

The ecology of Linnets *Carduelis cannabina* on lowland farmland

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The breeding ecology of Linnets *Carduelis cannabina* was studied from 1995 to 1998 on mixed farmland in southern England. Data were compared with long-term trends in breeding success and survival rates from the British Trust for Ornithology's Nest Record and Ringing Schemes in an attempt to understand the demographic and environmental causes of recent population trends on UK farmland (a severe decline during the 1970s and 1980s, followed by partial recovery during the 1990s). The field study found that Linnets had a long breeding season (first egg dates between 12 April and 13 August) with most females probably making 2 or 3 nesting attempts. Clutch size (mean = 4.72), nest failure rates (mean 0.026 per day during the egg stage, and 0.015 at the brood stage), and brood size (mean = 4.22) were all very similar to those recorded by the Nest Record Scheme since the 1960s. Overall, field data predict that the population was fledging between 4.5 nestlings per breeding female (if all females made 2 nesting attempts), and 7.1 (if all females made 3 nesting attempts). These levels of breeding productivity are sufficient to maintain or increase the population, given recent estimates of annual survival rates. This accords with the recent increase in Linnet abundance recorded on Common Birds Census plots. Losses of whole broods and individual nestlings through starvation were low and suggested that breeding success was not limited by food supply. Nest survival rates at the egg stage showed a strong seasonal increase, with predation of clutches by corvids early in the breeding season probably the main cause of loss. Part-ripe seed of oilseed rape is now the predominant food source for nestlings, leading to the hypothesis that increasing availability of this food source has ameliorated longer-term effects of agricultural intensification on weed seed abundance, and allowed the recent population recovery. This hypothesis is now being tested via comparative studies in an area of Norfolk where intensive arable farming is practised without oilseed rape in the rotation. The most likely demographic mechanisms underlying these recent population trends are changes in the number of nesting attempts being made by females and changes in post-fledging survival rate. However, the possibility that changes in population trend have been caused by subtle changes in the density-dependences of other demographic rates, without any marked, long-term effect on their absolute values, cannot be ruled out.

Changes in national and European agricultural policy since the Second World War, coupled with technological advances and large-scale public subsidy, have shifted the emphasis of agricultural land management progressively towards maximisation of food production (Pain & Pienkowski 1997). These changes are often grouped under the umbrella of 'intensification'. With this fundamental objective, an ever-increasing proportion of primary production has been directed into human consumption. The inevitable consequence of this has been to reduce the abundance of all other components of ecological communities, from the weed flora that competes with crops for primary production (e.g. Andreasen *et al.* 1996), to the consumers of natural and agricultural plant material and their predators, including invertebrates (e.g. Ewald & Aebischer 1999), birds (e.g. Tucker & Heath 1994) and mammals (e.g. Flowerdew 1997).

Many European farmland birds have declined in numbers and, in some cases, in geographical range in recent decades, notably in northern and western nations where agricultural intensification has been most apparent (Gibbons *et al.* 1993, Tucker & Heath 1994, Siriwardena *et al.* 1998a). The hypothesis that this association reflects cause and effect has been tested and supported in various ways. Firstly, community-wide studies indicate that population declines are associated particularly with farmland species and habitats (e.g. Marchant & Gregory 1994, Fuller *et al.* 1995, Siriwardena *et al.* 1998a), and that higher population densities of a wide range of species are associated with sites where intensive farming practices have either been avoided or reversed (e.g. Christensen *et al.* 1996, Chamberlain *et al.* 1999). Secondly, detailed autecological studies of individual species have often found negative associations between both behavioural (e.g. habitat

selection) and demographic (e.g. nest success, survival rates) measures and aspects of agricultural intensification (for a review see Baillie *et al.* 1997). Finally, in a few cases, formal experimental field manipulations have confirmed the effect of a particular component of agricultural change on breeding population size or productivity (e.g. Potts 1986, Green & Stowe 1993).

The effects of agricultural change on populations of the Linnet *Carduelis cannabina* L. have not, hitherto, been studied in the UK, even though almost 70% of the breeding population occupies agricultural habitats (Gregory & Baillie 1998). This population declined by 52% between 1968 and 1995 (Siriwardena *et al.* 1998a), with particularly steep declines on arable farmland (Marchant & Gregory 1994). The species has been placed on the Red List of birds of UK conservation concern (Gibbons *et al.* 1996), and similar losses have been reported elsewhere in central and north-west Europe (Hagemeijer & Blair 1997). In Britain, the main period of decline was between 1975 and 1986, with a gradual recovery during the 1990s (Siriwardena *et al.* 1998a), but was not accompanied by marked changes in the species' overall range (Gibbons *et al.* 1993).

On agricultural land, Linnets build their nests in the woody vegetation of field boundaries, typically in hedgerows, isolated bushes and patches of scrub (Cramp & Perrins 1994). In the UK, an unknown and probably seasonally variable proportion of the breeding population winters further south in France and Iberia, returning to breeding areas in March and April (Cramp & Perrins 1994). The breeding season is long, with the earliest nests built in early April and the last in August. Breeding territories are not defended, and many pairs nest and forage semi-colonially (Tast 1970), perhaps offering females opportunities for extra-pair copulation (Drachmann 1997). However, some pairs also nest in isolation (Tast 1970, Moorcroft pers. obs.). During the breeding season, most passerine birds in farmland habitats switch to a primarily invertebrate diet in response to the increased nutritional demands of reproduction (e.g. Evans *et al.* 1997). In contrast species of the genus *Carduelis*, including the Linnet, feed mainly on seeds all year. Invertebrate prey form a minor dietary component, even when provisioning nestlings (Newton 1967, Eybert & Constant 1992, 1998, Moorcroft *et al.* 1997). Linnets are known to forage at distances of up to 3 km from the nest in order to locate food when provisioning nestlings, although distances of up to 1 km are more typical (Frey 1989a, b, Eybert *et al.* 1995). Historically, the Linnet depended on seeds of the weeds of cultivation to a greater extent than any other UK species (Newton 1967) although, more recently, the part-ripe seed of cultivated oilseed rape has become a dominant dietary item, especially when feeding nestlings (Moorcroft *et al.* 1997).

Here we combine preliminary data from an ongoing intensive study of the breeding demography of Linnets carried out in southern England with the results of recent analyses of long-term demographic data at the national scale (Siriwardena *et al.* 1998b, 1999, 2000), with the aim of improving our understanding of the environmental and demographic causes of the species' recent population trend.

METHODS

Study sites

The study was carried out from April to September 1995–1998 across a total of nine lowland farms in Oxfordshire (1995–1998), Wiltshire (1996–1997) and Warwickshire (1996–1997), UK. Not all sites were studied in all years. All nine sites were mixed farmland plots comprising fields surrounded by various margins including hedgerows, tree-lines, woodland edges and ditches. Cropped areas consisted of approximately equal proportions given over to arable production (both autumn- and spring-sown varieties of wheat, oats, barley, legumes, oilseed rape, linseed, maize), and pastoral farming (hay and silage for winter feed, set-aside, and grazing pasture for cattle, sheep, and horses). On all farms, some land was set aside, either as a 'green cover' of weeds and crop volunteers regenerating naturally from the stubble of the preceding crop, or as a sown mixture of grass species. Four sites were managed organically with no agrochemical inputs, one was undergoing transition from a conventional farming regime to organic, and the remaining four were managed conventionally.

Monitoring of nest success

Nests were found by searching along field boundaries between 0700 and 1200 Greenwich Mean Time, using visual cues such as singing males and adult females carrying nesting material. Most were found during the building and incubation periods, when attendance at the nest site by the parents is at its most frequent. Nests were visited at three-day intervals in order to gain accurate data on all phases of the breeding cycle, and the following data were recorded; first-egg date, clutch size, date of hatching, brood size at hatching, and brood size at fledging. For nests which failed, the date of failure was recorded and, where possible, the cause (e.g. starvation, predation, nest collapse). The date of failure (or fledging) was estimated as the mid-point between the date when the nest was last known to be active and the date on which it was found to have failed (or the fledglings to have left the nest). Where a nest was found after clutch completion, first-egg date

was back-calculated after hatching by assuming that incubation lasted on average 13 days (Cramp & Perrins 1994), and that it began with the last egg. Where a clutch was found after clutch completion, but did not hatch, first-egg date was not estimated. Where a nest was found after hatching, brood age and, by extrapolation, first-egg date, were estimated from the degree of feather development of the largest nestling in the brood, based on experience of broods of known age.

An attempt to estimate the number of breeding attempts by individual females was made at one site in 1998, by flushing incubating females from the nest and capturing them in mist-nests. Captured birds were individually colour-ringed, and their activities followed for the remainder of the breeding season to determine the number of nesting attempts made.

Data analysis

Clutch size, daily nest failure rate between clutch initiation and hatching, daily nest failure rate between hatching and fledging, partial losses from successfully hatching clutches, partial losses from successfully fledging broods and brood size at fledging were all modelled as a function of year (four-level factor), farm (nine-level factor), farm type (two-level factor - organic versus conventional) and first-egg date (covariate) using generalised linear models. A quadratic term for first-egg date was included in order to account for curvilinear effects.

Clutch size and brood size at fledging were modelled using normal error and an identity link. Daily nest failure rates were modelled using binomial error and a logit link, with nest fate (failure = 1, success to hatching or fledging = 0) as the binomial response variable, and the numbers of days that the nest was exposed to the risk of failure after it had been found ('exposure days') as the binomial denominator, following the method recommended by Aebischer (1999). Partial losses were also modelled with binomial errors and a logit link, with the number of eggs or nestlings lost as the response variable and initial clutch or brood size as the binomial denominator.

Modelling was carried out in GLIM 3.77, and minimum adequate models were found by backwards selection from a 'full' model, until all retained predictors were significant at $P < 0.05$ (Crawley 1993). In all cases, the full model was considered to be that containing all the predictor variables, but no interaction terms. Interaction terms between the categorical variables could not be specified since they were confounded (e.g. each farm was always either organically or conventionally managed, and not all farms were studied in all years).

RESULTS

Breeding season

Clutches were laid between 12 April and 13 August, inclusive. The distribution of first-egg dates by 5-day intervals is presented in Fig. 1. This shows a clear peak of initiation of first breeding attempts in the second half of April, but with no clear pattern thereafter. Table 1 shows the nest fates of female Linnets captured and colour-ringed at one farm (University Farm, Wytham, Oxford) in 1998. Although the possibility that some of these birds may still have had undetected nesting attempts on the farm (e.g. attempts which failed before the nest was found) or may also have nested elsewhere cannot be ruled out, the overall pattern indicates that most female Linnets made between two or three nesting attempts during the course of the breeding season. The mean first-egg dates of probable first, second and third nesting attempts were 2 May, 13 June and 11 July, respectively.

Clutch size

Clutch size varied between 3 and 6 eggs, with the following distribution (3, 16; 4, 149; 5, 350; 6, 27; $n = 542$; mean = 4.72; $se = 0.0259$). Mean clutch size did not vary with year, farm or farm type but did vary seasonally, showing a weak quadratic relationship with first egg date:

$$\text{clutch size} = 3.70 + 0.03731 \text{ date} - 0.000267 \text{ date}^2$$

($n = 505$, adjusted $r^2 = 15.6\%$; date: $se = 0.00017$, $P < 0.001$; date²: $se = 0.000012$, $P < 0.001$).

This predicted a maximum mean clutch size of 5.00 (lower $se = 0.08$; upper $se = 0.07$) on day 70 (9 June), with minima at the extremes of the breeding season of 4.04 (lower $se = 0.15$; upper $se = 0.16$) on day 10 (10 April) and 3.69 (lower $se = 0.29$; upper $se = 0.28$) on day 140 (18 August).

Nest survival rates

Daily nest failure rates at the egg stage ($n = 537$ nests) were found to vary significantly between farms (Fig. 2) and with first-egg date. The latter relationship is presented in Fig. 3 after back-transformation and shows that predicted daily failure rates pooled across all farms declined from 0.0437

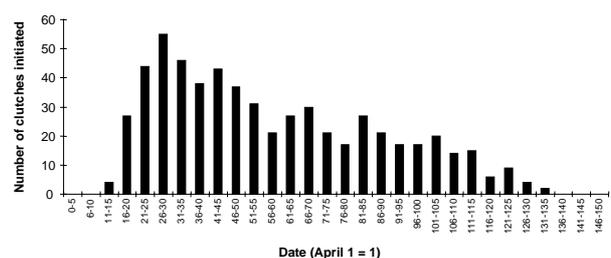


Figure 1. Seasonal distribution of first-egg dates of Linnets from an intensive field study in southern England, 1995-1998.

Table 1. First-egg dates and nest fates of 21 colour-ringed female Linnets at one farm in Oxfordshire, 1998. Day 1 = April 1. Known repeat nesting attempts by the same female are on the same row, in chronological order. Females 18-21 were colour-ringed late in the season, and it is likely that they made nesting attempts earlier than those recorded. For those nesting attempts ending in failure through predation, (e) indicates predation at the egg stage, and (n) indicates predation at the nestling stage. An asterisk indicates that it was unknown whether a nesting attempt took place.

Female	Date	Fate	Date	Fate	Date	Fate
1	19	fledged	59	fledged	*	*
2	22	fledged	60	fledged	*	*
3	24	pred (e)	*	*	*	*
4	25	pred (e)	*	*	100	pred (n)
5	26	pred (n)	51	pred (e)	*	*
6	30	fledged	76	fledged	105	fledged
7	32	fledged	*	*	*	*
8	33	fledged	75	fledged	*	*
9	34	pred (e)	*	*	*	*
10	37	pred (n)	66	pred (e)	80	fledged
11	37	pred (e)	83	fledged	115	fledged
12	38	fledged	76	fledged	*	*
13	38	starved	87	pred (n)	*	*
14	39	nest collapsed	70	fledged	104	fledged
15	40	pred (e)	51	pred (e)	*	*
16	48	fledged	*	*	95	fledged
17	41	fledged	*	*	*	*
18	?	?	80	fledged	*	*
19	?	?	83	fledged	*	*
20	?	?	97	fledged	*	*
21	?	?	98	pred (e)	113	pred (e)

(lower se = 0.0073; upper se = 0.0087) at the start of the breeding season (day 10 = 10 April) to 0.0090 (lower se = 0.0039; upper se = 0.0068) by the end (day 140 = 18 August). Extrapolated over a 17-day laying and incubation period (i.e. 4 days of laying and 13 days of incubation for a modal clutch of 5 eggs Cramp & Perrins 1994), this amounts to an increase in overall nest success rate over the period from first-egg to hatching from 46.8% (lower se = 6.7%; upper se = 6.4%) in early April, to 85.8% (lower se = 9.5%; upper se = 5.9%) by the end of the season in mid-August.

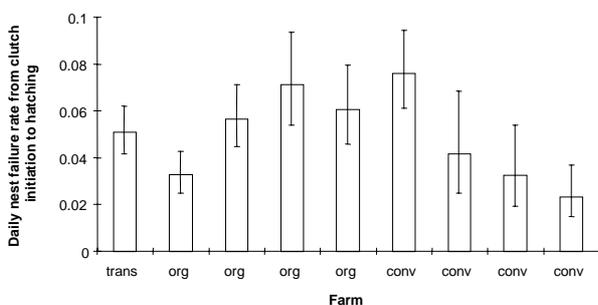


Figure 2. Daily failure rates (+/- se) of Linnet nests at the egg stage on nine study farms in southern England, 1995-1998. org = organic farm; conv = conventional farm; trans = farm in transition to organic status.

Daily nest failure rates during the brood period (n = 406) did not vary significantly with any of the predictor variables. After back-transformation, the mean was 0.0149 (lower se = 0.0016; upper se = 0.0019). Extrapolated over a 13-day brood period (Cramp & Perrins 1994, this study), this amounts to an overall success rate of nests from hatching to fledging of 82.3% (lower se = 2.1%; upper se = 1.7%).

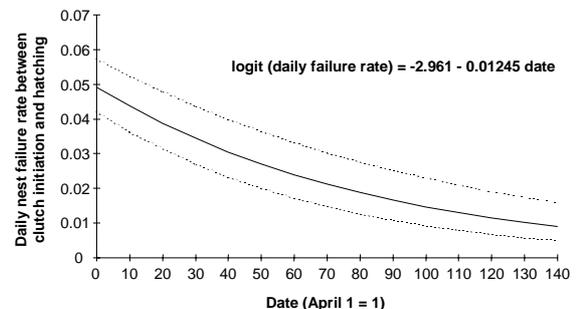


Figure 3. Regression (+/- se) of logit (daily failure rate during egg stage) on first egg date of Linnets from an intensive field study in southern England, 1995-1998. The relationship is plotted after back-transformation.

Partial losses of eggs and nestlings

Neither partial losses of eggs from clutches in which at least 1 egg hatched ($n = 385$) nor partial losses of nestlings from broods in which at least 1 nestling fledged ($n = 325$) varied significantly with any predictor variable. Partial losses of eggs occurred in only 106 of 385 (27.5%) of successfully hatching clutches and in 81 of 106 (76.4%) of these cases, only 1 egg failed to hatch. Partial losses of nestlings occurred in only 37 of 325 (11.4%) successfully fledging broods and in 26 of 37 (70.3%) of these cases only 1 nestling died. This was usually the smallest nestling in the brood (D. Moorcroft unpubl.).

Brood size at fledging

Brood size at fledging varied between 1 and 6 chicks, with the following distribution (1, 5; 2, 12; 3, 45; 4, 125; 5, 128; 6, 15; $n = 330$; mean = 4.22; se = 0.0534). Mean brood size at fledging did not vary with year, farm or farm type but did vary seasonally, showing a very weak quadratic relationship with first egg date:

$$\text{brood size} = 3.76 + 0.0203 \text{ date} - 0.000166 \text{ date}^2 \quad (1)$$

($n = 330$, adjusted $r^2 = 1.9\%$ date: se = 0.00047, $P < 0.017$; date²: se = 0.000003, $P = 0.008$).

This, like clutch size, exhibited a mid-season peak.

Demographic modelling

From the above results, we predicted the mean number of nestlings fledged per nesting attempt over the whole population for first, second and third nesting attempts respectively, using the following formula:

$$\text{fledglings/attempt} = (1-i)^{17}(1-n)^{13}b,$$

where i = daily nest failure rate during the incubation period, calculated for the mean first egg-date of the attempt in question (Table 1), using the formula in Fig. 3, n = daily nest failure rate during the nestling period, and b = mean brood size at fledging calculated for the mean first-egg date of the attempt in question (Table 1) using the formula presented at (1) above. Thus,

$$\begin{aligned} \text{attempt 1: fledglings/attempt} &= 0.564 \cdot 0.823 \cdot 4.25 = 1.97, \\ \text{attempt 2: fledglings/attempt} &= 0.707 \cdot 0.823 \cdot 4.35 = 2.53, \\ \text{attempt 3: fledglings/attempt} &= 0.782 \cdot 0.823 \cdot 4.10 = 2.64. \end{aligned}$$

These results predict that the study population was fledging approximately 4.5 nestlings per breeding female if each female made two nesting attempts, and 7.1 if each female made three nesting attempts.

We attempted to determine whether these levels of breeding success were likely to be sufficient to maintain or increase population levels (assuming no net effect of immigration or emigration) by combining them with national estimates of survival rates of full-grown,

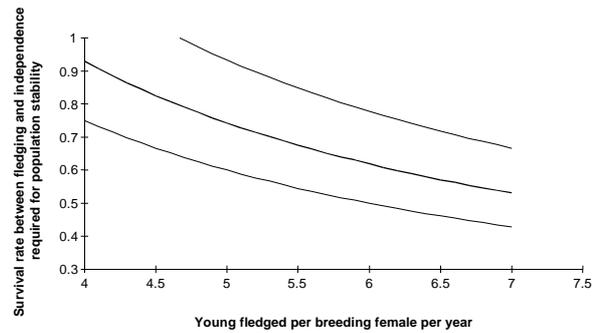


Figure 4. The survival rate of Linnets over the 14 days after fledging that would be required to maintain breeding population size the following year given varying breeding productivity (young fledged per breeding female per year), and survival rate during the remainder of the year. This model assumes that sex ratio is 1:1 and that all birds breed. Upper line = 30% annual survival rate of full-grown, independent birds; middle line = 35%; lower line = 40%.

independent birds recently calculated from ring-recovery data by Siriwardena *et al.* (1998b). Thus,

$$N_{t+1} = (N_t S_{fg}) + (N_t 0.5 P S_{pf} S_{fg})$$

where N_{t+1} and N_t are the breeding population sizes in years t and $t+1$, S_{fg} is the annual survival rate of full-grown, independent birds assuming no differences between sex or age-groups, monogamy and a 1:1 sex ratio (Siriwardena *et al.* 1998b), P = the number of young fledged per breeding female per year (from this study) and S_{pf} = the survival rate of young between fledging and independence, a period of approximately 14 days (Cramp & Perrins 1994).

Given that S_{pf} is unknown, Fig. 4 plots the values of S_{pf} that would be needed to yield $N_{t+1} = N_t$ (i.e. population stability) for realistic ranges of P suggested by the field breeding success data and S_{fg} suggested by ring-recovery analyses (0.3-0.4 in Siriwardena *et al.* 1998b, their Table 4), using the following re-arrangement of the above formula, for $N_{t+1} = N_t$:

$$S_{pf} = (1 - S_{fg}) / (0.5 P S_{fg})$$

Fig. 4 shows that if breeding productivity was limited to two attempts per female per year, then the post-fledging survival rates needed for population stability would vary between 0.667 (0.971 per day), where $S_{fg} = 0.4$, and 1 where $S_{fg} = 0.3$. With three nesting attempts per female per year, the required survival rates fall to between 0.423 (0.940 per day) where $S_{fg} = 0.4$, and 0.657 (0.970 per day) where $S_{fg} = 0.3$.

These figures compare with known survival rates of 0.95-0.97 per day during the immediate post-fledging period for other small passerines (e.g. Sullivan 1989, Zann & Runciman 1994, Anders *et al.* 1997, Hill 1998). In addition, Linnet survival rates between fledging and independence can be calculated indirectly, from a combination of British Trust for Ornithology (BTO) Nest Record Scheme, survival rate and Common Birds Census

(CBC) abundance data (1962-1995), as between 0.952 and 0.980, assuming a 14-day period from fledging to independence and two or three nesting attempts per female (Siriwardena *et al.* 2000). However, these estimates incorporate any measurement error in the estimates of abundance, survival and nesting success used to calculate them, and also make the tacit assumption of monogamy, a 1:1 sex ratio and a constant proportion of breeding adults in the population.

DISCUSSION

Given current levels of breeding productivity, and assuming that national estimates of survival rates of full-grown birds apply, our simple demographic models suggest that the Linnet population of the region in which this study was carried out is likely to be self-sustaining at present providing that some females are making three nesting attempts during the course of the breeding season. In this context, the very low proportion of broods where brood starvation (2.2% of 406 broods with known fate) or partial loss of nestlings occurred also suggests that few pairs were being constrained by food supply. A possible explanation for this is the high local availability of oilseed rape as a source of food for nestlings. From being absent in the 1960s and rare in the 1970s, oilseed rape has become a common crop on most arable farmland in the UK, covering some 0.3-0.4 million hectares annually (MAFF 1996). The part-ripe seed is now the predominant food source for nestling Linnets in rape-growing areas, including in this study (Moorcroft *et al.* 1997). Where both autumn- and spring-sown crops are grown, this food

source may be available from late May through to the end of the breeding season in August. The importance of oilseed rape as a nestling food source coupled with the distances Linnets routinely fly to collect food for nestlings may explain the weak effect of farm identity, and the absence of any effect of organic versus conventional farming regime, in explaining variation in breeding demography in this study; many Linnets were probably collecting food for their nestlings off the farm on which the nest was located.

The conclusion that this study population was likely to be self-sustaining accords with the recent gradual increase on farmland CBC plots (which are concentrated in lowland England) during the 1990s. It would be incautious to draw any more detailed conclusions than this since there are sources of sampling error and bias associated with all the demographic parameters estimated above. Despite these caveats, however, many of the demographic parameter estimates recorded in this study are very similar to those recorded by national monitoring schemes, which have remained fairly constant over recent decades, even during the period of severe population decline between the mid 1970s and the late 1980s (Table 2). Clutch size, nest survival rates during the nestling period, and brood size at fledging are all strikingly similar when comparing this study and BTO Nest Record Scheme data (Siriwardena *et al.* 2000), and estimated survival rates of full-grown birds have fluctuated without any clear trend in recent decades (Siriwardena *et al.* 1999).

Estimates of nest failure rate during the incubation period derived from Nest Record data were variable and were high enough in periods of population decline to explain those declines (Siriwardena *et al.* 2000 and Table

Table 2. Breeding success parameters of Linnets as estimated from Nest Record Scheme data for the main periods of population increase (+) and decline (-) from 1962-1995 (Siriwardena *et al.* 2000), compared with those recorded by the current field study. Mean (in bold) and 95% confidence limits are presented for nest failure rate. Mean \pm 1 se are presented for other parameters. Standard error of 'fledglings per attempt' was calculated using the formula for calculation of variance of products presented by Crick & Baillie (1996). * denotes the fact that a seasonal decline in daily nest failure rate was recorded in the field study; the overall mean is presented. ** denotes that brood size was recorded at fledging in the field study; brood size data from Nest Record Cards will involve broods of varying age but derive from maximum recorded brood size and so will tend towards brood size at hatching.

	Nest failure rate/day (eggs)	Nest failure rate/day (nestlings)	Clutch size (\pm se)	Brood size (\pm se)	Fledglings per attempt (\pm se)
1962-1966	0.0203- 0.0237 -0.0275	0.0109- 0.0140 -0.0179	4.78 \pm 0.029	4.08 \pm 0.046	2.43 \pm 0.091
1967-1969	0.0111- 0.0154 -0.0213	0.0069- 0.0121 -0.0212	4.74 \pm 0.050	4.01 \pm 0.085	2.80 \pm 0.168
1970-1974	0.0109- 0.0142 -0.0185	0.0074- 0.0111 -0.0167	4.71 \pm 0.036	4.13 \pm 0.060	2.98 \pm 0.127
1975-1978	0.0183- 0.0235 -0.0300	0.0115- 0.0173 -0.0259	4.72 \pm 0.048	4.15 \pm 0.076	2.38 \pm 0.152
1979-1986	0.0217- 0.0256 -0.0301	0.0131- 0.0171 -0.0224	4.81 \pm 0.033	4.18 \pm 0.054	2.34 \pm 0.106
1987-1995	0.0177- 0.0209 -0.0247	0.0137- 0.0173 -0.0218	4.66 \pm 0.031	4.35 \pm 0.040	2.56 \pm 0.099
This study	0.0244- 0.0263 -0.0284*	0.0133- 0.0149 -0.0168	4.72 \pm 0.026	4.22 \pm 0.053**	2.49 \pm 0.174

2). However, this temporal variation is small in comparison to the overall seasonal trend observed in this study (Fig. 3). This trend is caused largely by a seasonal decline in predation risk since 212 of 274 (77.4%) nest failures in this study were attributed to predation, probably mostly by Carrion Crows *Corvus corone* and Magpies *Pica pica*. Similar seasonal increases in nest success have been found for other hedgerow-nesting passerines in the UK (e.g. Evans *et al.* 1997). It would be valuable to examine the national nest record database for Linnets to examine whether this seasonal trend has become more apparent in recent years as populations of corvid predators have increased (Gregory & Marchant 1996), and changes in hedgerow management (e.g. mechanical flailing) may have made nests easier to reach.

So, overall, what can we conclude about the likely demographic cause of the severe decline from the mid-1970s and to the late 1980s, followed by recovery during the 1990s? There are at least four possible explanations, none of which are mutually exclusive:

1. The historical changes in nest success rate during the incubation stage that Siriwardena *et al.* (2000) found to be statistically capable of explaining the recent population trend are a true cause of that trend.
2. The trends were caused by changes in the number of nesting attempts that individual females are able to make. Such changes cannot be detected using Nest Record Card data since the identity of females is not known to observers.
3. The trends were caused by changes in survival rate between fledging and independence. This will not have been detected by the analyses of temporal changes in survival rate of full-grown, independent birds carried out by Siriwardena *et al.* (1998b, 1999).
4. The trends have been caused by a change in one or more of the demographic rates analysed above. However, those changes were density-dependent. They were thus ephemeral and difficult to detect as a cause of subsequent population change in a time series where subtle changes are likely to be masked by noise created by sampling error and stochastic effects such as weather. As Green (1999) has pointed out, a long-term population decline may be caused simply by a change in the density-dependence of one demographic rate (e.g. adult survival rate), whilst others remain constant. Such a change, alone, can cause a marked change in population size that is not associated with any simultaneous marked change in any demographic rate.

Given that predation is the main cause of nest loss of Linnets and most other open-nesting passerines (e.g. Newton 1998), hypothesis 1 leads us to consider whether predation, either directly or indirectly, may have been the cause of the fluctuations in nest success that in turn led to

the observed population trend. As the main nest predator of Linnets, Magpie and Crow populations have increased consistently in recent years (Gregory & Marchant 1996), so simple changes in corvid numbers seem unlikely to lie behind the fluctuating trends in nest survival rates. Similarly, trends in agricultural management that may have altered accessibility of Linnet nests (e.g. growth in mechanical flailing of hedgerows) are likely to have been consistent rather than fluctuating. A more probable explanation is that resource limitations on the length of the breeding season (e.g. the number of nesting attempts that individual females are able to make - hypothesis 2) may have prevented birds from making those later nesting attempts that tend to experience high success rates. This hypothesis remains to be tested but is biologically plausible given recent changes in agricultural management. Similarly, it is reasonable to hypothesise that post-fledging survival rates may have been reduced by resource limitations towards the end of the breeding season (hypothesis 3, above). Linnets traditionally fed on the seeds of a variety of agricultural weeds (Newton 1967, Eybert & Constant 1992, 1998, Wilson *et al.* 1996, Moorcroft *et al.* 1997), many of which are known to have been reduced in abundance over the past 40 years by intensive management practices such as herbicide and nitrogen application, and regular cultivation (Andreasen *et al.* 1996, Donald 1998, Ewald & Aebischer 1999, Wilson *et al.* 1999). Especially on arable land, the seeds of many formerly preferred weed species (e.g. Charlock *Sinapis arvensis*) are now scarce or absent. On grassland, where herbicide application is less intensive, some of the species, which Linnets rely on early in the breeding season (e.g. Dandelions *Taraxacum*, Meadow-grasses *Poa*, and Chickweeds *Stellaria*) are relatively competitive, nitrogen-responsive species and have remained abundant (Moorcroft *et al.* 1997). If stresses imposed by scarcer food sources resulted simply in failure to make later nesting attempts, rather than in birds nesting less successfully, then the periods of low incubation-stage nest success observed in the Nest Record Scheme would be an artefact of the reduced probability that individual females would make nesting attempts later in the breeding season when predation risk is low, rather than a reflection of any genuine decline in the nest success rates experienced by individual pairs. A test of this hypothesis by examining whether there have been changes over time in the seasonal distribution of farmland Linnet nests in annual samples of Nest Record Cards would be a valuable development of current work. Similarly, the apparently high incubation-stage nest failure rates observed in this study (Table 2) may be explained if the distribution of nests in this study was more dominated by early nests than are annual samples of Nest Record Scheme data. This possibility should also be tested by future work.

More recently, the increasing availability of oilseed rape

may have ameliorated or reversed the effects of declining agricultural weed populations and allowed Linnet populations to increase, perhaps by restoring the opportunity to make late nesting attempts when predation risk is low. We are now testing the hypothesis that the availability of oilseed rape as a nestling food source may be supporting the current Linnet population increase on farmland. The approach is to compare the data sets presented above with data collected from an arable area of north Norfolk where agricultural grassland is scarce, and oilseed rape absent within 3km of the study area. Although this study cannot test post-fledging survival rates (hypothesis 3) with the resources available to it, preliminary data collected during 1998 do show that breeding densities are lower in Norfolk than in the main study area, and that the breeding season is shorter, despite higher nest failure rates. This indicates the likely effect of a limitation on the number of nesting attempts being made by individual females that is more severe in Norfolk than in Oxfordshire.

Lastly, hypothesis 4 is impossible to test in a short-term field study. Density-dependence characterises the demographic rates of more than half of British small passerines but is difficult to detect even in relatively long-term CBC data (Holyoak & Baillie 1996a, b). However, Siriwardena *et al.* (in press) found that absolute population size (as estimated by CBC index) did not influence statistical models of the relationship between annual survival rates of Linnets and inter-annual population change on CBC plots, thus offering some reassurance that density-dependence may not have concealed the demographic cause of recent trends in British Linnet populations.

In conclusion, we suggest that the most likely explanation for the recent population trend of Linnets on lowland farmland in the UK, is that the severe decline during the 1970s and 1980s was caused by a reduction in the availability of breeding season food supplies on arable farmland as a result of agricultural intensification. The demographic mechanisms involved are less clear. Reductions in the number of nesting attempts being made by individual females and a reduction in immediate post-fledging survival rate are the most likely, but historical data on these two parameters are not available. The population recovery since the late 1980s is likely to have been caused by an increase in the breeding season food supply provided by the increased growing of oilseed rape. These ideas are now being investigated in more detail through collection of comparative breeding demography data from a Linnet population in an intensively arable area where oilseed rape is not grown. Farmland Linnet abundance in the UK may now depend heavily on the availability of oilseed rape. This crop is grown largely under subsidy support from the European Union's

Common Agricultural Policy (CAP). If reforms of the CAP to withdraw production subsidies are realised, and oilseed rape sowing declines, Linnet numbers are likely to decline in arable areas unless provisions are made either to restore their traditional weed seed food sources, or to grow favoured food sources such as oilseed rape as 'wildlife strips' under agri-environment scheme support.

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