Demographic mechanism of a historical bird population collapse reconstructed using museum specimens

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Long-term studies of demographic rates provide clues about the external causes of animal population declines, but systematic monitoring is rarely in place until after the decline has occurred. This study evaluates alternative hypotheses about the demographic mechanisms underlying the historical collapse of corncrake (*Crex crex*) populations in Britain and Ireland in the late nineteenth and early twentieth centuries using characteristics of museum specimens. The proportion of adult corncrakes that are 1-year old was estimated from feather characteristics of birds collected before, during and after the population decline and showed a marked transitory reduction during the decline. This pattern would be expected if the decline was caused by a large reduction in the recruitment of young birds to the breeding population and is the opposite of what would be expected if a change in adult survival had caused the decline. These results are consistent with previous suggestions that the corncrake population decline was caused by adverse effects on breeding productivity caused by the mechanization of the harvesting of hay crops.

Keywords: corncrake; demographic rate; population model; age structure; agriculture

1. INTRODUCTION

Studies of the demographic mechanisms underlying animal population declines make a useful contribution to the diagnosis of the external causes of adverse changes in population and conservation status (Caughley & Gunn 1996; Green 2002). However, they usually require long-term monitoring of reproductive performance and survival that is difficult to achieve, especially for threatened species. Recently, pioneering attempts have been made to reconstruct historical changes in the demography and diet of a threatened bird species, the marbled murrelet (*Brachyramphus marmoratus*), using information derived from museum specimens (Becker & Beissinger 2006; Beissinger & Peery 2007; Norris *et al.* 2007). In this paper, I test hypotheses about the demographic mechanism of a well-documented bird population collapse; the rapid decline of the corncrake (*Crex crex*) population in Britain and Ireland *ca* 100 yr ago.

Corncrakes are ground-dwelling rails (Rallidae) that nest, rear their chicks and forage in the concealment provided by tall grass and herbage. They breed in Eurasia and winter in sub-Saharan Africa. Much of the population breeds in agricultural grassland that is mown for hay or silage (Green *et al.* 1997a). Marked declines in the corncrake population have occurred in many parts of the global range, especially western Europe (Tucker & Heath 1994; Green *et al.* 1997a), including Britain and Ireland, where the species was formerly widespread (Holloway 1996). As a result, the species is classified in the highest category of conservation concern in the UK (Gregory *et al.* 2002) and Europe (BirdLife International 2004), and listed as Near Threatened globally (IUCN 2007). Studies

of the late nineteenth- and early twentieth-century declines in Britain, Ireland and Finland noted that they occurred after the introduction and spread of machines for mowing hay and silage (Norris 1947a,b, 1948; von Haartmann 1958) and proposed the destruction of nests, chicks and full-grown birds during machine mowing as the cause. Mowing occurs largely within the corncrake breeding season and machines can destroy many nests and chicks (Green *et al.* 1997b). Adult corncrakes are killed by mowing relatively rarely (Norris 1948; Tyler *et al.* 1998), so the presumed demographic mechanism of a population decline caused by mowing machines is a decrease in the production of young, and hence recruitment of young adults, rather than adult survival. In this paper, I present information on the age structure of adult corncrakes, collected during the decline and preserved in museums, which indicates that recruitment of young adults was markedly reduced during the decline.

2. MATERIAL AND METHODS

(a) Measurement of the shape of secondary remiges

The proportion of a sample of adult corncrakes that is 1-year old (i.e. those in their second calendar year) can be estimated by measuring the shape of the secondary remiges (Green *et al.* 2001; Green 2004a). The first set of these feathers, grown by chicks, have a more acutely angled shape at their tips than those of adults (Green 2004b). Remiges grown by chicks are not replaced until the late summer of the second calendar year, so the proportion of 1-year-old adults, sampled on the breeding grounds before the moult, can be estimated from the frequency distribution of the secondary shape. I located museum skins of adult corncrakes collected in parts of Britain and Ireland where a substantial population decline was reported prior to 1938

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Figure 1. Map of Britain and Ireland showing the locations (circles) of collection sites of corncrake skins used in the analyses. The map also shows zones in which corncrakes remained numerous with little change up to 1938 (dark grey), remained locally by 1938, but had undergone a considerable decrease (light grey), and remained only in isolated locations for a short period by 1938, having undergone a considerable decrease (white). These zones were defined by Norris (1947a, p. 143).

(Norris 1947a; figure 1). Adults (second calendar year and older) were distinguished from juveniles (first calendar year) by the presence of blue–grey contour feathers on the head, neck and breast. Only skins of adults for which the year and county of collection were given were used. All 65 eligible skins had worn primary tips, indicating remiges grown in the previous calendar year. The 62 birds for which the month of collection was recorded had been collected in April (15), May (37), June (9) and August (1).

I traced the outline of the tip of each of the third to the sixth secondary remiges (numbering from distal to proximal) onto a piece of thin card using a propelling pencil with a 0.5 mm lead. The angle at the tip of the feather was measured from the outline using a miniature protractor and the four angles summed. For further details of the method, see Green *et al.* (2001).

(b) *Timing of the corncrake population decline*

Norris (1947a,b) carried out the first national survey of the status of the corncrake in Britain and Ireland in 1938 by corresponding with ornithologists and naturalists. He requested information on the past and recent distribution and abundance of the species and the timing of any marked changes. I extracted from his papers the year in which a marked decline was first noted, for each county in the areas of Britain and Ireland where substantial corncrake population declines had been reported by the time of the survey.

Information on the timing of corncrake declines for some counties of England and Wales has also been extracted from county avifaunas independently by Shrubb (2003; fig. 9.8), with decline dates being attributed to decades. I assumed that the decline occurred at the midpoint of the decade to which Shrubb assigned it. Rapid population declines do not appear to have occurred after 1938 in parts of Britain and Ireland from which skins are available, although more gradual decreases in numbers occurred. This is evident from the similarity of the map of the corncrake population status in the 1930s, given by Norris, to that for *ca* 1970 given by Sharrock (1976).

Using the results from Norris's survey, I listed the year of population decline for the county from which each museum skin originated and calculated the mean, interquartile range and range of these dates. Norris did not give a decline date for three counties where five of the skins were collected, so I used the decline date for the county with available data whose centroid was nearest; in all cases an adjacent county. One of these skins was from a county covered by Shrubb's map, and the decade of decline given by Shrubb was the same as that given by him for the substitute.

(c) *Analyses*

I used a simple population model to assess how the proportion of 1-year-old adult corncrakes in the population would be expected to vary over time if the predominant demographic mechanism underlying the declines was a reduction in recruitment, a reduction in adult survival or a mixture of the two. The number of adult corncrakes in year i , N_i , was given by $N_i = N_{i-1} (S_{i-1} + R_{i-1})$, where S is the annual survival rate of adults and R is the number of 1-year-old adults recruited in the current year per adult present in the previous year. I assumed $S = 0.286$, the value estimated for the population of corncrakes in Scotland in the period 1991–2002 (Green 2004a). Assuming the population to be stable before the decline, $R = 0.714$ (i.e. $1 - 0.286$). Consider a hypothetical population with these initial demographic rates in which one rate changed abruptly and permanently in any particular geographical location, but this change occurred at different times in different locations. Suppose also that a proportion K of the corncrake's geographical range consisted of refugia in which the demographic rates remained constant and were not affected by the changes that caused the decline. The existence of small refugia is realistic, given that small scattered breeding populations persisted in 1970 in parts of Britain where population collapses had been reported *ca* 60 years earlier (Sharrock 1976). The year in which the change occurred in different parts of the remaining $1 - K$ of the range was taken to be normally distributed with a standard deviation arbitrarily set at 2 years. Young adults were assumed to return in the following year to locations with the same demographic rates as those in their natal sites. For illustrative purposes, I selected changes in the demographic rates that produced maximum rates of adult population decline of 25 and 50% per year, since these correspond to the most rapid sustained rates of population decline documented for globally threatened bird species (Green & Hirons 1991).

The purpose of the main analysis was then to describe changes in the observed proportion of 1-year-old adults over time that could be compared with those produced by the simulation model. The proportion of 1-year-olds was estimated from the secondary angle sums of the sample by

the maximum-likelihood method described by Green (2004a, eqn 3), using the values given in that paper for the mean and standard deviation of the angle sum for secondary remiges grown in the hatching year (carried by adults in the breeding season of their second calendar year) and those grown after the hatching year (carried by older adults). I estimated the proportion of 1-year-olds for subsets of the data corresponding to the main period of the population decline and the periods before and after that period, and also fitted a smoothed curve relating the proportion of 1-year-old adult corncrakes to the calendar year of collection. For both the approaches, 95% CIs of estimates were obtained by bootstrapping. A bootstrap sample of 65 angle sums was drawn at random, with replacement, from the real data and the analysis performed on the sample. This procedure was repeated for 1000 bootstrap samples and the central 950 of the values was used to define the 95% CI.

To produce a smoothed estimate of the proportion of 1-year-olds for a given focal year f , I used the angle sums from all 65 skins and a weighting factor dependent on the time interval between the focal year and the year of collection of each skin. I used the Gaussian weighting factor q_i to weight the component of the total log-likelihood associated with the i th individual collected in year c_i , before summing across all individuals to obtain the total weighted log-likelihood. The weighting factor was $q_i = \exp(-(c_i - f)^2 / 2s^2)$, where s is a smoothing parameter. Selection of the value of s to be used is arbitrary and depends upon the desired degree of smoothing. To assess the robustness of conclusions to using different values of s , I performed the analyses using six values; 5, 10, 15, 20, 25 and 30, thus encompassing a range that allows very short-term apparent fluctuations to be described at one extreme and only long-term trends at the other.

Skins were collected between 1862 and 1985, but only a few skins were available at the extremes, leading to smoothed proportions heavily dependent on results from one or two skins. I therefore restricted the calculation of the smoothed curve to the period 1869–1959, though the data from four skins collected before 1869 and three skins collected after 1959 were still used in the calculation of smoothed estimates.

I wished to assess the statistical significance of the observed pattern of change in the proportion of 1-year-old adults over time in relation to the hypotheses about the demographic mechanisms of the corncrake population decline discussed elsewhere in this paper. Specifically, I used randomization tests to assess the probability of observing by chance a depression in the proportion of 1-year-olds as large as that observed and coinciding as closely with the main period in which population declines were reported. For each randomization, I reshuffled the observed values of the 65 angle sums so that each was reassigned at random to one of the skin collection years. I carried out two tests. (i) I estimated the proportion of 1-year-olds for skins collected within the interquartile range of reported population decline dates, and for the periods before and after this. I calculated the difference in proportions between each of the three pairings of these time periods, repeated the procedure 1000 times and took the proportion of randomizations in which the difference was as large, or larger, than that seen in the real data as the probability that the observed difference arose by chance. (ii) I fitted a smoothed curve to the randomized data as described above. From this curve, I obtained the minimum

value of the smoothed proportion of 1-year-olds and the calendar year in which it occurred. I repeated this procedure 1000 times and counted the number of cases in which the minimum value of the smoothed proportion was equal to, or less than, the minimum obtained by smoothing the real data and also occurred closer to, or as close to, the mean date of the observed population declines as was seen in the real data. I took the proportion of such cases as the probability of observing by chance a result more extreme, or as extreme, as that obtained.

3. RESULTS

(a) *Contrasting expectations for changes in the proportion of 1-year-old adults from competing hypotheses about the demographic mechanism of a rapid population decline*

The observed rapid declines of corncrake populations might have been caused by a reduction in the recruitment of young adults, a reduction in the further survival of adults or by a combination of these two. A maximum population decline rate of 25% per year could be induced in a model population with refuge proportion $K=0.01$ by reducing either recruitment R by 37% or adult survival S by 92% of the initial values, in each case leaving the other demographic rate unchanged. The proportion of 1-year-olds was initially the same as the initial value of $R=1-S$. There were contrasting consequences of the two demographic mechanisms for the proportion of 1-year-old adults. If the decline was caused by the reduced recruitment of young, the proportion of 1-year-old adults underwent a transitory decline, and then returned gradually to its initial value as populations outside the refugia dwindled. However, if the decline was caused by reduced adult survival, the proportion of 1-year-old adults increased and later returned to its initial value (figure 2). A larger reduction in R (by 92%) was required to induce a population decline at a maximum rate of 50% per year and this produced a larger transitory depression of the proportion of 1-year-old adults (figure 2). It is not possible to induce a decline of 50% per year in this model population by reducing adult survival alone. In all cases, there was a lag of several years between the time when the decline was well advanced, and would probably be apparent to observers, and the minimum or maximum of the transient change in the proportion of 1-year-old adults. If I induced a population decline by reducing both S and R by the same proportion, the proportion of 1-year-old adults in the model population remained constant (results not shown).

(b) *Timing of the corncrake population decline*

Based upon the survey of Norris (1947a,b), the weighted average of the years in which marked population declines were first reported in the areas where the corncrake skins were collected was AD 1908 (mean AD 1907.8; range of county dates AD 1875–1936; interquartile range AD 1900–1920). The mean dates of decline for the 18 counties in England and Wales from which corncrake skins were available, and decline dates given both by Norris and from Shrubbs (2003), were very similar for the two sources (Norris, AD 1902.4 cf. Shrubbs, AD 1903.3). Variation among counties was highly correlated between the sources ($r=0.933$, $p<0.001$), which is not

Figure 2. (a) Trajectories of adult population size (scaled arbitrarily to 1 in the first year) for hypothetical corncrake populations subject to a change in adult survival or recruitment in part of their range. The solid curve shows the trajectory for a population in which adult survival remained constant, but recruitment declined abruptly by 37% in 99% of the region. The change occurred with an average onset in the year 20 (vertical line) and a standard deviation among places of 2 years. The same trajectory is followed by a population in which recruitment remained constant but adult survival declined abruptly by 92%, with the same spatial extent and variation in the timing of onset. Both of these populations declined at a maximum rate of 25% per year. The dashed curve shows results for a population that declined at a maximum rate of 50% per year because recruitment fell by 92%, with the same spatial pattern as above. (b) Changes over time in the proportion of 1-year-old adults in the populations shown in (a). The two solid curves show results for the two populations with a maximum decline rate of 25% per year. The proportion of 1-year-olds decreases during the period of decline in the case where the decline was caused by a change in recruitment but increases where the decline was caused by a change in adult survival. The dashed curve shows the result for the population that declined by a maximum of 50% per year owing to a 92% reduction in recruitment.

Table 1. Proportion of adult corncrakes estimated to be 1-year-old during the main period from which population declines were reported (the interquartile range of decline dates), compared with equivalent proportions from museum skins collected before and after the main decline period and a recent sample of adults live-trapped or found dead in Scotland.

period	range of collection years (AD)	<i>n</i>	proportion 1-year-old	95% CI
before decline	1862–1898	25	0.799	0.559–1.000
during decline	1901–1917	16	0.392	0.081–0.723
after decline	1927–1985	24	0.755	0.538–0.971
recent	1991–2002	136	0.720	0.619–0.809

surprising because much of the information used by both authors probably came from the same naturalists. Given that the results from the two sources were so similar, I used the information provided by Norris in all analyses because he provided data for Scotland and Ireland and estimates of timing to the nearest year.

(c) *Observed change in the proportion of 1-year-old adult corncrakes during the population decline*

The proportion of 1-year-old adult corncrakes estimated from the secondary angle sums of museum skins was considerably lower for those collected during the main period of reported population declines (defined as the interquartile range of county-specific decline years) than for the periods before and after (table 1). Randomization tests indicated that the reduction in the proportion of 1-year-olds was larger than expected by chance, comparing the main decline period with the period before it ($p=0.024$) and also for the comparison of the main decline period with the period after it ($p=0.040$). The proportions of 1-year-old adults before and after the decline were similar to one another and to the proportion of 1-year-old adults in a sample of 136 corncrakes captured or found dead in Scotland in 1991–2002

(table 1). Further details of this sample are given by Green (2004a).

The examination of the smoothed trajectory of the estimated proportion of 1-year-old adults shows that the minimum occurred between AD 1913 and 1918, 5–10 years after the average year in which population declines were reported (figure 3b; table 2). Randomization tests indicated that the combination of the observed magnitude of the reduction in the proportion of 1-year-olds with the closeness of its coincidence with the reported population declines was unlikely to have arisen by chance. As would be expected, the statistical significance of the variation declined as the degree of smoothing was increased, but significance remained until the smoothing parameter was quite large (above 25 years; table 2).

4. DISCUSSION

The simple population model does not provide a realistic simulation of corncrake population processes, but indicates the expected direction and broad pattern of changes in the proportion of 1-year-old adults under competing hypotheses about the predominant demographic mechanism underlying the population decline. In reality, natal and breeding dispersal would be expected

Figure 3. (a) Sums of angles at the tips of the third to the sixth secondary remiges of museum skins of adult corncrakes in relation to their year of collection. The horizontal lines show the mean and shaded zones the interquartile range of angle sums for a recent sample of birds with secondary remiges known to have been grown in the year of hatching (lower) or after the year of hatching (upper). The shapes at the right-hand side show the normal distributions of the secondary angle sum fitted to data for these known-age birds. (b) The smoothed curve, derived from the data in (a), represents variation over time in the proportion of adult corncrakes that had hatched in the previous calendar year (thick curve) and its 95% CI (thin curves) during the period 1869–1959. The value of the smoothing parameter s was 10. The filled square shows the proportion of 1-year-old adults estimated from a recent sample of corncrakes from Scotland and the vertical line represents the 95% CI for that estimate. Shown in (a, b) is the mean of calendar years (AD) in which substantial corncrake population declines were first detected (thick vertical line) and the interquartile range representing variation in this date among counties (thin vertical lines).

to be sufficient to allow some movement of young birds between areas with different demographic rates (Green 1999), but an elaborate model of this would be needed. However, a transitory reduction or increase in the proportion of 1-year-old adults, or no change, during a period of rapid decline is also likely to be a feature of more realistic models, with the direction of change being dependent on the demographic mechanism in the manner described.

The estimated proportion of 1-year-old adult corncrakes was similar across three time periods: (i) the late nineteenth century, before most marked population declines were reported, (ii) the mid-twentieth century after most declines had occurred and only small, stable or slowly declining relict populations remained, and (iii) the late twentieth and early twenty-first centuries when the

Table 2. Sensitivity to the value of the smoothing parameter s of the estimated minimum proportion of 1-year-old adult corncrakes in the period 1869–1959 and the year in which the minimum occurred. (Results from a randomization test of statistical significance (see text) are also shown.)

smoothing parameter s	minimum proportion 1-year-old	year of minimum (AD)	proportion of randomizations
5	0.246	1915	0.003
10	0.447	1914	0.006
15	0.575	1913	0.032
20	0.628	1913	0.047
25	0.654	1914	0.050
30	0.668	1918	0.069

remaining population in Scotland was increasing at approximately $5\% \text{ yr}^{-1}$ (O'Brien *et al.* 2006). However, during the main period when declines were reported, the proportion of 1-year-old adults was lower than in any of these three periods of relative stability. The minimum occurred a few years after the mean date of reported onset of declines. The pattern of change in the proportion of 1-year-old adults in relation to the timing of the decline resembled that of the simple population model (figure 2b cf. figure 3b), in which the mechanism of the decline was reduced recruitment, and contrasted with the pattern expected if reduced adult survival or similar reductions in both rates had caused the decline.

The low proportion of 1-year-old adults estimated for the main decline period implies a rapid rate of population decline. During a steady decline, the population multiplication rate λ can be calculated from adult survival S and the proportion of 1-year-old adults P_1 as $\lambda = S/(1 - P_1)$. Assuming that S remained at its recently determined average value (0.286) during the decline and that P_1 had the value estimated for the period within the interquartile range of county decline dates (0.392), λ is then estimated at 0.470 during 1900–1920: a decline rate of 53% per year. The fact that the declines really were rapid is evident from the reports of the amateur naturalists who witnessed them (Norris 1947a,b, 1948) and from the fact that they felt able to specify the time of onset of declines quite precisely, probably without having done any systematic survey work.

The use of age ratios in the study of avian demography is susceptible to a number of sampling errors and potential biases with various consequences for the estimation of demographic parameters (Beissinger & Peery 2007; Peery *et al.* 2007). In the present study, unpublished simulations incorporating uncertainty in the estimates of the mean and standard deviation of the secondary tip angle sum of corncrakes of known age showed that it had little effect on significance tests on changes over time in the estimated proportion of 1-year-old birds in the museum specimens or the year in which the minimum value occurred. The most plausible cause of bias would be for the circumstances of collection of birds that became museum specimens to differ over time in ways associated with the population decline and for age composition to vary with collection circumstances. There was no information on circumstances of collection of the great majority of

specimens, but this hypothesis seems unlikely. Specimens were not grossly damaged and most were obtained in spring (April and May), before the main mowing season, so collection of birds killed by machine mowing itself are not a plausible source of potential bias. The percentage of birds obtained in spring was similar before, during and after the main period of decline (83, 87 and 83%, respectively). Finally, there was no marked difference in age ratios between samples of live-trapped adult corncrakes and those found dead by the public (Green 2004a).

The results indicate that the predominant demographic mechanism of the corncrake decline was a reduction in recruitment instead of a reduction in adult survival or a comparable reduction in both rates. A plausible cause of this is low breeding productivity. Another possible explanation is the reduced survival of fully grown corncrakes in their first winter, with the survival of older birds remaining unchanged. Although this alternative cannot be excluded, it is difficult to suggest what could cause such a large change in overwinter survival of one age class, relative to the other. Overwinter survival of first-winter birds would need to be reduced by 74%, and the survival of older birds to remain unchanged, to account for the observed change in the proportion of 1-year-old adults. It was not possible to use the ratio of juvenile (first calendar year) museum skins to the number of adults as a measure of breeding productivity because only small numbers of juveniles were collected.

The apparent reduction in recruitment, coincident with the decline, is consistent with previous suggestions that it was caused by the effects on breeding productivity of the mechanization of grass mowing (Norris 1948). The timing of the mechanization of grass mowing in Britain and Ireland is difficult to establish precisely, but it began in the second half of the nineteenth century and the proportion of the hay crop in mainland Britain mown by machines probably exceeded 50% by the beginning of the twentieth century. The spread of machine mowing probably occurred later in wet meadows and upland margins where corncrakes were most likely to breed (Norris 1948; Shrubbs 2003). In addition to the direct mortality caused by machines, an important factor that probably affected corncrake breeding success was the speeding-up of the hay harvest by mechanization, so that more of it occurred early and within the corncrake breeding season. This change was caused not only by mowing machines, but also by the somewhat later introduction and spread of machines for turning and drying the cut hay (Shrubbs 2003). For these reasons, it is difficult to quantify precisely the degree of coincidence between the mechanization of hay production and the corncrake population declines and changes in demography. However, the timing of the mechanization of the hay harvest is consistent with it having been a major cause of the reduced recruitment that accompanied the collapse of the corncrake population.

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