Brood size of twelve farmland bird species in Sweden during 1962–2001

Kullstorlek hos tolv arter jordbruksfåglar i Sverige under perioden 1962–2001

HANS RYTTMAN & K. SUSANNA S. HALL-KARLSSON

──────────── **Abstract** ────────────

Several farmland bird species are declining in Sweden. We investigated if the population decreases are linked to smaller broods or a higher rate of unhatched eggs. The number of broods ringed and the average number of nestlings in these broods from 1962 to 2001 were analysed for twelve species: Skylark *Alauda arvensis*, Swallow *Hirundo rustica*, House Martin *Delichon urbica*, Meadow Pipit *Anthus pratensis*, White Wagtail *Motacilla alba*, Wheatear *Oenanthe oenanthe*, Whitethroat *Sylvia communis*, Starling *Sturnus vulgaris*, House Sparrow *Passer domesticus*, Tree Sparrow *Passer montanus*, Linnet *Carduelis cannabina* and Yellowhammer *Emberiza citrinella*. Only two of the investigated species, the Tree Sparrow and the Yellowhammer, showed a statistically significant decline in average brood size over time. We conclude that changes in brood size alone cannot explain the decline in several farmland bird species. The House Sparrow showed an increase in the number of dead nestlings and data for House Sparrow, Tree Sparrow and Whitethroat indicated that a higher rate of unhatched eggs might be a problem.

Hans Ryttman, Skönstaholmsvägen 68, 123 60 Farsta. E-mail: hans.ryttman@comhem.se
Susanna Hall-Karlsson, c/o Africa Groups of Sweden, P.O. Box 86 445, Windhoek, Namibia.
E-mail: susanna.hallkarlsson@gmail.com

Introduction

The number of European farmers has decreased over the last decades and the ones remaining have become more efficient and competitive. The more intense working methods, including the use of herbicides and pesticides, have caused a decline of insects and weeds and the farmers have also become more efficient when it comes to reducing their harvest spill. These and other changes have caused a decline the last decades in the populations of many bird species depending on farmland habitats (Fuller et al. 1995, Berg & Kvarnbäck 2005).

The annual monitoring of bird populations in Sweden, which started in 1975, has shown that many farmland species are declining (Lindström & Svensson 2003, 2006, Wretenberg et al. 2007). These declines must depend on either fewer offspring produced or decreased survival of nestlings or older birds, or a combination of both. The optimal brood size of a species depends on several factors such as survival probability of young, life expectancy of adults, habitat favourability and pre-dation pressure. In a stable population, the amount of offspring surviving to reproductive age will equal the number of adults dying each year.

We investigated the brood size and number of ringed broods from 1962 to 2001 for twelve bird species more or less dependent on farmland habitats. The aim was to investigate if changes in brood size and the proportion of unhatched eggs per brood have played any role in the declining populations of farmland birds.

Materials and methods

This study is based on bird ringing data from 1962 to 2001 reported to the Swedish Bird Ringing Centre (Swedish Museum of Natural History). The twelve species included, all more or less dependent of farmland habitats, are: Skylark *Alauda arvensis*, Swallow *Hirundo rustica*, House Martin *Delichon urbica*, Meadow Pipit *Anthus pratensis*, White Wagtail *Motacilla alba*, Wheatear *Oenanthe oenanthe*, Whitethroat *Sylvia communis*, Starling *Sturnus vulgaris*, House Sparrow *Passer domesti-*

cus, Tree Sparrow *Passer montanus*, Linnet *Carduelis cannabina* and Yellowhammer *Emberiza citrinella*. The total number of broods ringed, the average brood size and the range of brood sizes of each species are presented in Table 1. The term 'brood size' includes, in this study, all nestlings alive at the ringing occasion even if not all were ringed. Unhatched eggs and dead nestlings were not included, if nothing else is stated. From this material it is not possible to know how many nests with nestlings that were predated or failed for other reasons.

The number of nestlings included in this study is not the same as the number of nestlings of the same species ringed in Sweden. In some broods, not all nestlings were ringed, but they were included in this study as a member of the brood. Other nestlings were ringed outside the nest without any information about their original brood, and these were not included. The most important discrepancy, though, is due to research manipulations. Broods known to have been manipulated (eggs or young were added or removed) were not included in the study and this is most obvious among Starlings.

In a few cases the brood sizes of the Starlings were unusually large. In eight broods there were eight eggs and in two broods, nine eggs were found. Sometimes a female can lay one or a few eggs in another female's nest-box but, since this was not due to manipulations, these large broods of Starlings were included in this study.

A linear regression analysis was performed on the average brood size over time. For additional analyses the ringing data was divided into four "decades" 1962–1971, 1972–1981, 1982–1991 and 1992–2001. To investigate if there were any differences in brood size in different parts of the country, Sweden was divided into three regions, i.e. South (south of 59°N), Middle (59–62°N) and North (north of 62°N). The numbers of unhatched eggs and dead nestlings were also investigated, but this kind of data was not regularly reported until 1982.

All statistical analyses were performed with JMP (version 2 SAS inst inc.). Differences between means were tested with ANOVA and Tukey-Kramer HSD*. Changes in the number of ringed broods over time were tested with linear regressions.

Results

The number of broods included in this study varied from 484 broods of Yellowhammers to 14,653 broods of Starlings (Table 1). The species with the second highest number of broods was the Swallow with 8568 broods. The average brood size varied from 3.51 in the Yellowhammer to 4.99 in the Wheatear.

Number of ringed broods per year

For all species included in the study, the number of ringed broods varied over time but for some species a clear trend was shown. The number of broods ringed decreased since 1962 in three (Skylark, White Wagtail, Linnet) of the twelve species

Table 1. Number of broods of twelve farmland species ringed in Sweden in 1962–2001, as well as average and range of brood size (s.d. = standard deviation).
Antal kullar av tolv arter fåglar knutna till jordbrukslandskapet ringmärkta 1962–2001, medelantal ungar per kull vid märktillfället, samt spridning i kullstorlek.

Species *Art*	Scientific name *Vetenskapligt namn*	No. of broods *Antal kullar*	Av. brood size *Medelkull s.d.*	Brood size range *Spridning*
Skylark *Sånglärka*	*Alauda arvensis*	725	3.58 (0.96)	1–6
Swallow *Ladusvala*	*Hirundo rustica*	8568	4.42 (1.07)	1–8
House Martin *Hussvala*	*Delichon urbica*	1587	3.58 (1.09)	1–7
Meadow Pipit *Ängspiplärka*	*Anthus pratensis*	609	4.57 (1.14)	1–8
White Wagtail *Sädesärla*	*Motacilla alba*	4395	4.73 (1.23)	1–8
Wheatear *Stenskvätta*	*Oenathe oenanthe*	1833	4.99 (1.34)	1–8
Whitethroat *Törnsångare*	*Sylvia communis*	535	4.44 (1.08)	1–6
Starling *Stare*	*Sturnus vulgaris*	14653	4.19 (1.21)	1–9
House Sparrow *Gråsparv*	*Passer domesticus*	667	3.56 (1.21)	1–6
Tree Sparrow *Pilfink*	*Passer montanus*	1752	3.72 (1.48)	1–8
Linnet *Hämpling*	*Carduelis cannabina*	989	4.60 (1.12)	1–8
Yellowhammer *Gulsparv*	*Emberiza citrinella*	484	3.51 (1.06)	1–7
Total/*Summa*		36797		

Table 2. Average number of nestlings per brood, and number of broods, during four decades: 1962–1971, 1972–1981, 1982–1991 and 1992–2001. Differences in brood size between different decades were tested with ANOVA and Tukey-Kramer HSD* (P). Average brood sizes are marked with superscripts as combinations of the letters a–c. Averages with combinations containing the same letter are not significantly different from each other. For example, a and ab are not significantly different from each other, whereas a and bc are.

Medeltalet ringmärkta ungar per kull, samt antalet kullar, perioderna 1962–1971, 1972–1981, 1982–1991 och 1992–2001. Skillnader i kullstorlek mellan olika tidsperioder har testats med ANOVA och Tukey-Kramer HSD* (P). Medelvärdena för en given art är markerade med kombinationer av bokstäverna a–c i olika kombinationer. Värden där kombinationerna innehåller samma bokstav skiljer sig inte statistiskt från varandra. Till exempel, värden med a respektive ab är inte signifikant skilda åt, medan värden märkta med a respektive bc är det.

	Average brood size Medelkullstorlek					No. of broods Antal kullar			
Species Art	62-71	72-81	82-91	92-01	P	62-71	72-81	82-91	92-01
Skylark *Sånglärka*	3.59^a	3.60^a	3.68^a	3.25^b	0.055	315	223	133	52
Swallow *Ladusvala*	4.36^c	4.43^b	4.36^c	4.53^a	<0.001	2359	2604	1596	2009
House Martin *Hussvala*	3.49	3.66	3.58	3.55	NS	424	474	424	265
Meadow Pipit *Ängspiplärka*	4.44	4.39	4.71	4.64	0.044	156	106	188	159
White Wagtail *Sädesärla*	4.70	4.76	4.74	4.71	NS	1908	1403	557	528
Wheatear *Stenskvätta*	4.81^b	4.78^b	4.94^b	5.20^a	<0.001	490	328	276	739
Whitethroat *Törnsångare*	4.19^b	4.61^a	4.64^a	4.49^a	<0.001	194	105	139	97
Starling *Stare*	3.87^b	4.18^a	4.21^a	4.23^a	<0.001	1207	569	4122	8755
House Sparrow *Gråsparv*	3.42^a	3.68^a	3.59^a	3.00^b	0.02	201	288	160	18
Tree Sparrow *Pilfink*	3.86^{ab}	4.07^a	3.64^b	3.31^c	0.001	207	576	522	447
Linnet *Hämpling*	4.51^b	4.58^{ab}	4.71^{ab}	4.91^a	0.01	445	284	175	85
Yellowhammer *Gulsparv*	3.60	3.53	3.44	3.49	NS	105	152	121	106

investigated (Table 2), and since 1972 in another four species (House Martin, House Sparrow, Tree Sparrow, Yellowhammer). Swallow, Meadow Pipit and Whitethroat showed no temporal trend in the number of ringed broods. In the Wheatear and the Starling, ringing of nestlings increased, although for the Wheatear only from the 1980s, due to large species-specific projects (see more below).

A decreasing number of Wheatear broods were ringed from 1962 to the beginning of the 1990s when the ringing increased heavily. The increase in the number of ringed broods was caused by a research project at the Swedish University of Agriculture (SLU) in Uppsala, in Middle Sweden (Arlt & Pärt 2007). Since 1992 as many as 601 broods were ringed within this project, i.e. 83% of all broods ringed during the study period. If the ringing in this project is omitted, the number of ringed broods decreased from 1962 to 2001 (F=20.0, P=0.0001, b=−1.13).

The ringing of Starlings was restricted in 1962 because the Bird Ringing Centre in Stockholm was short of personnel and therefore did not have the possibility to handle a large material of ringed birds. As a consequence of this relatively few Starlings were ringed during 1963–1980; only around 40 broods per year (Fransson et al. 2005).

A research project has focussed on Starlings since 1990 (Smith & Bruun 2002), and from this on the number of ringed birds increased heavily, to more than 800 broods per year.

Changes in brood sizes over time

The Tree Sparrow and the Yellowhammer showed a significant decline in mean brood size over time (Table 2 and 3). However, if the only two broods of Yellowhammers during the last year (2001), is eliminated or replaced by the average for Yellowhammer (3.51 young) no significant decline is shown (P=0.133). The Tree Sparrow has a decline of 0.015 young per year (t=−2.8, P=0.008). The Meadow Pipit, House Sparrow, House Martin, White Wagtail and the Skylark show no statistically significant tendency and the five other species show significant positive trends in their mean brood sizes.

Differences in brood sizes between regions in Sweden

Six of the twelve species investigated had statistically significant differences in average brood size between one or more regions in Sweden (Table 4).

Table 3. Regression analysis of the mean annual brood size over the period 1962–2001.
Regressionsanalys av årlig medelkullstorlek för perioden 1962–2001.

Species *Art*	Regressions-koefficient *Slope*	t-value *t-värde*	P
Skylark *Sånglärka*	-0.0072	-0.20	NS
Swallow *Ladusvala*	0.0045	2.39	0.022
House Martin *Hussvala*	0.0010	0.27	NS
Meadow Pipit *Ängspiplärka*	0.0070	1.15	NS
White Wagtail *Sädesärla*	-0.0017	-0.52	NS
Wheatear *Stenskvätta*	0.0146	3.34	0.012
Whitethroat *Törnsångare*	0.0117	2.25	0.030
Starling *Stare*	0.0088	2.11	0.042
House Sparrow *Gråsparv*	0.0040	0.53	NS
Tree Sparrow *Pilfink*	-0.0150	-2.80	0.008
Linnet *Hämpling*	0.0120	2.03	0.050
Yellowhammer *Gulsparv*	-0.0100	-2.21	0.033

Table 4. Mean number of nestlings per brood (x̄) and number of ringed broods (N) in South (south of 59°N), Middle (59–62°N) and North (north of 62°N) Sweden. Differences in brood size between regions were tested with ANOVA and Tukey-Kramer HSD* (P). Bold indicates average brood size statistically significantly different from the other brood sizes.
Medeltalet ungar per kull (x̄) och antalet märkta kullar (N) i Södra (söder om 59°N), Mellan (59–62°N) och Norra (norr om 62°N) Sverige. Skillnader i kullstorlek mellan olika regioner har testats med ANOVA och Tukey-Kramer HSD (P). Fetstil indikerar kullstorlekar som statistiskt skiljer sig från övriga kullstorlekar.*

Species *Art*	South Södra (x̄)	N	Middle Mellan (x̄)	N	North Norra (x̄)	N	P
Skylark *Sånglärka*	3.61	637	**3.28**	76	4.00	14	0.005
Swallow *Ladusvala*	**4.38**	5521	4.50	2908	4.36	139	<0.001
House Martin *Hussvala*	3.57	620	3.58	938	3.69	29	NS
Meadow Pipit *Ängspiplärka*	4.22	297	4.28	36	**4.99**	276	<0.001
White Wagtail *Sädesärla*	4.74	2521	4.72	1480	4.66	394	NS
Wheatear *Stenskvätta*	4.88	999	**5.18**	722	4.67	112	<0.001
Whitethroat *Törnsångare*	4.43	413	4.49	110	4.50	12	NS
Starling *Stare*	**4.24**	10935	**4.07**	3185	**3.90**	533	<0.001
House Sparrow *Gråsparv*	3.56	529	3.54	130	4.38	8	NS
Tree Sparrow *Pilfink*	**3.80**	1327	3.47	387	3.66	38	<0.001
Linnet *Hämpling*	4.56	775	4.73	160	4.81	54	NS
Yellowhammer *Gulsparv*	3.50	285	3.50	164	3.74	35	NS

In the North region Meadow Pipits had their largest broods, whereas the Starlings had their smallest broods there. In the Middle region, Skylarks had their smallest broods and in the South region both Starlings and Tree Sparrows had their largest broods. The average brood size of Starlings decreased northwards. In the SLU research project on the Wheatears (Arlt & Pärt 2007), a very large average brood size was noted. Depending on this, the Middle region had a significantly larger brood size compared to the other regions. Excluding the broods from the research project, the mean was 4.69 (n=121) in the Middle region, which is not significantly different from the other regions.

Six species showed no significant differences in average brood size between regions but the relative numbers of broods ringed in the north was, for some of these species, extremely low in relation to the numbers ringed in the south. In total, 80% of the House Sparrow broods were ringed in the South region and only eight broods (1.2%) were ringed in the North. Most of the Linnets were also ringed in the South region (78%) and fewest in the North (5%). Similarly, the numbers of ringed broods of

Yellowhammers and Whitethroats were much lower in northern Sweden compared to the more southern areas but there were no significant differences in average brood sizes.

Unhatched eggs and dead nestlings

For many broods (but not all) it has been reported whether unhatched eggs were present or not. In a total of 174 such broods of House Sparrows ringed 1982–2001, the number of unhatched eggs was on average 0.48 per brood (Table 5). The corresponding figures were 0.46 unhatched eggs in 158 broods in 1982–1991, and 0.69 unhatched eggs in 16 broods in 1992–2001. This indicates an increase in the number of unhatched eggs per brood, but none of the means were significantly different from each other ($t=1.13$, $P=0.26$, $df=172$). However, the number of dead nestlings was significantly higher in the last decade (mean for 1982–1991 was 0.04 and mean for 1992–2001 was 0.38; $t=3.66$, $P<0.001$, $df=172$, Table 6).

A rather exceptionally high number of unhatched eggs was found in the Tree Sparrows. Nearly one egg per brood (0.97 eggs) was unhatched among the 1055 broods with relevant information during 1982–2001 (Table 5). The number of unhatched eggs seems to have been stable over time, i.e. the means were not significantly different from each other (mean for 1982–1991 was 0.92, $n=612$ and mean for 1992–2001 was 1.01, $n=443$; $t=1.04$, $P=0.30$, $df=1053$). During 1972–1981 unhatched eggs were reported in only 26 broods. Among these

broods there was on average 1.15 unhatched eggs per brood. No difference in the number of dead nestlings was found between the decades (1982–1991 mean=0.071 and 1992–2001 mean = 0.061, $P = 0.62$, $df = 952$, Table 6).

Compared to the other species in this study the number of unhatched eggs found were high for the Tree Sparrow and the House Sparrow. The other species had between 0.1 (Skylark) to 0.3 (Linnet) unhatched eggs per clutch during 1982–2001 (Table 6). The Meadow Pipit had a higher number the first decade 0.285 ($n=140$) compared to the last 0.081 ($n=159$, $t=2.81$, $P=0.005$). The pattern was similar in the Wheatear, with on average 0.226 the first decade ($n=270$) and 0.109 the second decade ($n=137$, $t=2.40$, $P=0.017$, the data from the SLU research project was excluded). In contrast, the Whitethroat had 0.073 ($n=136$) the first decade and 0.237 the last decade ($n=97$, $t=3.00$, $P=0.003$, Table 6).

A significantly higher number of dead nestlings (Table 7) was found among the Wheatears during 1982–1991 (mean=0.129, $n=271$) compared to 1992–2001 (mean=0.029, $n=665$, $t=3.42$, $df=934$, $P<0.001$). However, dead nestlings and unhatched eggs were not always reported in the protocols from the SLU project, which makes the comparison somewhat uncertain. If the data from the SLU project is omitted the average number of dead nestlings in 1992–2001 was 0.051 ($n=136$) which is not significantly different from the decade 1982–1991 ($P=0.07$)

Table 5. Number of broods with information on presence/absence of unhatched eggs, number and proportion of broods with unhatched eggs, and the average number of unhatched eggs in all broods, for House Sparrows *P. domesticus* and Tree Sparrows *Passer montanus*, respectively.
Antal kullar med information om förekomst av rötägg, antal kullar där rötägg noterats, andelen kullar med rötägg i, samt medelantalet rötägg i alla kullar, för gråsparv respektive pilfink.

Decade *Årtionde*	Number of broods *Antal kullar*	Number of broods with unhatched eggs *Antal kullar med rötägg*	% broods with unhatched eggs *% med rötägg*	Unhatched eggs per brood *Rötägg per kull*
House Sparrow				
Gråsparv				
1972–1981	288	17*		0.35
1982–1991	158	49	31.0	0.46
1992–2001	16	6	37.5	0.69
Tree Sparrow				
Pilfink				
1972–1981	576	26*		1.15
1982–1991	612	254	41.5	0.92
1992–2001	443	202	45.6	1.01

* not compulsory to report

Table 6. Average number of dead nestlings and average number of unhatched eggs per brood (number of broods) during the decades 1982–1991 and 1992–2001. *data from the SLU project is excluded.
Medelantal döda ungar och rötägg per kull under årtiondena 1982–1991 och 1992–2001.
*data från SLU-projektet har uteslutits.

Species *Art*	Dead nestlings *Döda ungar*			Unhatched eggs *Rötägg*		
	82-91	92-01	P	82-91	92-01	P
Skylark *Sånglärka*	0.023 (131)	0 (52)	0.54	0.083 (131)	0.154 (52)	0.16
Swallow *Ladusvala*	0.021 (1581)	0.017 (1998)	0.12	0.176 (1581)	0.160 (1998)	0.30
House Martin *Hussvala*	0.030 (406)	0.016 (253)	0.50	0.030 (406)	0.147 (252)	0.75
Meadow Pipit *Ängspiplärka*	0 (140)	0 (159)		0.285 (140)	0.081 (159)	0.015
White Wagtail *Sädesärla*	0.036 (549)	0.034 (522)	0.90	0.156 (550)	0.132 (522)	0.38
Wheatear *Stenskvätta*	0.129 (271)	0.051* (136)	0.07	0.226 (270)	0.109* (137)	0.017
Whitethroat *Törnsångare*	0.051 (136)	0.010 (97)	0.31	0.073 (136)	0.237 (97)	0.003
Starling *Stare*	0.044 (3932)	0.043 (7551)	0.81	0.114 (3930)	0.123 (7559)	0.33
House Sparrow *Gråsparv*	0.044 (158)	0.375 (16)	<0.001	0.46 (158)	0.69 (16)	0.26
Tree Sparrow *Pilfink*	0.071 (508)	0.061 (444)	0.62	0.92 (507)	1.01 (443)	0.21
Linnet *Hämpling*	0.011 (171)	0.058 (85)	0.22 (169)	0.226 (85)	0.308	0.67
Yellowhammer *Gulsparv*	0.100 (120)	0.057 (105)	0.65	0.225 (120)	0.257 (105)	0.66

Table 7. The brood size of the Swallow in different regions and months.
Kullstorlek för ladusvala i olika regioner och månader.

Month *Månad*	No. of broods in South (% of all) *Antal fåglar i södra regionen (% av alla)*	Average brood size *Medelvärde för kull*	No. of broods in Middle (% of all) *Antal fåglar i mellanregionen (% av alla)*	Average brood size *Medelvärde för kull*	No. of broods in North (% of all) *Antal fåglar i norra regionen (% av alla)*	Average brood size *Medelvärde för kull*
June	2076 (37.6%)	4.70	708 (24.4%)	4.86	5(3.6%)	4.80
July	1953 (35.4%)	4.29	1766 (60.8%)	4.50	119(85.6%)	4.50
August	1440 (26.1%)	4.08	405 (13.9%)	3.93	15(10.8%)	4.33
September	51 (0.9%)	3.46	26(0.9%)	3.73	0	

Differences between migrating/non-migrating species

The twelve species in this study can be divided into three migratory categories; stationary, short-migrating and long-migrating species. Three species, the Tree Sparrow, House Sparrow and Yellowhammer are stationary and two of them, the Tree Sparrow and Yellowhammer, show smaller average brood size over time. The House Sparrow shows a smaller average brood size during the last decade, although not statistically significant. Of the short migrating species (Meadow Pipit, Linnet, Skylark, Starling and Wheatear) three (Linnet, Starling and

Wheatear) show positive trends in average brood size and the other no trend at all. Among the long distance migrating species (House Swallow, Swallow, White Wagtail and Whitethroat) two show positive trends (Swallow and Whitethroat) and the other ones show no trend (Table 3).

Discussion

Number of broods ringed

The number of ringed broods declined in seven of the twelve species investigated. One explanation for less broods ringed would be a population decline, and ten of the twelve species in this study showed decreasing population numbers in Sweden after 1975 (Lindström & Svensson 2007). The population trends of the two remaining species (Swallow and Whitethroat) were long-term stable. In two species, the Wheatear and the Starling, the number of ringed broods increased in spite of decreasing populations due to species-specific research projects. The Starling breeds readily in nest boxes which does not only provide the species with excellent breeding opportunities as the number of nest-boxes increase, but the nestlings are also much more easy to ring. Thus, the number of, for example, Tree Sparrow broods ringed could, without doubt, depend on the availability of nest-boxes in the vicinity of bird ringers. On the other hand, ringing nestlings is extremely time consuming in free-breeding species with well-hidden nests, for example Skylarks and Yellowhammers. Searching for nests was popular before the introduction of mist-nets in the late 1950s (Fransson & Pettersson 2001) and fewer bird ringers engage in this type of ringing nowadays.

Changes in brood size over time

The Starling has increased its brood size compared to the 1960s, maybe because the Starlings suffered from intake of mercury, which was used in mould protection of seeds, in the late 1950s and beginning of the 1960s. In contrast to the decreasing number of Wheatears and Linnets, showing a decline of 50–75% in Sweden, the Wheatear and Linnet increased their brood sizes over time. Possibly, Wheatear and Linnet nowadays breed only in the most favourable habitats as a consequence of a decreasing population density. Another explanation may be that in declining populations the birds left are not competing so much with each other. However, in comparison with the Wryneck (Ryttman 2003), this explanation is not so likely, as the

Wryneck shows an identical pattern with larger brood size during the last decades compared to the earlier time periods. The Wryneck has never been a common species in Sweden. Also, in the present study, Wheatear had their largest brood sizes in a rather dense population.

One of the species with increasing brood size, the Whitethroat, did not have a negative population trend (Svensson & Lindström 2003, 2007) which might indicate that larger brood sizes, in some areas, could compensate for an otherwise decreasing breeding population.

The average brood size of Swallows increased during the last decade, thereby maybe enabling a population increase. The Swallow population index in Sweden shows a slight increase from 1995 onwards (Lindström & Svensson 2006)..

The average brood size of Skylarks decreased by 12% during the last decade but the decline of the Skylark population begun already in the late 1970s (Lindström & Svensson 2003), before the decrease in brood size is apparent.

In conclusion, comparing brood size changes over time to the population trends (Lindström & Svensson 2007) reveals no obvious pattern of connection between brood size and population size. Only one species, the Tree Sparrow, and maybe the Yellowhammer, showed decreasing average brood sizes over time. All the other species showed increasing average brood size or showed no trend at all.

Differences in brood size between north to south

Seven of the twelve species investigated showed tendencies towards larger broods in northern Sweden compared to more southern regions but five species had their largest broods in the South (White Wagtail, Starling, Tree Sparrow) or Middle (Swallow, Wheatear) regions.

These regional differences might be influenced by changes in ringing efforts over time of the year in different areas of Sweden. For example, the brood size of Swallows in the South region was smaller compared to the Middle region, in June and July but somewhat larger in August (cf. Table 8). During 1992–2001 the average brood size of Swallows was significantly larger (4.53) than in earlier decades (4.36 in 1962–1971, 4.43 in 1972–1981 and 4.36 in 1982–1991, respectively). This might reflect a lower number of broods ringed late in the South region during this decade (10% compared to at most 32% during the decade 1982–1991).

Unhatched eggs and dead nestlings

The number of unhatched eggs gives another ambiguous pattern. The number of unhatched eggs as well as the number of dead nestlings in House Sparrow broods increased over time, although the sample size is small for 1972–1981 (Table 7). The House Sparrows had a very small average brood size, only 3.0 nestlings per brood, in 1992–2001 and it is possible that the increasing proportion of unhatched eggs over time could be a cause of this. Interesting, though, is that this very low average brood size is not significantly lower compared to the earlier decades. In the following years, 2002–2005, 11 broods of House Sparrows were ringed, including 36 nestlings (mean brood size 3.27). The average brood size including these years, i.e. 14 years in the 1990s and early 2000s, was 3.10 nestlings per brood. Although somewhat higher, this is still lower than the average brood sizes in the earlier decades. Very few broods of House Sparrows are ringed each year and it is difficult to conclude anything of the fate of the House Sparrow in the future, but the annual bird monitoring has reported a slow but steady population decline during both winter and summer for the last 30 years (Lindström & Svensson 2007).

The population of Tree Sparrows is slowly decreasing in Sweden, but in the northern part of the country (Bergquist 2004) as well as in Finland (Väpsäläinen et al. 2005) the population is increasing. Väpsäläinen et al. (2005) suggested that the increasing habit of putting up nest-boxes and feeding birds during winter was the cause of the increasing numbers of Tree Sparrows in Finland and this might be true also for the Swedish population in the northern part of the country. The present study shows that the average brood size for Tree Sparrows is decreasing over time and one reason for this may be that Tree Sparrows has a high proportion of broods with unhatched eggs and a high average number of unhatched eggs in these broods. On average, almost every Tree Sparrow brood has one unhatched egg. One unhatched egg per brood is comparable to the 0.9 unhatched eggs found in Wryneck broods (Linkola 1978, Ryttman 2003) but the Wrynecks lay on average 10 eggs in a brood and, consequently, the proportion of unhatched eggs in a brood is much lower and less severe for Wrynecks. The average brood size of Tree Sparrows during the last decade, 1992–2001, concerning living nestlings, was 3.31 and the largest average brood size, 4.08, was found in 1972–1981 (in the present study), i.e. one unhatched egg equals

25–30% of the reproductive investment. Also, Whitethroats showed an increase in the number of unhatched eggs, a statistically significant increase that may influence the future Whitethroat population size.

Brood size and migration strategy

Two sedentary species, the Tree Sparrow and Yellowhammer, show smaller average brood sizes over time. All other short migrating and long migrating species show larger brood sizes or no trend at all during the investigated time, i.e. migratory habits do not seem to have influenced the current changes in brood size.

Concluding remarks

In conclusion, there is a trend towards smaller broods in the Tree Sparrow and possibly the Yellowhammer, but for the remaining ten of the twelve farmland species investigated in this study the trend is positive or insignificant. This result indicates that brood size alone cannot explain why a population is increasing or decreasing. There is some indication that the proportion of unhatched eggs is a problem for Tree Sparrows and House Sparrows as well as an increase in the number of dead nestlings for House Sparrows, but longer time series are needed for a thorough investigation of this.

Acknowledgements

References

Arlt, D. & Pärt, T. 2007. Nonideal breeding habitat selection: a mismatch between preference and fitness. *Ecology* 88: 792–801.

Berg, Å. & Kvarnbäck, O. 2005. Preferenser för olika fälttyper hos häckande jordbruksfåglar – en litteraturstudie. *Ornis Svecica* 15: 31–42.

Bergquist, M. 2004. Pilfinken i Norrbottens län – från sällsynthet till vardagsart. *Fåglar i Norrbotten* 23: 116–118.

Fransson, T. & Pettersson, J. 2001. *Svensk ringmärkningsatlas*, Vol. 1. Stockholm.

Fransson, T., Hall, S., Karp, K., Kroon, C., Staav, R., Sällström, B. & Sällström U. B. 2005. *Report on Swedish Bird Ringing for 2003*. Swedish Museum of Natural History, Stockholm.

Fuller, R. J., Gregory, R. D., Gibbons, D. W., Marchant, J. H., Wilson, J.,D. Baillie, S. R. & Carter, N. 1995. Population declines and range contractions among lowland farmland birds in Britain. *Conserv. Biol.* 9: 1425–1441.

Linkola, P.1978. Häckningsbiologiska undersökningar av göktyta i Finland 1952–1977. (On the breeding biology of the wryneck *Jynx torquilla* in Finland) *Anser*, Suppl. 3: 155–162.

Lindström, Å. & Svensson, S. 2003. *Övervakning av fåglarnas populationsutveckling och starens häckningsframgång. Årsrapport för 2002.* (Monitoring population changes of birds in Sweden and breeding success of the Starling. Annual report for 2002.) Department of Ecology, Lund University, 88 pp.

Lindström, Å. & Svensson, S. 2006. *Övervakning av fåglarnas populationsutveckling. Årsrapport för 2005.* (Monitoring population changes of birds in Sweden. Annual reportfor 2005). Department of Ecology, Lund University, 68 pp.

Lindström, Å. & Svensson, S. 2007. *Övervakning av fåglarnas populationsutveckling. Årsrapport för 2006.* (Monitoring population changes of birds in Sweden. Annual reportfor 2006). Department of Ecology, Lund University, 68 pp.

Ryttman, H. 2003. Breeding success of Wryneck *Jynx torquilla* during the last 40 years in Sweden. *Ornis Svecia* 13: 25–28.

Smith, H. G. & Bruun, M. 2002. The effect of pasture on starling (*Sturnus vulgaris*) breeding success and population density in a heterogeneous agricultural landscape in southern Sweden. *Agricult. Ecosyst. Environm*. 92: 107–114

Vepsäläinen, V., Pakkala, T. & Tianen, J. 2005. Population increase and aspects of colonization of the Tree Sparrow *Passer montanus*, and its relationships with the House Sparrow *Passer domesticus*, in the agricultural landscapes of Southern Finland. *Ornis Fennica* 82: 117–128.

Wretenberg, J., Lindström, Å., Svensson, S. & Pärt, T. 2007. Linking agricultural policies to population trends of Swedish farmland birds in different agricultural regions. *J. Appl*. Ecol. 44: 933–941.

Sammanfattning

Många fågelarter knutna till jordbruk har minskat i antal de senaste decennierna enligt de årligen utförda inventeringarna som genomförs av Naturvårdsverket i Lunds universitets regi. För att om möjligt få klarhet i varför minskningarna sker har vi i denna studie undersökt antalet ringmärkta kullar och kullstorlekar av tolv olika arter som företrädesvis finns i närheten av odlade arealer (Tabell 1). De tolv arterna är: sånglärka *Alauda arvensis*, ladusvala *Hirundo rustica*, hussvala *Delichon urbica*, ängspiplärka *Anthus pratensis*, sädesärla *Motacilla alba*, stenskvätta *Oenanthe oenanthe*, törnsångare *Sylvia communis*, stare *Sturnus vulgaris*, gråsparv *Passer domesticus*, pilfink *Passer montanus*, hämpling *Carduelis cannabina* och gulsparv *Emberiza citrinella*.

Studien bygger på de uppgifter som ringmärkare rapporterat till Ringmärkningscentralen under åren 1962–2001. Förändringar i kullstorlek över tid analyserades med regressionsanalys. För vissa frågeställningar har tidsperioden delats in i fyra perioder som motsvarar de fyra decennierna som undersökningen omfattar och medelantalet ungar per kull har jämförts mellan dessa tidsperioder. För att undersöka om det finns geografiska skillnader i antalet ungar per kull har Sverige delats in i tre regioner: Södra (söder om 59°N), Mellan (59°N–62°N) och Norra (norr om 62°N) regionen.

För sju av de tolv arterna minskade antalet ringmärkta kullar tämligen kontinuerligt från 1960-talet till år 2001. Hur många kullar som ringmärks beror dock på många olika faktorer och det är svårt att dra någon generell slutsats utifrån detta. En orsak kan vara att när arten minskar i antal så blir det också svårare att finna dess bon. Det är också möjligt att ringmärkare idag inte arbetar lika hårt på att finna mer eller mindre svårupptäckta bon som de äldre ringmärkare gjorde som började ringmärka fåglar innan slöjnäten fanns tillgängliga. Ett samband som är tydligt är att arter som ingår i forskningsprojekt ringmärks i högre antal. Utöver detta ringmärks arter som häckar i holkar eller i människans närhet i större antal än frihäckande arter med svårfunna bon.

Antalet levande ungar per kull borde kunna ge en fingervisning om huruvida arten har svårt att reproducera sig eller inte. I två fall, gråsparv och gulsparv, visar ringmärkningsdata på en reduktion av kullstorleken över tiden men gulsparvens minskning påverkas av att endast två kullar ringmärktes år 2001. Om dessa kullar utesluts är förändringen inte längre statistiskt signifikant. Hos ladusvala, stenskvätta, stare, törnsångare och hämpling ökade medelantalet ungar per kull över de senaste decennierna. Detta trots att inventeringarna visar på en kraftig minskning av framförallt populationerna av stenskvätta och hämpling, vilka numera har en tredjedel så stor population som arterna hade vid inventeringarnas början. En tolkning kan vara att stenskvätta och hämpling endast finns kvar i de mest gynnsamma biotoperna men att de i dessa biotoper kan föda upp fler ungar än i normalbiotopen. Detta tycks i alla fall vara fallet för stenskvätta där ett forskningsprojekt i Uppsala står för drygt 80% av all ringmärkning. I detta projekt har de ett signifikant högre medelantal ungar per kull i jämförelse

med andra delar av landet. Det är också möjligt att kullstorleken ökar vid minskande populationstäthet, på grund av minskande inomartskonkurrens.

Sju av de tolv arterna visar en tendens till större kullar i norra delen av landet medan sädesärla, stare, pilfink hade störst kullar i den södra regionen och ladusvala och stenskvätta hade störst kullar i mellanregionen.

Två arter som tycks ha det bekymmersamt är gråsparv och pilfink. Båda arterna har en tämligen låg kullstorlek med 3,5–4 ungar per kull men också en ovanligt hög andel rötägg. Pilfinken, som har fler ringmärkta kullar i förhållande till gråsparven, har haft i genomsnitt ett rötägg per kull (25–30 % av kullen!) under de två årtionden som ringmärkare har rapporterat rötägg i kullarna mer systematiskt.

För gråsparven är siffrorna mer osäkra för de olika årtiondena men totalt har i medeltal 0,5 rötägg per kull rapporterats under perioden 1982–2001. Utöver detta kan noteras att antalet döda ungar i boet har ökat signifikant för gråsparv under perioden 1982 till 2001, liksom antalet rötägg har ökat signifikant för törnsångare under samma tidsperiod.

Denna studie kan inte påvisa något tydligt samband mellan förändringar i kullstorlek och förändringar i populationsstorlek. Således kan förändringar i kullstorlek inte ensamt förklara minskande populationer av flera arter jordbruksfåglar. En ökad andel rötägg skulle kunna vara en förklaring, men längre tidsserier krävs för att kunna avgöra om så är fallet.