Illegal killing slows population recovery of a re-introduced raptor of high conservation concern – The red kite *Milvus milvus*

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ABSTRACT

The re-introduction of extirpated species is a valuable conservation tool. Red kites *Milvus milvus* are declining over much of their European range and have been re-introduced to England and Scotland, following their extinction due to widespread human persecution during the 19th century. Considerable regional variation in population growth exists. This study aims to identify the proximate demographic and ultimate environmental constraints on red kites in north Scotland, a region with low population growth. Productivity in north Scotland was high compared to other Scottish and Welsh populations and equal to English populations with high population growth rates. In north Scotland, annual survival of wild-fledged birds was low for first-year birds compared to other Scottish populations and second-year survival declined over time. In north Scotland, 40% of 103 red kites found dead were killed illegally, mainly by direct poisoning. In the absence of illegal killing, we estimate that annual survival rates in wild red kites might increase from 0.37 to 0.54, 0.72 to 0.78 and 0.87 to 0.92 for first, second-year and adult birds respectively. Demographic rates from this study produce population trends that recapitulate observed trends for the north Scotland population (leading to a population of c40 pairs by 2006). Models in which the additive illegal killing mortality is excluded, predict a population trajectory and size (c300 pairs by 2006) very similar to that found in the Chilterns, a rapidly growing population (320 pairs in 2006) in south-east England re-introduced at the same time, but where rates of illegal killing are much lower. We conclude that illegal killing of red kites is the cause of poor population growth in north Scotland and the key challenge facing government is to find a way to eliminate this killing.

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1. Introduction

The re-introduction of extirpated species is now firmly established as a valuable management practice in conservation biology (Griffith et al., 1989; Seddon et al., 2007). The IUCN re-introduction guidelines provide robust criteria under which decisions on re-introductions can be assessed (IUCN, 1998). A key component of these guidelines are the identification and elimination, or reduction to a sufficient level, of the previous causes of decline. The cause of extinction for many predatory species, including raptors, within Europe and elsewhere has been human persecution (Breitenmoser, 1998; Newton, 1998). However, improvements in protective legislation have meant that most of these species are now protected in Europe, and as such many re-introductions over the

last 30 years have focused on re-establishing wild predator populations (Breitenmoser et al., 1998; Evans et al., 2009). Unfortunately in some situations, despite changes to the law, illegal killing by some stakeholders continues, and in these circumstances, re-introduced populations may fail to establish or may show reduced population growth rates than would otherwise be supported by the environment (Breitenmoser et al., 1993; Margalida et al., 2008).

The red kite was formerly widespread and common in Britain, but became extinct in Scotland and England by the end of the 19th century due to human persecution. A small remnant population remained in Wales, but numbers increased very slowly due to a restricted genetic pool, an unfavourable climate, poor land productivity and continued illegal killing (Lovegrove et al., 1990; May et al., 1993; Walters-Davies and Davis, 1973). Because of the low population size and productivity in Wales, and because the species is highly philopatric (Newton et al., 1994), the potential

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for expansion to the rest of the UK was considered low. Thus, in 1989 a re-introduction program was initiated. Ninety-three juveniles of Spanish, Swedish and Welsh origin were released into the Chilterns in southern England, and exactly the same numbers of juveniles of Swedish origin were released on the Black Isle in north Scotland (Evans et al., 1999). Releases were carried out over a 5 and 6-year period in Scotland and the Chilterns, respectively, and successful breeding began in both populations in 1992. Subsequent releases successfully established populations at a further two Scottish areas and at three English areas (Fig. 1). These releases, combined with a substantial increase in the Welsh population, thought to result from a combination of reduced persecution and increased protection, meant that by the time of the national survey in 2000 the UK breeding population had increased to 430 pairs (Wotton et al., 2002), and by 2005, an estimated 901–971

breeding pairs were present (www.gigrin.co.uk). As a result, the UK population now represents some 4–5% of the European population, which although stable during 1970–1990, has declined by almost 20% during 1990–2000 and consequently was listed on the IUCN European Red list of species of greatest conservation concern (BirdLife International, 2004). Direct illegal poisoning and indirect poisoning from pesticides and rodenticides, particularly in the wintering ranges in France and Spain, and changes in agricultural practices and refuse treatment reducing food resources, are considered to be the main causes of decline (BirdLife International, 2004; Villafuerte et al., 1998).

Artificial supplementary feeding has the potential to impact on population processes. This activity is widespread in the UK, ranging from individuals feeding kites in their gardens (Chilterns and East Midlands) to more organised supplementary feeding (Wales and
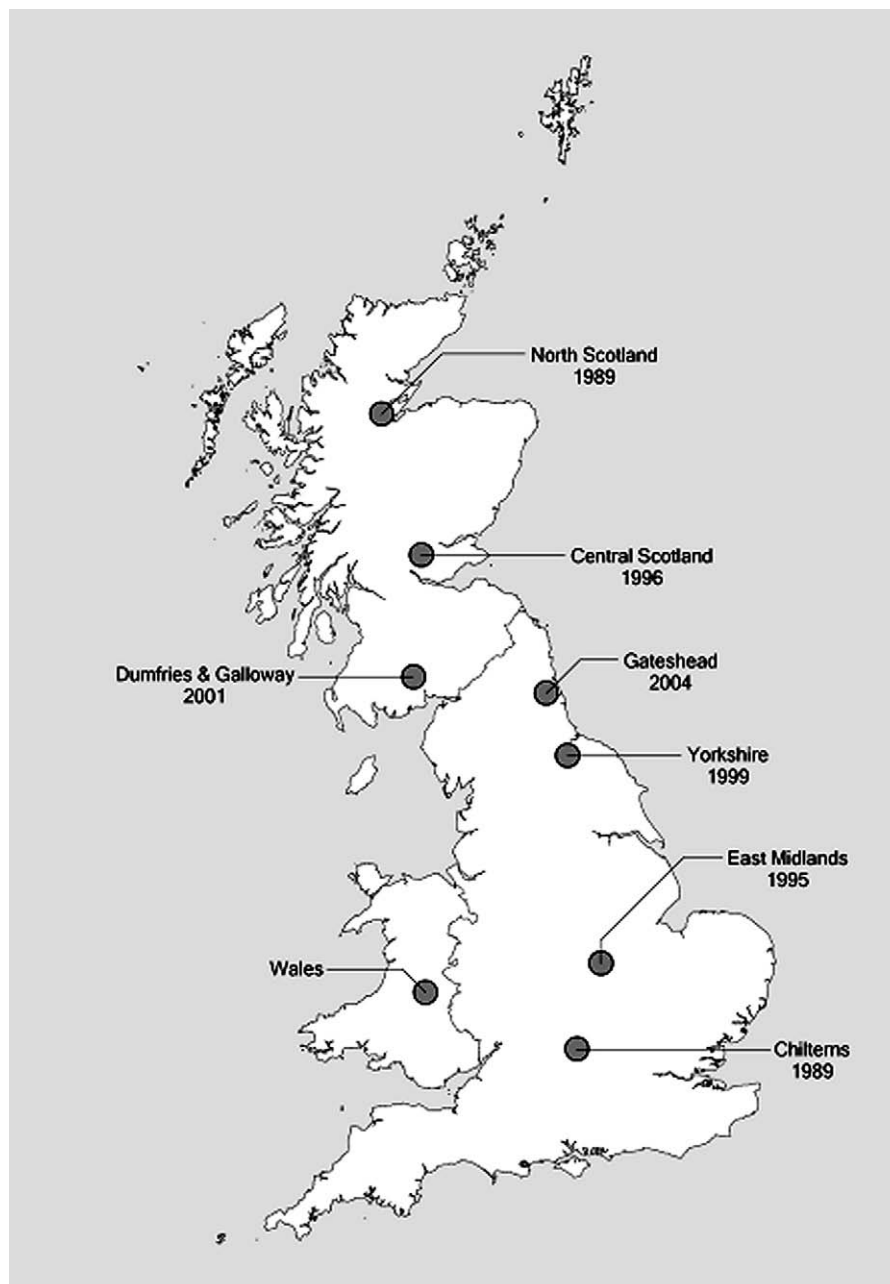
Fig. 1. The approximate central location of each red kite re-introduction scheme (greater than 5-years old) and the year in which red kites were first released in each area. *Note*: Wales is a natural not a re-introduced population hence no year is given.

Central Scotland) but it is likely that this has occurred to some extent a round all release areas at some time. However, the ad hoc and unregulated way in which this is implemented means there is no way of quantifying the effects on red kites re-introduced in the UK.

Within the apparent success of these re-introduction schemes in Britain, there remains significant regional variation in population growth rates (Fig. 2). In particular, there has been a marked contrast in the fortunes of the two initial releases in north Scotland and the Chilterns (Fig. 1). In 2006, the north Scotland population was only 41 pairs, whereas the Chilterns population exceeded 300 pairs, and the population size of many of the later releases were already higher than found in north Scotland. Over the same period, reported crimes against birds of prey have increased each year in the UK, and in 2006, Scotland had the highest rate of illegal poisoning for 25 years (Anon., 2006; http://www.rspb.org.uk/Images/birdcrime%2006_tcm9-169702.pdf). In addition, there has been speculation that differences between the growth rates of these populations are due to higher reported levels of illegal poisoning in the North Scotland population (Carter et al., 2003).

In this paper, we compare variation in population trends and variation in demographic rates across populations. Specifically, we:

(i) compare productivity between Scottish populations, and between north Scotland and English and Welsh populations,

(ii) compare age-specific annual survival rates between the three Scottish populations and changes in survival over time,

(iii) quantify the causes of mortality in kites found dead from north Scotland and,

(iv) use population models to examine whether the estimates of demographic rates from this study explain observed population trends in north Scotland, and explore how the population might have grown in the absence of illegal killing.

2. Methods

Red kites have been monitored annually in Scotland (NS = north Scotland; CS = central Scotland; DG = Dumfries and Galloway), since their re-introduction in 1989; this has included individually colour-marking released and wild-fledged kites using patagial wing-tags and monitoring the success of nests in each population (Table 1). In all populations and years, the nests of a large percentage of the breeding population were monitored (mean%: NS = 99.7; CS = 100; DG = 100) and a large percentage of fledged chicks were individually wing-tagged (mean%: NS = 85.7; CS = 96.2; DG = 100).

2.1. Productivity

Nest success data was recorded as the number of fledged young or the number of young kites close to fledging per occupied territory (integer range 0–4). While individual kites would have bred in subsequent years, we could not assign every nest to an individual adult kite. Furthermore, re-nesting following clutch loss is rare in red kites (Evans et al., 1999). Thus, we used nest as our independent replicate.

Annual productivity data from all the UK red kite populations is collated on the Welsh Kite Trust website (www.gigrin.co.uk/red_kites_in_the_united_kingdom_breeding_pairs_1989-2007) and we used this to compare annual productivity (young fledged laying pair^{-1}) of all populations greater than five years old. Where alternative sources exist (e.g. population newsletters), the records were checked for accuracy.

2.2. Estimation of survival rates

To estimate survival rates we used data from 1154 red kite chicks that were individually marked in the nest using patagial wing-tags between 1989 and 2006 from the three Scottish populations (NS = 708, CS = 293, DG = 153; Table 1). We classify whether a bird was alive in a given year based on at least one re-sighting in
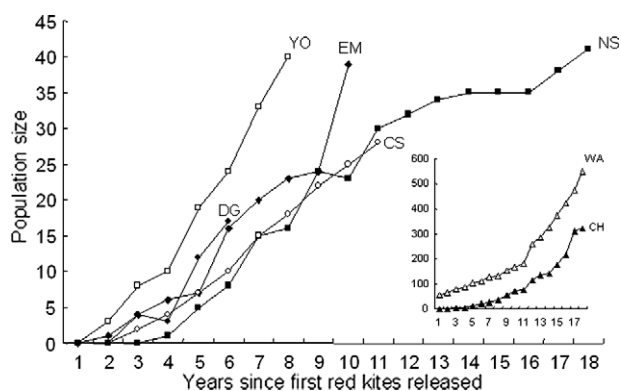
Fig. 2. The breeding population (pairs laying eggs) of red kites in seven populations in England, Wales and Scotland between 1989 and 2006 in relation to years since the first red kites were released. The main graph shows data for north Scotland (NS, closed squares), east Midlands (EM, closed diamond), Yorkshire (YO, open squares), central Scotland (CS, open dots) and Dumfries and Galloway (DG, closed dots). The inset graph shows data for Wales (WA, open triangle) and the Chilterns (CH, closed triangle). Note the different y-axis scales between the main and inset graph. Data are sourced for Welsh and English populations from http://www.gigrin.co.uk and for Scotland from the Scottish Red Kite Co-ordination group.

Table 1
The number of juvenile red kites with wing-tags that were released (R-WT), wild-fledged (W-WT), fledged without wing-tags (W), harvested for release elsewhere (H) and the number of nests monitored for productivity for each year in each of the Scottish populations (NS = north Scotland, CS = central Scotland and DG = Dumfries and Galloway).

Pop	Measure	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	Totals
NS	R-WT	6	19	20	24	24														93
	W-WT				1	4	13	24	38	33	41	49	68	55	58	40	49	63	73	609
	W[a]				3	0	2	0	6		3	5	6	10	10	11	31	22	6	115
	H													12	20	20				52
	Nests				1	5	9	15	17	23	23	30	32	34	35	35	35	39	40	373
CS	R-WT								19	18	20	20	20	6						103
	W-WT										5	6	7	15	22	33	32	28	42	190
	W										0	0	3	0	3	1	0	0	2	9
	Nests										2	4	8	11	15	20	22	25	29	136
DG	R-WT													33	24	33	10	4		104
	W-WT														1	3	18	27		49
	W														0	0	0	0	0	0
	Nests														4	3	12	17		36

[a] Figure excludes the juveniles harvested.

Table 2
Comparisons of model results for red kite survival analysis. Only models with a model likelihood > 0 are shown. $\hat{c}$ adjustment of 1.18 has been applied using the median $\hat{c}$ method. Models are ranked by QAIC$_c$ value (quasi-Akaike information criterion), ΔQAIC$_c$ values of models are relative to the top model. Φ = survival, P = encounter, WR = wild/released status, 3a = 3 age classes, 2a = 2 age classes, c = population, t = time-dependence.

Model	QAIC$_c$	ΔQAIC$_c$	AIC$_c$ weights	Model likelihood	Num. par	QDeviance
{ΦcWR3a–/t/t Pc2a}	2809.2	0	0.95101	1	72	625.3
{ΦcWR3a–/t/tP}	2815.8	6.6	0.03537	0.0372	67	642.5
{ΦcWR3a–/t/tP2a}	2817.9	8.9	0.01243	0.0131	68	642.5
{ΦcWR3at/t/tPc}	2823.5	14.3	0.00075	0.0008	101	576.7
{ΦcWR3at/t/tPc2a}	2824.5	15.3	0.00044	0.0005	103	573.4

that year, with a year starting on 1st July, the approximate fledging time for kites, and using all re-sightings up to and including June 2007. Birds were grouped by their natal population and whether they were released or wild-fledged because previous studies of red kites (Evans et al., 1999) and white-tailed eagles *Haliaeetus albicilla* (Evans et al., 2009) have found that survival rates differ between released and wild-fledged birds. Young red kites lead a nomadic lifestyle prior to breeding, which occurs when they are aged 2–3 years, so our survival models included three age classes, first-year (<1 year old), second-year (1–2 years) and adult birds (>2 years). To explore whether survival had changed over time, we also examine whether the inclusion of time-dependence in age-specific survival was supported in the models. Thus, our global model was [(ΦcWR3a:$t_1t_2t_3$)(Pc2a)] where Φ is survival rate, P is encounter rate, c is the natal population, WR is whether a bird was released or wild, 3a and 2a is age in three and two classes respectively and $t_1t_2t_3$ denotes time-dependence in the three age classes. We included population and age-specific survival in all models, since we were particularly interested in changes in age-specific survival over time and between populations. Other key terms were added and removed until all possible combinations were tested, and thus we could explore whether the inclusion of: (i) population differences in encounter rate, (ii) survival differences between wild and released red kites and (iii) time-dependence in survival for the different age classes, improved the fit of the models. All models were fitted in program MARK version 5.1 (Cooch and White, 2008) with models selected on the basis of AIC statistics (White and Burnham, 1999), allowing the best model to be selected in terms of both parsimony (fewest model parameters) and adequate description of the data. This program can incorporate variation over time and among classes of individuals in both encounter probabilities and survival rates and is an extension of the Cormack-Jolly-Seber model. Models with the lowest AICc values were retained as good candidate models and were interpreted in terms of their 'relative value' (Burnham and Anderson, 1998).

When differences in AICc scores (ΔQAIC$_c$) between models were less than 2, models were considered statistically indistinguishable. The goodness of fit of the global model was assessed via the median $\hat{c}$ method and this variance inflation term ($\hat{c}$) was used to calculate the quasi-Akaike information criterion (QAIC$_c$) which corrected for small sample size and overdispersion (Burnham and Anderson, 1998). The median $\hat{c}$ method usually gives a slightly higher estimate of $\hat{c}$ than other methods and therefore its use makes model selection more conservative, thereby reducing the risk of a Type II error (Cooch and White, 2008). To accommodate uncertainty in the model selection process, we use model averaging to estimate our survival parameters. More specifically, we use the average value of each estimated parameter from each model with ΔQAIC$_c$ value <7. Models with ΔQAIC$_c$ > 7 are considered to have no support from the data, and were thus not considered further. The values from each model are weighted by the normalised QAIC$_c$ model weights. In our reporting of age-specific and annual survival rates, we present the model averaged parameter estimates and the unconditional SE. Where annual survival rates are averaged, we used

variance component estimation in program MARK to calculate mean (±SD) survival rates.

2.3. Quantifying causes of mortality

To examine the proportion of deaths that were attributable to illegal and non-illegal causes, we collated information on the cause of death of all North Scotland kites found dead (identified through wing-tags, and/or rings and through radio-tracking).

Radio tags were fitted to either fully grown juveniles pre-release or nestlings greater than six weeks old. Two tag types were used, either 12-month lifespan tail-mounted tags (single cell TW-3: Biotrack, Dorset, UK; tag weight 18.5 g, 1.9% male mass, 1.7% female mass) in 1989–1993 and in 2006 (n = 109, 90 released birds, 19 wild-fledged), or 2–3 year lifespan back-mounted tags onto wild-fledged birds between 2004–2006 (n = 57, single cell TW-5: Biotrack, Dorset, UK; tag weight 29 g, 3% male mass, 2.7% female mass). In general, tail-mounted tags were fitted to birds during the early releases because red kite tail feathers must be fully grown to use tail-mounted tags and additionally, these tags are more discreet and thus are better for studies of illegal killing (B. Etheridge pers. comm.) All causes of death were recorded and were then categorised as: (i) unknown, when the cause of death could not be established, for example when a very old carcass was found, (ii) non-illegal causes (e.g. collisions with cars/trains/wind turbines/pylons, accidental indirect poisoning through the consumption of rodents killed by legal rodenticides (Whitfield et al., 2003) and natural causes) and (iii) illegal causes, including direct deliberate poisoning (see Whitfield et al., 2003 for full description), shooting and a small number of cases where evidence strongly suggested illegal activities (e.g. no body recovered but radio tag found which had been cut off). Using these sources of data, we estimated the proportion of birds that died due to illegal causes and those to non-illegal causes, for which we also included those where the cause of death was unknown. Thus, the proportion of birds whose deaths were attributed to illegal causes will be an underestimate, and therefore conservative given that some of the unknown causes are also likely to have been instances of illegal killing. Data were examined in relation to the same three age classes used in the survival analysis.

2.4. Population modelling

We modelled the population growth rates and the resulting population size of north Scotland red kites over 18 years using VORTEX (Lacy et al., 2005). A number of assumptions were made. Models assumed that red kites are monogamous, with 80% and 20% of the population breeding for the first time at two or three years old respectively, can breed until 20 years old and can fledge up to four young per year (Evans et al., 1999; Newton et al., 1989). The models also assumed that 100% of males and females of breeding age attempt to breed and that the initial population size is zero, with the population being initiated and then supplemented by the actual number of birds released during the first 5 years of the re-introduction program (Table 1). We also account for the small number of birds harvested to source other populations (Table 1).

Table 3
For the north Scotland population, averaged estimates of survival rates (±SD) and survival rates in the absence of known illegal killing for released and wild-fledged first-year, second-year and adult red kites.

Survival	Age	Released		Wild	
		Φ	SD	Φ	SD
Estimate	1st	0.52	0.00	0.37	0.00
	2nd	0.87	0.16	0.72	0.25
	Adult	0.85	0.20	0.87	0.12
Estimated minus illegal mortality	1st	0.66		0.54	
	2nd	0.90		0.78	
	Adult	0.91		0.92	

The predicted breeding population size (measured as number of adult territorial pairs in each year) was estimated for each scenario as the mean from 1000 iterations, assuming no density-dependence or limitation by carrying capacity, and a 1:1 sex ratio. Models incorporated demographic stochasticity in reproductive and mortality rates, and environmental stochasticity measured as annual variation (SD) in reproductive rates and mortality rates (see Section 3). Using this model, we first examined whether we are able to recapitulate the observed population trajectory from 1989–2006 using the average productivity and survival rates from this study (Table 3). Secondly, we calculated revised survival estimates for each age class across the two release classes (wild-fledged and released) removing the additive effect of mortality by illegal killing, with a right censoring approach ensuring we accounted for individuals that would have subsequently died of natural causes had they not been persecuted, and re-run the models with these revised estimates. We calculated the survival rate in the absence of illegal killing (S) as follows:

$$S = 1 - [(Mn)(Mi) + Mn]$$

where M = observed overall mortality rate, i = proportion of total mortality caused by illegal killing, n = proportion of total mortality attributable to natural or unknown causes.

2.5. Population comparisons of productivity

We used a Generalised Linear Model (GLM) with a log link function and a Poisson error structure to examine differences in productivity between the Scottish populations. First, we tested for overall differences between the three populations by including year and population as fixed effects. However, because the three populations have become established over different periods, we also wanted to compare the productivity of populations over similar periods of population establishment. We therefore also tested for differences in productivity between (i) north and central Scotland over the first 9 years after establishment and (ii) all three populations over the first 4 years after establishment. We included years since re-introduction as a fixed effect to control for possible effects of population age on productivity, and then tested for effects of breeding population on productivity.

For all other UK populations, we simply had an annual estimate of productivity, thus, comparisons of productivity between all UK populations greater than five years old were carried out using a Kruskal–Wallis test (non-parametric equivalent of ANOVA) with Mann–Whitney tests for specific comparisons between north Scotland and the other populations.

3. Results

3.1. Productivity

Across all years, average annual productivity is significantly higher in north Scotland (NS) compared to both the central (CS) and Dumfries (DG) populations (mean ± SE chicks fledged pair^{-1}: NS = 1.87 ± 0.16, 1992–2006; CS = 1.27 ± 0.13, 1998–2006; DG = 1.21 ± 0.19, 2003–2006; year: χ^2_{14} = 12.2, P = 0.59; population: χ^2_2 = 28.0, $P < 0.001$). This could simply be an artefact of the NS population being established for six and 11 years longer than the CS and DG populations respectively. Comparing the NS and CS populations in the first 9 years after re-introductions began, productivity was again significantly higher in NS compared to CS (mean ± SE chicks fledged pair^{-1}: NS = 1.89 ± 0.14, 1992–2000; CS = 1.44 ± 0.12, 1998–2006; year established: χ^2_8 = 6.29, P = 0.62; population: χ^2_1 = 8.9, P = 0.003). However, during the period when we have information for all Scottish populations (i.e. the first 4 years after re-introduction), productivity did not vary across the three populations (mean ± SE chicks fledged pair^{-1}: NS = 1.39 ± 0.22, 1992–1995; CS = 1.38 ± 0.23, 1998–2001; DG = 1.23 ± 0.19, 2003–2006; year established: χ^2_3 = 2.01, P = 0.57; population: χ^2_2 = 0.43, P = 0.81).

There were significant differences between the productivity of populations in NS, England and Wales (Kruskal–Wallis, H = 39.0, df = 5, $P < 0.0001$), which was driven by the low productivity in Wales compared to the other populations (Median: NS = 1.97, CH = 1.89, EM = 1.87, Yorkshire = 1.87, Wales = 0.91). Productivity in NS is significantly higher than Wales (W = 385.0, $P < 0.0001$) but is similar to the Chilterns (W = 217.5, P = 0.70), East Midlands (W = 209.0, P = 0.21) and Yorkshire (W = 173.0, P = 0.56).

3.2. Annual survival estimates from wing-tagged kites

Our global model examining apparent survival of all wing-tagged red kites in Scotland adequately fit the data and was only slightly over-dispersed (median $\hat{c}$ goodness of fit test: $\hat{c}$ = 1.18). In the global model, survival rate is time dependent for each age class, varies with breeding population and status (wild-fledged or released) and encounter rates vary with both population and age class. Five models had model likelihoods >0 (Table 2). However, two models had clearly more support and were the most parsimonious (combined QAIC$_c$ weight = 0.986), both of which supported constant first-year survival, time-dependence in second-year and adult survival and effects of status on survival. These two models differed in relation to the inclusion of breeding population and age class on encounter rates (Table 2). The best model (most parsimonious) has 26.9 times more support than the second model (ΔQAIC$_c$ of 6.6 between top two models). Model averaged estimates of population and status specific estimates of first-year survival, annual estimates of second-year and adult survival and population estimates of encounter rate and their standard errors derived from these two models are presented in Supplementary table A. These standard errors incorporate both sampling error and uncertainty in model selection.

Survival rates of first and second-year wild-fledged individuals tend to be higher than released birds in CS and DG (CS: 1st wild = 0.64, 1st released = 0.59, 2nd wild = 0.81, 2nd released = 0.55; DG: 1st wild = 0.7, 1st released = 0.45, 2nd wild = 1.0, 2nd released = 0.83; Fig. 3). However, in NS released first- and second-year birds have higher survival than wild-fledged birds (1st wild = 0.37, 1st released = 0.52, 2nd wild = 0.72, 2nd released = 0.77; Fig. 3). It is likely that this relates more to changes in survival rates over time, rather than inherent differences in survival of birds of different release status (see later). Comparing only wild-fledged individuals across all years, first-year survival in DG was 1.1 and 1.9 times higher than CS and NS, respectively (Table 3).

Survival of wild-fledged second-year kites varied between populations and between-years (Fig. 4A). Second-year survival in NS declined, although this was marginally non-significant (r_p = −0.58, n = 11, P = 0.06). Prior to and including 1998 (when the population was increasing), average second-year survival was
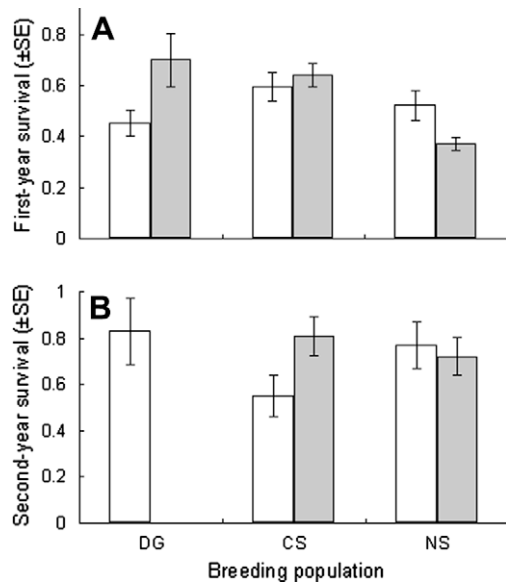
Fig. 3. Comparisons of the survival rates (SE) of wild-fledged (grey bars) and released (white bars) red kites for (A) first-year birds and (B) second-year birds from the three Scottish populations (NS = north Scotland, DG = Dumfries and Galloway, CS = central Scotland).

Table 4
Red kites found dead from the NS population and the number and (%) dead from different causes of death in each age class.

	N		<1	Year old	1–2	Years old	2+	Years
All dead kites	103		67		16		20	
Illegally killed	41	(40)	28	(42)	4	(25)	9	(45)
Unknown	29	(28)	14	(21)	8	(50)	7	(35)
Non-illegal causes	33	(32)	25	(37)	4	(25)	4	(20)

3.3. Cause of mortality and population models

A total of 103 red kites from NS were recovered dead between 1989 and 2006. Of these, 41 (40%) were killed illegally mainly due to poisoning ($n = 38$), 33 (32%) died due to non-illegal causes and for a further 29 (28%) the cause of death was unknown (Table 4). The recovery of 25 of these birds was aided because they had radio tags fitted (either tail-mounted or back-packs). If the causes of mortality of only radio-tagged birds is examined, the figures are similar, but suggest an even higher proportion of illegally killed birds; 52% compared to 32% due to non-illegal causes and 16% where the cause of death was unknown. Thus, our estimates from all birds found dead are unlikely to be heavily biased, but if anything, will underestimate the proportion killed illegally. Table 4 shows the proportion of birds that were illegally killed or died through other causes (including unknown cases) in each age class; these data were used to recalculate survival rates with illegal causes of mortality removed. Based on our estimates of survival and the levels of killing, we calculated that on average 12 first-year red kites, 4 second-year and 5 adults were killed illegally each year in north Scotland. Between 1999 and 2006, the period when the population increase halted, we estimate that 166 red kites have been killed illegally (first-year = 95, second-year = 33, adults = 39).

0.99 ± 0.01, compared to 0.59 ± 0.11 in later years (when population increase halted). Second-year survival in CS declined during 2000–2005 ($r_p = -0.88$, $n = 6$, $P = 0.02$; Fig. 4A). Adult survival of wild-fledged red kites also varied between populations and years (Fig. 4B). There was no significant change in adult survival over time in NS ($r_s = 0.22$, $n = 10$, $P = 0.53$), but there was a significant decline in CS ($r_s = -0.96$, $n = 5$, $P = 0.01$; Fig. 4B).
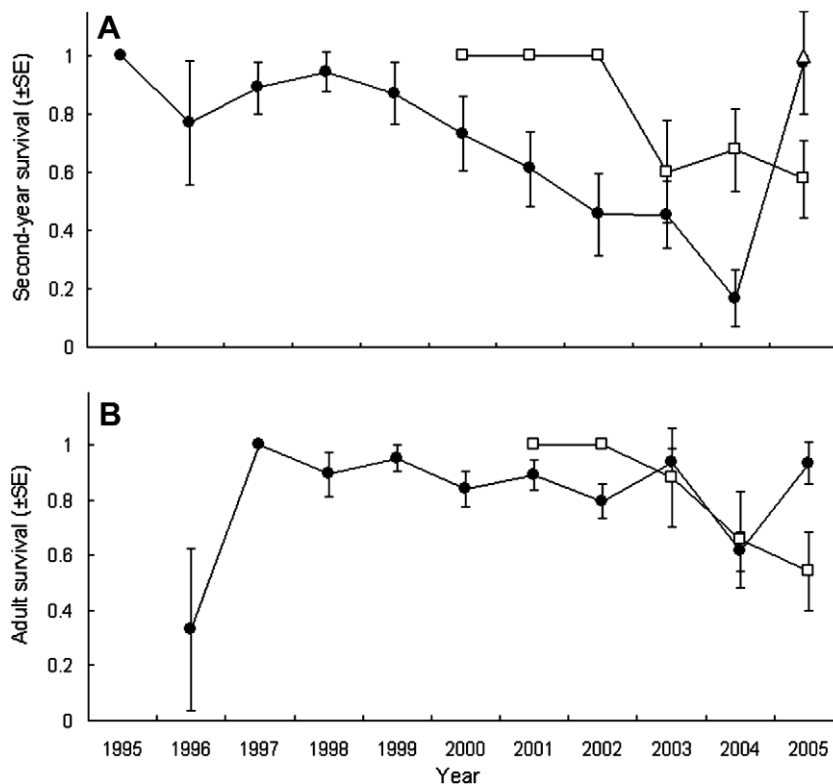
Fig. 4. A comparison of the annual survival probabilities (±SE) of wild-fledged (A) second-year and (B) adult red kites from the three Scottish populations (north Scotland: filled dots, central Scotland: open squares, Dumfries and Galloway: open triangles – single point).
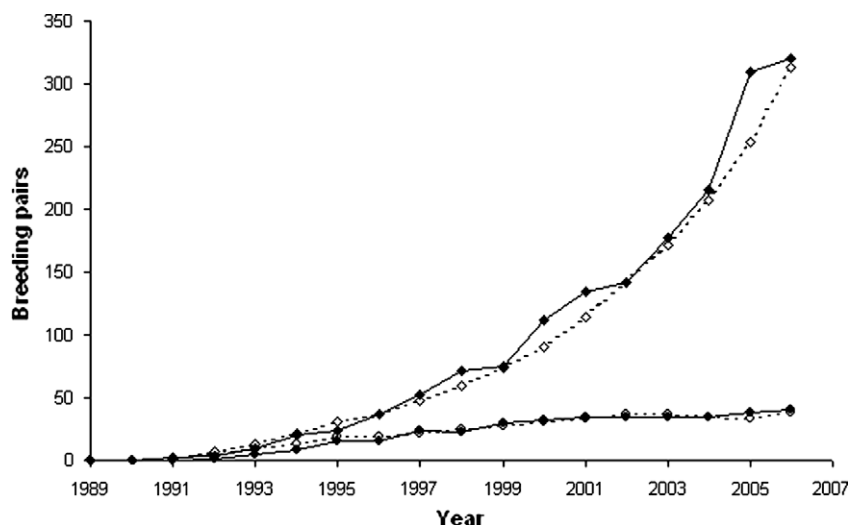
Fig. 5. The observed population trajectories (solid lines) for north Scotland (solid circles) and the Chilterns (solid diamonds) and two modelled trajectories for north Scotland. The first (open circles/dashed line) seeks to recapitulate the observed trajectory using the estimates of productivity and survival rates from this study. The second (open diamonds/dashed line) models the north Scotland population trajectory using survival rates adjusted assuming the removal of illegal killing (Table 3). Modelled population trajectories present means for each year based on 1000 simulations.

Population models using the average productivity and survival rates recorded for NS, predicted a population growth rate (λ in the absence of supplementation and harvesting = 1.069) and a current population size that was extremely close to that observed (Fig. 5). Models suggested that by 2006 the population would be 40 pairs, only one less than the actual population size of 41 pairs (Fig. 5).

Running these models with the survival rates adjusted to remove illegal causes of mortality (Table 3), predicted a considerably higher population growth rate (λ in the absence of supplementation and harvesting = 1.21) and a population size of 293 (95% CI: 283–302) pairs by 2006 (Fig. 5). This is very similar to the actual population size of 320 pairs present in the Chilterns in 2006, a population initiated with the same number of released individuals and over the same span of years as in north Scotland (Fig. 5), but that suffers far lower levels of illegal killing. Between 1989 and 2005, the period where comparable data are available for both north Scotland and the Chilterns, 13 red kites from the Chilterns were found dead for illegal reasons (Evans et al., 1999; Snell, 2005) compared to 37 for north Scotland. Thus in north Scotland, a population which was on average 3.6 times smaller than the Chilterns, rates of illegal killing were 2.8 times higher.

4. Discussion

A previous assessment of the demographic rates of the re-introduced red kite populations in the Chilterns and north Scotland, up to and including 1995, predicted that these populations would exceed 100 pairs by 1998 and 2007, respectively (Evans et al., 1999). Whilst the population in the Chilterns exceeded 100 pairs in the year 2000, just two years later than predicted, north Scotland has yet to reach half of that target, with only 41 pairs breeding in 2006. It is clear from a comparison of the population trends of red kite in England, Wales and Scotland that the population growth of north Scotland differs from other populations in the UK. Our study shows that the north Scotland population is limited by poor and declining survival rates linked to high levels of illegal killing principally from poisoning. The north Scotland population is not limited by poor reproductive output because productivity is higher than, or similar to other populations with strong population growth across the UK and, compares favourably with studies of

productivity in other European countries (Mougeot and Bretagnolle, 2006). Density dependence is unlikely to complicate these comparisons because in suitable habitats, red kites will breed at high densities without affecting productivity (Newton et al., 1996). Our population models predict that without illegal killing the NS population would have increased at a similar rate to the Chilterns and, by 2006, would have held over 300 breeding pairs. Should illegal killing continue, then based on the current population growth rate we would not expect the population to exceed 300 pairs until after 2035; however, if illegal killing ceased we predict that the population might reach 300 pairs by 2017.

Undetected dispersal is also a very unlikely cause of low survival rate estimates. Red kites are highly philopatric (Newton et al., 1989; Evans et al., 1999; Carter et al., 2003), and the small number (*n* = 4) of red kites that have dispersed between Scottish populations were detected in the population where they settled and have therefore been accounted for in survival rate estimation.

Our finding that, across study populations, survival rates of wild-bred red kites are higher than those of released birds matches recent studies of the re-introduced Scottish white-tailed eagle population (Evans et al., 2009). However, in the case of red kites, the effect differed between populations with higher survival rates for first and second-year wild-fledged red kites in Dumfries and central Scotland but higher survival rates for released red kites in north Scotland. It is likely that these differences are related to the bigger impacts of illegal killing on north Scotland survival rates in later years when the population had become dominated by wild-bred birds.

Illegal killing was responsible for 55% of the north Scotland red kites that were recovered dead where the cause of death could be established, and of the birds illegally killed, the vast majority were killed through direct poisoning, usually using carrion baits laced with poison. Our sample of dead kites is unlikely to be heavily biased toward illegally killed birds. Using causes of death from radio-tagged birds alone is the best way to obtain unbiased data (González et al., 2007), although as a result sample size is usually compromised. Data obtained purely from radio-tagged birds (which formed c. 25% of our sample) produced similar results, albeit with slightly higher estimates of death through illegal killing. Other studies have found similar findings with radio-tagged birds usually revealing higher levels of non-natural mortality than birds found through other means (González et al., 2007; Margalida et al.,

2008). Thus, our estimates and subsequent modelling are likely to be, if anything, slightly conservative with respect to the influence of illegal killing.

Reported crimes against birds of prey are increasing (Clare, 2008) with Scotland having some of the highest figures for illegal poisoning (Anon., 2006). Furthermore, a recent study (Whitfield et al., 2003), showed that records of illegal poison use in Scotland between 1981–2000 were closely associated with grouse moor management, that this association had increased in recent years, and found no evidence to suggest a decline in poisoning incidents on grouse moors over their study period.

Our study demonstrates that illegal killing, principally through the use of poison, is the key factor constraining the conservation status of the north Scotland red kite population. If this killing is not reduced or eliminated, this population will at best only increase slowly. Other recent studies of raptors in Scotland have drawn similar conclusions. The conservation status of golden eagle *Aquila chrysaetos* populations in Scotland is currently unfavourable; largely due to problems of poisoning in the south and east of the country in areas where grouse moor management is most prevalent (Whitfield et al., 2008). In the absence of this persecution, it is anticipated that the population could expand and fill currently vacant territories (Whitfield et al., 2004b). Similarly, the hen harrier *Circus cyaneus* population, although increasing as a whole in the UK, remains constrained and declining in areas dominated by grouse moor management due to persecution (Anderson et al., 2009; Etheridge et al., 1997; Sim et al., 2007).

Various aspects of red kite foraging and dispersal behaviour make them vulnerable to illegal killing (Carter et al., 2003; Villafuerte et al., 1998). Red kites pose little threat to game interests as they forage mainly on carrion (Carter et al., 2003), but because of this, they are particularly vulnerable to use of illegal poisoned meat baits. Many of the baits they consume may well not have been set specifically to target red kites, and may have been set for red foxes *Vulpes vulpes* or other raptor species, which are viewed as being more damaging to game (Whitfield et al., 2004a). However, the indiscriminate nature of poison baits, means that other non-target species often become the victims. The dispersal behaviour of kites in their first-year means that they are more likely to wander out of areas where project officers have been working with local estates to encourage more tolerant attitude and to discourage the use of poisons. Moreover, the north Scotland population is established in a lowland area surrounded by large areas of active grouse moor management in the nearby uplands (Anderson et al., 2009). Since 1992, when the breeding population became established in north Scotland, 81.1% of illegally killed red kites were found within 50 km of the core breeding area and are on average 37.1 km (±95% CI = 14.6) from the core breeding area (RSPB unpublished data). This demonstrates that this killing is local to the population and targeted action to halt it in a relatively small area around core populations could be an effective conservation tool.

Firmer law enforcement that focuses on known problem areas and the implementation of more effective crime prevention and detection strategies, as recommended by the recent Thematic Review of Wildlife Crime in Scotland (Her Majesty's Inspectorate of Constabulary, 2008), is an urgent conservation action for this population and it is hoped this study will stimulate the implementation of this action. This, together with a recently launched conservation initiative using satellite transmitters on kites fledged from the north Scotland population, could act as a deterrent to those who would use illegal poisons. Locating nests and wing-tagging young kites will remain crucial for subsequent monitoring of survival and to understand whether any measures to reduced illegal mortality have been successful.

Re-introduction schemes have been criticised for poor levels of post-release monitoring (Seddon et al., 2007). When monitoring does occur, it must be sufficient to enable problems with re-introduced populations to be investigated and understood. Post-release monitoring of the Scottish red kite re-introductions have been well resourced and has enabled the current study to take place to identity the cause of the slow population growth rate in north Scotland. This study itself has wider implications for other re-introduced populations, and other raptors populations suffering from slow growth or declines, and provides further support for the IUCN guideline which states that past causes of extinctions must be tackled if re-introductions are to be successful.

Acknowledgements

Appendix A. Supplementary material

Model averaged estimates of annual survival rates (Phi ± SE) of released and wild-fledged first-year, second-year and adult red kites and estimates of encounter rates (*P* ± SE) of first-year and older red kites from three Scottish populations in North Scotland, Central Scotland and Dumfries and Galloway. Estimates come from model outputs from program MARK. Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2010.03.002.

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