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A new method for estimating the adult survival rate of the Corncrake *Crex crex* and comparison with estimates from ring-recovery and ring-recapture data

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The mean annual survival rate of adult Corncrakes *Crex crex* was estimated by three independent approaches: ring-recovery, ring-recapture and the shape of secondary remiges. The last method is new and uses measurements of the shape of the tips of the secondaries, which changes in the first post-juvenile wing moult to become less pointed. The estimates obtained by the three approaches were mutually compatible and indicated that annual survival is likely to be within the range 0.2–0.3. This low survival rate is likely to make the growth rate of Corncrake populations particularly sensitive to the effects of agricultural and conservation management on breeding success and recruitment. The survival rate of adult female Corncrakes was estimated for the first time (0.259) and was found not to differ significantly from an estimate for adult males (0.298) made in the same study area by the same method. It is concluded that the method based upon population counts and measurements of the shape of remiges has potential value for studies of the demography of Corncrakes and other species.

Estimates of the demographic rates of birds are important for studies of population dynamics and can provide insights relevant to conservation management (Green 2002), but practical problems often make reliable estimates difficult to obtain, in spite of considerable advances in analytical methods (White & Burnham 1999). This is especially true for the estimation of survival rates in the Corncrake *Crex crex*. Several workers have noted the low return rate of ringed Corncrakes to restricted study areas in subsequent years (Alnås 1974, Swann 1986, van den Berg 1991, Fox 1993). Estimates of dispersal distance and survival of male Corncrakes in Scotland and Ireland by Green (1999) indicated that there was much long-distance (> 10 km) natal dispersal, leading to low return rates of birds ringed as chicks, but that breeding dispersal was restricted and adult survival was low (< 0.2), even after allowing for emigration from the study areas. In these circumstances, it has not been practical to obtain sufficient recaptures for robust estimation of survival from conventional Cormack–Jolly–Seber analysis. The ringing of 900 Corncrakes and considerable efforts to recapture them in subsequent years resulted in only 40 recaptures, and, more importantly, the low survival rate led to only six of these recaptures being made more than 1 year after ringing and there were none at all more than 2 years after ringing (Green 1999). This lack of recaptures over periods of more than about 2 years has also been noted in studies in Sweden (Alnås 1974), The Netherlands (van den Berg 1991) and Ireland (Fox 1993). This makes the estimation of recapture and survival rates by Cormack–Jolly–Seber methods problematic.

In this paper I describe a new approach to the estimation of the adult survival rate of Corncrakes based on surveys of males calling during the breeding season and measurements on captured birds of a plumage characteristic that changes with age. As well as yielding a new estimate for males, this method produces the first survival estimate for adult female Corncrakes. I also estimate adult survival from the few available ring recoveries and compare this with the estimate from the new method and the existing estimate from ring-recapture.

METHODS

The plumage characteristic upon which the new method for survival estimation depends is the shape

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of the tips of the secondary remiges. One-year-old adults have secondaries grown in the hatching year (HY). These have more pointed tips than the secondaries of older adults, which are grown after the hatching year (AHY) (Green *et al.* 2001). In this section, I describe the method used to measure secondary shape and the source of the birds that were measured.

Capture of wild birds

At the beginning of the breeding season in May, adult Corncrakes were caught on the Isle of Coll, Argyll, Scotland (56°40′N, 6°35′W) in 1999, 2000, 2001 and 2002 by tape luring them at night or by driving them into cage traps (see Green 1999 for details). Partly grown chicks, full-grown juveniles and adults were also caught in August–September on Coll by driving them into cage traps and funnel traps in 1998, 1999, 2000, 2001 and 2002. In late summer to autumn, full-grown birds were aged as juveniles if they had greyish green irides and as adult if they had brown or reddish-brown irides (Salzer & Schäffer 1997). Adults were sexed from their behaviour if possible, but otherwise from measurements of wing length and head and bill length (see Tyler *et al.* 1996).

All 96 adult Corncrakes (83 males, 13 females) captured on Coll in 1999–2002 that had remiges grown in the previous year were included in the analysis. Most of these birds (92) were measured in May.

Carcasses

The carcasses of 40 Corncrakes found dead in Scotland by members of the public and RSPB staff between 1991 and 2002 were sexed by dissection or measurements of wing length and head and bill length (see Tyler *et al.* 1996). The collection comprised 25 males, seven females and eight that were not sexed because they were decomposed or partly eaten. Only data from adults with old remiges (i.e. grown in the previous year) were included. The specimens were collected on Barra (1), Benbecula (3), Coll (3), Colonsay (1), Lewis (2), North Uist (7), Orkney (2), South Uist (1), Tiree (19) and the Scottish Highland mainland (1).

Measurement of secondaries

Each of the tips of the third to sixth secondaries (numbering ascendantly) was outlined on to a piece of thin white card using a propelling pencil with a 0.5-mm lead (Method 3 of Green *et al.* 2001). The angle at the tip of the feather was read off from the cards using a transparent miniature protractor (Green *et al.* 2001). All tracings and measurements were made by the author.

STATISTICAL ANALYSIS

Modified inventory method

It is possible to estimate annual survival from the proportion of birds in different age classes and annual census data. Indeed, Snow (1956) estimated adult survival rates from proportions of 1-year-old adults alone by assuming that adult population size was stable. The most frequent use of this method is to estimate survival rates of geese from complete winter counts that also include measurements of the proportion of first winter birds (e.g. Kirby *et al.* 1985). I modified this method to allow the estimation of adult survival from annual censuses of Corncrakes and a proxy for direct measurements of their age structure. Suppose that the population of adult Corncrakes in year i is N_i, of which a proportion v_i is more than 1 year old, and that the adult population in the previous year was N_{i-1}. Assume also that there is no net immigration or emigration after recruitment to the adult population. It is evident that

$$N_i = N_{i-1} \times \varphi_i + (1 - v_i) \times N_i \quad (1)$$

where φ_i is the adult survival rate between years $i - 1$ and i. When rearranged, this gives

$$v_i = \varphi_i \times N_{i-1}/N_i. \quad (2)$$

Green *et al.* (2001) found that the sums of the angles at the tips of secondary remiges 3–6 were approximately normally distributed and differed between 1-year-old adults and older birds because HY feathers were more pointed than AHY feathers. Suppose that the mean and standard deviation of this angle sum are m_1 and s_1 for HY and m_2 and s_2 for AHY feathers and that a sample of n adults is captured in year i before the late summer moult and the secondary angle sum a is measured for each bird. Using the approach of Green *et al.* (2001), the proportion of birds older than 1 year, v_i, can be estimated by modelling the distribution of the a as a mixture of two normal distributions and minimizing the deviance

$$\text{deviance} = -2 \sum_{j=1}^{n} \log_e[(1 - v_i) \times f(a_j, m_1, s_1) + v_i \times f(a_j, m_2, s_2)], \quad (3)$$

where $f(a, m, s)$ denotes the normal probability density function for a bird with secondary angle sum a, given a mean and standard deviation m and s.

Substituting for v_i in Eq. (3) using Eq. (2) allows adult survival φ to be estimated if m_1, s_1, m_2 and s_2 are known from previous studies and estimates of N_i and N_{i-1} can be obtained for the area in which each of the birds in the sample was captured.

Although Green *et al.* (2001) gave estimates of m_1, s_1, m_2 and s_2, their samples were small (54 HY and 14 AHY birds), so I augmented them with new measurements made in 2001 and 2002. Data were added for 18 birds with HY feathers (17 juveniles captured in autumn on Coll and a juvenile found dead on Tiree (Argyll)) and eight birds with AHY feathers (three ringed adults recaptured on Coll in a year after ringing, four adults captured in moult on Coll and an adult with freshly grown feathers found dead on Tiree in September 2001). Details of the criteria used to determine the minimum age at which the adults grew their remiges are given by Green *et al.* (2001). Using the augmented samples, the mean and standard deviation of the sum of the angles at the tips of secondaries 3–6 were 401.2° and 20.4°, respectively, for HY feathers and 450.1° and 16.4° for AHY feathers.[a] These values are similar to those obtained previously from the smaller samples of Green *et al.* (2001, 399.4° (sd = ± 21.1°) and 452.9° (sd = ± 16.5°)).

It was assumed that N_i and N_{i-1} could be approximated by counts of singing male Corncrakes in the current year and the previous year. Census data for the island on which each Corncrake was measured were obtained from Table 1 of Green and Gibbons (2000) or updates thereof using the same survey method (R.E. Green unpubl. data). Because all captures on Coll were made at the western end of the island, within the RSPB reserve, the census figures used were confined to this area, i.e. west of National Grid reference easting 200 and south of northing 590. The value of φ that gave the minimum deviance was found using the NONLIN module of SYSTAT 5.03. A 95% confidence interval was defined by the central 950 of estimates made from 1000 bootstrap samples drawn with replacement from the original data. This confidence interval does not incorporate uncertainty in the estimates of m_1, s_1, m_2 and s_2. However, the standard errors of these estimates are quite small,[a] so the interval would probably not be much wider if this source of error was included.

The goodness-of-fit of the modelled distribution of secondary angle sum to the data was assessed by a χ^2 test. Observed and expected numbers of birds in each of the nine 10° bins between 370° and 459° and for birds with angle sums < 370° and > 459° were compared. Amalgamation of bins at the extremes of the distribution was necessary to avoid expected values less than five.

Ring recovery analysis

Recoveries were used of Corncrakes ringed in all years up to 1998 inclusive in Britain and Ireland under the British Trust for Ornithology's (BTO) Ringing Scheme. Details of the geographical distribution and timing of Corncrake ringing are given in Green (1999). Corncrakes have mainly been captured for ringing by luring them into traps or nets by reproducing the *crek-crek* call or by capturing flightless chicks during the mowing of hay and silage meadows. Methods for determining the sex of Corncrakes from measurements have only become available recently, so most ringed adults were not sexed. However, it is likely that most of the birds ringed as adults were males because the most frequently used trapping methods bias captures in favour of males (Tyler *et al.* 1996, Green 1999).

The recoveries used were restricted to those of birds found dead or in poor condition by the public. Recoveries of dead radiotagged adults made by research workers during recent intensive studies were excluded because the carcasses would almost certainly not have been found without radiotracking. Because the radio-tags and attachment methods used are short term (tags detach within 4 months) inclusion of these recoveries would have biased estimates of survival to be too low. Recoveries were grouped by age at ringing (chick or adult), year of ringing and time since ringing divided into 365-day periods. I considered recoveries made up to the breeding season of 2000 to be eligible for analysis, so birds ringed in 1998 could only be recovered within 2 years of ringing, those ringed in 1997 within 3 years of ringing and so on. Some analyses required the numbers of birds ringed by age at ringing and year. From 1974 onwards these totals are available from the records of individual ringers (Green 1999), but for earlier years annual ringing totals were obtained from BTO Ringing Scheme reports. Birds ringed as pulli were taken to be chicks or juveniles and those ringed as full-grown were taken to be adults. A few fledged juveniles reported as full-grown were probably misclassified as adults by this procedure, but this problem is believed to be negligible, given the difficulty of capturing fully fledged Corncrakes in late summer before mist-nets were widely available and before the recent (1998) development of methods for driving birds into cage traps. Annual ringing totals broken down by age classes for the period prior to 1954 were not available, so it was assumed, from the proportions of the age classes ringed in the period 1954–61, that 90% of birds were ringed as chicks and 10% as adults. This is a much greater proportion of chicks than that for the period 1954–98 for which the proportion of chicks is known (37%), but the use of mist-nets and tape-recorded calls as lures is certain to have increased the ease with which adults can be captured. Seven of the recoveries used relate to birds ringed before 1954.

Two methods were used to estimate adult survival from ring recoveries. The model of Haldane (1955) was fitted to the 11 recoveries ringed as adults and the single recovery of a bird ringed as a chick and recovered more than 365 days after ringing. This method uses only the recovery data and not the numbers of birds ringed. The maximum-likelihood method of Brownie *et al*. (1985) for birds ringed as young and adults, modified to estimate reporting rate rather than recovery rate, was also used on all 17 recoveries. This method requires the numbers of birds ringed for each age class as well as the recoveries. It was assumed that survival in the first year of life differed from that of older birds, but that neither survival nor reporting rate varied with calendar year. Although these assumptions are unlikely to be entirely realistic, they are accepted here because the data are insufficient to support more elaborate models and should provide reasonable estimates of average survival rate, even though survival really varied among years. For both analyses, the NONLIN module of SYSTAT 5.03 was used to obtain maximum-likelihood estimates. A 95% confidence interval was defined by the central 950 estimates made from 1000 bootstrap samples drawn with replacement from the recovery data (Haldane method) or histories of all birds ringed (Brownie method).

Ring-recapture analysis

Green (1999) reported an analysis of recaptures of male Corncrakes ringed as chicks and adults in Scotland and Ireland between 1974 and 1996. The results of that analysis are used here, together with a modified analysis of the same data that allows for possible under-recording of singing male Corncrakes in annual censuses. Such under-recording would make the estimated values of the probability of detection too high and survival rate too low. The model was altered to include a factor q, which is the proportion of the true population of singing males that is counted. This proportion was assumed to be the same throughout the study area and was incorporated[b] into equations 3 and 4 of Green (1999). Estimation and the calculation of confidence intervals were carried out as previously described (Green 1999).

RESULTS

Modified inventory method

The adult survival rate estimated from the distribution of secondary angle sums for captured birds and carcasses combined was 0.286 (Table 1). As the estimates derived from captured birds did not differ from those from carcasses (survival estimates 0.301 cf. 0.252, respectively; likelihood-ratio test, $\chi^2 = 0.20$,

Table 1. Annual survival rates of adult Corncrakes estimated from the distribution of secondary angle sums, ring-recovery and ring-recapture. Dataset codes (A, B, C) identify groups of estimates made from the same dataset by different methods or estimates for subdivisions of a dataset. Sample sizes are numbers of (1) secondary angle sum measurements, (2) recoveries of dead birds and (3) live recaptures of ringed birds in years after ringing.

Method	Dataset	Sex	Survival estimate	95% CI Lower	95% CI Upper	Sample size
Secondary shape	A	Both	0.286	0.191	0.393	136[1]
Secondary shape	A	Male	0.298	0.188	0.421	108[1]
Secondary shape	A	Female	0.259	0.050	0.545	20[1]
Ring-recovery (Haldane)	B	Both	0.201	0.041	0.496	12[2]
Ring-recovery (Brownie)	B	Both	0.217	0.048	0.502	17[2]
Ring-recapture	C	Male	0.186	0.123	0.237	43[3]
Ring-recapture (modified)	C	Male	0.229	0.085	0.525	43[3]

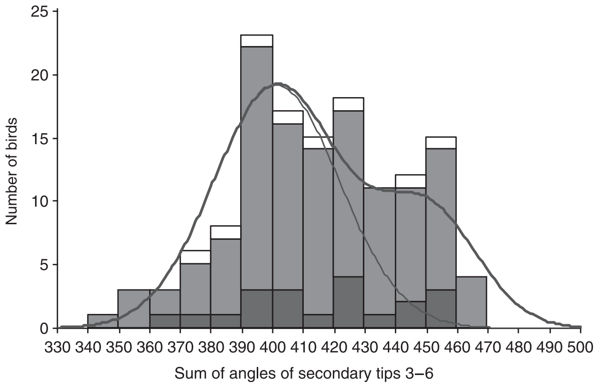

Figure 1. Numbers of female (dark grey bars), male (light grey bars) and unsexed Corncrakes (open bars) by 10° bins of the sum of the angles at the tips of secondaries 3–6. Samples of live trapped birds from the Isle of Coll and carcasses of birds found dead throughout the Corncrake's range in Scotland have been pooled. The curves show the expected distribution for a population in which the proportion of birds older than 1 year is 0.280 (thick line) and the distribution for the 1-year-old component (thin line).

df = 1, $P > 0.6$), data from these two sources were pooled in making the estimates given in Table 1. Neither was there a significant difference between the estimates for males and females (0.298 cf. 0.259, respectively; $\chi^2 = 0.08$, *df* = 1, $P > 0.7$). Considering the Corncrakes captured on Coll in 1999–2002, the survival estimates for the four years did not differ ($\chi^2 = 6.81$, *df* = 3, $P = 0.08$). There were insufficient data to make a meaningful test of variation in survival among years from the carcass data. The observed distribution of secondary angle sums conformed reasonably well with that expected from the means and standard deviations of birds of known age and the fitted proportion of birds older than 1 year (Fig. 1; $\chi^2 = 14.83$, *df* = 10, $P = 0.14$).

Based on these analyses, it is concluded that a survival rate estimate derived from the pooled data for all years, sources and both sexes is a reasonable summary.

Ring-recovery analysis

Of six recoveries of Corncrakes ringed as chicks, five occurred within 1 year of ringing, with one bird being recovered between 1 and 2 years after ringing. Of 11 recoveries of Corncrakes ringed as adults, eight occurred within 1 year of ringing, with three birds being recovered between 1 and 2 years after ringing. The estimates of adult survival rate made using the Haldane and Brownie models were similar (Table 1). Because reporting rates often vary among age classes (Brownie *et al.* 1985), an alternative Brownie model was also fitted in which both survival and reporting rates differed between birds in their first year and older birds. Comparison of this model with that in which reporting rate did not vary with age showed no significant effect of age on reporting rate (likelihood-ratio test, $\chi^2 = 2.96$, *df* = 1, $P = 0.08$), although the test has little power with such a small number of recoveries. The estimate of adult survival rate was the same whether reporting rate was assumed to vary with age or not.

Ring-recapture analysis

The previously published estimate of the survival rate of adult males from the ring-recapture analysis of Green (1999) was 0.186. When the model was modified to allow for possible under-recording of male Corncrakes in censuses, the estimate was somewhat higher (0.229), but the confidence interval became much wider[b] (Table 1). The estimated proportion of males present that were recorded on the censuses, *q*, was 0.768, which, initially, suggests that males were under-recorded by 23%. However, the 95% confidence interval for *q* was very wide (0.290–2.010), so this cannot be regarded as reliable evidence for substantial under-recording.

DISCUSSION

The modified inventory method is a new development of existing methods of survival estimation that use proportions of age classes and assumptions about, or surveys of, population changes (Snow 1956, Kirby *et al.* 1985). The novel aspect of the present study is that it uses the distribution of measurements of a character whose average value differs between age classes, but with sufficient overlap that it is not possible to age all individuals reliably. If valid, it will be useful for comparing the demography of Corncrake populations and could be applied to other species in which it is not currently possible to age all adults reliably. For example, in many passerines the tips of rectrices grown in the hatching year tend to be more pointed than those of older birds, but it is difficult to make reliable assignments, based on this character, of all adults to age classes (Svensson 1992). The method has the advantage over the ring-recovery and ring-recapture approaches that it is practical to base the estimates directly on measurements of large samples of adults, rather than on relatively small numbers of recoveries or recaptures. For Corncrakes, the precision of estimates based on ring-recovery and ring-recapture is severely limited by the small proportion of ringed birds that are recovered (*c.* 1%) or recaptured (*c.* 5%).

The main assumptions of the modified inventory method are (1) that there is no net emigration or immigration of adults from/to the study area, (2) that the sample of adults from which the proportion that are 1 year old is estimated is representative with respect to age, (3) that the ratio N_{i-1}/N_i is measured with negligible error, and (4) that the distributions of secondary angle sums are normal with parameters accurately estimated from samples of known-age birds. Assumption (1) is likely to be approximately correct because it is known that only a small proportion (< 10%) of adult male Corncrakes move sufficiently far (> 10 km) after their first year to result in movement between islands or study areas (Green 1999). Little is known of the movements of adult females, but even if a greater proportion of them make long-distance movements, there is no reason to believe that emigration and immigration would not balance for a particular study area. Assumption (2) is difficult to check. It might be that young adults are more or less likely to respond to tape lures and be captured than older birds. It is also possible that the proportion of ages in the captured sample might not be representative because most trapping effort is concentrated early in the breeding season. If age classes differ in the date of arrival on the breeding grounds this could lead to bias in the proportions of 1-year-old and older birds captured. Most Corncrake trapping has been carried out over too short a period of the breeding season to test this conjecture. Assumption (3) cannot be checked because Corncrake surveys in Scotland are treated as censuses and the standard errors of these cannot be obtained from existing data. However, it is not assumed here that the entire adult population is counted in each of the two years, only that the counts represent a constant proportion of the true population. Assumption (4) appears to be reasonable because goodness-of-fit tests, on secondary angle sum measurements of Corncrakes of known age, indicate good agreement between the observed data and fitted normal distributions of angle sums. This agreement was good both for birds with HY feathers ($\chi^2 = 3.14$, $df = 6$, $P > 0.70$) and for birds with AHY feathers ($\chi^2 = 1.84$, $df = 3$, $P > 0.60$). The good fit of the mixture distribution fitted to the secondary sum angles of Corncrakes of unknown age (see Results and Fig. 1) also supports this assumption.

Estimates of adult survival based on the three approaches ranged between 0.186 (ring-recapture) and 0.286 (modified inventory), but there was no significant difference between any pair of the survival estimates based on the three approaches. All the methods yielded estimates with quite wide confidence intervals, with the sparse ring-recovery data giving the most imprecise estimate. The difference that came nearest to significance was that between the estimate based on secondary angle sums from captures and carcasses and the unmodified ring-recapture estimate ($P = 0.09$). Some differences among estimates might be expected from differences among datasets in the time periods and geographical areas from which the data were drawn. Differences attributable to variation in the proportion of males and females in the samples of captured birds seem unlikely because there was no indication of a difference between the survival rate of males and females as estimated by the modified inventory method.

As indicated by Green (1999), the ring-recapture estimate of survival should be too low if the census data used in its calculation underestimated the number of adult males present. Peake and McGregor (2001) have suggested, on the basis of analyses of the voice characteristics of untagged male Corncrakes, that census techniques used in Britain and Ireland would lead to under-recording by about 30%. In their study area they estimated, from vocal identity assessments, that the mean number of males present per night during the census period was about 21. This compares with an estimate from night-time surveys of about 15 for the survey pattern that most resembles typical surveys (three night-time visits between 20 May and 10 July, avoiding windy nights). This apparent survey underestimate arises because males only called on an average of 41.5% of nights. This assumes that those identified from their calls were present continuously in the study area between their first and last records. This finding contrasts with estimates of census efficiency from two independent studies in which the proportion of nights on which radiotagged males were singing was recorded (Hudson *et al.* 1990, Tyler & Green 1996). These found that males called on 70–80% of nights. This higher efficiency value leads to estimates of under-recording for a two- or three-visit survey of about 5% (Green 1996). The reason for this difference cannot be resolved using the present data, but it should be noted that Peake and McGregor were unable to allow fully for mortality and temporary and permanent movements of males into and out of their restricted study area. Studies of radiotagged males suggest that this occurs more often than they assumed. Monitoring of 74 radiotagged adult male Corncrakes during the breeding season on the Isle of Coll indicates a daily probability of death of 0.005 and a daily probability of apparently leaving the study area of 0.003 (R.E. Green unpubl. data). As the proportion of false matches generated by the voice-matching protocol that they used was not negligible, it is possible that some of the instances when they considered that an individual had called and then apparently remained silent for several nights might really have been due to one male dying or leaving the study area and later being falsely matched by voice characteristics with a different bird that arrived or began to sing later. Inclusion of such cases would lead to underestimation of the probability of a male singing per night and over-estimation of the mean number of males that were present. Resolving this issue is a complicated problem, which will probably require the estimation of movement rates of marked birds independently of vocal identity studies, so the real extent of under-recording is likely to remain uncertain for some time. If it is assumed that under-recording does occur and it is incorporated in the ring-recapture model, the estimate of adult survival increases to 0.229 (cf. 0.186 with under-recording not allowed for).

Given the sparseness of the data available and the substantial differences in the methods used and their underlying assumptions, the estimates of adult survival rate for Corncrakes are in reasonably good agreement. It seems probable that the mean rate lies between 0.2 and 0.3. This survival rate is at the lower end of the range for bird species (Ricklefs 2000) and supports the suggestion that the growth rate of Corncrake populations is likely to be particularly sensitive to the effects of agricultural and conservation management on breeding success and recruitment (Green 1999).

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ENDNOTES

[a]The standard errors of the estimates of m_1, s_1, m_2, s_2 from the augmented samples are 2.4, 1.7, 3.5 and 2.4, respectively.

[b]Equations (3) and (4) of Green (1999) were modified as follows. The expressions for the expected probabilities of recapture in the first, second and third years after ringing as a chick were altered to $0.5 \times q \times S' \times P_{iv+1}$, $0.5 \times q \times S' \times S \times P_{iv+2}$ and $0.5 \times q \times S' \times S^2 \times P_{iv+3}$, respectively. The expressions for Eq. (4) were the same except that the factor 0.5 was omitted. Note that the estimation of q means that the information on the number of recaptures relative to the number of birds ringed is essentially not used in the estimation of the survival rate, whereas this information is used when it is assumed that $q = 1$. This is the reason that the standard error of the survival rate increases markedly when this modification is made (see Table 1).

REFERENCES

Alnås, I. 1974. Die Ortstreue der gotländischen Wachtelkönige *Crex crex* (L.). *Ornis Scand.* **5**: 123–129.

van den Berg, L. 1991. Status, distribution and research on Corncrakes in the Netherlands. *Vogelwelt* **112**: 78–83.

Brownie, C., Anderson, D.R., Burnham, K.P. & Robson, D.S. 1985. *Statistical Inference from Band Recovery – a Handbook*. Washington, DC: US Department of the Interior Fish and Wildlife Service.

Fox, J.B. 1993. Corncrake ringing near Dublin, 1939–1959. *Irish Birds* **5**: 61–66.

Green, R.E. 1996. Factors affecting the population density of the corncrake *Crex crex* in Britain and Ireland. *J. Appl. Ecol.* **33**: 237–248.

Green, R.E. 1999. Survival and dispersal of male Corncrakes *Crex crex* in a threatened population. *Bird Study* **46** (Suppl.): 218–229.

Green, R.E. 2002. Diagnosing causes of population declines and selecting remedial actions. In Norris, K. & Pain, D.J. (eds) *Conserving Bird Biodiversity*: 139–156. Cambridge, UK: Cambridge University Press.

Green, R.E. & Gibbons, D.W. 2000. The status of the Corncrake *Crex crex* in Britain in 1998. *Bird Study* **47**: 129–137.

Green, R.E., Schäffer, N. & Wend, D. 2001. A method for ageing adult Corncrakes *Crex crex*. *Ring. Migr.* **20**: 352–357.

Haldane, J.B.S. 1955. The calculation of mortality rates from ringing data. *Proc. Int. Ornithol. Congr.* **11**: 454–458.

Hudson, A.V., Stowe, T.J. & Aspinall, S.J. 1990. Status and distribution of Corncrakes in Britain. *Br. Birds* **83**: 13–186.

Kirby, R.E., Barry, T.W., Kerbes, R.H. & Obrecht, H.H. 1985. Population dynamics of North American Light-bellied Brent Geese as determined by productivity and harvest surveys. *Wildfowl* **36**: 49–52.

Peake, T.M. & McGregor, P.K. 2001. Corncrake *Crex crex* census estimates: a conservation application of vocal individuality. *Anim. Biodiversity Conserv.* **24**: 81–90.

Ricklefs, R.E. 2000. Density-dependence, evolutionary optimisation and the diversification of avian life-history strategies. *Condor* **102**: 9–22.

Salzer, U. & Schäffer, N. 1997. Alterbestimmung von Wachtelkönigen *Crex crex*. *Vogelwelt* **118**: 135–139.

Snow, D.W. 1956. The annual mortality of the Blue Tit in different parts of its range. *Br. Birds* **49**: 174–177.

Svensson, L. 1992. *Identification Guide to European Passerines*. Stockholm: Lars Svensson.

Swann, R.L. 1986. The recent decline of the Corncrake *Crex crex* on the Isle of Canna. *Bird Study* **33**: 201–205.

Tyler, G.A. & Green, R.E. 1996. The incidence of nocturnal song by male Corncrakes *Crex crex* is reduced during pairing. *Bird Study* **43**: 214–219.

Tyler, G.A., Green, R.E., Stowe, T.J. & Newton, A.V. 1996. Sex differences in the behaviour and measurements of Corncrakes *Crex crex* in Scotland. *Ring. Migr.* **17**: 15–19.

White, G.C. & Burnham, K.P. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* **46** (Suppl.): S120–S139.

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