertion	Days between broods	Median date of 1st egg	Days from 1st egg to fledging	Length of breeding period
	Antal honor	*Median-datum 1:a ägg*	*Botid från 1:a ägg till utflygning/övergivning*	*Dagar mellan kullarna*	*Median-datum för 1:a ägg*	*Botid från 1:a ägg till utflygning*	*Häcknings-tidens längd*
Successful first and second brood *Lyckad första- och andrakull*	15	23 April (15/4–2/5)	37.8±1.8	2.5±2.1	2 June (19/5–13/6)	34.5±1.1	74.9±3.2
Failed first and successful replacement brood *Misslyckad förstakull och lyckad omläggning*	15	20 April (10/4–3/5)	20.8±7.2	9.5±3.9	19 May (7/5–5/6)	36.8±1.9	67.1±6.5

Table 3. The mean sizes (+S.D.) of the first, second, and replacement clutches from the seasons 1995–2005, distributed across ten- or eleven-day periods from the start of laying. n = number of clutches.

Medelstorleken på första- och andrakullarna samt omläggningarna från säsongerna 1995–2005, fördelade på de tio- eller elva-dagarsperioder då första ägget värptes. n = antal kullar.

Clutch	April		May			June		April–
Kull	11–20	21–30	1–10	11–20	21–31	1–10	11–20	June
First *Första*	5.52 ±0.59	5.68 ±0.53	5.88 ±0.64	6	6	–	–	5.66 ±0.56
n	24	40	8	1	1	–	–	74
Second *Andra*	–	–	–	5	5.55 ±0.82	5.09 ±0.68	5	5.22 ±0.72
n	–	–	–	1	11	22	2	36
Replacem. *Omläggn.*	–	–	6	6.25 ±0.45	5.52 ±0.77	4.83 ±0.75	5	5.63 ±0.82
n	–	–	1	11	19	6	1	38
All *Alla*	5.52 ±0.59	5.68 ±0.53	5.89 ±0.60	6.15 ±0.55	5.55 ±0.77	5.04 ±0.69	5	5.55 ±0.69
n	24	40	9	13	31	28	3	148

Table 4. The mean egg volumes of the first and repeat clutches of 24 and 30 treecreeper females that started second and replacement broods, respectively. /corr. indicates that the volume has been corrected for the difference in clutch size and environmental temperature.
Äggens medelvolym hos förstakullarna samt de därpå följande andrakullarna för 24 trädkryparhonor och. omläggningskullarna för 30 honor. /korr. anger att den del av volymändringen som beror på skillnaden i kullstorlek och omgivningstemperatur har dragits ifrån.

Number of broods	Clutch	Mean egg volume, cm^3	Change from first to repeat clutch	Matched pairs t-test of difference *Parvis test på skillnaden*	
Antal kullar	*Kull*	*Äggens medelvolym, cm^3*	*Skillnad mellan kullar*	t	p
24 success-ful lyckade	Second *Andra*	1.17±0.07			
			+0.018±0.047	0.502	>0.6
	First *Första*	1.15±0.07			
			+0.035±0.054	4.511	<0.001
	Second/*corr.* *Andra*/korr.	1.12±0.09			
30 failed *miss-lyckade*	Replacement *Omläggning*	1.19±0.08			
			+0.031±0.031	3.134	<0.01
	First *Första*	1.16±0.08			
			+0.010±0.024	2.209	<0.05
	Replacement/*corr.* *Omläggning*/korr.	1.17±0.11			

a small but statistically significant reduction (matched pairs t=2.16, df =35, p<0.05). The first (5.76±0.54) and repeat clutches (5.63±0.81) of 38 replacement-breeding females did not differ in size (matched pairs t=0.75, 0.5>p>0.4). The replacement clutches were larger than the second clutches (t=2.29, p<0.05). The mean size of the first clutches of 32 double-brooded females (5.6±0.62) did not differ significantly from that of 23 single-brooded females (5.8±0.47) (t = l.360, p>0.1). Both samples emanated from the same eight seasons and only clutches laid within the three weeks after the appearance of the season's first egg were included.

The clutch means of the egg volumes are known for 24 double-brooded females (Table 4). The volumes of the first and second clutches of each individual female are strongly correlated (Figure 1). The small increase in the mean volumes from 1.15 cm^3 to 1.17 cm^3 is not significant ($F_{1,46}$ = 1.29, p>0.2), nor did the individual females lay significantly larger second clutch eggs (matched pairs t-test, Table 4). On the contrary, they laid on average significantly smaller second clutch eggs after controlling for differences in clutch size and mean ambient temperature during the laying period (Table 4).

The mean egg volumes of 16 single-brooded females (1.13±0.079 cm^3) do not differ from those of the first clutches of the double-brooded females in Table 4 ($F_{1,38}$= 0.49, p>0.2).

The mean egg volumes of 30 replacement clutches are strongly correlated to the means of the preceding first clutches (Figure 1). The mean egg size of the replacement clutches does not differ from that of the failed first clutches ($F_{1,58}$ = 3.40, 0.1>p>0.05) although the individual females laid on average significantly larger replacement eggs (Table 4). A minor increase remains, even after the effect of the differences in clutch size and temperature during laying has been subtracted from the egg volumes (Table 4).

Discussion

The frequency of the three brood categories

Classification of successful and failed first broods in the nest pockets requires knowledge of the presence as well as the absence of repeat breeding. The problem is that some repeat clutches may be laid in nest sites other than the nest pockets within or outside the study area. Such suitable nest sites behind loosened bark and similar crevices are probably rather common in the study area. Moreover, there are indications that the Treecreepers prefer natural
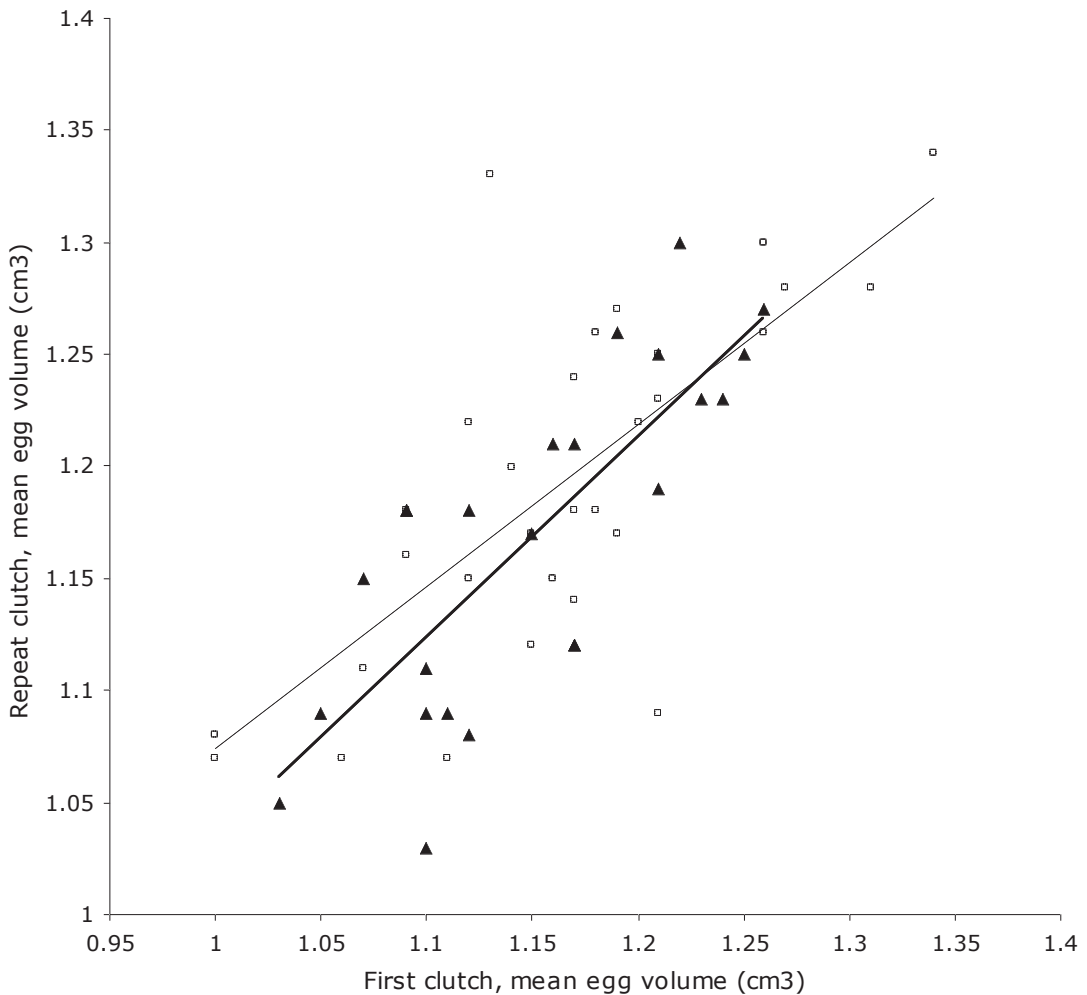
Figure 1. The correlation between the egg sizes (clutch means) within 24 pairs of first and second clutches (triangles, coarse regression line, y = 0.89x + 0.14, r² = 0.62, p<0.001) and within 30 pairs of first and replacement clutches (small open circles, thin regression line, y = 0.72x + 0.35, r² = 0.54, p<0.001).

Sambandet mellan äggstorlekarna (kullmedelvärden) inom 24 par av första- och andrakullar (tringlar, den grova linjen) och inom 30 par av förstakullar och omläggningskullar (små cirklar, den tunna linjen). Förstakullarnas äggvolymer kan avläsas på den horisontella axeln, andrakullarnas och omläggningskullarnas volymer på den vertikala axeln. De båda linjerna visar att då äggen i första kullen ökar i storlek så ökar också andra- och omläggningskullens äggstorlek. Sambanden är statistiskt säkerställda.

sites (Kuitunen & Aleknonis 1992). Unidentified repeat nests lead to an over-estimation of the number of single-brooded pairs and an under-estimation of the double-brooded and the replacement-breeding pairs. However, most of the double-brooded and replacement-breeding females in the population of the study area probably used the pockets for their repeat nests. This assumption is based on the following observations.

1. The Treecreeper females were extremely site tenacious, as only one out of 25 returning females was absent the season after colour ringing, but returned the following season.
2. The Treecreepers only moved fairly short distances within the study area between the first and the repeat breeding (see Results).
3. There was plenty of space available for re-breeding within the study area because its Treecreeper

population was sparse. The mean density was 5 ± 1.7 breeding pairs/km² (n=9), which corresponds to Treecreeper populations elsewhere (e.g. Steinfatt 1939, Kuitunen & Helle 1988, but see Schönfeld 1983, Schwerdtfeger 1987).

4. Each breeding pair had access to a surplus of unoccupied nest pockets within the territory.
5. During the field work in the study area, Treecreeper nests were never discovered in positions other than nest pockets.

Nevertheless, the numbers of repeat clutches accounted for in Table 1 most likely represent minimum values. New females without coloured rings that showed up every season in June and bred in the nest pockets might support this assumption. However, their number was small and represented a seasonal mean of three breeding females (3.0±1.7, n=9). Only once has a colour-ringed female from the preceding season appeared among these late newcomers. Obviously, female Treecreepers move into the study area (or have been overlooked when breeding in natural cavities there) in the middle of the breeding season to start second or replacement clutches. It is reasonable to assume that some Treecreepers may have crossed the study area border in the opposite direction, however probably fewer than the immigrants, because of the lack of nest pockets in surrounding areas. The average number of females that could not be found re-breeding in the study area after their first successful or failed brood is between four and five per year (4.6±2.5, n=10) as calculated on the basis of the last two columns of Table 1. Some may have started repeat clutches elsewhere, at a guess about the same number as the immigrating re-breeding females, i.e. three clutches equally divided into 1.5 second clutches and 1.5 replacement clutches per season. Adding these to the annual number of repeat clutches (Table 1) increases the number of second clutches to 43.5 (75%) (the exceptional year 1996 excluded), and the number of replacement clutches to 57.0 (97%).

These adjustments, although precarious, indicate that at least two thirds of the successful first broods were followed by a second breeding attempt, i.e. a doubled second brood frequency compared with those found in other Treecreeper populations (references below). It follows from the adjusted frequency of the double-brooded Treecreepers that about one third of the females were single-brooded. According to the adjusted values, practically all failed first broods were followed by replacement-breeding attempts.

The average rate of the second clutches as presented in Table 1 is rather high, 51%, when compared with the investigated nest-box populations in Finland (37%, Kuitunen 1987). A second clutch frequency of 32% was found in a Lithuanian population breeding in natural cavities (Kuitunen & Aleknonis 1992). The British nest card data indicate a rate of less than 20% (Flegg 1973). The percentage of the replacement broods also differs remarkably from those of the Finnish and Lithuanian populations (see below).

The high frequency of second broods occurring in the population of the study area is not unique, as it has been observed in another double-brooded small passerine, namely the likewise resident and forest-living Coal Tit *Parus ater* (Winkel & Winkel 1995).

The breeding season: time schedule and course of events

When comparing the time course and sequence of breeding events of the double-brooded and replacement-breeding females it is apparent that the latter normally managed to rear only one brood (Table 2). The start of a second clutch after a successful replacement brood has never been observed in the study area, and a replacement laying after a failed second brood has been noted only once in Finland by Kuitunen (1987). In order to rear two successive broods in the same season, the first clutch must obviously be laid in early spring and result in fledged young. A successful first brood started too late may preclude the laying of a second clutch (see below). Only once has a second brood followed a first brood started in May.

On average, the failed breeding was interrupted 17 days before the fledging day of the successful broods, a time span that was reduced to 14 days between the subsequent laying starts of replacement and second clutches (Table 2). Therefore the fledging of the replacement broods will be too late to make successful second brood rearing possible (see below).

The double-brooded female ensures time for the second brood by starting nest building (Kuitunen 1987, own observations) as well as oocyte growth and egg formation several days before the fledging of the first brood. The first egg of the second clutch was sometimes laid as soon as the day after the fledging day (mean interval 2.5 days, Table 2). The two broods were never observed to overlap. Elsewhere in Sweden, Durango (1963) found one breeding pair that had one nest with fledglings and one with eggs at the same time. Rare cases of over-

lapping have been reported from Germany and Finland (Bäsecke 1957, Kuitunen 1987). The absence of overlapping broods in the study area indicates that the normal food supply is not sufficiently rich to permit the female to lay eggs and feed young simultaneously (cf. Burley 1980).

The failed females started replacement laying in a new nest after one to two weeks (mean 9.5 days, Table 2) corresponding to the 6 to 12 days reported by Schönfeld (1983). The length of the interval may be at least partly dependent on the age of the first brood when destroyed. The lengths of the total breeding period of the double-brooded and replacement-brooding females differed significantly (U=26, p<0.05). The difference only amounts to approximately one week, as it takes longer to start laying a replacement clutch and fledge the young compared with the second brood (Table 2). The average fledging date of a replacement brood is around 25 June, which means that a hypothetical second brood would not fledge until about 1 August. Only two repeat broods fledged after 15 July. It is probably the advanced time of the season that somehow signals to the female to abstain from another breeding attempt when her replacement brood has fledged.

The distance between the nest site of the first and the repeat breeding

The nest-pocket of the first brood was never re-used in the same season. The distance between the two nests of the replacement-breeding female tended to be greater than that of the double-brooded female, although the difference was not significant (see Results). One third of both repeat clutch categories were laid in a pocket within 100 m of the first one. This means that the neighbouring empty pocket was used, as they were erected, on average, 75 m apart. As regards the double-brooded females, one would expect most of them to select a neighbouring pocket because the quality of the local habitat proved good enough to support successful breeding. Nevertheless, about one third (12 out of 32) of the females chose a more distant pocket, often ignoring unoccupied pockets in between. The reason might be that the food supply around the first nest site had been so depleted during the first brood rearing (cf. Jäntti et al. 2001) that it paid to move further away to the second nest site.

The same proportion (14 out of 40) of the failed females laid their replacement clutches beyond the nearest unoccupied pocket. Most of them lost their first brood more than one week prior to fledging,

i.e. maybe before the food resources of the surrounding habitat were exploited heavily enough to necessitate a more distant move. Nevertheless, the double-brooded and replacement-breeding female Treecreepers did not differ significantly when selecting a nest pocket in order to start repeat breeding (see Results).

Clutch size

The clutch size variation during the breeding season illustrates the well known "calendar curve" in the Treecreeper (Kuitunen 1987, Enemar 1992). It peaked in the middle of the laying season, i.e. during the second ten days of May, when replacement laying has started (Table 3). The second clutches had significantly fewer eggs than the first clutches, which is in accordance with the "calendar curve" but may also be a consequence of the reduced egg-producing capacity of the females after having successfully reared a first brood.

Most replacement clutches are laid in the last 11-day period of May, when the peak-sized clutches of the preceding 10-day period have already started to decline and become similar to the size of the first appearing second clutches (Table 3). The mean size of all replacement clutches equals that of the preceding first clutches.

More detailed comparisons with Kuitunen's (1987) results as regards Treecreeper clutch size have been made by Enemar (1992).

Egg-size

The double-brooded females laid approximately equal-sized eggs throughout the breeding season, although the second clutch eggs tended to be larger (Table 4). However, adjusting for the size-promoting effects of fewer eggs in the second clutch and the prevailing higher temperature during the egg formation period unveils a considerable reduction of the egg volumes. The latter may be a consequence of the weakened egg formation capacity of the female after rearing the first brood. This drawback may be compensated for not only by the somewhat reduced clutch size and the increased ambient temperature in June, but also by the longer days with a more favourable feeding situation in June (Kuitunen & Suhonen 1991).

The replacement-brooding females laid larger eggs in the repeat clutch than in the first failed one (Table 4). A significant minor size increase remains even after controlling for more favourable temperature during the replacement laying. The replace-

ment-breeding females probably had a better physical condition than the double-brooded females, as they had on average invested in only part of what was required to fledge a first brood and they also waited ca. 7 days longer before starting the repeat brood (Table 2). The average temperature change between the laying periods of the first and the repeat clutch was of minor or no importance, as in both cases the interval is the same, increasing from +8°C to +13°C between the first and second clutches and from +7°C to +12°C between the first and replacement clutches.

The fitness gains, if any, related to the slightly larger replacement eggs are hard to judge. It is, however, a general rule among the small passerine species that larger eggs give rise to heavier hatchlings, although the lifetime fitness value of this relationship has not been sufficiently investigated (Williams 1994, Christians 2002, and see below).

The resident Great Tits *Parus major* in northern Finland (Ojanen et al. 1979) and Switzerland (Nager & Zandt 1994) exhibit much the same variation as the Treecreeper with regard to egg size in the different clutch categories. The replacement-brooding female lays significantly larger eggs in the repeat clutch (Ojanen et al. 1979) representing an increase of 3.2%. The corresponding percentage is 2.6% in the Treecreeper. Ojanen et al. also established high heritability of the egg dimensions of the first and second clutches. As indicated by the regression lines (Figure 1), heritable factors may also affect egg size in the Treecreeper. Females that laid small eggs in the first clutch generally did the same in the repeat clutch, and large first clutch eggs were followed by large repeat eggs, a highly significant correlation in both double-brooded and replacement-breeding Treecreepers.

To lay or not to lay a repeat clutch?

This question does not seem to be of immediate interest in a frequently double-brooded species such as the Treecreeper, especially as it has been demonstrated in other multi-brooded species that reproductive success is more a function of the number of reared broods than of e.g. clutch size (e.g. Smith & Roff 1980, Holmes et al. 1992, Soler et al. 1995, Winkel & Winkel 1995, Palomino et al. 1999). It is reasonable to assume, therefore, that all Treecreepers are hereditarily double-brooded although with a varying readiness to lay a second clutch. The females may differ in their sensibility to external or internal factors that inhibit a second breeding attempt. In any case and according to the interpretations above, about a third of the Treecreeper pairs do not seem to make a second breeding attempt and remain single-brooded when the first brood has fledged. The conditions and adaptive value of the two breeding strategies will be considered in the following. The replacement breeding will also be treated, as it is so frequent in the Treecreeper and, furthermore, because this breeding category, according to Roonem & Robertson (1997), has rarely been described in detail (but see e.g. Einloft-Aschenbach & Schmidt 1984).

The double-brooded female

Females that have fledged the first brood have to decide whether or not to invest in a second clutch. They have already fledged one brood, an achievement that probably took a considerable toll on their physical condition. Consequently, they invest less when producing the second clutch compared with the first one (Table 3 and 4). Rearing a second brood may further negatively affect their physical status, involving reduced prospects of surviving the subsequent winter as demonstrated in other small passerine species (e.g. Askenmo 1979, Bryant 1979, Verhulst 1998, but see Einloft-Achenbach & Schmidt 1984, Smith & Marquiss 1995, Winkel & Winkel 1995, Hario 1997). The delayed onset of moult following double-brooding may have important consequences for winter survival, at least in a long-distant migrant (Evans Ogden & Stutchbury 1996). Furthermore, the male Treecreeper participates only sporadically or not at all in feeding the second brood (Kuitunen et al. 1996, own studies), which further increases the rearing load on the female. Nevertheless, between half and two thirds of the successful females laid a second clutch. The low adult survival rate (Enemar & Nilsson 2008) together with an even lower, although unknown, survival rate of the juvenile birds may strongly select for double-broodedness. Therefore, the best strategy to maximise the presence of own reproducing offspring in the next generation is probably to be double-brooded.

The single-brooded female

A good strategy could also be to remain single-brooded, as at least third of the females that had fledged their first brood did not breed a second time. A large number of investigations regarding other double-brooded small passerines (references below) indicate that the frequency of single-brooded pairs may depend on 1. the weather conditions

around the fledging time of the first brood, 2. the size of the first clutch and its eggs, 3. the timing of the start of breeding, 4. the quality of the female and of the territory, and 5. the age of the female. The relation between the listed factors and breeding behaviour has not been experimentally investigated in the study area. However, the descriptive information in the Results section makes it possible to assess the relevance of the listed factors.

1. Periods of rainy and cold weather or scarcity of food may inhibit a second breeding attempt. The breeding Treecreeper is very sensitive to bad weather, which often leads to desertion of nests containing eggs or young (Enemar 1995) (see also year 1996 in Table 1), thus indicating that an environmental impact on the frequency of laid second clutches is plausible.

2. Single and double-brooded females laid first clutches of the same size and comprising eggs of the same volume (see Results). This indicates that the Treecreeper has not evolved the trading-off strategy between single-broodedness with larger clutches and double-broodedness with smaller clutches, as experimentally demonstrated by e.g. Lindén (1988) in the Great Tit and Siefferman & Hill (2008) in the Eastern Bluebird *Sialia sialis*. The equal clutch size of the two categories of females is a trait not unique to the Treecreeper, as it also applies to e.g. the Song Sparrow *Melospiza melodia* (Smith & Roff 1980) and the Snow Bunting *Plectrophenax nivalis* (Smith & Marquiss 1995).

3. In contrast to some other double-brooded passerines (e.g. Banbura & Zielinski 1998, Weggler 2006, but see Evans Ogden & Stutchbury 1996) the single-brooded Treecreepers did not start laying later than the double-brooded pairs. Thus the Treecreepers do not postpone the laying, which would lead to increased clutch size due to the course of the "calendar curve" as described by e.g. Lack (1954) and Crick et al. (1993). Nor did the single-brooded Treecreepers fledge their broods later in the season than the double-brooded pairs. This indicates that the species does not comply with the "date hypothesis", which was experimentally tested and demonstrated in the Great Tit by Verboven & Verhulst (1996).

4. Possible differences in individual and territorial quality between the single and double-brooded pairs, as discussed by Drent & Daan (1980), have not been investigated in this study. The fact that the clutch size and egg volume of the two breeding strategies did not differ (point 2 above) indicates that the females in question may be of equal quality (but see Smith et al. 1995). However, the quality of their territories is unknown.

5. The effect of age on the frequency of repeat broods can be preliminarily evaluated by using the information from the five seasons 1997 to 2001 (Table 1). Most probably the majority of the females that start breeding unringed are first-year breeders (Enemar & Nilsson 2008). In any case, they are, on average, one year younger than the returning females that have been ringed the previous season. No less than 15 out of 22 unringed birds (68%) laid second clutches in comparison to a mere 5 out of 13 ringed birds (38%). Although the difference is not statistically significant (Gadj=2.959, $0.10>p>0.05$), perhaps due to the small sample size, it does not rule out the possibility that the frequency of second clutches declines with age. If so, it is contrary to what has been found in other passerine species (e.g. Hario 1997, Banbura & Zielinski 1998, Weggler 2006) but it may be supported by the fact that the egg size decreases from the first to the second breeding season in the Treecreeper as a suggested consequence of senescence (Enemar & Nilsson 2008).

To conclude, the first of the five factors listed above seems to have the greatest influence on the frequency of single-brooded Treecreeper females, i.e. the prevailing environmental conditions around the fledging time of the first brood. The females could be expected to refrain from a second laying when the prospects of success seem so poor that the average addition to the reproductive result tends to be less than the advantage of using the late season to improve physical condition and increase the winter survival rate. Therefore they appear, on average, as more productive and fitter than the double-brooded females in cases where the second breedings of the latter fail. Moreover, the co-operation between the single-brooded parents is probably a more efficient method of raising high quality fledglings than that of the double-brooded pairs, where the feeding around the fledging day is to a varying extent left to the male alone, while the female is away preparing for the second breeding (own observations). Consequently, both breeding strategies are conserved in the gene pool of the population and found side by side during most seasons in the study area.

The replacement-breeding female

A Treecreeper female that has lost her first nest containing eggs or young has to decide whether to

make a new breeding attempt or give up and instead improve her physical condition in order to survive the winter and breed again. The latter option is risky, because the adult survival rate is low, only about 32% (Enemar & Nilsson 2008, but see Peach et al. 1995). As plenty of breeding time remains after the breeding failure, as demonstrated by the double-brooded females, most or all of the failed females attempt to rear a replacement brood (see Results). The laying capacity can be considerable, as demonstrated by one female that finally succeeded in fledging the last of three consecutively laid 6-egg clutches. Apparently, the failed female has no better alternative but to invest in replacement breeding attempts while there is still time, despite the fact that it only implies "making the best of a bad lot" as described below.

To what extent, then, does the replacement breeding compensate for the failed first attempt? The size of replacement clutches did not differ from that of successful ones, i.e. clutches of the single-brooded female and the first clutch of the double-brooded female (see Results). However, the eggs of the replacement clutches were significantly larger and heavier than those of the first and second clutches, even after controlling for the effect of clutch size and temperature (Table 4). This means that the replacement-breeding females produce the heaviest hatchlings, especially as the Treecreeper hatchling increases in weight proportionally more than the weight increase of the egg, a unique situation among investigated small passerines (Enemar 2001). It is possible that the heavier hatchlings have a better start than those of the first brood, with increased prospects of reaching reproductive age, although studies supporting a positive relationship between egg size and offspring fitness among passerines are equivocal (Williams 1994, Christians 2002, but see Wagner & Williams 2007).

A number of the replacement-breeding females will continue to fail due to depredation, bad weather and other untoward events, resulting in a zero result for the season's breeding attempts. The presumptive single-brooded females that re-breed after failing may fully compensate for the interrupted first brood, even if negative consequences, i.e. the cost of the wasted investment in the first brood and the delayed breeding start, are unavoidable compared with the successful single-brooded females. Both aspects may negatively affect the restoration of their physical condition for the winter period ahead. The larger eggs and heavier hatchlings of the replacement clutch may compensate for only a tiny share, if any, of this loss of fitness. As mentioned above, the presumptive double-brooded and re-breeding female is prevented by lack of time from rearing a second replacement brood. Therefore the failed first brood means a heavier reproductive loss for this category of breeding Treecreepers. Obviously, the presumptive single-brooded and double-brooded females behave in the same way after failure and cannot be identified when acting as replacement breeders. The unavoidable reproductive shortcomings of the replacement-breeding Treecreepers compared to the successful single-brooded as well as double-brooded pairs indicate that those Treecreepers that start breeding early in spring and minimize the risk of failure by choosing good territories and safest possible nest sites are strongly favoured by natural selection.

The contribution of the three breeding categories to the total output of fledged broods

The calculations below are a simplified application of the precise and exhaustive method employed by Bryant (1979) to investigate the "reproductive values of the breeding patterns" in a House Martin *Delichon urbica* population. They were carried out in order to allow certain comparisons, in the area of "reproductive pattern", between my population and the investigated Treecreeper populations in Finland and Lithuania. The fledged brood was used as a unit when measuring the reproductive output, because the number of fledglings in each brood is often unknown.

The "reproductive quotient" was calculated, i.e. the quotient between the total number of fledged broods in the population and the number of breeding pairs. The percentage distribution of the fledged broods among the three breeding categories was also calculated. The totals of the breeding parameters in Table 1 have been used, both the original ones as well as those adjusted to approximately compensate for overlooked repeat broods. The resulting values are averages of the seasons and provide a rough idea of the "reproductive efficiency and pattern" of the study area population. The calculations are based on the rate of failed first breeding attempts and the proportion of the replacement breeding attempts together with the frequencies of fledged broods of the double and single-brooded pairs. The calculations were carried out on the assumption that the failure rate holds not only for the first broods but also for the second and replacement broods. The results are presented in Table 5 with the values based on the adjusted data in parentheses.

The reproductive quotient of the population of

Table 5. Frequency of failed and repeat broods, reproductive quotient (number of fledged broods per breeding pair) and percentage distribution of the total number of fledged broods among the three breeding categories as established in three different study areas. Numbers in parentheses denote adjusted values (see text).
Frekvensvärden för boförluster, andrakullar och omläggningar, samt förökningskvoten (antalet flygga kullar per häckande par) och den procentuella fördelningen av totalantalet flygga kullar på de tre häckningskategorierna i tre olika provytor. Siffrorna inom parentes gäller uppräknade värden (jfr huvudtexten).

Locality, nest site *Plats, bolägen*	Proportion of (%) *Andel (%)*			Reproductive quotient Förökningskvot	Breeding category (%) *Häckningskategori (%)*		
	Failed broods *Boförluster*	Second broods *Andrakullar*	Replacement broods *Omläggningar*		Doublebrooded *Tvåkullarpar*	Singlebrooded *Enkullpar*	Replacementbreeding *Omläggarpar*
This study, nest pockets *Denna studie, häckningsfickor*	50 (50)	51 (66)	71 (100)	0.80 (0.92)	47 (54)	31 (19)	22 (27)
SW Finland, nest boxes *holkar*	29.8*	6.9*	0.89*	46	52	2	
Lithuania, natural *Litauen, naturliga*	45.4*	32.3*	22.1*	0.70	39	53	8

*) From Kuitunen & Aleknonis (1992).

the study area, representing a measure of the reproductive efficiency, is less than unity (0.80–0.92, Table 5) and implies that the total number of fledged broods is 10% to 20% less than the number of breeding pairs. Roughly speaking, the double-brooded pairs rear 50% of fledged broods in the study area, and each of the single-brooded and replacement-breeding pairs rear 25% of the remainder (Table 5). Had the population consisted of only single-brooded pairs, the quotient would have dropped to 0.75. Double-brooded pairs are the most efficient contributors in terms of fledged broods. This is true of most failure rates in the population and frequencies in the different breeding categories. Moreover, thanks to the double-brooded pairs, the quotient will exceed unity when the brood failure rate is reduced to about 40% or less (the other parameters remaining unchanged), i.e. a reproductive efficiency that is impossible to attain in an exclusively single-brooded population. Obviously, the double-brooded pairs play an important role in maintaining the high reproductive rate that is necessary considering the low survival rate of the Treecreeper (Enemar & Nilsson 2008). Another adaptive consequence of the low survival rate is probably that so many, if not all, females start replacement breeding after a failed first attempt.

The frequency values used in the calculations above tend to differ from those obtained in a Finnish population breeding in nest-boxes and a Lithuanian population using natural nest sites (Kuitunen & Aleknonis 1992), both of which studies were conducted over many years. The Finnish study area is mainly covered by coniferous and the Lithuanian by mixed coniferous and broad-leaved forests. The breeding data that are used for the calculations are presented in Table 5.

The differences between the three investigations are considerable not only in terms of the habitat of the study areas but also their size, density of the Treecreeper populations, the number and density of breeding facilities, various environmental factors and the main aim and direction of the research programs. Close comparative interpretations are therefore not advisable, all the more so as they cannot be tested statistically. Nevertheless, a couple of observations deserve attention.

The Lithuanian investigation is of special interest because it is based on naturally breeding Treecreepers. The high rate of unsuccessful broods, about 45%, indicates that the frequency of failed breeding in my population, 50%, is not much higher than what may occur in a population breeding without access to a surplus of breeding facilities. According to Kuitunen & Aleknonis (1992), the disturbing trapping and ringing activities lead to a "surplus"

of failed broods that could be substantial, at least 9% of all interrupted breeding attempts.

The three investigated populations differ significantly with regard to the frequency of the three breeding categories, with the replacement-breeding pairs as the most obvious example. The latter are very few in the Finnish and Lithuanian populations. This also applies to their percentage share of the reproductive output (Table 5). Regarding the Finnish and Swedish studies, the considerable difference in the density of nesting facilities (2.5 nest-boxes/km^2 and 80 nest pockets/km^2, respectively) might partly explain the dissimilar repeat nest frequencies. The high density of nest pockets may have made it easier to keep up with the re-laying activities in my study area.

The reproductive quotients and the distribution of the fledged broods among the three breeding categories (both my calculations) are presented in Table 5. The frequency of the single-brooded pairs and their contribution to the total offspring production in Finland and Lithuania considerably outnumber the corresponding data for my population. This is a consequence of the fact that only about 33% of the successful first broods are followed by second breeding attempts, i.e. only about two thirds or less of the percentage found in my study area, as stated above. Obviously, the low frequency of established repeat broods (second and replacement broods) is the main cause of these differences. Compared with the Swedish population, the low rate of repeat broods in the Finnish population is compensated for by a lower failure rate, which means that a larger part of the population, the single and double-brooded pairs, produces at least one fledged brood per pair. Moreover, the second broods of the relatively fewer double-brooded pairs in Finland have a higher fledging rate due to the lower failure frequency. To conclude, the average number of fledged broods per breeding pair, the reproductive quotient, is about the same in the three populations (Table 5), with the naturally breeding Lithuanian population tending to lag slightly behind.

Acknowledgements

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Sammanfattning

Trädkryparen är en liten stannfågel som börjar att häcka tidigt på våren. Enligt forskare med erfarenhet från andra arter, kan en fågel med de nämnda egenskaperna förväntas föda upp två kullar årligen och dessutom uppvisa en bågformad kullstorlekskurva (den s.k. kalenderkurvan) under den långa häckningssäsongen. Kurvan visar att äggkullarna är relativt små i början av säsongen för att sedan successivt öka fram till säsongmitten, varefter de minskar igen. Allt detta stämmer in på trädkryparen, vilket tidigare visats och även kan utläsas av Tabell 3. Syftet med denna uppsats är att identifiera och närmare skärskåda trädkryparens tre kategorier av häckande par. Dessa är 1. par eller honor, som föder upp endast den först värpta kullen, här benämnda "enkullpar" eller "enkullhonor", 2. "tvåkullarpar" eller "tvåkullarhonor", som satsar på att få två kullar flygga, nämligen en förstakull och en andrakull, samt 3. "omläggarpar" eller "omläggarhonor", vars häckningssätt uppkommer av tvång som följd av att första häckningen misslyckats på grund av

borövning, hårt väderläge eller annan störning, varefter ett eller flera nya försök görs för att få en omläggningskull flygg. Den mängd häckningsdata, som insamlats under en 10-årsperiod, redovisas i sammanfattad form i syfte att karakterisera delar av de olika häckningsförloppen i populationen. Därtill undersöks dels hur effektiv provytans population är på att producera flygga kullar, dels hur stora de olika häckningskategoriernas andelar är i denna produktion. Bland fältarbetets brister bör främst nämnas att antalet flygga ungar ej kunnat bestämmas under senaste delen av säsongen samt att variationen i näringstillgången ej studerats.

Metoder

Studierna genomfördes 1995–2005 (med uppehåll 2004) i Gunnebo-området, ca 10 km sydöst om Göteborg, i en 2,5 km² stor provyta. Denna är till största delen täckt av ädellövskog med inslag av planterad granskog. De öppna ytorna består mest av betad ängsmark. Provytan är försedd med 200 häckningsfickor, gjorda av takpapp och särskilt anpassade för trädkrypare (se Enemar 1992). Varje häckningsficka innehållande bo med ägg täcktes av perforerad aluminiumplåt som skydd mot angrepp av större hackspett. Den häckande trädkryparhonan fångades genom att fösas ut ur häckningsfickan rakt in i en genomskinlig plastpåse. Hon försågs därefter dels med en metallring, dels med en för varje individ unik kombination av tre färgringar. Ringmärkningen genomfördes för att eventuell förekomst av andrakullar och omläggningskullar skulle kunna påvisas senare under säsongen. Häckningsfickorna inspekterades med varierande tidsmellanrum beroende på forskningsuppgiftens karaktär för säsongen, dock alltid tillräckligt ofta för att säkert kunna räkna antalet häckningar och följa dessas förlopp. För varje tvåkullarpar och omläggarpar mättes avståndet mellan de använda häckningsfickorna på en kartskiss i skala 1:10000. Temperaturdata hämtades från mätningarna vid Säve flygplats (SMHI 1995–2005) vilka tidigare visats stämma väl med temperaturen i provytan. Volymen eller storleken på äggen beräknades med hjälp av måtten på längden och bredden. Äggmätningarna gjordes på fotografier av genomlysta kullar (se Enemar 1997, 1999).

Resultat med kommentarer

De häckande trädkryparnas fördelning på tvåkullarpar och omläggarpar presenteras i Tabell 1. Även antalet enkullar redovisas där (se spalten

"None") liksom de tidiga förstakullarnas fördelning på fullföljda och avbrutna häckningar. I genomsnitt fick hälften av paren sin förstakull flygg. Av dessa par startade runt 50% därefter en andra kull (tvåkullarparen), medan resten (enkullparen) avstod från en ny satsning. Av de par som misslyckats, gjorde ca 70% ett nytt häckningsförsök (omläggarparen). Andelen såväl tvåkullarpar som omläggarpar är hög jämfört med erfarenheterna från finska studier (ca 30% resp. ca 10%). Icke desto mindre kunde antalet upprepade häckningar i provytan misstänkas vara för lågt. Anledningen är att beräkningarna bygger på förutsättningen, att alla trädkrypare vid förnyade häckningsförsök stannar inom provytan och därtill väljer en häckningsficka som ny boplats. Används naturliga boplatser kommer dessa att förbises och antalet enkullpar därmed att överskattas och antalet tvåkullarpar och omläggarpar att underskattas. Följande fakta talar dock för att de allra flesta häckande paren höll sig till fickorna vid upprepade häckningsförsök: 1. De trädkrypare som återkommit efter övervintringen har häckat nära eller ibland i fjolårets häckningsficka. 2. Förflyttningarna mellan två häckningsförsök samma säsong var mycket korta (se nedan). 3. Tillgången på lediga häckningsfickor har varit riklig (medeltätheten häckande har varit 5 par/km² med 80 fickor/km² till förfogande). 4. Inte ett enda trädkryparbo har upptäckts utanför fickorna inom provytan i samband med fältarbetet. Men mot dessa fyra punkter talar det faktum att i medeltal tre icke ringmärkta honor dykt upp sent och häckat i provytan i juni varje år. Det är rimligt att anta, att denna inflyttning till provytan har motsvarats av ungefär lika stor utflyttning av områdets färgmärkta honor i syfte att starta säsongens andra och därmed förbisedda häckningsförsök. Tas hänsyn till detta, blir andelen andrakullar och omläggningar något högre jämfört med värdena i Tabell 1. Resultatet av denna uppräkning blir att mellan hälften och två tredjedelar av de flygga förstakullarnas honor värper en andrakull medan resten avstår. Vidare gör i stort sett alla honor med avbrutna förstakullar ett nytt häckningsförsök.

Häckningssäsongens tidsschema framgår i grova drag av Tabell 2, som visar tidsåtgången för de olika momenten i häckningen för tvåkullarhonan och omläggarhonan. Skillnaden mellan dem vad gäller säsongens längd, räknad från första kullens första ägg till sista kullens utflygning, var i medeltal endast ca en vecka, en liten men statistiskt säker skillnad. Man hade annars väntat sig mer eftersom omläggarhonans första häckning ofta avbröts åtskilliga dagar (medelvärde 17 dagar) innan kullen

skulle ha flugit ut. Hon hade därmed haft möjlighet att börja omläggningen långt innan tvåkullarhonan kunde börja värpa sin andrakull. Av någon anledning har det gått trögt för omläggarhonan att få igång den nya häckningen. Tvåkullarhonan har däremot förberett sin andra häckning (bobygge, äggutveckling m.m.) i så god tid att första ägget ibland värpts redan dagen efter första kullens utflygning. Detta var möjligt tack vare att hanen matade ungarna oftare än honan, stundtals ensam, under dagarna strax före och efter utflygningen. Hanen tog sedan skadan igen genom att så gott som helt utebli från matningen av den något mindre andrakullen, som honan trots sin ensamhet ofta nog lyckades få på vingarna.

Den "trögstartade" omläggarhonan värpte den nya kullens första ägg i medeltal först 9,5 dagar efter katastrofen med första kullen (Tabell 2). Jämfört med den lyckosamma honans andra kull tog det dessutom två dagar längre tid att få omläggningsungarna flygga. Dessa förseningar bidrog uppenbarligen till att den resterande säsongen blev för kort för att räcka till uppfödning av ytterligare en kull, eftersom inga försök till en andra kull har kunnat noteras efter de många kontrollerade omläggningskullarnas utflygning.

Medeldatum för första kullens start och ungarnas utflygning var densamma för alla kategorier av häckande par.

Medelavstånden mellan häckningarna var för 32 tvåkullarpar 146±90 m och för 40 omläggarpar 166±110 m. Medelskillnaden på 20 m är inte statistiskt säker. Man hade annars väntat sig att de honor som misslyckats, t.ex. genom att boet rövats, skulle flytta längre bort än de som lyckats med första kullen. I stället valde en tredjedel av båda kategorierna den närmaste häckningsfickan i grannskapet för den nya kullen och en tiondel en ficka mer än 250 bort.

I Tabell 3 redovisas antalet ägg i de tre olika häckningskategoriernas kullar för varje tio- eller elvadagarsperiod under säsongen. Summaraden längst ned i tabellen avspeglar den bågformade kullstorlekskurvan under säsongen med sin topp i mitten, dvs andra perioden i maj. Det är som synes omläggarhonorna som då svarar för ägglägningen. Sorterar man fram de förstakullar, som svarar mot de 36 andrakullarna i tabellen, visar det sig att medelantalet ägg i förstakullen (5,51±0,56) är signifikant större än i den påföljande andrakullen (5,22±0,72). Motsvarande jämförelse för omläggningskullarna visar att ingen skillnad föreligger mellan den havererade förstakullen och omläggningskullen.

Även det enskilda äggets medelvolym kan variera mellan de olika kategorierna av kullar, vilket framgår av Tabell 4. Tvåkullarhonan värper lika stora ägg i båda kullarna. Men räknar man bort "den hjälp" honan fått av varmare väder och lägre äggantal under andra kullens värpperiod, så hade äggen blivit signifikant mindre. För omläggarhonan är det tvärtom. Honan värper klart större ägg i andra häckningsförsöket, vilket betyder att de nykläckta ungarna också blir är större. Det råder nämligen ett klart positivt samband mellan äggets och den nykläcktas storlek hos trädkryparen (se Enemar 2001). Om sedan en nykläckt unge på sikt har någon fördel av att vara särskilt stor är fortfarande en omtvistad fråga. Enkullhonans ägg är lika stora som tvåkullarhonans och omläggarhonans ägg i förstakullen.

Diskussion

Att värpa en kull till eller ej, det är frågan

Eftersom trädkryparen är en etablerad uppfödare av två kullar, kan den i rubriken ställda frågan verka onödig, i synnerhet som det visats för andra arter att de honor, som försöker sig på att dra upp två kullar genomsnittligt får fler ungar på vingarna än de som nöjer sig med en enda flygg kull. Man kan därför förvänta sig, att alla trädkryparpar har siktet inställt på att föda upp två kullar. Men däri ligger ett moment av chansning. Detta skall här något kommenteras tillsammans med synpunkter på de övriga häckningskategoriernas för- och nackdelar.

De honor, som lyckats få säsongens först värpta kull flygg, har gott om tid att häcka en gång till. Vinsten är alltså uppenbar, men det finns även skäl att "tänka sig för". En andrakull innebär nämligen en mödosam arbetsinsats som tär på en honas krafter utöver vad den lyckade förstakullen redan kostat och detta i synnerhet som trädkryparhanen endast obetydligt eller inte alls deltar i matningen av andrakullen. Den konditionskrävande dubbla häckningen innebär för honan, att hon kommer i ett sämre läge vad gäller att bygga upp nödvändig styrka för att framgångsrikt klara instundande övervintring. Icke desto mindre väljer bortåt två tredjedelar av de framgångsrika honorna i provytan att satsa på en andrakull. Detta torde vara taktiskt välbetänkt eftersom syftet med all fortplantning är att få egen könsmogen avkomma med i nästa generation, dvs i det häckande beståndet nästa säsong. Det angelägna i tvåkullartaktiken understryks av att trädkryparen är en mycket kortlivad art bland småfåglarna (endast 32% överlevnad enligt preliminära beräkningar på provytans bestånd), dvs chansen att klara sig över vintern och kunna häcka igen är

under alla förhållanden ganska liten. Därtill kommer att den flygga avkommans överlevnad säkerligen är betydligt lägre. Därför torde den produktiva tvåkullartaktiken inom provytan under nuvarande förhållanden favoriseras av det naturliga urvalet.

Det kan dock inte vara "helt fel" av en trädkryparhona att nöja sig med den utflugna första kullen för säsongen, eftersom runt en tredjedel av dem förblir enkullhonor. Många ornitologer har forskat i möjliga orsaker till detta val men med olika resultat, delvis beroende på vilken art som studerats. Det har föreslagits att väderförsämring och födoknapphet vid tiden för första kullens utflygning kan få en hona att avstå från en andra häckning. Sannolikt gäller detta för trädkryparen, eftersom arten påfallande ofta reagerar på dåligt väder genom att överge både ägg och ungar. Hos vissa arter värper honan antingen en stor kull (enkullhonan) eller två små (tvåkullarhonan), men ett sådant laborerande med kullstorlekar gäller ej för trädkryparen, eftersom förstakullarnas medelstorlek är densamma för en- och tvåkullarhonorna. Det kan tilläggas att någon skillnad i äggstorlek mellan dem inte heller föreligger. Denna likhet vad gäller ägg och kullar betyder sannolikt att de två honorna befinner sig konditionsmässigt på samma nivå. För andra arter har visats att enkullhonorna ligger efter i vikt, men detta gäller sannolikt inte för trädkryparen. Inte heller uppvisar de blivande enkullhonorna någon försening i häckningsstarten på våren jämfört med tvåkullarhonorna. Sammanfattningsvis verkar det sannolikt att det i många, kanske de flesta, fall är omständigheternas tryck (uselt väder, dålig näringstillgång) som hejdar en hona från att fullfölja sin häckningsdrift och värpa en andrakull.

Man kan fråga sig om vissa trädkryparhonor kan vara helt inställda på att producera en enda flygg kull för säsongen, alltså även under gynnsamma omständigheter. I så fall borde denna häckningsmodell, i varje fall i vissa lägen, medföra någon eller några fördelar jämfört med tvåkullarhonans häckning. En sådan kan vara att enkullhonan kan ägna all sin tid att delta i matningen av kullens ungar tillsammans med hanen ända fram till självständighet. Resultatet av samarbetet bör bli en avkomma av bättre kvalitet och högre överlevnad jämfört med tvåkullarhonans förstakull, som mot botidens slut och därefter mer eller mindre lämnas därhän av honan, som blivit upptagen med att förbereda andrakullen (bobygge, äggbildning, m.m.). Enkullhonan får däremot gott om tid att rugga och bygga upp sin kondition inför vintern med förhöjd överlevnadschans som följd. Dessa fördelar blir än mer uppenbara i jämförelse med de många tvåkul-

larhonor som misslyckas med andra häckningen, alltså en konditionskrävande satsning utan resultat med risk för sänkt vinteröverlevnad. I detta läge framstår enkullhonorna avgjort som vinnare i "kampen" om det naturliga urvalets gunst. Både enkull- och tvåkullartaktiken kan alltså ha sina fördelar och därmed chans att tillämpas samtidigt i ett och samma trädkryparbestånd.

Den trädkryparhona som misslyckats helt med första kullen står inför valet att antingen starta en ny häckning eller också ägna resten av säsongen till att rugga och bygga upp sin kondition inför vintern och sikta på nästa säsongs häckning. Detta senare är en riskfull chansning eftersom trädkryparen, som ovan påpekats, är så kortlivad. Icke oväntat värper därför så gott som alla honor på nytt en kull, som är lika stor som den första. De har därmed ersatt den förlorade kullen fullt ut oberoende av om förlusten drabbat en blivande enkullhona eller tvåkullarhona. Däremot finns ej tid att efter en lyckad omläggning föda upp ytterligare en kull och uppnå den från början avsedda produktionsnivån som tvåkullarhona. Den hona, som fått en omläggningskull flygg, befinner sig förmodligen i visst underläge även gentemot den framgångsrika enkullhonan, eftersom den förspillda kraftinsatsen på den misslyckade första häckningen tillsammans med den senarelagda enda flygga kullen kan betyda att hon inte hinner nå toppkondition innan vintern sätter in. En omläggarhona får finna sig i att med sin nya kull förhoppningsvis i alla fall undvika att drabbas av vad värre är, nämligen en häckningssäsong helt utan avkomma.

Sammanfattningsvis tycks följande gälla för provytans population: Den trädkrypare är framgångsrikast som börjar häcka tidigt på våren med säker boplacering i ett näringsrikt revir och som hinner med att föda upp två kullar. Den förlust som ett avbrutet första häckningsförsök innebär kan aldrig fullt ut repareras genom omhäckning.

De olika häckningskategoriernas andel i populationens totala produktion av flygga kullar

Dessa beräkningar utfördes för att möjliggöra jämförelser med andra trädkryparpopulationer, gällande främst sammansättningen av de olika häckningskategorierna och produktionen av flygga ungar. Eftersom antalet flygga ungar inte är känt för alla häckningar, används istället antalet flygga kullar vid jämförelsen. Resultaten är sammanfattade i Tabell 5.

Den i tabellen angivna "förökningskvoten" för provytans trädkryparbestånd erhålls genom att to-

tala antalet flygga kullar divideras med totala antalet häckande par. Som synes är kvoten mindre än ett (Tabell 5), vilket betyder att flera par misslyckats helt med att få en kull flygg. Detta beror på att andelen boförluster varit så omfattande, 50% (Tabell 1). Att kvoten ändå är så hög, beror på att tillräckligt många tvåkullarhonor lyckats med båda häckningarna men även på att de olycksdrabbade honorna efter den avbrutna första häckningen i så hög grad startat ett nytt häckningsförsök (Tabell 1). Som väntat är fördelningen av flygga kullar på de tre häckningskategorierna ojämn. Tvåkullarparen svarar för omkring hälften av antalet flygga kullar i provytan, medan enkullparen och omläggarparen vardera står för ungefär hälften av återstoden (Tabell 5).

Avslutningsvis görs en enkel jämförelse med resultaten från en finsk undersökning som bygger på häckningar i trädkryparanpassade holkar i barrskog, och en litauisk, där naturliga boplatser letats upp i blandskog. Studiernas olikartade karaktär tillåter inte att mer ingående jämförelser görs. Men man kan lägga märke till att förökningskvoterna är mindre än ett i båda fallen och av samma storleksordning som den i provytan (Tabell 5). Boförlusterna är betydande och ligger omkring 30% i den finska och 45% i den litauiska studien, varav de finska tenderar att vara färre än i provytan. Frekvensen omläggningar är klart lägre, 7% resp 22%, vilket avspeglas även i den låga andelen omläggningskullar i den totala produktionen av flygga kullar (Tabell 5). Detta torde vara den enda säkra skillnaden jämfört med beståndet i provytan. Den är emellertid svårtolkad och kan möjligen till icke ringa del bero på att i den finska undersökningen vissa omhäckningar inte fångats upp av holkarna. Detta kan i sin tur vara en följd av att det tillgängliga antalet holkar i den finska populationen varit avsevärt lägre än antalet häckningsfickor i provytan (2,5 holkar/km^2 resp. 80 häckningsfickor/km^2). En tätare uppsättning av häckningsanordningar torde rimligen innebära en säkrare registrering av andrakullar och omläggningar.

Den låga andelen förnyande häckningar (andrakullar och omläggningar) i den finska och den litauiska studien tillsammans med de färre boförlusterna motsvaras av högre frekvens av framförallt enkullhäckningar. Dessa svarar för störst andel i produktionen av flygga kullar. Även tvåkullarhäckningarna har ganska stor andel trots den klart lägre frekvensen par jämfört med beståndet i min provyta, vilket återigen är en effekt av den nyssnämnda låga nivån på boförlusterna.

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