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Breeding performance of the Fieldfare *Turdus pilaris* in the subalpine birch zone in southern Lapland: a 20 year study

Björktrastens Turdus pilaris *häckning i den subalpina björkzonen i södra Lappland: en 20-årig studie*

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Abstract

A Fieldfare population, on average c. 160 pairs, was studied in subalpine birch forest in southern Lapland (c. 66°N; 500–600 m.a.s.l.) in 1983–2002. Onset of egg-laying showed no temporal trend, consistent with absence of spring temperature trend. Eggs were laid with an interval of c. 21 hours and 45 minutes, not 24 hours as normal in passerines. This reduces the exposure time to depredation during egg-laying with 9%. Egg hatchability was 96%. Egg parasitism never occurred. Depredation of nests was 46%, but very variable. Replacement and second clutches did not occur. Although an average of 4.45 young fledged from successful nests (≥1 fledgling), only 2.11 fledglings were produced per pair and year. The population varied without trend over the study period. Adult survival, estimated by the proportion of adults at the start of breeding, was 58%. This infers that first year survival must be at least c. 40%. Since this is a likely value, it seems that the Fieldfare population of the subalpine birch forest is self-sustained and not dependent upon immigration.

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Introduction

Three species of thrushes are common in the Scandinavian subalpine birch zone: Redwing *Turdus iliacus*, Fieldfare *T. pilaris*, and Song Thrush *T. philomelos*. Two of the species, the Redwing and the Fieldfare, have been studied within a long-term project on population dynamics in the birch and alpine zones near the village of Ammarnäs (65° 58’ N; 16° 13’ E) in southern Swedish Lapland, the so called Luvre project, started in 1963 (Enemar 1969, Andersson & Sandberg 1996). The results on the Redwing have been published previously (Arheimer 1978a, 1978b, 1978c, 1979). Early results on the Fieldfare have also been published (Arheimer 1987). The Fieldfare study has continued and in this paper we expand the coverage to the period 1983–2002, which means that we can use a much larger data set permitting several new analyses, particularly those that are connected with long time series, the effect of exceptional years, and estimates of recruitment versus mortality. A number of dedicated studies of methods or of special problems were also conducted, for example assessment of the interval between laying of the eggs and the dispersal after breeding.

Study area

The study area, located 3–8 kilometers west of Ammarnäs village (Figure 1), was the south-facing slope of the mountains Gaisatjåkke and Valle, approximately from an elevation of c. 750 meters (near the forest line) down to the lake Tjulträsk and the river Tjulån at an elevation of c. 500 meters. In the west, the area was bordered by Rödingbäcken and in the east by Karsbäcken. The size of the area was approximately nine square kilometers. Most of the study area is located within the Vindelfjällen nature reserve. Excellent maps are provided by several web services, for example www.eniro.se, where high-resolution aerial photographs demonstrate many habitat details, especially open patches versus closed forest.

Almost all Fieldfares were breeding in six colonies in the eastern part of the area with only a small number of solitary pairs in the rest of the area. The elevation of the colonies was 500–600 meters. The

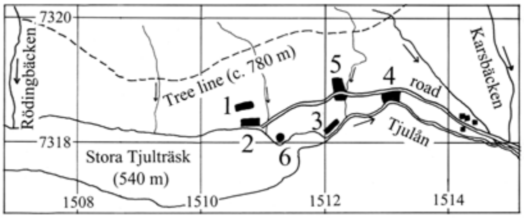


Figure 1. Map of the study area, limited in the west and east by the streams Rödingbäcken and Karsbäcken, in the north by the tree line, and in the south by lake Stora Tjulträsk and river Tjulån. Numbers 1–6 indicate the location of the six Fieldfare colonies. Bird trapping sites were located at colony 3 (late summer) and colony 5 (spring). The kilometer coordinates of the Swedish national grid are given. North is up.
Karta över undersökningsområdet, begränsat i väster och öster av Rödingbäcken och Karsbäcken, i norr av trädgränsen och i söder av Stora Tjulträsk och Tjulån. Siffrorna 1–6 markerar läget för de sex björktrastkolonierna. Fångstplatser låg vid koloni 3 (sensommar) och koloni 5 (vår). Kilometerkoordinater anges enligt Rikets nät. Norr är uppåt.

approximate areas covered by the six study colonies were 3, 4, 3, 8, 8, and 2 ha (colony 1–6, respectively; we refer to the colonies with these numbers; Figure 1). The nearest big colony was located at Rödingvik about three kilometres west of colony 1 and 2 of this study, and just outside the study area.

The habitat within the whole study area was birch forest, partly a rich and moist meadow-type forest with dense undergrowth of willows and tall herbs (wolfsbane *Aconitum septentrionale* and blue sow thistle *Cicerbita alpine* were common), and partly a drier, heath-type forest on more well-drained ridges with undergrowth dominated by low junipers *Juniperus communis* and scattered willows *Salix* spp. There were numerous small mires and streams. The Fieldfare colonies were located in meadow-type patches with 10–15 m tall birches *Betula pubescens* and sallows *Salix caprea*. In the eastern part of the study area human influence was apparent with many open areas that had been used for hay harvest and grazing. All the colonies were found in the vicinity of such areas or small mires. The whole area between the westernmost study colonies 1 and 2 and Rödingvik is closed forest, but Rödingvik is a human settlement with open meadows. Figure 2 shows habitats from the colonies. It should be observed, however, that when the Fieldfares initiated egg-laying in early spring, the trees and bushes had no leaves yet, snow often still covered parts of the ground, and the herbs were only just about to emerge. The nests were most often built at a height of 2–5 meters.

Methods

All six colonies could not be studied every year, but three of them were studied in almost all years (Table 1). Colony 6 declined during the late 1980s, and was no longer included in the study after 1988. Upon arrival in Ammarnäs, the colonies known from previous years were visited and the nests inspected. Surrounding areas were searched in order to determine the size of each whole colony, including peripheral nests up to 75 meters from the nearest nest towards the centre of the colony. The whole study area was also surveyed every year in order to locate new colonies. No new colony was ever found, only dispersed solitary nests. We are certain about the absence of other colonies both because we made our own surveys and because the whole study area was carefully covered by line transects during the counts of all the passerines (Enemar et al. 2004). The nests were easy to find visually during the early part of the season when the trees had no leaves, and the Fieldfares were very noisy when their nests were approached. One rather large colony that had existed during the 1960s and was included in Arheimer (1987) disappeared during the 1970s before the start of this project.

In order to estimate the average total population size we assumed that colony size in years when a colony had not been studied was the same as the average in years when it had been studied. We also assumed that the proportion of nests that were not inspected was the same in 1983–1991 as it was lat-

Figure 2. Typical breeding and feeding habitats of the Fieldfare in the study area. Top: River Tjulån from Juomovare westwards with the fjeld Stor-Aigert in the background. Colony 4 was located on the slope to the right. The birds often gathered food in the open meadow that is a remnant of larger hay fields on the slope. Lower left: a small stream where much feeding took place in early spring. Lower right: breeding habitat with tall birches and a moderately dense field layer. The photos were taken on 16 June 2007. This year was very early and most young had just left the nests. When the birds start to breed there are no leaves on the trees and often much snow.
Typiska biotoper för häckning och födosök för björktrast i undersökningsområdet. Upptill: Tjulån från Juomovare västerut med fjället Stor-Aigert i bakgrunden. Koloni 4 låg på sluttningen till höger. Fåglarna samlade ofta föda på den öppna ängen som är en rest från tidigare större slåttermarker på sluttningen. Nere till vänster: en liten bäck där fåglarna ofta sökte föda tidigt på våren. Nere till höger: häckningsbiotop med höga björkar och ett måttligt tätt fältskikt. Fotona togs den 16 juni 2007. Detta år var mycket tidigt och de flesta björktrastungar hade just lämnat bona. När fåglarna börjar häcka finns det inga löv på träden och ofta mycket snö.

Table 1. Number of nests in the colonies. Empty cells are years without study. No colony was studied in 1986 and 1989.
Antal bon i kolonierna. Tomma celler är år utan undersökning. Ingen koloni studerades 1986 och 1989.

	No. of nests in colony no. *Antal bon i koloni nr*					
	1	2	3	4	5	6
1983					54	
1984		6			55	
1985		17	13		46	19
1986						
1987	23	20	16	20	30	23
1988	12	15	34	35	28	16
1989						
1990	21	11		42		
1991	27	7		55	27	
1992		19	8	57	34	
1993		23		68	60	
1994		10	16	58	53	
1995		16	15	69	31	
1996	11	11		64	44	
1997		21		52	19	
1998	15	10		39	30	
1999		21		44	37	
2000		19	10	65	33	
2001		17		73	59	
2002		8		53	38	
Mean	18	15	16	53	41	19

er, when these nests were inspected (about 5%). We also accounted for the fact that colony 6 declined so much that it no longer was studied after 1988.

The visits were made at least every second day throughout the annual study periods. In most years the first visit was made after the earliest Fieldfares had laid the first egg or after completion of the clutch. Hence it was not possible to directly determine the date of the first egg in each clutch. This date was instead calculated by subtracting 10 days plus clutch size from the date of hatching of the first egg (14 days for 4-egg, 15 days for 5-egg, 16 days for 6-egg, and 17 days for 7-egg clutches). The date of hatching of the first egg was always known. The fieldwork periods and the date of the first egg are given in Appendix 1.

The values used for calculation of the date of the first egg were based on previous knowledge of the breeding biology of the Fieldfare in the study area (Arheimer 1987). One egg is laid per day, although with an interval of less than twenty-four hours (see below). Incubation starts successively after egg number two or three (Enemar & Arheimer 1980). Because of this, the first 2–3 eggs hatch within 24 hours and before the eggs laid later. A special study of this involved 12 clutches with five eggs and 30 clutches with six eggs. These 42 clutches were selected because all eggs hatched. They were visited every 12 hours through egg-laying and hatching. Every new egg was marked with a number.

In another special study the hour of egg-laying and the interval between eggs were determined in 18 clutches with five and 12 clutches with six eggs. These nests were inspected throughout the laying period one to three (most often two) times per 24 hours. The time of the visit of each particular nest was adapted according to the knowledge of the time of the previous egg. The hour of a visit was recorded with a precision of plus/minus 15 minutes. The interval between the eggs in each clutch was calculated according to Watson et al. (1993): maximum interval = [time(last egg found) − time(visit before egg 1 found)]/(clutch size − 1); minimum interval = [time(visit before last egg found) − time(egg 1 found)]/(clutch size − 1).

When hatching date had been determined, another visit was always made 10 days after hatching of the first eggs. The number of young in the nest on that day was considered to be the number of fledged young. The normal nestling period in undisturbed nests is 13–14 days, but checks involving handling of the young cannot be made after day 10 because this may easily cause the nestlings to leave the nest prematurely. Hence an unknown amount of desertions or depredations may have occurred after the last inspection. Therefore, a special study with careful counts of the number of nestlings in thirteen nests with a spotting scope or binoculars from a safe distance without disturbance was made in order to assess late mortality during the last 3–4 days in the nest.

On the first visit in a colony, when the nests were first located and inspected, some of them were already empty. A nest was recorded as depredated if it contained remains of egg shells, if the nest cup was torn asunder, or if a completed nest cup was undisturbed but empty for at least three days. Nests were recorded as deserted if they contained cold eggs during at least three days without any increase of number of eggs. All deserted nests contained at least three eggs. A few nests where all young died just after hatching were also recorded as deserted.

A small number of nests were not inspected at all. These nests were either difficult to access because they were placed too high up in a tree or were located in a very distant part of a colony. In 1983–1991, such nests were not exactly counted because time did not permit the extra work needed. However, from 1992, these inaccessible and peripheral nests could be counted thanks to access to field assistance. When it was relevant to include these nests in a calculation (e.g. total reproductive success in relation to number of pairs), their fate was assumed to be the same as that of the inspected nests. The number of nests belonging to the different categories is shown in Appendix 2.

Hatching success was determined by deducting the number of remaining unhatched eggs from clutch size. Only nests for which both clutch size and hatching were observed and in which at least one egg hatched were included. Nests in which no egg hatched were classified as total losses (desertion or depredation). The unhatched eggs were collected and examined in the field two or three days after hatching of the last young, since the last egg may hatch up to 24 hours after the previous one. They were classified as eggs with or without an embryo, the former if an embryo larger than one mm could be detected and the latter if no embryo could be seen (i.e. including non-fertilized eggs).

Colony size was determined with different levels of accuracy. In 1992–2002, the accuracy was high, and we know precisely the number of (1) inspected nests with at least one egg laid, (2) inspected nests that were depredated before the first visit, and (3) nest that were known to be active but could not be inspected (usually too high up). Thus, for these years we know the total number of pairs that attempted to breed in all colonies. For 1983–1991 we do not know the number of nests belonging to category (3).

For the calculation of the final production of fledglings per pair, different categories of nests had to be treated differently. The following assumptions were made: (1) Pairs that deserted their nests or got their nests depredated, did not lay a replacement clutch; (2) With the possible exception of very few pairs in one single year, no true second clutches ever occurred; (3) The few nests that were not at all inspected but observed to be active produced the same average number of fledglings as the inspected nests with known outcome, and (4) The nests that were inspected and where eggs or hatched young were recorded but not followed until fledgling produced the same average number of fledglings as the inspected nests with known outcome.

In most years the field work at Ammarnäs continued for two to three weeks after initiation of the very latest clutches. During the last few days of each season, the colonies and their surroundings were carefully searched for late clutches. In addition to this, most of the rest of the nine square kilometre study area was also surveyed in detail towards the end of the field period to check whether any late clutches were to be found.

We got unpublished data on number of trapped birds in two standardized trapping schemes operating in our study area (early spring trapping at a site within colony 5; courtesy Roland Sandberg) and (late summer trapping at a site in colony 3; courtesy Åke Lindström). The former scheme distinguished between one year old and older birds providing us with an estimate of adult survival.

In order to study dispersal, nine females in colony 4 and 5 were supplied with battery-powered radio transmitters (PIP 1.45±0.05 g., Biotrack Ltd.) in late May and early June 2002. Four of them got their transmitters 3–5 days before and five of them 2–4 days after hatching date. To check the possibility to detect a transmitter during the test period, one transmitter was placed on the ground in each of the two colonies. These two transmitters could be received from suitable higher points in the valley at a minimum distance of 1.5 km, and they retained their transmitting power throughout the field work period. Between 30 May and 25 June, effort was made to receive signals from the transmitters of the females every second day from eight suitable elevated points within three kilometers west and east of the colonies. On 18–25 June, signals were also searched every kilometer up to four kilometers southeast of the colonies in the valley towards Ammarnäs village. During the same period, signals were also searched along ten kilometers of the nearest adjacent valley with birch forest, namely the Vindel river valley northwest of Ammarnäs (at a distance of 5–10 km from the colonies).

In order to follow the development and survival of individual nestlings, their claws were marked with nail polish of different colour immediately after hatching. They were ringed when 6–8 days old. Data on all Fieldfares that had been ringed in the study area and the recoveries were obtained from the Ringing centre at the Museum of Natural History, Stockholm. Supplementary information of recoveries was also obtained from the two ringing projects within the study area (courtesy Roland Sandberg and Åke Lindström). Throughout the study years, temperature (maximum and minimum), precipitation and wind were recorded at colony 5. For overall description of spring temperature in relation to onset of breeding, we used data from the Swedish Meteorological and Hydrological institute.

Results

Notes on method tests

The special study of the hatching sequence showed that hatching was completed within 48–72 hours. The mean values were 57 hours for 5-egg clutches and 60 hours for 6-egg clutches. The penultimate egg hatched after the previous eggs in all clutches, and the last laid egg was always the last one to hatch, 12–24 hours after the penultimate one. In 46 clutches with 4–6 eggs, the incubation period of the last numbered egg was 11–12 (mean 11.6) days irrespective of clutch size. Since the first 2–3 eggs normally hatched 1.5 days before the last egg, the date of laying the first egg could be calculated with great accuracy from the date of hatching of the first 2–3 eggs, a date that was always known.

The special study of late nestling mortality showed that there was no mortality during the last few days. Hence, the number of nestlings on day 10 is likely to be a close estimate of the true number of fledglings.

Size of population and colonies

For the whole study period, the average number of pairs in all six colonies was estimated at 155–165 pairs (Table 1). The uncertainty depends on the decline of colony 6 that was not followed after 1988. In good years twice as many pairs bred in the colonies as in poor years. No linear trends were found, neither in single colonies nor when all colonies were pooled. Not even when colony 6 was explicitly given zeros after 1988 was any significant trend found (TRIM index slope = −0.0083; SE=0.0168; NS; van Strien et al. 2000).

Time of start of breeding and length of laying period

Considering all years, the total clutch initiation period at Ammarnäs was 39 days long. The earliest date was 16 May 2002 in colony 4 and the latest date 23 June 1998 in colony 5 (Figure 3 Left, Appendix 1). The mean date of all clutches was 31 May, the median date 1 June, and the modal date 2 June. Very few clutches were initiated after 11 June.

In each separate year, the clutch initiation period was always shorter than 39 days, most often 20 days or less (mean 22 days; s.d. 6.7 days; Figure 4). Only in one year (1984) was it almost as long as the period of all years (37 days). The number of clutch initiations reached a peak already three days after the very first ones (Figure 3 Right). Almost fifty percent of all clutches were initiated within five days, and almost all during the first two weeks. Only one year, 2001, differed from all the other. This year will be examined separately below.

The dates varied without any long-term trend in any of the first egg dates calculated (first, mean or last date), and there was no trend toward a longer or shorter period of clutch initiation dates during the study period (Figure 4). The date for the first egg was somewhat different in the different colonies (Appendix 1), but none of the differences was significant.

Both first lay date and mean lay date were strong-

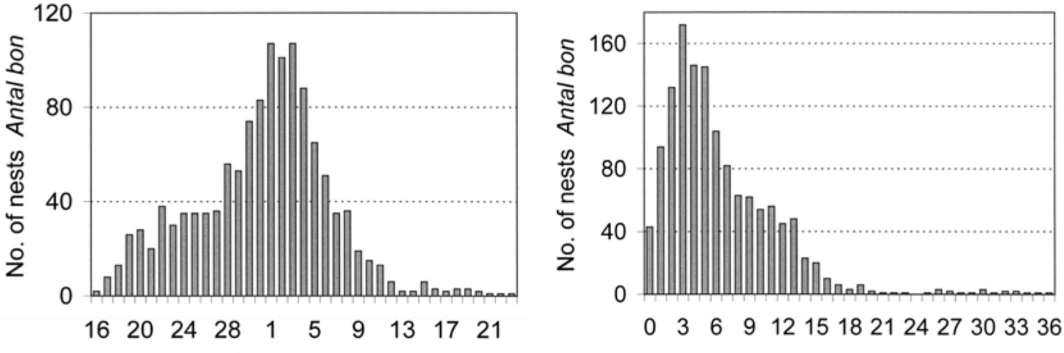


Figure 3. Lay date of first egg in 1983–2002. Left: Number of initiated clutches on different calendar dates. Right: Number of initiated clutches on different days, relative to the date of the earliest egg in each season (this day is called day zero).
Läggdatum för första ägget 1983–2002. Vänster: Antal påbörjade kullar olika kalenderdatum. Höger: Antal påbörjade kullar olika dagar i relation till det första äggets datum varje säsong (detta datum kallas datum noll).

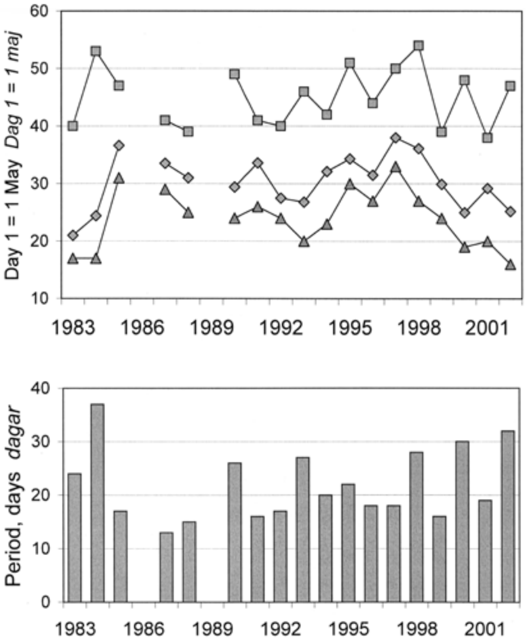


Figure 4. Upper panel: Calendar dates of clutch initiation in different years: the first clutch, the mean clutch, and the latest clutch. Lower panel: Period of clutch initiations in different years, the dates of the first and last clutches included.
Övre diagrammet: Läggdatum för första ägget för tidigaste, genomsnittliga och senaste kullen. Nedre diagrammet: Antal dagar mellan tidigast och senast lagda första ägg, inklusive dessa dagar.

ly temporally correlated between the colonies. We compared only colonies 2, 4, and 5, because dates were available from many years. The correlation coefficients were all significant and varied between 0.64 and 0.92.

The size of the colonies was correlated with the date of the first egg, both for colony 5 alone (r=0.64; p<0.01; 18 years) and colony 2, 4, and 5 together (r=0.53; p<0.05; 15 years).

Special case: 2001

As said above, one year, 2001, was exceptional. The first clutch was initiated on 20 May in colony 5. Egg-laying started in colony 4 one day later. On 24–27 May, bad weather with much snow (more than 10 cm) and low temperature made the birds desert their nests (6 nests with eggs and 5 completed nests yet without eggs). The birds in colony 2 had not started to lay before the snowfall. After the snowfall laying was resumed on 29 and 30 May (1 and 2 clutches) and 52 clutches were initiated within the next four days. There was no significant difference in clutch size between the first and second peak (5.55 eggs and 5.32 eggs, respectively).

Hour of egg-laying and interval between eggs

Among the 30 studied clutches, the first egg was laid between 0900 and 1100 hours in three nests, between 1100 and 1600 hours in 18 nests, rather evenly distributed between 1600 and 2300 hours in 7 nests, and soon after midnight in only two nests. The last egg was laid during the hours 2300–0700 in 21 nests and during 0700–1200 in seven nests. In the two nests where the first egg was laid very early after midnight, the last egg was laid in the afternoon.

The possible intervals between successive eggs for all 30 nests are given in Table 2. In the same table, detailed data for four typical nests are given as examples. The average interval between eggs was shorter than 24 hours, namely 21 hours and 45 minutes for both five and six egg clutches. Three times during the field work the visits were so timed that it could be directly ascertained that the interval really was shorter than 22 hours. The total period of egg-laying was thus reduced with 9 hours for a 5-egg clutch and with more than 11 hours for a 6-egg clutch, compared with what it would be with 24 hour intervals. This is a reduction of the egg-laying period with 9%.

Clutch size

Clutch size varied between three and seven eggs with five or six eggs being most common (92% of 1136 completed clutches; Table 3). The average clutch size of all completed clutches was 5.42 (s.d. = 0.66). Clutch size varied between both colonies (F=3.09; p<0.01) and years (details in Appendix 3).

Both the size of the completed clutch and date of the first egg were known in 1097 nests. Using this pooled data set, clutch size was found to decline over the season, both in relation to calendar date (slope for the period 22 May–9 June was –0.023 egg/day; r=0.83; p<0.001; Figure 5A) and in relation to the date relative to the earliest clutch in each season (slope during the first ten days was –0.090 eggs/day; r=0.97; p<0.001; Figure 5B). In relation to calendar date, clutch size was lower during the five earliest dates. However, 15 of the 21 clutches initiated during these days, 16–20 May, emanated

Table 2. Upper part: Possible maximum and minimum intervals between laying of eggs in 18 clutches with five and 12 clutches with six eggs. Superscripts refer to the nest numbers in the lower part of the table. Lower part: Example of original data from two of the five egg and two of the six egg clutches. The first record of each new egg is marked with a grey cell and bold face. Nests no. 9, 12 and 21 are examples of the most common case when the first egg was laid after noon and the last egg in early morning. Nest no. 25 is one of the few where the first egg was laid early and the last one after noon.

Övre delen: Möjliga längsta och kortaste intervall mellan äggens läggning i 18 femäggskullar och 12 sexäggskullar. Upphöjda siffror avser bonumren i tabellens nedre del. Nedre delen: Exempel på originaldata från två av femäggs- och två av sexäggskullarna. Första besöket med ett nytt ägg har markerats med grå celler. Bona nr 9, 12 och 21 är exempel på de oftast förekommande kullarna, där första ägget lades på eftermiddagen och det sista under morgontimmarna. Nr 25 är exempel på ett av de få bon där första ägget lades tidigt på dygnet och det sista på eftermiddagen. Upphöjda siffror är bonumren.

Five egg clutches *5 ägg*			Six egg clutches *6 ägg*		
Max.	Min.	Mean	Max.	Min.	Mean
23,75	17,50	20,63	22,80	17,20	20,00
24,00	18,00	21,00	22,80	18,00	20,40
23,75	18,50	21,13	22,80	19,60	21,20^{21}
23,75	18,50	21,13	24,20	19,20	21,70
24,25	18,25	21,25	24,20	19,40	21,80
24,00	18,75	21,38	25,40	18,40	21,90
24,50	18,50	21,50	24,00	19,80	21,90^{25}
23,50	19,75	21,63	23,20	21,00	22,10
22,25	21,25	21,75^{9}	25,40	19,20	22,30
24,00	19,75	21,88	24,00	20,80	22,40
24,25	19,75	22,00	25,40	19,60	22,50
24,00	20,00	22,00^{12}	23,20	22,20	22,70
24,25	19,75	22,00			
24,25	20,00	22,13			
24,50	20,00	22,25			
25,00	19,75	22,38			
23,00	22,50	22,75			
24,50	21,25	22,88			
Mean *Medelvärde*		21,76	Mean *Medelvärde*		21,74

	Nest *Bo* 9						Nest *Bo* 12						Nest *Bo* 21							Nest *Bo* 25					
Hr	Day *Dag*						Day *Dag*						Day *Dag*							Day *Dag*					
Kl	1	2	3	4	5		1	2	3	4	5		1	2	3	4	5	6		1	2	3	4	5	6
1																									
2																									
3																									
4					4													5							
5			2	3	**5**										**2**										
6																									
7																						**2**			
8				**4**													**5**	**6**			**1**				
9									**3**							3							**3**		5
10		**2**	**3**				0			**4**	**5**													4	
11								**2**							**3**	**4**									
12	0												0	1											
13																									
14																									
15													**1**												
16							**1**	2														2	3	4	
17	**1**																								
18																									
19																									
20																								**5**	
21								2												0			**4**		**6**
22									3	4															
23																4									
24																									

from the unusually early year 2002. If this year is excluded, there is no sign of lower clutch size during the very early part of the season. The relation between clutch size and date is demonstrated in a different way in Figure 5C. Here it can be seen that 3-egg clutches are laid two weeks after the first clutches each year and ten days after the 7-egg clutches which are laid only four days after the very earliest clutch. Between the two predominant clutch sizes with five and six eggs, there was a difference of one and a half day.

The average seasonal clutch size was independent of whether breeding started early or late (Figure 5D, 16 years). This was the case when mean annual clutch size was correlated with the date of the first

Table 3. The frequency and proportion of different clutch sizes in the total material from 1983–2002
Frekvens och andel för olika kullstorlekar i hela materialet från 1983–2002.

Clutch size *Kullstorlek*	Nests *Bon*	%
3	6	0.5
4	69	6.1
5	513	45.2
6	531	46.7
7	17	1.5
Total	1136	100.0

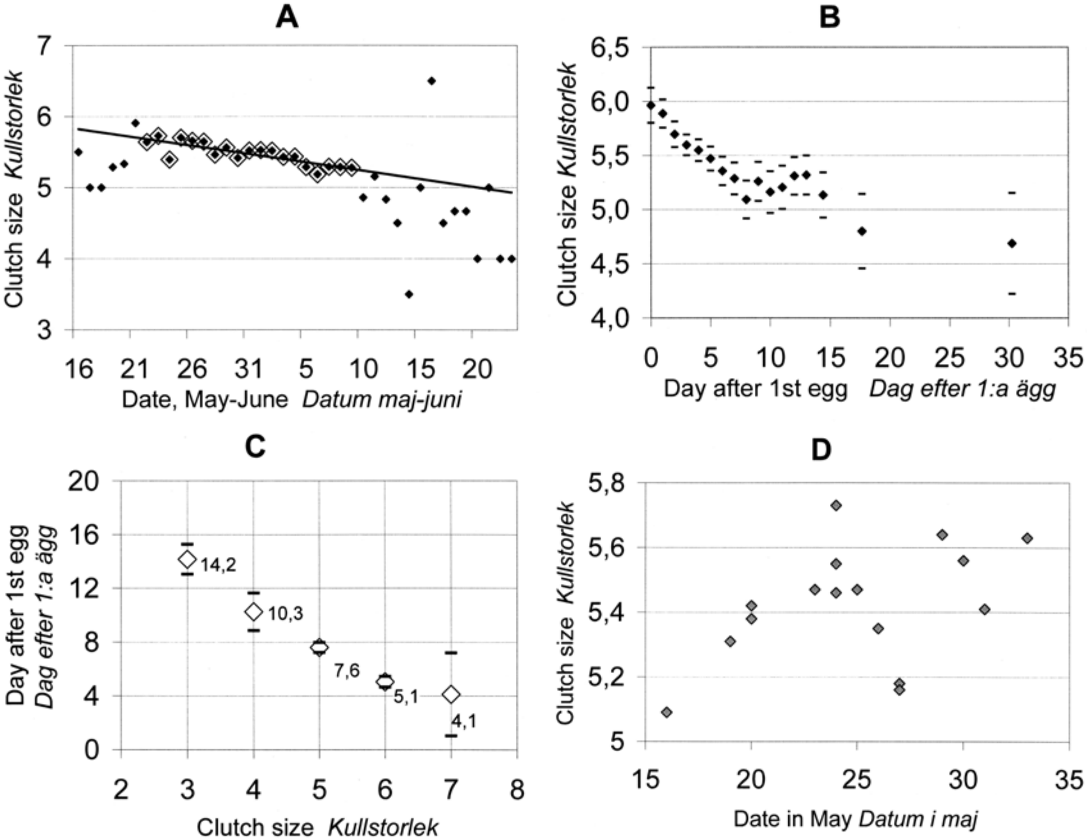


Figure 5. Clutch size versus lay date within and between years. A: Clutch size vs. calendar date. The regression line (y=−0.024x+5.8) is for the period 22 May–9 June (indicated by different symbols). B: Clutch size vs. relative date. Two standard errors are indicated about the means. C: Relative date vs. clutch size. Means and two standard errors are given. D: Mean clutch size vs. first date in each year. No significant correlation: r=0.43. The leftmost value is for year 2002.
Kullstorleken mot läggningsdatum inom och mellan år. A: Kullstorlek mot kalenderdatum. Regressionslinjen (y=−0.024x+5.8) avser perioden 22 maj–9 juni (indikerad med särskilda symboler). B: Kullstorlek mot relativdatum. Medelvärde och två standardfel ges. C: Relativdatum mot kullstorlek. Medelvärde och två standardfel ges. D: Kullstorlek mot första läggdatum olika år. Ingen korrelation: r=0.43. Symbolen längst ner till vänster är för år 2002.

Table 4. Hatchability of eggs.
Äggens kläckbarhet.

Clutch size	No. of nests	No. of eggs	Dead embryo	Without embryo	% with	% without	% total
Kull-storlek	*Antal bon*	*Antal ägg*	*Döda embryon*	*Utan embryo*	*% med*	*% utan*	*% total*
3-4	47	185	0	3	0	1.6	1.6
5	339	1695	35	47	2.1	2.8	4.8
6	384	2304	29	57	1.3	2.5	3.7
7	13	91	3	5	3.3	5.5	8.8
All	783	4275	67	112	1.6	2.6	4.2

egg each season (r=0.43; p>0.05) as well as when it was correlated with the mean date of egg-laying (r=0.22; p>0.10).

Egg hatchability

Data on hatchability are available for 4275 eggs in 783 nests, for which all relevant data (clutch size, and number of hatched and unhatched eggs) were recorded (Table 4). All eggs hatched in 628 nests (80%). In the 155 nests where all eggs did not hatch, the most common case was that only one egg did not hatch, which was the case in 144 (92%) of these nests. Two eggs did not hatch in fifteen nests and five eggs (all without embryo) in one nest (a 6-egg clutch). Only five nests contained unhatched eggs both with and without embryo. Of all laid eggs, only 179 (4.2%) did not hatch, 67 (1.6%) with a dead embryo and 112 (2.6%) without a visible embryo.

The difference in hatchability between different clutch sizes is not significant (Chi-square test). The proportion of nests where all eggs hatched differed little between years, and was on average 80% (s.d. 5.4%; range 76–88 in all years but one, 1998, when it was 64%). The proportion of all eggs that hatched was high (average 96%; s.d. 1.1%; range 93–97%). There were no significant temporal trends in either the proportion of hatched eggs or proportion of nests where all eggs hatched.

Losses of nests and nestlings

A large proportion of the nests were lost already before the first visit in the colonies (Figure 6). This early depredation always referred to clutches that had not yet been completed or clutches in the stage of incubation. On average, 29% (S.E.=4.3%) of the inspected nests were depredated early. The early depredation rate was extremely variable between both years and colonies. In 1992 colony 3 and in 1999 colony 2 were completely depredated and already deserted at the first visit. The year 1995 was particularly free of early depredation and none of 131 nests in four inspected colonies was depredated early. Additional depredation occurred after the first visit, making the total depredation of nests as high as 46% (S.E.=5.4%). A number of desertions (6% of the nests) added to the depredation so that only 48% (S.E.=5.5%) of all nests were successful (at least one fledgling).

Starvation due to cold weather was an important cause of death among the nestlings in some years. We have reliable data on this for the period 1992–2002 (Figure 7). Total losses of whole broods

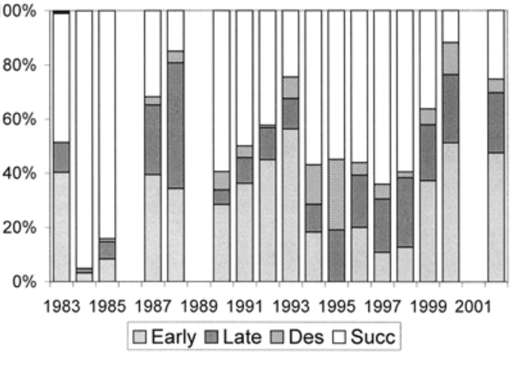
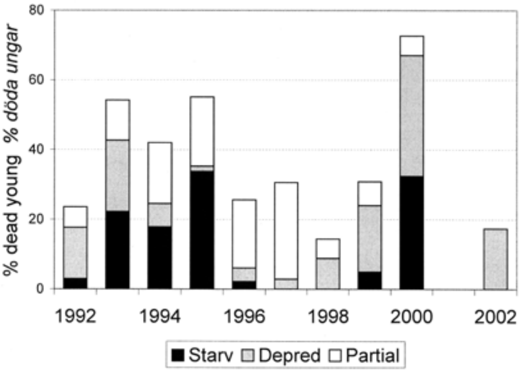


Figure 6. Proportion of nests with total loss of eggs or young and successful nests (Succ; nests with at least one fledgling). The total losses depended on either depredation or desertion (Des) of nestlings that starved to death during periods of cold weather. Depredation was early (before first visit in a colony) or late.
Andel bon med total förlust av ägg eller ungar och lyckade bon (Succ; bon med minst en flygg unge). Totalförlusterna berodde på att boet prederades eller övergavs (Des) på grund av att ungarna dog av svält under perioder med kallt väder. Predationen var antingen tidig (Early; före första besöket i en koloni) eller sen (Late).



Figur 7. Proportion of hatched young that died because of starvation of the whole brood, partial starvation, and depredation of whole broods.
Andelen kläckta ungar som dog på grund av svält av hela kullen (Starv), del av kullen (Partial) och predation (Depred) av hela kullen.

due to starvation were concentrated to four years. In three of these years (1993, 1994 and 2000), the weather was unusually bad during large parts of the nestling phase, with several long periods of heavy rain (a total of 40–50 mm) combined with mean daily temperature close to zero. The females could not both incubate the young and feed themselves. In 1995 it was a twenty-four hour storm on 26 June that caused the losses. Some trees with nests fell, and several nests were blown down. The strong wind was combined with a temperature of only 5–7 degrees and many broods could not be kept warm, and the combination of this and insufficient provision of food resulted in many total losses toward the end of the storm.

Partial loss of nestlings was also important in several years, and in 1996 and 1997, partial losses were more important than total losses (Figure 7). The nestlings that died were those that were the last ones to hatch. These nestlings were also the smallest ones. If more than one nestling died in the same nest, death occurred in reverse order of hatching sequence.

In 2002, depredation was strong. However, in the nests that were not depredated, not a single young died (Figure 7). All the 17% of the nestlings that were lost, were lost due to depredation of whole broods. During the whole nestling period, day-time temperature was 15–25 degrees, night-time temperature 5–10 degrees, and brief rains fell, that made earthworms easily accessible at the ground surface.

The average number of hatchlings in nests where all young were lost before fledging was 5.34 (s.d. 0.78; n=148) and it was 5.25 (s.d. 0.80; n=487) in nests with partial losses; the difference was not significant, indicating that initial brood size did not affect the destiny of a brood.

Number of fledglings

The number of fledglings can be expressed in different ways depending on the categories of nests that are included in the calculations (Appendix 4). The average number of fledglings from successful nests (at least one fledgling) was 4.45 (SE=0.134; N=17 years; 609 nests). The average number of fledglings from all nests with a completed clutch, i.e. nests with total loss of nestlings included, was 2.92 (SE=0.273; N=17 years; 975 nests), which is 1.5 nestlings less. If we include also the nests that were depredated early, the average number of fledglings per pair making a breeding attempt was only 2.11 (SE=0.283; N=17 years; 1906 nests). For the period 1992–2002, we could also include the young that were produced in the nests that were not accessible for inspection, assuming that these nests produced the same average number of young as the other nests with a completed clutch. However, this increased the estimates with only 0.06 fledglings or 3.6%, which is little compared with the standard errors of the estimates. However, if we add this value to the estimate we get a final average production of 2.17 young per pair making a breeding attempt in the study population.

The number of fledglings increased with increasing clutch size until a clutch size of six eggs (Table 5). But the increase with one egg between the two predominant clutch sizes, five and six eggs, resulted in an increase of less than half a fledgling. If all nests, also deserted and depredated ones, were included about 50% of the eggs resulted in fledglings in both five and six egg clutches. However, the percentage of nests with all young fledged was lower for six than for five egg clutches.

Although there was no decline of average brood size (Figure 8) for successful nests (slope –0.04; R^2=0.19; NS), the other two categories of nests showed some decline during the study period (slope 0.10–0.11; R^2=0.25–0.31; p<0.05). However, the decline showed by the category that included all nests, that is with early depredated nests included, depended solely on the two aberrantly successful years 1984 and 1985. In the perspective of all seventeen study years, a low production is the normal situation and very successful years constitute exceptions.

Tabell 5. Breeding success in nests of different egg clutch size.
Häckningsutfallet för bon med olika äggkullstorlek.

		Egg clutch size *Äggkullens storlek*				
		3	4	5	6	7
Number of nests with *Antal bon med*	0 fledglings *flygga ungar*	1	9	137	152	5
	1	0	0	4	3	0
	2	1	0	11	12	0
	3	2	3	36	31	3
	4	–	25	65	67	3
	5	–	–	99	76	1
	6	–	–	–	70	0
	7	–	–	–	–	1
No. of nests *Antal bon*		4	37	352	411	13
No. of successful nests (≥1 fledgling) *Antal lyckade bon (≥1 flygg)*		3	28	215	259	8
No. of fledglings *Antal flygga ungar*		8	109	889	1188	33
Fledglings per nest *Flygga ungar per bo*		2.00	2.95	2.53	2.89	2.54
Fledglings per successful nest *Flygga ungar per lyckat bo*		2.67	3.89	4.13	4.59	4.12

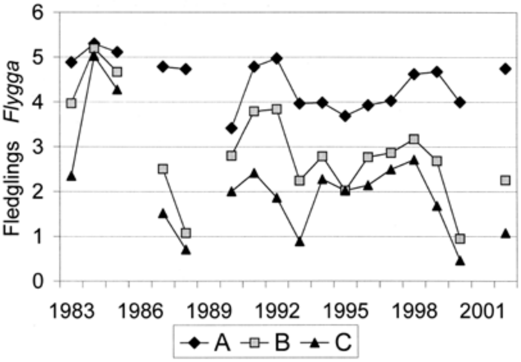


Figure 8. Mean number of fledglings in all colonies in different years. Values were calculated for three categories of nests. A: Successful nests, i.e. nests with at least one fledged young (= at least ten days old). B: Nests with at least one egg recorded (i.e. early depredations excluded). C: Nests of category B plus nests known to have been depredated before the first visit. Category C is assumed to represent all pairs that attempted to breed in each year, i.e. gives the true final breeding success.
Medeltalet flygga ungar i alla kolonier olika år. Värden har beräknats för olika kategorier av bon. A: Lyckade häckningar, dvs. minst en unge flygg (minst 10 dagar gammal). B: Bon med minst ett ägg observerat (dvs. tidigt prederade bon ej medräknade). C: Bon av kategori B plus de tidigt prederade bona. Kategori C antas representera det antal par som gjorde häckningsförsök respektive år, dvs. visar den sanna och slutliga häckningsframgången.

Recordings of the transmitters

Five of the nine females with transmitters lost their eggs or broods by depredation on 3–11 June. The dates of loss in relation to the date of hatching in each nest were: 3 days before, at hatching date, 2, 3, and 8 days after. These females moved about near the nest site for 1–4 days after the loss. Four of them were not recorded anywhere in the two monitored valleys later on. One of them was recorded once in the birch forest on the south-western slope of Björkfjället c. 10 km north-west of Ammarnäs village on 23 June. The distance between her nest, that was depredated in colony 4 on 6 June with 5 nestlings 3–5 days old, was 11 km. Intensive search of this female during the next two days in the area where she was discovered did not give any further contact.

The four successful females got their nestlings fledged at the normal age of 13–14 days on 11–17 June. The young were fed in the colony area for 2–4 days. After this brief period, the absence of further contact indicated that the females did not stay anywhere in the two surveyed valleys.

Ringing and recoveries

In the spring trapping project, that was active during the last week of May and the first week of June in 1988–2001 at the edge of colony 5 (Roland Sandberg; the data kindly provided by him), 419 Fieldfares were ringed (237 males, 163 females and 10 adults that were not sexed). In the other project, carried out within colony 3 in the latter half of July and the first half of August in 1983–2001 (Lindström & Lind 2001), 30 adult males, 33 adult females, and 58 juveniles were ringed. Other ringing activities in 1982–2001 resulted in the ringing of 9 male, 11 female and 1 non-sexed adults. A total of 2481 nestlings were ringed in 1982–2000.

Of this total of 3042 ringed Fieldfares, only five were recovered in 1983–2002 within the study area and in the breeding season. Three birds ringed as adult males were trapped one, two and five years later. Two females, ringed as nestlings, were trapped one and two years later. Eleven recoveries were made outside the study area. They were all made in the winter, six in England, four in France, and one in Scotland.

Discussion

Size and dispersal of colonies

The absence of any long-term trend of the size of the study population was in agreement with the results from the line transects of Enemar et al. (2004) in the same years. Their study also showed that there had been no trend since 1963. Also the Swedish Breeding Bird Survey (BBS; Lindström & Svensson 2006) indicates the absence of any long-term population trend of this species. This permits us to consider the study population stable for the purpose of survival estimates later on.

The dispersal pattern of breeding Fieldfares seems to differ between different breeding areas. At Ammarnäs, solitary pairs were few. The only colonies ever found in our study area were the six colonies, and these colonies were located at the same places every year. The big colony at Rödingvik was also recorded at the same place every year.

Contrary to this, other studies report a majority of solitary pairs or non-permanent colony locations. In a heath birch forest at Budal (62°45'N, 10°30' E; 750–900 m a.s.l.), 116 pairs bred solitarily and 83 pairs in small colonies during a ten year period (Hogstad 1983a, Hogstad et al. 2003). In a mixed heath and meadow birch forest at Staloluokta (67°18' N, 16°43' E; 600–800 m), also during a period of ten years, 533 pairs nested in 57 colonies with a mean size of 9.2±8.3 pairs and with different locations in different years (Wiklund 1982, Wiklund & Andersson 1994). During a five year study in a predominantly meadow birch forest at Innerdalen (62°32' N, 10°08' E; 800–900 m), located along a 10 km long artificial lake, between 123 and 255 Fieldfares nests were spread within a study area that was 2700 m long and between 200 and 500 m broad (Reitan & Sandvik 1994).

The explanation of the different patterns may be effects of vegetation. The distribution pattern of nests differed between the poorer heath forest habitats of Budal and Staloluokta and the richer meadow habitats of Innerdalen and Ammarnäs. The latter two areas were also similar in having more stable population size than the former, poorer areas. Thus it seems that habitat patches with a rich food source within a matrix of poorer habitats attract Fieldfares to form colonies.

Egg-laying

In southern Germany (49–52° N), the Fieldfare laid eggs during more than three months, from late March to mid-July (Hohlt 1957, Gülland et al. 1972, Lübcke 1975, Haas 1982). At Trondheim (63° N) at the Atlantic coast of Norway, the eggs were laid from early May to mid-June (Slagsvold & Sæther 1979), a period that was only half of that in central Europe. The climate conditions in spring made the start of the laying period later at higher elevations in the Scandinavian mountains, but the length of the period was about the same, from mid-May to end of June, but it varied with up to two weeks between years (62° N; 800–900 m a.s.l.; Reitan & Sandvik 1994; 67° N; 600–800 m; Wiklund 1984). In the tree-less low alpine part of Hardangervidda in southern Norway (60° N; 1200 m), where the birds nested in Salix bushes and on the ground, the laying period was concentrated to only two weeks in the middle of June due to the severe climate (Håland 1984).

The period of first eggs, 39 days from 16 May to 23 June (Figure 3A), and the concentration of clutch initiation to the first 15 days in each season (Figure 3B) were the same as found in other studies in subalpine birch forest in northern Scandinavia (Wiklund 1984, Reitan & Sandvik 1994).

Onset of breeding in the second half of May was mainly determined by the occurrence of earthworms (Lumbricideae) that became available at the uppermost soil level as the snow melted away. When the snow melted late or when the ground was frozen in their feeding areas, the females could not gather enough food for early egg-laying. The time difference for first egg-laying that depends on temperature and snow conditions has earlier been shown to be up to 14 days in the current study area (in the years 1965–1985; figure 1 and 2 in Arheimer 1987). During the 20 years of this new study, the earliest date was 16 May 2002 and the latest date 2 June 1997, a period of 16 days (Appendix 1). In the earliest year, 2002, the study area was free of snow and the lake free of ice already on 14 May (Lasse Strömgren). In the latest year, 1997, only the tops of some hills were free of snow whereas the snow was 0.5–1 m deep in the depressions with the most important feeding habitats, and the lake was still ice-bound when the study started on 5 June. The exceptional year 2001 showed that snowfall could temporarily interrupt egg-laying, and similar interruption because of snowfall has been observed earlier in the subalpine birch zone (Reitan & Sandvik 1994).

The absence of any long-term trend in the date of breeding was explained by a similar absence of any spring temperature trend. For three different periods during the sensitive phase (15–31 May, 1–15 June, and 15 May–15 June) the temperature trends were +0.078, –0.005, and +0.038 °C per day. Corresponding R^2-values were 0.041, 0.000, and 0.113. All trends were far from significant ($p>>0.10$).

Our finding that more Fieldfares tended to breed in early than in late springs was also found at Budalen by Hogstad et al. (2003). This may be an effect of the snow situation when the birds first arrive; if the spring is late with much snow some birds may return to an adjacent area that is more benevolent. Another explanation is that the birds are discouraged from continuing migration to their breeding area if the weather is bad over larger areas which they pass during migration. A third explanation is that a proportion of the birds, mainly yearlings, refrain from breeding in late seasons.

Hour of laying and interval between eggs

Earlier studies of egg-laying were often influenced by the data compiled and interpreted by Skutch (1952) for Central America (9°N) and Schifferli (1979) for Europe. During the 1990s several authors considered these reviews to be based on poor data and that they were not reliable about the laying interval. However, many recent papers from North America and Europe confirm that the majority of passerines lay the eggs in early morning soon after sunrise 24 hours apart. Four species of tits Paridae, breeding in nest-boxes, is an example of this very regular egg-laying; Haftorn (1996) found that the eggs were laid within a narrow interval of 1–43 minutes after sunrise at Trondheim (63° N) in Norway. The selective advantage of laying in the early morning, i.e. about sunrise directly after the night rest, is most often explained by the female having reduced agility with an egg ready to be laid, which in turn reduces here ability to feed and avoid predation.

Already Skutch (1952) found that thrushes Turdidae were exceptional and that the hour of egg-laying could vary. According to Hohlt (1957) the first egg was laid between 0900 and 1630 in seven Fieldfare clutches. The second egg was laid next day before 1200 hours, but regrettably the exact interval for each clutch was not given. Our data now demonstrate clearly that Fieldfares lay the first egg at different times of the day although with concentration in the afternoon, and that laying then continues with an interval of c. 22 hours (Table 2).

Also the Redwing *Turdus iliacus* lays eggs during all parts of the day, the interval between eggs being c. 20 hours (Arheimer 1978a). For the Blackbird *Turdus merula*, Steinbacher (1941) found that it also laid eggs during different hours of the day, and Snow (1958) found that it most often laid between 0800 and 1200, but also after noon. Song Thrushes *Turdus philomelos* laid 48 eggs before 1300 hours and 12 eggs 1300–1800 hours (Picula 1969). In the American Robin *Turdus migratorius*, 37 eggs in 17 clutches were laid 0730–1800, average 1130 hours (Weatherhead et al. 1991). However, in none of these studies was the interval between the eggs measured; hence our studies seem to be the only ones explicitly addressing this question. It would be very interesting to investigate whether not only the Redwing and Fieldfare but also other thrushes lay eggs less than 24 hours apart, a strategy that may have developed because of the heavy nest depredation in the early part of the nesting season.

A study by Håland (1986) raises another question related to the laying interval, namely intra-specific egg parasitism. Håland suggests that this phenomenon may occur in the Fieldfare, based on finding two new eggs in a nest between his daily visits. However, this interpretation is based on the assumption of a 24 hour laying interval. In our study, comprising about one hundred nests where laying was monitored closely and the eggs were numbered as they were laid, no extra egg has ever been found. It is therefore likely that Håland's observation was a misinterpretation of a case when the same female laid two eggs within the 24 hours between his visits. In our opinion, this was also the case in the study by Ringsby et al. (1993). They interpreted their results as a parasitism rate of 11.5% (they found two eggs within 24 hours in 26 of 226 nests). They visited the nests once a day at about noon. If the interval between eggs were the same at their site as at Ammarnäs, c. 22 hours, one would expect a high incidence of two eggs between visits. A simple calculation shows that a frequency as high as 37% is to be expected if visits are paid 24 hours apart, the laying interval is 22 hours, the laying of the first egg is randomly distributed over all 24 hours, and if clutch size is equally divided between five and six eggs. Hence, there is no reason to believe that parasitism exists at all in the Fieldfare; occasional foreign eggs in a nest can easily be explained as mistakes, not a parasitic strategy. It is therefore a vain attempt to base a discussion of anti-parasite strategies on the erroneous assumption that parasitism is common (Ringsby et al. 1993). Also a paper by Grendstad et al. (1999) deals with anti-parasite strategies in the Redwing. We like to point out that also these authors accept the erroneous assumption of intra-specific egg parasitism in this species.

The Cuckoo *Cuculus canorus* was common in our study area but eggs or nestlings of the Cuckoo were never recorded in any of our c. 2600 nests. It was the same in the Redwing with c. 600 nest records during forty years. We have also never found eggs or nestlings of the Fieldfare in a Redwing nest, or vice versa. We therefore conclude that the Fieldfare neither lays parasitic eggs, nor is exposed to parasitic laying, neither by other thrushes, nor by the Cuckoo. No *Turdus* species is known to be a preferred Cuckoo host (Soler et al. 1999).

Clutch size

It has earlier been shown that there is no significant difference between clutch size in Germany and northern Scandinavia (table 4 in Arheimer 1987). More recent publications do not change this conclusion. Near the Atlantic coast at Trondheim (63° N), Lerkelund et al. (1993) found clutch size to be 5.50 (s.d.=0.64; n=102 nests) and 5.41 (s.d.=0.61; n=99) in two different data sets. Reitan & Sandvik (1994) gave the value 5.25 (s.d.=0.72;n=701) for the pooled five year data at Innerdalen (62° N). In the latter study, 87% of the clutches were 5 or 6 eggs, which is very close to the same predominant sizes at Ammarnäs (92%). However, there is a difference in the proportion of five and six egg clutches at the two sites, explaining a small difference. At Innerdalen, 51% of all clutches were 5-egg clutches and 36% 6-egg clutches. At Ammarnäs the corresponding proportions were 45% and 47%. There is no significant difference between Trondheim and Ammarnäs, whereas the lower value at Innerdalen is significantly different from both Trondheim (t=3.66; p<0.001) and Ammarnäs (t=5.53; p<0.001).

The difference between the highest annual mean clutch size in 1992 (5.74; s.d.=0.52; n=47) and the lowest one in 2001 (5.11; s.d.=0.46; n=36) is significant (t=5.7; p<0.001), and a few other annual means were also significantly different. However, in the vast majority of cases, the annual means did not differ between colonies. In contrast, there was no difference between the colony averages. The three colonies that were studied in most years (colony 2, 4, and 5) had very similar mean clutch sizes with a maximum difference of only 0.06 eggs, which was far from significant (Appendix 2). The declining clutch size with the progress of the season is similar to what has been found in other Scandinavian studies (von Haartman 1969, Otto 1979, Slagsvold & Sæther 1979, Wiklund 1983, Arheimer 1987, Reitan & Sandvik 1994).

That mean clutch size did not differ between early and late years (Figure 5D) deserves comment. In two other species a significant decline of mean clutch size with average egg-laying date has been found at Ammarnäs: Sand Martin *Riparia riparia* (1969–1985; Svensson 1986) and Pied Flycatcher *Ficedula hypoleuca* (1972–1985; Svensson 1987). Interestingly, this absence of decline was also found in the Redwing (Arheimer 1978b). According to the review by Klomp (1970) the former pattern seems to be more common than the latter. Since most explanations of smaller clutch size in late than in early seasons involve food we note that the species with such decline at Ammarnäs are insectivorous whereas the thrushes feed mainly on eartworms that live in soil and litter. This food source may be more stable over a longer period of time as soon as the snow has melted away. If so, adaptation to an early decline of food for the nestlings has not been necessary.

Incubation and egg hatchability

The result of our study, with 96% of all eggs hatched in clutches that survived through hatching and with all eggs hatching in 80% of the clutches, is somewhat better than found in other Scandinavian studies. Slagsvold (1982) reported that all eggs hatched in 64% of 74 5-egg and 77 6-egg clutches. In 5-egg and 6-egg clutches, 11.1% and 9.5% of the eggs did not hatch, which is more than twice as high as in our study (Table 4). The proportion of clutches with one egg that did not hatch was as high as 23%, compared with 8% in our study. In contrast, Lerkelund et al. (1993), working in the same habitat as Slagsvold at the coast near Trondheim, found about the same hatchability as at Ammarnäs; 95% of all eggs hatched, and all eggs hatched in 74% of the clutches.

Wiklund (1984) found that 93% of the eggs hatched at Staloluokta, and he also found one exceptional year (1979) with only 88% of the eggs hatching (Wiklund 1985); no such year was recorded at Ammarnäs, where the lowest value was 93% in 1998. Wiklund also found that the proportion of clutches with at least one unhatched egg was twice as high (32%) in 6-egg as in 4- and 5-egg clutches (15% and 16%). No such difference was found at Ammarnäs.

The three eggs with dead embryos in 7-egg clutches (Table 4) belonged to different clutches. Of the five eggs without visible embryos in three other clutches, two were found in each of two different clutches. The suggestion by Lerkelund et al. (1993), that a larger proportion of eggs would remain unhatched in naturally large clutches "because of wear and tear" by the parents is not supported by our findings. The proportion of unhatched eggs was not greater in 6-egg than in 5-egg clutches in our study (Table 4), and there is no indication that failed hatching in the 7-egg clutches should be a result of "wear and tear" since most of the eggs had no visible embryo.

No single eggs ever disappeared during the incubation period in our study, where the eggs of hundreds of clutches were numbered from the time the eggs were laid. The hatched eggs that did not result in a growing young were eggs where the young died during the 2–3 days long hatching phase, and the dead young were removed from the nest by the parents. This was concluded from the repeated visits during the incubation period and the frequent visits during the hatching phase.

Nest predation

Nest predators were the most important cause of complete loss of eggs and young (Figure 6), whereas starvation of whole broods due to cold weather was important only in occasional years (Figure 7). It was difficult to determine which predator that depredated a particular nest. However, a large number of spontaneous observations permit the following general account.

In most years it was probably the Hooded Crow *Corvus corone cornix* that was responsible for most of the depredation. Crows were breeding within the study area, and they flew rapidly into a colony in order to be able to take eggs or young before the attacks of the Fieldfares became so heavy that they were forced to leave. That the Fieldfare's nest defence by defecation (Bezzel 1975, Fürrer 1975, Meister 1976, Hogstad 1991) increases as breeding proceeds also when humans visit the nest (Hogstad 1991) was really confirmed during our field work. The precision of homing in on the intruder and hitting his face was impressive when the nestlings were almost fledged.

The Raven *Corvus corax* did not breed in the study area but depredated heavily in occasional years. In one year, a colony with c. 20 nests was almost completely depredated during two days in mid-June by one Raven pair. About every second hour they flew to their nest four kilometres away with their beaks loaded with Fieldfare nestlings.

The weasel *Mustela vulgaris* sometimes had its nest under one of a few small buildings at colony 5 and was often observed with thrush nestlings in its mouth. When it had depredated a nest with large nestlings, the nest often contained rests of body parts, wing quills or blood spots. On one occasion, nine undamaged eggs were found under a tree stump, probably gathered by a weasel. Damaged eggs that remained in depredated nests sometimes showed the symmetric bite marks from the canine teeth of a weasel. When a crow damaged eggs in the nest, the shells were crushed irregularly. A stoat *Mustela erminea* was one day seen passing through colony 2, preying upon several nests, and leaving remains of dead nestlings in the nests. In 1978, nine Fieldfare nests in colony 1 were supplied with activity recorders of the same kind as used for Redwings (Arheimer 1978c). On 20 June a female stoat with three large young was observed in the colony. In five of the nests, intensive activity for about one minute was recorded during the next twenty-four hours. After these brief spurts of activity, no further activity was recorded. At two of the depredated nests, a killed adult female Fieldfare was found. In the nests, there were remains of nestlings about one week old.

In 1984, 1988, and 2001, a Merlin *Falco columbarius* pair was breeding within colony 5. The total predation in that colony was zero in 1984 and 1988, and in 2001 only 3% of the nests were depredated early in the periphery of the colony (only early depredation known in this year). The predation rate in the other colonies these years was about average or higher. Hence this is another observation of the well-known protective effect that the Merlin has when these two species breed at the same place (Hogstad 1981, Wiklund 1982).

Reported predation rates in other Scandinavian studies vary. Low rates were found at Trondheim, namely 15–25% (Slagsvold 1982, Lerkelund et al. 1993) and 20–25% (Meilvang et al. 1997). Both Slagsvold and Meilvang found several dead adult Fieldfares in the nests, indicating depredation by a weasel or stoat. At Staloluokta (Wiklund 1985), nest predation (45%) was similar to that at Ammarnäs (46%; Appendix 2), and the variation was also very large, from 8–9% in 1972 to 100 in 1975 (5–81% at Ammarnäs). The study at Budal (Hogstad 1983a) showed a predation pattern that was quite different from all the other. First, it was extremely high, 90%. Second, 13% of the depredation was partial. Partial depredation has not been observed in any other study, including ours. And even if one excludes partial predation, predation was higher at Budal than at any other site.

Nestling mortality and weather

Bad weather with ensuing starvation was the most important factor of nestling death in broods that were not depredated. This was the case in four of the ten years when this mortality factor was recorded. In other years weather was marginal or absent as a cause of nestling mortality. This means that the frequency of years with bad weather during the nestling phase is a key factor for long-term recruitment. Should future climate change involve cooler and rainier weather in June, the Fieldfare may encounter difficulties in maintaining population size.

In broods with partial losses, it was always the youngest nestling that died first, thereafter the next youngest. The explanation is the different size of the young (Wiklund 1985), in turn explained by the hatching sequence of the eggs (Enemar & Arheimer 1980, Slagsvold 1982). When the parents had difficulties of finding enough food for all their young in the brood, the smallest ones were rapidly trampled down by the larger ones. This brood reduction occurred almost always during the first days after hatching. In1990, the pattern of mortality was unusual. The proportion of nests that was lost was low after the high early depredation (Figure 6). The late total losses were peculiar, especially in nests along the shore of the lake. Several broods with 4–5 young died almost simultaneously after slow weight gain in the middle of the nestling period. Bad weather could not explain their death. Eight young from three of these nests were examined by the National Veterinary Institute at Uppsala. The young were emaciated, but there was no sign of bacteriological, parasitological or histological disease. Emaciation was indicated already in the field by easily visible small subcutaneous blood-filled oedema. Obviously, the parents were not able to collect enough food for their young but for reasons that we could not determine.

Replacement and second clutches

In central Europe, where the Fieldfare may lay eggs during more than three months, a female that looses a clutch most often move to a new breeding area if attempting to lay a replacement clutch. True second clutches, proved by ringed females, are rare (Gülland et al. 1972, Lübcke 1975, Fürrer 1978, 1979, Haas 1978, 1982).

At Ammarnäs, egg-laying was initiated within a period of 20 days and almost all clutches were started during the first two weeks of an individual year. In the distribution of dates (Figure 3B) there is no indication that replacement clutches occur at Ammarnäs. The high early depredation of nests (Figure 6) in many years must have caused a much more distributed period of egg-laying than the one we found. This conclusion is supported by the fact that the five females with radio transmitters rapidly disappeared after depredation. Wiklund (1983) also found that all Fieldfares left the area without any attempt of replacement clutches in 1975, a year with total depredation.

A true second clutch has been recorded only once in the Scandinavian mountain range, namely at Budal (62°45' N; Hogstad 1983b). The interval between the first eggs of the two clutches would have been as short as about 28 days. In the Ammarnäs data set (65° 58'), 28 days or more between the first and a later clutch in a season has occurred only in 1984, 2000 and 2002 (Figure 4). Only twelve clutches are involved, eight of them in 1984. In these eight clutches the first egg was laid 31–37 days after the earliest clutch (figure 2 in Arheimer 1987). These could possibly have been second clutches since June was favourable with rather high temperature without cold spells and with light rains evenly distributed. Food was abundant since 1984 was a peak year of the autumn moth *Epirrita autumnata* (Selås et al. 2001), and the Fieldfares were observed to exploit this food source instead of their usual earthworms. That they fed the young with the caterpillars was evidenced by the expanded bellies that appeared greenish because of the large content of caterpillars. Hence, the combination of several beneficial conditions might have inspired some Fieldfares to try a second clutch this particular year.

Wiklund (1984), at Staloluokta (67°18' N), found during eight years only one clutch that theoretically could have been a second clutch. Also in this area, the adults usually left the breeding site together with their young immediately after fledging, as did the Ammarnäs birds with radio transmitters. In conclusion, both replacement and true second clutches are extremely rare exceptions of the breeding strategy of Fieldfares in the subalpine birch forests of Scandinavia.

Final reproductive result

The result of 4.45 ten days old young in successful broods (Appendix 4) is good. It means that only 0.97 eggs did not result in a fledgling in these broods since the mean clutch size was 5.42 (Appendix 3). The final reproductive output (2.11 fledglings per pair in the population (Appendix 4) is similar to what was found in studies from both Scandinavia (1.4–1.6 by Pulliainen & Saari 2002) and Germany (1.8 by Hohlt 1957, and 2.4 by Gülland et al. 1972).

We would like to stress how important it is to calculate reproductive success on the basis of a correct estimate of population size, that is with all pairs, also those that fail, included. Figure 8 illustrates this. If only successful nests were included, average number of fledglings was between four and five with moderate variation between years. If all breeding attempts, representing the total number of pairs in the population, were included, breeding success declined to only about two fledglings per pair. The fact that this correct estimate of breeding success could be calculated in our study depended on the intensive field work that made it possible to include the nests of all pairs, including those that were depredated early.

Mortality and recruitment

It was not possible to determine all necessary demographic parameters to see whether the Ammarnäs Fieldfares represent a source or sink population. The number of fledglings is known, but how many of them that survived until next year could not be determined explicitly. However, thanks to the spring trapping project (Roland Sandberg) we could estimate adult survival. Since our study population was stable over a long period of time, mortality must have been balanced by recruitment (local or immigration). We assume that the spring trappings which were made in the period 18 May to 10 June, 1988–2002, trapped one year old and older birds in unbiased proportions. Then the proportion of birds older than one year equals adult survival. This was found to be 58% (S.E=3.4%; 14 years and 434 trapped Fieldfares). With 2.11 fledglings per pair, first year survival rate of fledglings must then be 39–40% to balance adult mortality. Whether this value of forty percent is high or low evades our objective judgment. Fieldfare young left the study area soon after they had fledged, and could not be followed during the post-fledging period, when mortality is assumed to be high. We know that the Fieldfares left the area soon both from the radio transmitter experiment in late June and from trappings from 15 July to 20 August (1983–2000) when an annual average of only three adults and three yearlings were trapped (Lindström & Lind 2001). The estimate of adult survival of the Fieldfare was similar to that of the Redwing at Ammarnäs that was 61% (234 trapped birds).

About two fledglings or less per pair and year also seems to be a typical outcome and the same result has been found in several studies, both of Fieldfares and other large thrushes (e.g. 2.5 in Blackbird in spite of two annual broods; Tomiałojć 1994). The critical question is whether the indirectly calculated survival rate of 40% during the first year is representative of the local population or if immigration is involved (which must be the case if 40% is an overestimate). In a study of Song Thrush *Turdus philomelos* Thomson et al. (1997) found first-year survival to be 48% during a period with stable population size and 40% during a period of population decline. In spite of some uncertainties, we conclude that it is likely that the Ammarnäs Fieldfare population is stable because reproduction is sufficient to balance mortality. This means that we refute the statement by Pulliainen & Saari (2002) that the Fieldfare is poorly adapted to the climatic conditions in northern Scandinavia. That their particular study population showed very low fecundity must be a local exception. Generally the phenomenal expansion of the species over much of northern Europe and in most wooded habitats proves the opposite, that the Fieldfare is a well adapted species under most prevailing conditions.

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Sammanfattning

Tre arter av trast häckar regelbundet i fjällbjörkskog, nämligen rödvingetrast, björktrast och taltrast. Häckningsbiologin hos de två förstnämnda arterna studerades i denna biotop i trakten av Ammarnäs i södra Lappland från 1960-talet fram till början av 1980-talet. Särskilt rödvingetrasten var föremål för en omfattande studie. En analys av på olika sätt insamlade data om björktrasten åren 1965–1985 har publicerats (Arheimer 1987). Från 1983 systematiserades studierna av björktrasten och har sedan fortsatt till och med 2002. Det är resultaten från denna tjugoårsperiod som redovisas i denna uppsats. Undersökningen bedrevs under arton av de tjugo åren (undantag var 1986 och 1989). Studien utgör en del av det s.k. Luvre-projektet, som bedrivits i Ammarnästrakten sedan 1963.

Undersökningsområdet omfattade björkskogen på sluttningarna av Gaisatjåkke och Valle 3–8 km väster om Ammarnäs by (Figur 1). Området begränsades i norr av skogsgränsen, i söder av Stora Tjulträsk och Tjulån, i väster av Rödingbäcken och i öster av Karsbäcken. Området var totalt nio kvadratkilometer och omfattade höjdnivåerna mellan 500 och 750 meter över havet. Björktrastarna häckade i sex kolonier i områdets östra del på 500–600 meters nivå. Vi hänvisar till kolonierna med siffrorna 1–6 enligt Figur 1. Närmaste större koloni låg vid Rödingvik alldeles väster om undersökningsområdet. Hela det nio kvadratkilometer stora området undersöktes varje år, men någon ny koloni upptäcktes aldrig. Inom hela västra delen av området, mellan kolonierna 1 och 2 och Rödingbäcken, häckade bara ett mindre antal solitära par.

Biotopen var björkskog med inslag av främst sälg, delvis rik och frodig ängsbjörkskog, delvis torrare hedbjörkskog. Undervegetationen bestod av viden, enbuskar och höga örter, bl.a. stormhatt och tolta. I östra delen av området, där kolonierna låg, fanns också flera små myrar och öppna områden som tidigare använts för slåtter. I Figur 2 visas några biotopfoton. Dessa är tagna på sommaren. När trastarna börjar häcka är träden fortfarande kala och örterna håller just på att komma upp. Snö kan ofta täcka en stor del av skogen vid denna tidpunkt.

Antal par

Tabell 1 visar antal par de år en koloni studerades. Alla sex kolonierna kunde inte studeras alla år, men tre av kolonierna följdes nästan alla år. Koloni 6 minskade mot slutet av 1980-talet och följdes inte efter 1988. För att uppskatta den totala populationsstorleken med alla kolonier inräknade antog vi att antal par i en koloni ett år då kolonin inte räknades var lika med medeltalet för åren då den räknades. Vi får då en genomsnittlig populationsstorlek på 155–165 par. Osäkerheten beror på koloni 6. Vi gjorde en trendberäkning med hjälp av TRIM (van Strien m.fl. 2000), en metod som optimerar informationen från tidsserier med luckor. Det fanns ingen långtidstrend i beståndet vare sig vi inte gjorde något antagande om koloni 6 eller antog att dess storlek var noll efter 1988. Fastän det inte fanns någon långtidstrend var variationen mellan åren betydande med ungefär halva antalet par de sämsta jämfört med de bästa åren. Även ett annat inventeringsprojekt inom undersökningsområdet fann att långtidstrend för björktrasten saknades, och därutöver visar Svenska häckfågeltaxeringen på samma sak för landet som helhet. Slutsatsen om stabil population är viktig för vår kommande beräkning av huruvida rekryteringen balanserar dödligheten eller om fjällbjörkskogens björktrastar är beroende av immigration.

Häckningsstarten

Den totala perioden för häckningsstart (första ägget) var 39 dagar. Det tidigaste datumet var 16 maj 2002 i koloni 4 och det senaste 23 juni 1998 i koloni 5 (Figur 3A; Appendix 1). Medeldatum för alla kullar var 31 maj. Inom varje enskilt år var koncentrationen större, oftast 20 dagar eller mindre (Figur 4). De flesta kullar startades inom fem dagar från första läggningen (Figur 3B). Varken första datum, medeldatum eller mediandatum visade någon trend över tiden. Detta stämmer överens med att det inte heller fanns någon trend för temperaturen under de tjugo åren. Förekomsten av eventuella temperaturtrender analyserades för perioderna 15–31 maj, 1–15 juni och 15 maj–15 juni, dvs. perioder som är kritiska för björktrastens häckningsstart. Regressionernas lutning skilde sig föga från noll och var fjärran från signifikanta. Samma avsaknad av temperaturförändring under fåglarnas häckningsstart i Ammarnäs har för övrigt gällt under hela den period som vi bedrivit fågelstudier i Ammarnäs (sedan 1963).

Klockslag och intervall mellan äggläggning

Trettio kullar studerades noga i detta avseende. Första ägget i kullen lades mellan klockan 09.00 och 11.00 i tre bon, mellan 11.00 och 16.00 i arton bon, mellan 16.00 och 23.00 i sju bon och omedelbart efter midnatt i två bon. Sista ägget lades mellan klockan 23.00 och 07.00 i 21 bon och mellan 07.00 och 12.00 i sju bon. I de två bon där första ägget lades omedelbart efter midnatt lades sista ägget på eftermiddagen. Resultaten visas i Tabell 2 där också detaljdata för fyra typiska bon redovisas. Med hjälp av sådana detaljdata för samtliga bon beräknades de möjliga intervallen mellan äggen med hjälp av följande formel (Watson m.fl. 1993): längsta intervall = [klockslag(sista ägg funnet) − klockslag(besöket före första ägg funnet)]/(kullstorlek − 1); kortaste intervall = [klockslag(besöket före sista ägg funnet) − klockslag(första ägg funnet)]/(kullstorlek − 1). Vi fann att björktrasten lägger sina ägg med kortare intervall än 24 timmar, nämligen i medeltal ca 21 timmar och 45 minuter. Förutom att björktrasten kan börja äggläggningen nästan när som helst under dygnet, innebär det kortare intervallet att äggläggningen blir spridd på nästan vilka klockslag som helst. I detta avseende liknar björktrasten rödvingetrasten, som lägger ägg med ca 20 timmars mellanrum i Ammarnäs. De flesta fåglar lägger ägg tidigt på morgonen och med 24 timmars intervall. Björktrasten förkortar således tiden för äggläggningen med nio procent, vilket kan vara av betydelse för att reducera predationen. Det vore intressant att undersöka om denna förkortning även förekommer hos andra trastarter.

Kullstorlek

De dominerande kullstorlekarna var 5 och 6 ägg, i medeltal 5,42 ägg (Tabell 3). Kullstorleken varierade både mellan år och mellan kolonier (Appendix 3). Kullstorleken minskade under säsongen. I förhållande till kalenderdatum var nedgången 0,023 ägg per dag under perioden 22 maj–9 juni (Figur 5A). Inom säsongen, dvs. i relation till första läggdatum, var nedgången ännu snabbare, nämligen 0,090 ägg per dag under de första tio dagarna (Figur 5B, 5C). Av diagrammet i Figur 5A framgår att de allra tidigaste kullarna var mindre än de som lades några få dagar senare. Nästan alla dessa kullar kommer dock från ett starkt avvikande år (2002) och kan därför inte tolkas som ett allmängiltigt mönster för kullstorleksförändringen hos björktrast.

Björktrasten uppvisade inte någon trend för medelkullen mot medeldatum för läggningen (Figur 5D). I detta avseende liknar björktrasten rödvingetrasten men skiljer sig från andra arter i samma biotop i Ammarnäs. Svartvit flugsnappare och backsvala lägger signifikant mindre medelkullar under sena jämfört med tidiga år. Det senare verkar vara det vanligaste mönstret bland fåglar i allmänhet. Möjligen kan detta ha att göra med olika arters födoval och därmed födotillgång under häckningstiden. Trastar matar sina ungar med evertebrater som lever i jorden (mest daggmask) och i förnan. Kanske är denna födokälla stabil under en lång period under våren medan insektsätare måste anpassa sig till en kortvarigare födotillgång.

Kläckbarhet

Kläckbarheten hos äggen var hög (Tabell 4). Om boet inte plundrades eller övergavs kläcktes 96% (93–97%) av äggen och i 80% (76–88%, undantag 64% 1998) av bona kläcktes samtliga ägg, och variationen mellan åren var liten. I bon där inte alla ägg kläcktes var det vanligaste att bara ett ägg förblev okläckt. Av 179 okläckta ägg hade 67 ett dött embryo. Det fanns ingen skillnad i kläckbarhet mellan olika kullstorlekar. Det fanns heller ingen tidsmässig trend i kläckbarhet över åren. Variationer i äggens kläckbarhet synes alltså vara en faktor som har ringa betydelse för björktrastens populationsdynamik.

Förlust av bon och ungar

En stor andel av alla bon hade förlorats på ett tidigt stadium, redan före första besöket (Figur 6). I alla dessa bon pågick äggläggning eller ruvning. Denna tidiga predation uppgick till 29% under alla år men var extremt variabel. Exempelvis var koloni 3 1992 och koloni 2 1999 redan helt plundrade vid första besöket medan 1995 var helt fri från tidig predation. Efter första besöket varje år tillkom sedan ytterligare predation under resten av ruvningen och under ungtiden. Den totala predationen uppgick till 46% av alla bon. Till detta kom sedan 6% av bona som registrerades som övergivna. Predationen innebar att endast 48% (S.E.=5.5%) av häckningsförsöken blev framgångsrika, dvs. producerade minst en flygg unge.

Svält vid kallt väder var en betydande dödsorsak bland ungarna vissa år (Figur 7). Förluster av hela kullar på grund av svält var koncentrerade till fyra år. Tre av åren (1993, 1994 och 2000) var vädret dåligt under stora delar av boungetiden. Det var flera perioder med mycket regn (40–50 mm totalt) i kombination med mycket låga medeldygnstemperaturer. Det fjärde året, 1995, var det en 24 timmar lång storm med temperaturer på fem till sju grader som orsakade kullarnas död mot slutet av stormen. Flera år var svält också orsak till omfattande partiell dödlighet, särskilt 1996 och 1997. De ungar som dog i bon där inte alla ungar dog var alltid de minsta. De klarade inte konkurrensen när mattillförseln tröt utan trampades ner av de större ungarna. Under år med gynnsamt väder var ungdödligheten ringa i bon som inte plundrades. Ett sådant år var 2002 då dagstemperaturen var 15–25 grader, nattemperaturen 5–10 grader och lätta regn föll och gjorde maskar lätt tillgängliga.

Antal flygga ungar

Antal flygga ungar kan uttryckas på olika sätt beroende på vilka kategorier av bon som räknas in (Appendix 2 och 4). Medeltalet flygga ungar i framgångsrika bon (minst en flygg unge) var 4,45 (S.E. 0,134; 609 bon). Samma beräkning för bon med fullagd kull ger medelvärdet 2,92 flygga (S.E.=0,273; 975 bon), vilket är 1,5 ungar mindre. Om vi också inkluderar de bon som plundrades före full kull blir medelvärdet 2,11 (S.E.=0,283; 1906 bon). Detta värde är således det antal ungar som producerades per par som gjorde häckningsförsök i vår studiepopulation.

Antalet flygga ungar ökade med ökande kullstorlek till en kullstorlek om 6 ägg (Tabell 5). Men ökningen med ett ägg från fem till sex ägg, de två dominerande kullstorlekarna, resulterade i mindre än en halv unge mer.

Det fanns ingen trend i antal ungar per lyckad häckning över studieperioden (Figur 8). Däremot fanns det en signifikant negativ trend för de andra två kategorierna i Figur 8. Dessa negativa trender beror dock helt på de osedvanligt framgångsrika åren 1984 och 1985. I perspektivet av hela tjugoårsperioden tror vi därför att de låga värdena med ungefär två ungar per par är det mest typiska för björktrasten i fjällbjörkskogen.

Föräldrarnas beteende efter häckningen

För att studera vad honorna gör om de förlorar sin kull försågs nio honor med radiosändare. Radiosändarnas funktion kontrollerades med hjälp av två sändare som placerades på marken i två av kolonierna. Fåglarna pejlades från upphöjda punkter i terrängen. Räckvidden visade sig vara minst 1,5 km och sändarna fungerade under hela undersökningsperioden. Fem av honorna utsattes för predation. De förlorade sina kullar 3 dagar före kläckningen, vid kläckningen samt 2, 3 respektive 8 dagar efter kläckningen. Dessa honor uppehöll sig i boets närhet 1–4 dagar efter förlusten av äggen eller ungarna. Fyra av honorna försvann därefter helt och hållet från området. En hona registrerades vid ett enda tillfälle i en annan dalgång elva kilometer från boplatsen 17 dygn efter förlusten av sin kull, som innehöll ca fyra dagar gamla ungar. De fyra honor som lyckades med häckningen matade sina ungar i kolonin 2–4 dagar efter utflygningen. Men därefter lämnade även dessa området helt och hållet.

Försöket visar att björktrastarna lämnar häckningsområdet nästan omedelbart vare sig de misslyckas eller lyckas med häckningen. Orsaken till detta är okänd. Det faktum att honorna som misslyckades med häckningen genast försvann kan inte förklaras med födobrist eftersom övriga honor kunde fortsätta att föda upp sina ungar. Huruvida övergivandet av området efter framgångsrik häckning har något med födotillgången att göra har inte studerats. Försöket visar också att det inte sker några omläggningar efter predation i slutet av ruvningstiden eller under ungtiden utan fåglarna upphör med häckningen för säsongen.

Att björktrastarna evakuerar häckningsterrängen snabbt stöds också av många års standardiserad ringmärkning under senare halvan av juli och början av augusti inom området för koloni 3. Under perioden 1983–2001 fångades endast 63 adulta och 58 juvenila björktrastar, vilket bara är sex björktrastar per år. Totalt har vi ringmärkt över 3000 björktrastar inom undersökningsområdet men bara fått fem återfynd under häckningstid. Detta är dock inte överraskande eftersom flertalet märkta fåglar varit boungar som normalt saknar hemortstrohet.

Omläggning och andrakullar

Vi har inga indikationer på att omläggning eller andrakullar förekommer hos björktrasten i fjällbjörkskogen. Läggningstiderna (Figur 5), särskilt inom säsongen (Figur 5B), visar att äggläggningen är starkt koncentrerad och saknar nämnvärt antal sena kullar. Om omläggning förekom borde det finnas ett betydande antal sena kullar med tanke på den höga tidiga predationen. Förekom andrakullar borde det finnas en andra topp av läggningsdatum ett lämpligt tidsintervall efter den första toppen, men någon sådan topp finns inte. Vi är säkra på att vi inte har missat några sena häckningar eftersom hela det nio kvadratkilometer stora undersökningsområdet genomsöktes varje år de sista dagarna av häckningsperioden.

Ett enda år, 1984, var äggläggningen så utsträckt i tiden (Figur 4) att åtta kullar rent teoretiskt skulle ha kunnat vara andrakullar. Just 1984 var speciellt såtillvida att juni var varm utan köldperioder och med lätta spridda regn. Födotillgången var extremt god tack vare toppår för larver av fjällbjörkmätare. Björktrastarna sågs exploatera denna födokälla i stället för de sedvanliga daggmaskarna. Det kan alltså ha varit de ovanligt gynnsamma betingelserna som fick några par att försöka sig på en andra kull detta år, men i avsaknad av ringmärkta honor saknas bevis. Endast en gång har en säker andrakull hos björktrast konstaterats i de skandinaviska fjällen, nämligen i Budal i Norge. En flerårig undersökning i Staloluokta visar samma sak; en enda kull kunde teoretiskt ha varit en andrakull. Slutsatsen är att de få ungar som undantagsvis kan ha producerats genom omläggningar och andrakullar inte behöver beaktas när man uppskattar ungproduktionen i fjällbjörkskogen.

Dödlighet och rekrytering

För att undersöka om en population är självförsörjande med ungar eller beroende av inflyttning från andra populationer måste egentligen alla populationsparametrar vara kända. För björktrasten i Ammarnäs känner vi produktionen av flygga ungar som är 2,11 per par. Dödligheten för de adulta fåglarna har vi kunnat beräkna tack vare ett annat projekt som bedrivits inom koloni 5 under perioden 18 maj–19 jun 1988–2002. Där bedrevs standardiserad nätfångst av fåglar varvid 434 björktrastar fångades. Av dessa var 58% (S.E. 3,4%) äldre än ett år. Under förutsättning att fåglar av olika ålder fångas i korrekta proportioner är andelen adulta fåglar lika med dödligheten hos dessa. Eftersom björktrastbeståndet i Ammarnäs var långsiktigt stabilt kan vi därför uppskatta hur stor överlevnaden för ungarna minst måste vara i genomsitt under deras första levnadsår. Den måste vara minst 39–40%. Huruvida detta är ett rimligt värde kan vi inte säkert avgöra från egna data eftersom vi inte vet något om ungarnas öden efter utflygningen. Men med tanke på motsvarande data från många olika arter och björktrastens storlek förefaller värdet vara rimligt.

Ungefär två ungar per par och år tycks vara ett rätt typiskt värde för björktrast och andra större trastar. Inte ens hos koltrasten, som studerats noga i naturlig skogsmiljö i Polen, där den lägger två kullar om året, producerades mer än 2,5 ungar per par och år. Den kritiska frågan är överlevnaden bland ungfåglarna under det första året. En beräkning för taltrast i England visade på 48% överlevnad under en period av stabilt bestånd och 40% under en period av populationsnedgång. Vi har inte hittat några tillförlitliga värden för björktrastens ungfåglar, men bedömer ändå att det är högst rimligt att mer än 40% av ungfåglarna överlever och därför kan rekryteras som häckare nästa år. Vår slutsats är därför att björktrasten utgör en självföryngrande population i fjällbjörkskogen i Ammarnäs.

Appendix 1. Periods of inspection and date of first and last first egg in the different colonies and years. M = May, J = June. When the June date is larger than 30 it refers to a July date (e.g. J 32 is 2 July). Shaded cells for colony 2 show unreliable first dates because of depredations before first visit.

Perioder då kontroller utförts samt datum för tidigaste och senaste första ägg i de olika kolonierna olika år. M = maj, J = juni. När ett junidatum är större än 30 avses datum i juli (t.ex. J 32 är 2 juli). Skuggade celler för koloni 2 anger otillförlitliga tidigaste datum på grund av predation före första besöket.

	Colony 1				**Colony 2**				**Colony 3**				**Colony 4**				**Colony 5**				**Colony 6**			
	First visit	Last visit	First egg1	Last egg1	First visit	Last visit	First egg1	Last egg1	First visit	Last visit	First egg1	Last egg1	First visit	Last visit	First egg1	Last egg1	First visit	Last visit	First egg1	Last egg1	First visit	Last visit	First egg1	Last egg1
1983																	J 12	J 28	M 17	J 09				
1984					J 12	J 33	*M24*	J 12									J 11	J 33	M 17	J 22				
1985					J 19	J 30	*J 01*	J 16	J 15	J 32	J 03	J 11					J 13	J 32	M 31	J 15	J 14	J 32	J 03	J 09
1986																								
1987	J 12	J 32	M 29	J 08	J 12	J 32	M 30	J 06	J 09	J 32	J 02	J 06	J 11	J 32	J 01	J 04	J 08	J 32	M 31	J 10	J 10	J 32	M 30	J 06
1988	J 07	J 30	M 25	M 30	J 07	J 30	M 29	J 07	J 09	J 30	M 28	J 01	J 06	J 30	M 26	J 05	J 08	J 30	M 26	J 08	J 10	J 30	M 28	J 02
1989																								
1990	J 14	J 33	M 26	J 18	J 14	J 33	*M 27*	J 03					J 14	J 33	M 24	J 07								
1991	J 08	J 32	M 26	J 06	J 08	J 32	*J 06*	J 10					J 09	J 32	M 30	J 09	J 09	J32	M 27	J 08				
1992					J 07	J 26	M 25	M 31	J 07	J 26			J 06	J 26	M 24	J 09	J 05	J26	M 24	J 01				
1993					J 08	J 30	*M 28*	J 15					J 07	J 30	M 22	J 08	J 06	J30	M 20	J 09				
1994					J 10	J 32	*J 01*	J 11	J 10	J32	M 26	J 05	J 08	J 32	M 23	J 11	J 07	J 32	M 23	J 10				
1995					J 08	J 28	J 03	J 09	J 09	J 18	J 01	J 09	J 06	J 28	M 30	J 20	J 05	J 28	M 31	J 10				
1996	J 12	J 30	M 29	J 07	J 07	J 30	M 28	J 13					J 04	J 30	M 27	J 10	J 03	J 30	M 28	J 05				
1997					J 06	J 30	J 03	J 17					J 07	J 30	J 02	J 19	J 05	J 30	J 04	J 12				
1998	J 11	J 22	M 27	J 11	J 04	J 29	J 01	J 15					J 02	J 29	M30	J 11	J 03	J 29	J 03	J 23				
1999					J 06	J 27							J 05	J 27	M 24	J 08	J 04	J 27	M 26	J 08				
2000					J 04	J 24	M 21	M 24	J 05	J 24	M 20	J 15	J 07	J 24	M 19	J 04	J 06	J 24	M 21	J 17				
2001					M 26	J 09	*M 31*	J 04					M 25	J 09	M 21	J 04	M 24	J 09	M 20	J 07				
2002					J 03	J 26	*M 27*	M 28					M 28	J 26	M 16	J 16	M 28	J 26	M 19	J 15				

Appendix 2. Number of nests found and inspected in different years. No data for 1986 and 1989. ?* = Active nests that were not inspected were not recorded before 1992. ?** = No data on fledglings in 2001; study closed before hatching. Calc. = How numbers were calculated from other columns (Col.). *** These totals exclude cells with unknown value.

Antal påträffade och inspekterade bon olika år. Inga data för 1986 och 1989. ? = aktiva bon som inte inspekterades registrerades ej före 1992. ?** = Inga data om antal flygga 2001; studien avslutades före kläckningen. Calc. = Hur antal beräknades från andra kolumner (Col.). *** Dessa totaler exkluderar celler med okänt värde.*

	Active nests *Aktiva bon*		Nests with known fate (total loss or successful) *Bon med känt utfall (totalförlust eller lyckade)*						Nests with unknown fate *Bon med okänt utfall*			
	insp- ected *insp- ekte- rade*	not insp- ected *ej insp- ekte- rade*	Total *Totalt*	Lost before 1st visit *Förlust före 1:a besök*	Lost after 1st visit *Förlust efter 1:a besök*	Depre- dated *Prede- rade*	Des- erted *Över- givna*	Successful: ≥1 young 10 days old *Lyckade: ≥1 unge 10 dagar gammal*	Total *Totalt*	With egg laid *Med ägg lagt*	With full clutch *Med full kull*	With young hatched *Med unge kläckt*
Col.	A	B	C	D	E	F	G	H	I	J	K	L
Calc.	C+I		D+E+H		F+G				J+K+L			
1983	54	?*	54	22	6	6	0	26	0	0	0	0
1984	61	?*	53	2	1	1	0	50	8	0	8	0
1985	95	?*	66	8	5	4	1	53	29	0	7	22
1987	132	?*	115	52	30	27	3	33	17	1	5	11
1988	140	?*	114	48	51	47	4	15	26	0	15	11
1990	74	?*	71	21	9	4	5	41	3	0	0	3
1991	116	?*	90	42	10	7	3	38	26	0	2	24
1992	103	15	97	53	10	9	1	34	6	0	2	4
1993	141	10	138	85	23	14	9	30	3	0	1	2
1994	137	0	115	25	27	11	16	63	22	0	0	22
1995	121	10	82	0	37	16	21	45	39	1	22	16
1996	115	15	104	26	23	19	4	55	11	0	3	8
1997	78	14	62	10	15	12	3	37	16	2	6	8
1998	83	11	47	12	11	10	1	24	36	1	18	17
1999	102	0	92	38	23	18	5	31	10	0	6	4
2000	127	0	124	65	45	31	14	14	3	0	2	1
2001	137	12	66	48	18	12	6	?**	71	3	68	?**
2002	90	9	89	47	22	18	4	20	1	0	1	0
Total	1906	96***	1579	604	366	266	100	609***	327	8	166	153***

Appendix 3. Clutch size in different years and colonies. No survey of any colony in 1986 and 1989. A zero in the N column means that the colony was visited, but no clutch size could be determined. No value means that the colony was not visited.

Kullstorleken för olika år och kolonier. Inga studier gjordes i någon koloni 1986 och 1989. En nolla i kolumn N betyder att kolonin besöktes men att ingen kullstorlek kunde bestämmas. Avsaknad av värde betyder att kolonin inte besöktes.

Year	Colony 1			Colony 2			Colony 3			Colony 4			Colony 5			Colony 6			All colonies		
	m	sd	N	M	sd	N	m	sd	N	m	sd	N	m	sd	N	m	sd	N	m	sd	N
1983															0						0
1984						0							5.13	0.78	8				5.13	0.78	8
1985			0	5.75	0.43	16	5.33	0.62	12				5.22	0.72	41	5.61	0.59	18	5.41	0.67	87
1986																					-
1987	5.88	0.60	16	5.73	0.45	11	5.71	0.45	7	5.80	0.40	5	5.43	0.58	23	5.54	0.63	13	5.64	0.58	75
1988	6.17	0.37	6	5.43	0.73	7	5.60	0.61	15	5.23	0.73	22	5.43	0.56	28	5.50	0.76	6	5.46	0.68	84
1989																					-
1990	5.47	0.78	17	5.57	0.49	7				5.62	0.58	21							5.56	0.65	45
1991	5.37	0.58	19	5.40	0.49	5				5.37	0.62	27	5.21	0.61	19				5.33	0.60	70
1992				6.00	0.67	9				5.70	0.46	20	5.67	0.49	18				5.74	0.52	47
1993				5.43	0.49	7				5.07	0.70	14	5.55	0.61	31				5.40	0.66	52
1994				5.25	0.43	4	5.56	0.50	16	5.42	0.62	43	5.49	0.50	47				5.46	0.55	110
1995				5.44	0.50	16	5.47	0.62	15	5.54	0.72	68	5.75	0.70	20				5.55	0.68	119
1996	5.45	0.50	11	5.00	1.00	8				5.16	0.65	49	5.14	0.56	21				5.18	0.66	89
1997				5.67	0.58	18				5.58	0.63	26	5.63	0.58	19				5.62	0.60	63
1998	5.83	0.37	12	4.60	0.66	10				5.00	0.55	20	5.14	0.55	22				5.14	0.66	64
1999						0				5.65	0.60	31	5.30	0.78	30				5.48	0.72	61
2000				5.31	0.46	16	5.50	0.50	2	5.54	0.50	13	5.00	0.82	18				5.27	0.66	49
2001				5.38	0.48	8				5.47	0.72	15	5.35	0.58	54				5.38	0.60	77
2002				5.00	0.00	2				5.12	0.47	17	5.12	0.47	17				5.11	0.46	36
All	5.58	0.63	114	5.37	0.73	158	5.52	0.58	67	5.41	0.66	417	5.35	0.65	432	5.60	0.61	45	5.42	0.66	1233

Appendix 4. Number of fledglings per pair for different categories of nests. The row “Calc.” indicates how the values were calculated, with reference to column letters shown in row “Col”. No studies were made in 1986 and 1989, and no fledgling data were collected in 2001. The letters in rows “Nests” and “Calc.” with subscript one refer to corresponding columns in Appendix 2.

Antal flygga ungar per par för olika kategorier av bon. Raden ”Calc” anger hur värdena har beräknats med referens till kolumnernas bokstavsmarkeringar i raden ”Col”. Inga undersökningar gjordes åren 1986 och 1989 och inga data om antal flygga ungar insamlades 2001. Bokstäverna med en nedsänkt etta i raderna ”Nests” and ”Calc.” hänvisar till motsvarande kolumner i Appendix 2.

	Number of fledglings in nests *Antal flygga ungar i bon*					Mean number of fledglings per pair *Medeltal flygga ungar per par*			
	with known no. of fledglings *med känt antal flygga*	with unknown no. of fledglings *med okänt antal flygga*	inspected *inspekterade*	non-inspected *ej inspekterade*	all categories *alla kategorier*	With ≥1 fledgling *med ≥1 flygg unge*	Early depredated nests excluded *tidigt plundrade bon uteslutna*	Early depredated nests included *tidigt plundrade bon inkluderade*	Inspected and non-inspected nests *inspekterade och ej inspekterade bon*
Col.	M	N	O	P	Q	R	S	T	U
Nests	C_1-D_1	I_1	C_1-D_1+I_1	B_1	A_1+B_1	H_1	E_1+H_1+I_1	C_1+I_1	A_1+B_1
Calc.		$I_1 \times S$	M+N	$B_1 \times S$	O+P	M/H_1	O/(E_1+H_1+I_1)	O/(C_1+I_1)	N/(A_1+B_1)
1983	127	0	127	-	-	4.88	3.97	2.35	-
1984	265	42	307	-	-	5.30	5.20	5.03	-
1985	271	136	407	-	-	5.11	4.67	4.28	-
1987	158	43	201	-	-	4.79	2.51	1.52	-
1988	71	28	99	-	-	4.73	1.08	0.71	-
1990	140	8	148	-	-	3.41	2.80	2.01	-
1991	182	99	281	-	-	4.79	3.79	2.42	-
1992	169	23	192	58	250	4.97	3.84	1.86	2.12
1993	119	7	126	22	148	3.97	2.25	0.89	0.98
1994	251	61	312	0	312	3.98	2.79	2.28	2.28
1995	166	79	245	20	265	3.69	2.02	2.02	2.02
1996	216	30	246	42	288	3.93	2.77	2.14	2.22
1997	149	46	195	40	235	4.03	2.87	2.50	2.55
1998	111	114	225	35	260	4.63	3.17	2.71	2.77
1999	145	27	172	0	172	4.68	2.69	1.68	1.68
2000	56	3	59	0	59	4.00	0.95	0.46	0.46
2002	95	2	97	20	118	4.75	2.26	1.08	1.19
Sum	2691	747	3438	237	2107				
Mean all yrs						4.45	2.92	2.11	1.82
St.dev.						0.55	1.13	1.17	0.75