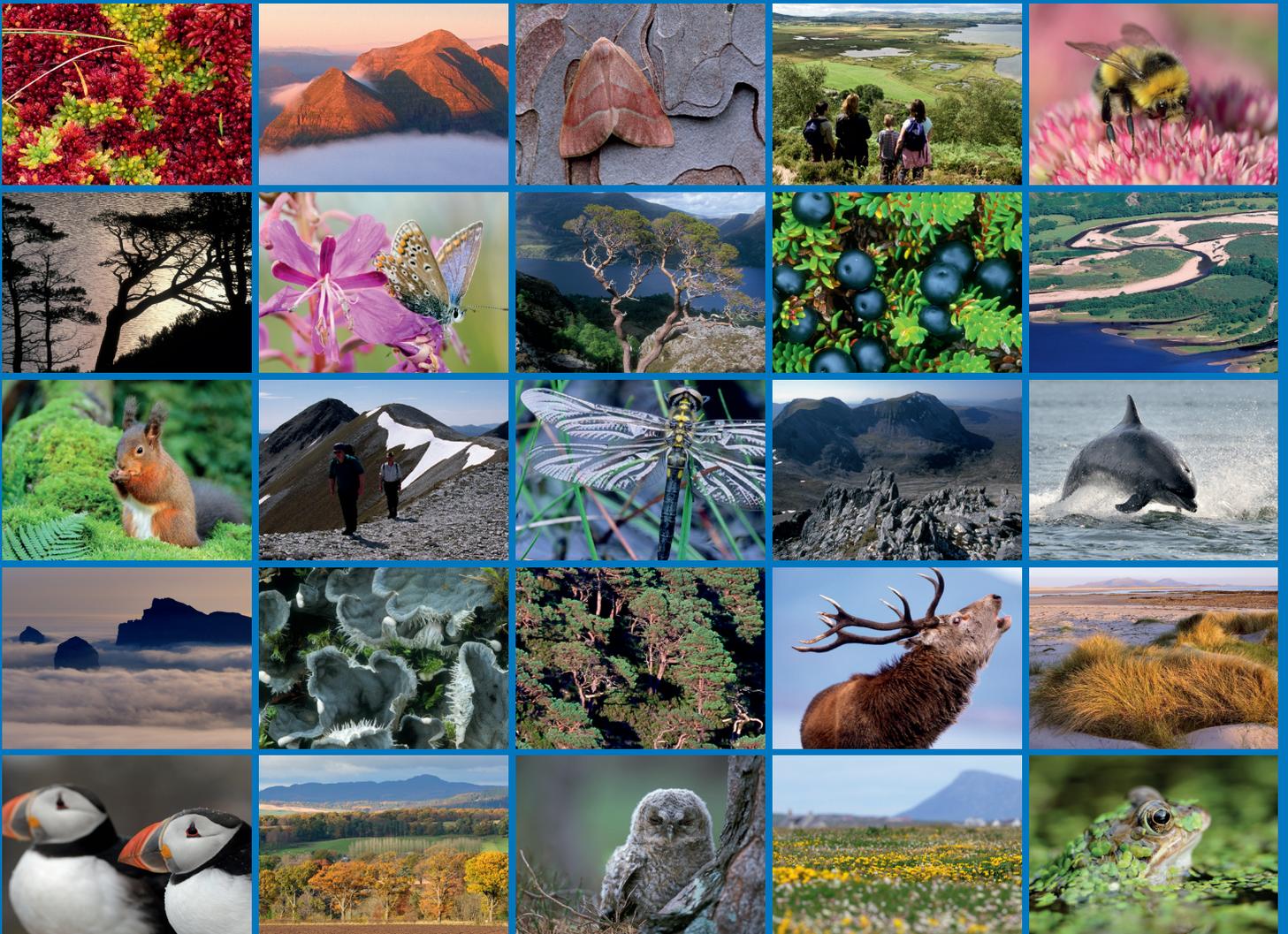


Population modelling for the Scottish Northern raven population





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RESEARCH REPORT

Research Report No. 1012

Population modelling for the Scottish Northern raven population

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RESEARCH REPORT

Summary

Population modelling for the Scottish Northern raven population

Research Report No. 1012

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Keywords

Raven; *Corvus corax*; licensing; wildlife management; demography; population modelling; breeding productivity; survival rates

Background

The northern raven (*Corvus corax*) is a highly intelligent member of the crow family that has adapted to a wide range of ecological circumstances. Ravens rely on eating carrion in many situations but they are not obligate scavengers, and also take a wide range of live prey, eggs and plants. This bird species was once widespread across upland, lowland and urban habitats in the UK. Numbers declined steadily from the mid-17th Century, reaching a population low point at the start of the 20th Century, by which time the distribution had contracted into the rugged and upland parts of western Britain. The decreases were caused by a range of factors including changes in livestock farming practices, reduction in human waste associated with settlements and deliberate killing associated with farming and game management. Since the mid to late 20th Century, the UK population of ravens has increased in size and expanded its range once more. The species has recovered and re-expanded back into most of its previous range, with the exception of some eastern areas (e.g. north-east Scotland). The recovery in both range and numbers has led to concerns about renewed damage to livestock and, in some cases, also to game bird and other wild bird populations.

Ravens come into conflict with people because of their potential to kill, injure and harass livestock, particularly recently born lambs and lambing ewes. The geographic extent, regularity and economic effects of such attacks are still poorly documented but the impacts reported by farmers on some sheep farms can be high. Ravens are protected under the Wildlife and Countryside Act, so it is illegal for farmers and other land managers to capture or kill wild ravens unless under the terms of a licence for the purpose of preventing serious damage to livestock. The numbers of applications for such licences submitted to SNH, the number of licences granted in response to these applications, and overall bag limits, have all increased in recent years. SNH has a duty to ensure that such licenced control does not impact adversely on the conservation status of the raven in Scotland. This study aimed to use population modelling to assess the current level of knowledge of Scottish raven populations and the likely effects of different levels of licensed control, using the best available demographic information from a range of sources. It also aimed to assess the levels of certainty that can currently be attached to the predicted outcomes of licensed control, and to give guidance on any gaps in knowledge that it would be most beneficial to fill in order to increase confidence in model predictions and therefore licensing decisions.

Main findings

- Using the best available information on the demography and population dynamics of the Scottish raven population, and a broadly realistic set of modelling assumptions, it is likely that the maximum level of sustainable removal of non-breeding ravens is around 200 birds per 100 x 100 km area in much of Scotland.
- In order to ensure that licenced control is sustainable however, lower limits should be set in situations where: productivity or survival are known or suspected to be lower than the average values used in these analyses; raven numbers have not yet reached carrying capacity; carrying capacity is lower; or control might affect both breeding and non-breeding birds.
- For the purposes of this report, ‘sustainable take’ is defined as a level of removal of ravens from the population that does not result in a long-term decline (modelled over a 50-year period) in the raven breeding population.
- During the years 2014 to 2016, the suggested sustainable level of take has been exceeded in some parts of western Scotland, particularly on the Uists, but without any related evidence that breeding ravens have declined there. It is not possible to assess for certain whether these particular levels of take are sustainable without more detailed information on population size, demographic rates and trends in and around the affected areas.
- The sustainable levels of control estimated by the modelling are sensitive to the range of uncertainty around the information inputs to the models, and in particular to variation in adult survival rates and breeding densities. Breeding density values determine the maximum number of breeding pairs that can be supported in any 100 x 100 km area (the ‘carrying capacity’) as defined in the preferred models.
- Conclusions from the modelling are also influenced by several other considerations, including: the mechanism by which the Scottish raven population is regulated; the shape of any density dependent relationships and the (related) extent to which mortality due to licensed control is additional to background mortality; whether regional populations are stable or expanding; and whether or not control is limited to non-breeders or also impacts some breeding adults.
- Assessments of the likely effects of licensed control on regional Scottish raven populations would benefit from: an improved understanding of age-specific survival rates; continued and enhanced monitoring of breeding raven populations (particularly in those parts of Scotland where levels of control are highest); and better understanding of the movements and behaviour of ravens in relation to their age and breeding status.
- Continued support for the monitoring studies of breeding ravens that currently contribute to the Scottish Raptor Monitoring Scheme, support for new initiatives like Raptor Patch that seek to enhance raven monitoring across Scotland, and the establishment of colour-marking and/or tracking studies of ravens in Scotland could all contribute to an enhanced future understanding of the likely impacts of licensed control and a reduced level of uncertainty around licensing decision making.

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Table of Contents	Page
1. BACKGROUND	1
2. AIMS	2
2.1 Analysis of survival and dispersal	2
2.2 Analysis of productivity	2
2.3 Analysis of breeding population size	2
2.4 Analysis of non-breeding Raven numbers and mobility	2
2.5 Population scenarios and sensitivity analyses	2
3. SOURCES OF INFORMATION	3
3.1 Ringing Scheme	3
3.2 Scottish Raptor Monitoring Scheme (SRMS)	3
3.3 Bird Atlas 2007-2011	3
3.4 Breeding Bird Survey	4
3.5 BirdTrack	4
3.6 The Raven – monograph by Derek Ratcliffe	5
4. ANALYSIS OF DISPERSAL AND SURVIVAL	6
4.1 Background	6
4.2 Methods	6
4.2.1 Data selection	6
4.2.2 Survival rates: Model fitting and selection	6
4.2.3 Dispersal and finding conditions	6
4.3 Results	9
4.3.1 Survival probabilities	9
4.3.2 Recovery probabilities	10
4.3.3 Dispersal	10
4.4 Discussion	11
5. ANALYSIS OF PRODUCTIVITY	16
5.1 Background	16
5.2 Methods	16
5.3 Results	17
5.4 Discussion	20
6. ESTIMATION OF BREEDING POPULATION SIZE	23
6.1 Background	23
6.2 Methods	23
6.3 Results	24
6.4 Discussion	26
7. ANALYSIS OF NON-BREEDING RAVEN NUMBERS	28
7.1 Background	28
7.2 Methods	28
7.3 Results	28
7.4 Discussion	31
8. EXISTING LEVELS OF LICENCED CONTROL	33
8.1 Introduction	33
8.2 Methods	33
8.3 Results	33
8.4 Discussion	36
9. POPULATION SCENARIOS AND SENSITIVITY ANALYSES	37
9.1 Background	37
9.1.1 Demographic data	37

9.2	Population models	38
9.3	Model Structure	38
9.3.1	Basic model	38
9.3.2	Density dependence model	39
9.3.3	Capped number of breeders model or threshold density dependence	39
9.4	Population growth rates under different scenarios	40
9.4.1	Density dependence	40
9.4.2	Capped number of breeders	41
9.5	Impact of licenced control	43
9.5.1	Density dependence	43
9.5.2	Capped number of breeders scenario 1: Baseline scenario	46
9.5.3	Capped number of breeders scenario 2: Expanding population	47
9.5.4	Capped number of breeders scenario 3: Breeding adults subject to licenced control	48
9.6	Sensitivity analysis	49
9.6.1	Density dependence	50
9.6.2	Capped number of breeders	55
9.6.3	Capped number of breeders, expanding population	57
9.7	Discussion	58
9.7.1	Sustainable harvest levels	58
9.7.2	Model sensitivity	60
9.7.3	Conclusions	61
10.	REFERENCES	63
	ANNEX 1: DISPERSAL AND SURVIVAL	65
	ANNEX 2: PRODUCTIVITY	71
	ANNEX 3: POPULATION SCENARIOS AND SENSITIVITY ANALYSES	73

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1. BACKGROUND

The northern raven (*Corvus corax*; henceforth simply raven) is the UK's largest passerine bird. Like other members of the crow family it is highly intelligent and has adapted to a diversity of ecological circumstances. Although it relies heavily on carrion in many situations, it is not an obligate scavenger and has been known to take a wide range of live prey, eggs and plants (Cramp & Perrins, 1994; Ratcliffe, 1997).

Ravens were once widespread birds in the UK, occurring across upland, lowland and urban habitats (Ratcliffe, 1997). However, a number of factors including changes in livestock farming, a reduction in the availability to ravens of waste associated with human settlements, and increased human persecution associated with farming and game management, resulted in a steady reduction in raven numbers from the middle of the 17th Century onwards. During this period the distribution of the raven contracted westwards, concentrating populations in more rugged and upland parts of Britain. The lowest ebb of the population was probably reached at the start of the 20th century, after which time populations started to recover in many upland areas, aided by reduction in the levels of population control associated with the two World Wars, and legislative protection of the species enacted (and subsequently reinforced) in the mid and late 20th Century. Expansion of numbers and range appear to have greatly increased towards the end of the 20th Century and the beginning of the 21st, with raven populations extending to many eastern, lowland areas from which they had been absent for well over 100 years (Ratcliffe, 1997; Balmer *et al.*, 2013). With this expansion in numbers, conflict between people and ravens has become more common.

Ravens come into conflict with people over their interactions with livestock, due to their ability to kill, injure and harass livestock, particularly recently born lambs and lambing ewes. The geographic extent, regularity and economic effects of such attacks are poorly understood but, at least in some cases, the impacts reported by individual sheep farmers can be high. Ravens are protected under the Wildlife and Countryside Act, so it is illegal for farmers and other land managers to capture or kill wild ravens unless under the terms of a licence for the purpose of preventing serious damage to livestock. The numbers of applications for such licences submitted to Scottish Natural Heritage (SNH), as well as the number of licences granted in response to these applications, and overall bag limits, have increased in recent years. In order to ensure that licenced control of ravens does not impact adversely on the conservation status of this species, it is important for SNH to understand as much as possible about numbers of ravens in Scotland, the processes underlying their population trends, and the likely effects of increased mortality through licenced control on population size and growth, at regional as well as national scales.

2. AIMS

This project aimed to:

- provide information to inform decisions made by policy makers, regulators and managers regarding the management of raven populations;
- give guidance about the most important limitations of this information and how these affect the reliability of the conclusions that can be drawn from it; and
- indicate what kind of future work might be most useful in filling existing gaps in understanding, and the ways in which such work might improve decision-making.

Specifically, the project addressed the following aspects of Raven ecology:

2.1 Analysis of survival and dispersal

Ringed recovery information from the BTO Ringing Scheme is used to derive survival estimates for different age classes of UK ravens, and to produce information on movements (natal and breeding dispersal as well as seasonal movements) of Scottish ravens.

2.2 Analysis of productivity

Breeding productivity information from the Scottish Raptor Monitoring Scheme (SRMS) is analysed to provide national and regional estimates of productivity for ravens, including assessment of the extent to which this information is representative of Scottish and regional raven populations (including a check for any biases because non-crag nesting ravens are likely to be under-represented in the sample monitored annually).

2.3 Analysis of breeding population size

Information from the SRMS is used to derive breeding raven densities in areas where intensive surveys of breeding ravens have been undertaken. These are compared with spatial variation in relative abundance estimates from the BTO/BirdWatch Ireland/SOC Bird Atlas 2007-11 project, in order to derive population estimates for Scotland.

2.4 Analysis of non-breeding Raven numbers and mobility

Current knowledge of non-breeding raven populations in Scotland is collated and reviewed for any information on the size of the non-breeding population, dispersal and seasonal movement of non-breeding birds, and observed distributions of flock size.

2.5 Population scenarios and sensitivity analyses

Demographic information and estimates from the other project elements are used in population models to simulate recent changes in the Scottish raven population, at national and sub-national scales. At the latter scale, it is important to contrast the established raven populations in the west with recovering populations in the east of Scotland.

3. SOURCES OF INFORMATION

3.1 Ringing Scheme

The British and Irish Ringing Scheme is organised by the BTO, with the aim of generating information on the survival, productivity and movements of birds, in order to understand why populations are changing. The value of the scheme relies on the fact that ringed birds are identifiable as individuals, whenever they are captured or encountered after they have died. Across all ringed birds, spatial and temporal patterns of recapture and recorded death yield valuable information on age structure of populations, how long individuals live, and where they go.

Most ringing of Ravens has been of pulli (young birds in nests), as adult ravens are very hard to capture. Accordingly, the analyses we present in this report focussed on 13 762 ravens ringed as chicks, and, in particular, the 662 of these individuals which were subsequently recovered and identified after their death. Data relating to birds ringed prior to 1950 were excluded in order to minimise problems with small annual cohort sizes.

3.2 Scottish Raptor Monitoring Scheme (SRMS)

Information from the SRMS (Challis *et al.*, 2016) was used to inform estimates of breeding densities of ravens in areas where this species has been studied intensively. This Scheme collates records from across Scotland, and gathers information on annual monitoring, territorial occupancy, breeding success and productivity at nest sites of raptors. The SRMS includes raven as an 'honorary raptor', due to many similarities between it and true raptor species in aspects of foraging, breeding and population ecology. As of March 2016, the SRMS contained records for the whole of Scotland for the period between 2003 and 2015, comprising summarised information about territorial and breeding behaviour, as well as breeding success and productivity, for individual raven nest sites.

Contributions to the SRMS are not necessarily the result of comprehensive surveys of any given area, so using the information on numbers of pairs of ravens to compute levels of abundance requires care. However, the dataset contains information from several contributors in different parts of Scotland who have carried out relatively intensive studies of ravens in which it is thought that the majority of raven pairs were recorded in one or more years.

Because SRMS data typically include information on breeding success and fledged brood sizes, they can also be used to assess levels of productivity of ravens in different parts of Scotland. If this information on productivity was to be drawn from unrepresentative subsets of the raven population, any estimates of productivity parameters based on the data could be biased, so it was important to consider the potential for this when using this data and interpreting the outputs.

3.3 Bird Atlas 2007-2011

Relative abundance information from the Bird Atlas 2007-2011 (Balmer *et al.*, 2013), summarised at a 20 km scale, was used to extend information on breeding densities from the SRMS to parts of Scotland where ravens had not been studied intensively. Bird Atlas relative breeding abundance data are based on timed surveys of tetrads (2 km x 2 km grid squares) carried out by thousands of volunteers in the breeding seasons of 2008 to 2011. Counts made during these surveys were used in conjunction with information on habitat and location to model the relative abundance of ravens across Britain and Ireland.

Atlas surveys during the breeding season were intended not to include juvenile birds, and so for many species the birds counted in these surveys are treated as breeding adults. There

are two reasons why this assumption could be problematic for ravens. Firstly, ravens are unusually early breeders with young fledging as early as mid-April. This means that, during the time that breeding season surveys were carried out for the Atlas, many juvenile ravens would have been difficult or impossible to distinguish from adults during Atlas surveys. Secondly, non-breeding adults form a substantial proportion of many raven populations (e.g. Hardey *et al.*, 2013; Loretto *et al.*, 2017; Ratcliffe, 1997), and are likely to have been recorded alongside breeding adults during atlas surveys, without any way of distinguishing them. This second issue likely poses the greater problem for interpretation of Atlas relative abundance information, as it is likely that the potential for a high proportion of resident birds to be non-breeders varies substantially from one area to another, and may be related to the size and stability of the breeding population (Ratcliffe, 1997).

Finally, total numbers of ravens detected during Atlas surveys in both the breeding and winter seasons can be used, together with BirdTrack data, to look at the distribution of flock sizes across different parts of Scotland and at different times of year.

3.4 Breeding Bird Survey

In the population models used to evaluate the likely effects of licenced control on ravens, population growth rates are modelled in response to other parameters such as survival and productivity. External information about population growth rates, although not directly input into the models, was used to check that the results produced by these models were broadly realistic. Year to year information on trends in numbers of ravens in Scotland can be derived from the BTO/JNCC/RSPB Breeding Bird Survey (BBS) (Harris *et al.*, 2017), which is the main scheme for monitoring the population changes of the UK's common breeding birds. It is a national volunteer project aimed at keeping track of changes in the breeding populations of widespread bird species in the UK. Every year, the relative abundance of many species is calculated for the whole of the UK, as well as for individual countries, provided that the BBS holds enough data for these species to yield robust measures of population size and change. A BBS trend for raven is available for Scotland, as well as for the UK as a whole. The trend may not be representative of changes in breeding raven numbers across Scotland as a whole, however, as the survey squares covered may be biased towards lowland areas in which the increases in the breeding raven population during the last 20 years have been relatively large, and because BBS methodology is not designed to allow breeding pairs to be distinguished from non-breeding 'floaters' (see Roos *et al.*, 2015).

3.5 BirdTrack

BirdTrack is an on-line recording scheme run by a partnership of the BTO, the RSPB, Birdwatch Ireland, the Scottish Ornithologists' Club and the Welsh Ornithological Society (<http://www.bto.org/birdtrack/>). It aims to provide broad-scale information on the seasonal movements and distributions of (particularly less common) birds throughout Britain and Ireland. It developed from Migration Watch, which ran in the springs of 2002-2004, and expanded on this to provide a year-round recording package that can be used to study migration and other aspects of bird ecology associated with their movement and distribution.

BirdTrack data fall into two main categories – complete lists (in which birds of all species seen during a period of observation are recorded) and casual observations, which typically comprise counts or observations of single species. Unlike information collected by fully standardised surveys such as Bird Atlas and BBS, BirdTrack observations are not generally associated with areas of known size, so it is not possible to interpret the numbers counted in terms of spatial densities of observations. However, the BirdTrack dataset contains useful information about the distribution of raven observations between different group sizes and across different times of the year.

3.6 The Raven – monograph by Derek Ratcliffe

This book (Ratcliffe, 1997) is a thorough review of raven ecology and population biology, based on a comprehensive knowledge of the existing literature at the time, as well as on the author's own extensive observations of raven individuals and populations. Although it is now 20 years old, and pre-dates the most recent expansion of ravens into lowland parts of Britain, many aspects of the understanding outlined in the book have not been superseded.

4. ANALYSIS OF DISPERSAL AND SURVIVAL

4.1 Background

The survival rates of different age classes form an important input parameter to population models. In a closed population (one from which individuals do not emigrate, and into which individuals do not immigrate), the balance of survival and productivity determines the annual surplus (or deficit) of birds. In the context of an open population (one in which changes in numbers can be influenced by birds entering and leaving from other populations), the direction and difference between productivity and mortality determines whether a population is a 'source' or a 'sink'. Knowledge of dispersal behaviour, and the factors affecting it, is essential in order to determine the extent to which sub-populations are 'closed' or can act as 'sources' (net producers of emigrants) or 'sinks' (net recipients of immigrants).

4.2 Methods

4.2.1 Data selection

The analysis considered all ravens ringed in Britain and Ireland since 1950 and subsequently recovered after their death. Ringing of ravens happens throughout Britain and Ireland, albeit with a patchy distribution (). Chicks were tagged between February and May each year from 1950 to 2013. Consequently, the survival interval extended from 1 January to 31 December in the same year, and during the first year from ringing as chicks until the 31 December of the same year (7-11 months). The data set contained 13 762 ravens ringed as chicks resulting in 662 dead ringed birds ('recoveries') reported by the end of 2013. Each recovery of a dead ringed bird had an associated finding condition (Figure 4.2).

4.2.2 Survival rates: Model fitting and selection

Model fitting and parameter estimation was conducted in Program MARK using the Seber parameterisation (White & Burnham, 1999; Catchpole *et al.*, 1995). The starting model separated birds into two age classes (juveniles and all birds older than age one), with year-specific values for both survival (S) and recapture (r) probabilities (Table 4.1; Model 16). Model simplification involved removing the effect of age class on survival, summarising survival rates over 10 year periods (rather than including rates for individual years), and modelling survival and recapture probabilities as linear and quadratic trends over time. Modelling survival and recapture as continuous functions of time, rather than as annual or 10-year values, reduced the number of parameters needed from 64 to 2 for the linear function, and from 64 to 3 for the quadratic function. Constant survival probability over time was also tested.

Variation in marking effort during the study period suggested that recovery probability was likely to vary between years. Because the dataset used to model survival probabilities was comprised of birds ringed solely as chicks, we also had to assume that reporting probability of dead birds did not vary with the age of these birds (Anderson *et al.*, 1985). For ravens, this may not be an unreasonable assumption, as dispersal and habitat use do not vary strongly with age. However, the relative importance of different causes of mortality could be affected by age, which could lead to differences in reporting rates between age classes. The best candidate model was selected using QAIC (Quasi-likelihood Akaike Information Criterion) scores. AIC scores reflect how well balanced models are between complexity and goodness of fit, with lower scores indicating more parsimonious models. QAIC is adapted from AIC to increase its suitability for heterogenous data (see Table 4.1 for details).

4.2.3 Dispersal and finding conditions

The distance that ravens dispersed (km) between ringing as chicks and subsequent ring recovery was examined for birds ringed in the Republic of Ireland, England, Isle of Man,

Northern Ireland, Scotland and Wales. The difference in dispersal between each country was tested in a linear model fitted in Program R (R Core Team, 2015).

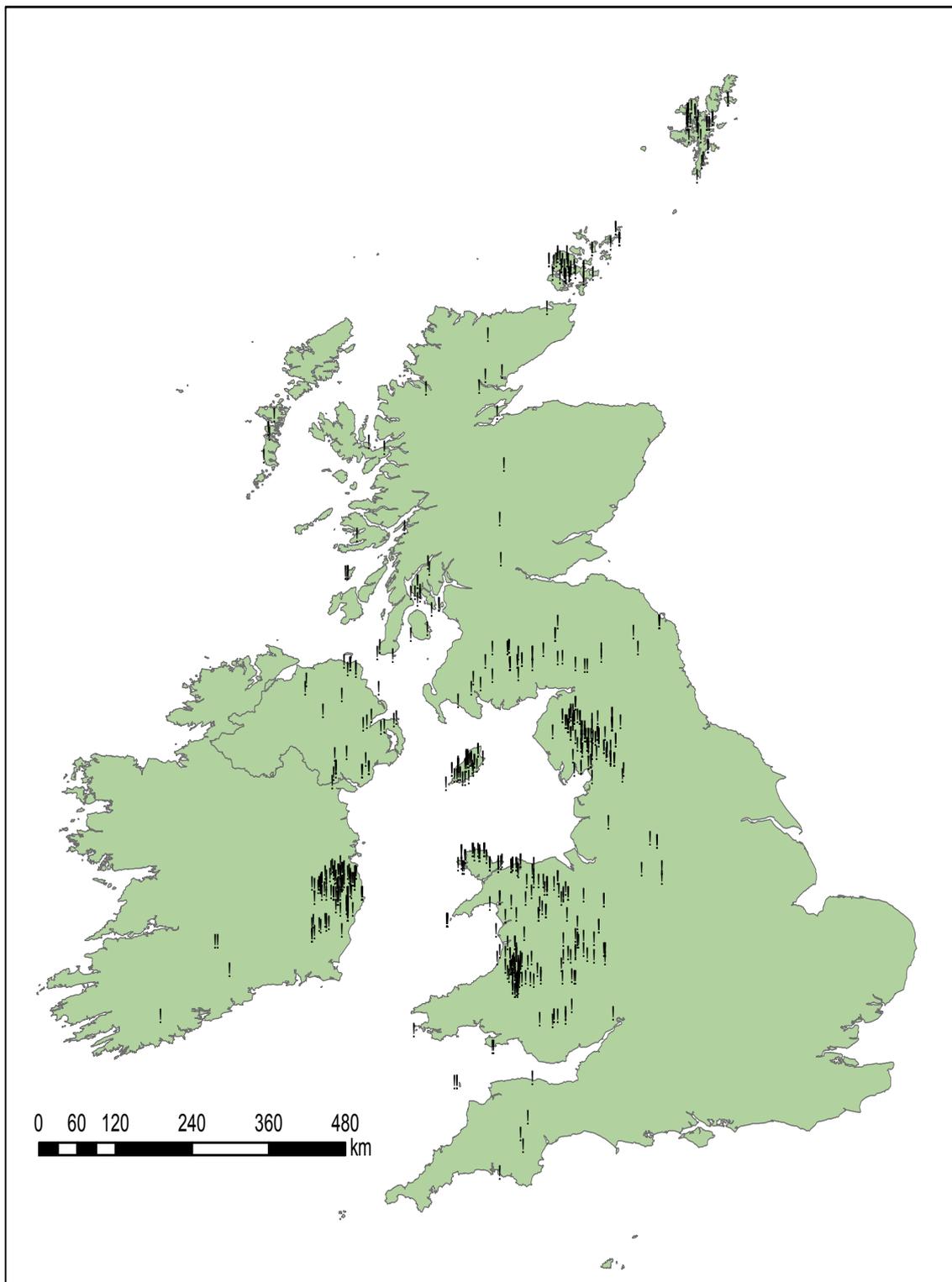


Figure 4.1 Raven ringing locations in the UK and Eire between 1950 and 2013.

Table 4.1 Modelling survival (S) and recovery (r) probabilities for ravens (1950-2012) (k is the number of parameters in the model; Model lik is the model likelihood; Dev. is the model deviance; and a_2 is a two-factor term representing age class, with a forward slash '/')

separating terms applying to juvenile and adult age classes. *S* and *r* terms are denoted as **lin.** or **quad.** if included in the model as linear or quadratic continuous variables, and as **10yr.** or **time** if represented as categories (10 year bins or individual years, respectively). Model 16 is the starting model). QAIC_c values were calculated in the program MARK, as described by Cooch & White (1999), with 10 replicates, a lower bound of 1.00 and an upper bound of 3.10, yielding a \hat{c} score of 2.16.

No.	Model	<i>k</i>	QAIC _c	ΔQAIC _c	Model lik.	Dev.
1	S (lin.) r (quad.)	5	3564.63	0.00	1.00	334.89
2	S (a2 age*lin. / age*lin.) r (quad.)	7	3565.01	0.38	0.82	331.27
3	S (10 yr) r (quad.)	10	3566.18	1.55	0.46	326.42
4	S (quad.) r (quad.)	6	3566.33	1.70	0.43	334.59
5	S (a2 lin. / lin.) r (quad.)	6	3566.56	1.93	0.38	334.82
6	S (a2 10yr / 10yr) r (quad.)	11	3568.17	3.54	0.17	326.41
7	S (a2 quad. / quad.) r (quad.)	8	3568.28	3.65	0.16	334.54
8	S (a2 age*quad. / age*quad.) r (quad.)	9	3568.31	3.68	0.16	330.56
9	S (a2 age*10yr / age*10yr) r (quad.)	17	3573.30	8.67	0.01	319.52
10	S (.) r (quad.)	4	3577.36	12.73	0.00	349.62
11	S (. / .) r (quad.)	5	3578.64	14.01	0.00	348.89
12	S (t) r (quad.)	67	3645.46	80.83	0.00	293.08
13	S (a2 time / time) r (quad.)	68	3647.47	82.84	0.00	293.07
14	S (a2 age*time / age*time) r (quad.)	122	3722.04	157.41	0.00	254.07
15	S (a2 age*time / age*time) r (linear)	121	3724.70	160.07	0.00	256.72
16	S (a2 age*time / age*time) r (t)	191	3822.83	258.20	0.00	215.69

4.3 Results

The distribution of the ravens considered in this analysis only represents part of the raven's breeding range. In particular, there were few recoveries from much of mainland Scotland (Figure 4.1). The ringing locations of birds not subsequently recovered are not currently stored on the BTO ringing database, so it is difficult to conclude whether this reflects a low ringing effort or a particularly low recovery probability. The highest frequency of ring recovery occurred in the 1980s (Figure 4.2). Apart from undefined circumstances, the most common finding circumstance for rings was associated with birds being shot. The number of rings recovered from shooting was highest in the 1970s and 1980s (Figure 4.2).

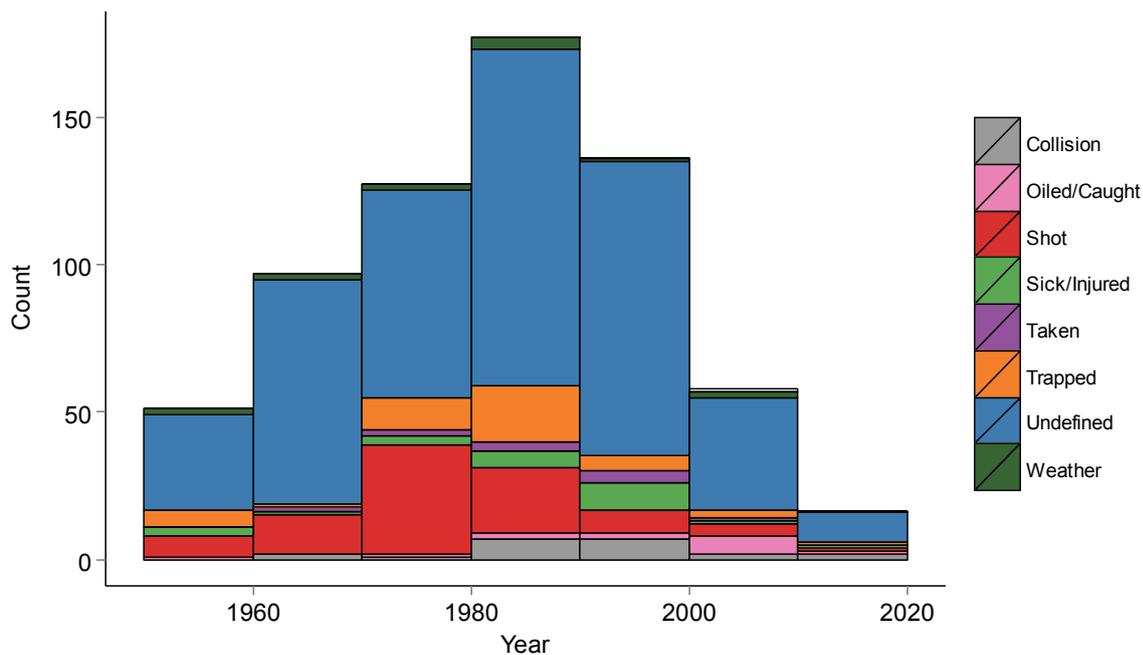


Figure 4.2 Frequency histogram of finding circumstances for recovered rings. Finding circumstance from top to bottom as follows: road or railway collision; oiled / caught in human artefact / caught in natural object; shot; found sick or injured; taken by another animal; intentionally trapped or poisoned; undefined circumstances; death associated with weather.

4.3.1 Survival probabilities

There were five candidate models that scored within two QAIC units of the best candidate model (Figure 4.1; Models 1-5). The estimates of survival from the three candidate models that did not include an age effect (Figure 4.1; Models 1, 3 and 4) indicated that the survival rates of ravens increased from about 0.60 (+/- 0.07 S.E.) to about 0.80 (+/- 0.07 S.E.) between 1950 and 2000. However, the models diverge in the last decade; Model 3 indicates that survival may have declined (albeit with a large confidence interval – see Figure 1i.1A, Annex 1). This lack of precision is likely to reflect the reduced rate of ring recovery in the last decade. The estimates of age-specific survival from the three candidate models that included an additive age effect (Figure 4.1; Models 5-7), also indicated that the survival rates of ravens have increased between 1950 and 2000 (Annex 1). The estimates of juvenile and adult survival in these models were very similar. Therefore, it seems unlikely that these models provide more information than those that did not include an age effect. Finally, the three candidate models that included an interactive age effect (Figure 4.1; Models 2, 8 and 9), indicated that the survival rates of juvenile ravens may have remained relatively stable between 1950 and 2010 (Figure 4.3.A), but adult survival may have increased over the same

time period (Figure 4.3.B). Once again, the estimate of survival for the last decade was considerably less precise (Figure 4.3.B).

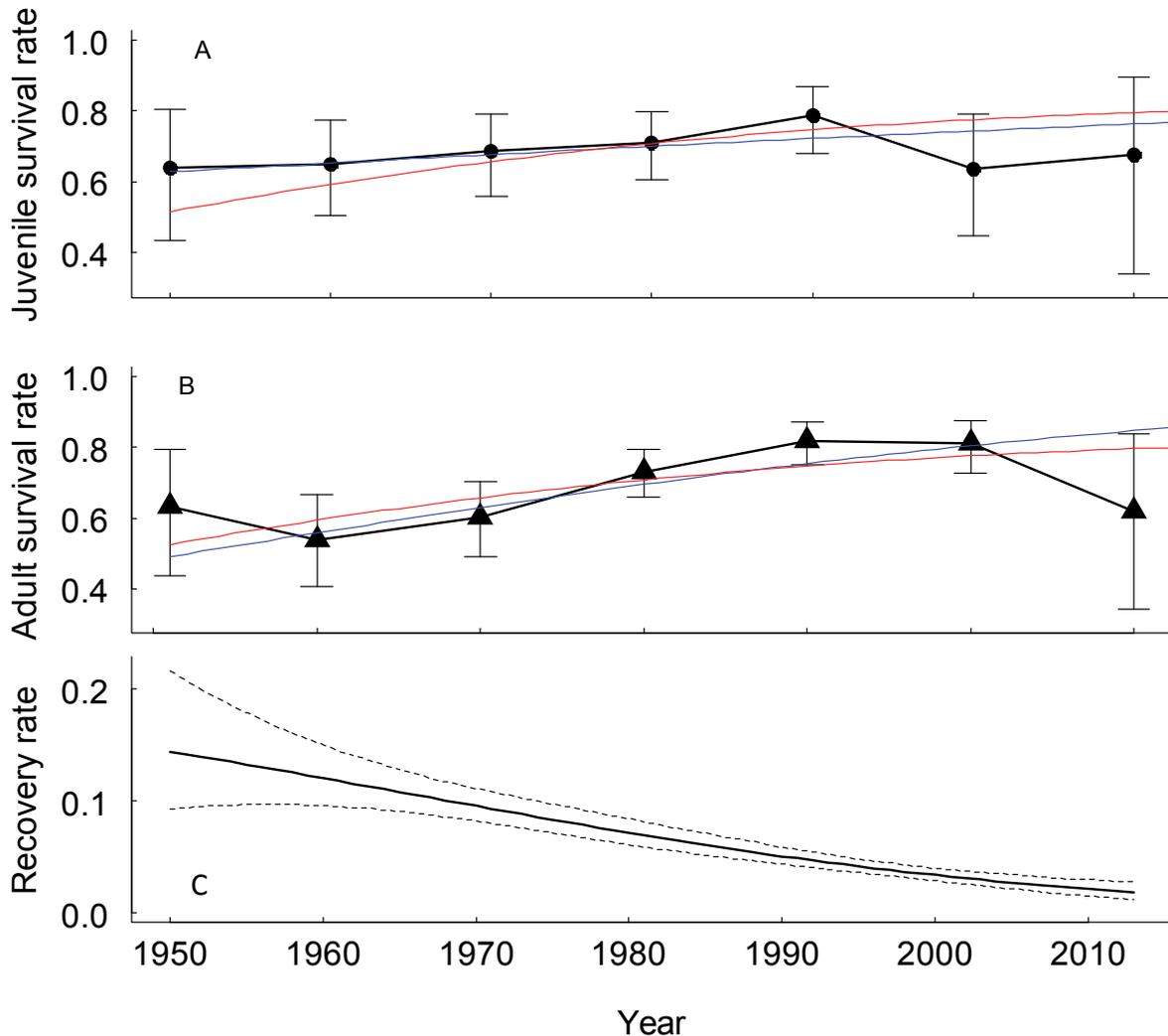


Figure 4.3 A. The survival rates of juvenile British ravens 1950-2013; modelled in 10 year blocks with an interaction between the age classes (model 9, black line and 95% confidence interval), modelled as a linear function with an interaction between the age classes (model 2, red line), and modelled as a quadratic function with an interaction between the age classes (model 8, blue line). B. The survival rates of British ravens older than age one, model structures as detailed for plot A. C. The recovery rate of rings from British ravens 1950-2013 modelled as a quadratic function of time.

4.3.2 Recovery probabilities

Recovery was best described by a quadratic function (Table 4.1; Model 14 vs. Models 15-16). The estimated recovery probability declined over the study period from ~0.16 (SE=0.03) to 0.02 (SE<0.01) (Figure 4.3.C).

4.3.3 Dispersal

Although the amount of variation explained by country was very small, inter-country differences in the distance between ringing and recovery of ravens was statistically significant between countries ($R^2=0.02$, $F_{5,648}=3.00$, $p=0.01$) being lowest for birds ringed on the Isle of Man (mean=13.00 km, sd=9.42; Annex Figure 1.i.8) and highest for those ringed

in Northern Ireland (mean=49.85 km, sd=106.09; Annex Figure 1.i.3). The mean distance travelled in Scotland was 33.36 km (sd=38.32; Figure 4.4). This was comparable to the mean distance travelled in the Republic of Ireland (mean=33.07 km, sd=35.49; Annex Figure 1.i.3), England (mean=32.69 km, sd=27.10; Annex Figure 1.i.4), and Wales (mean=29.78 km, sd=40.16; Annex Figure 1.i.5).

A breakdown of dispersal distance by age class suggests that movements of more than 50 km away from the natal site are commonest among birds aged 4 or less (Figure 4.6), suggesting that birds typically establish territories within 50 km of their natal site. Only 8% of British and Irish birds aged 5 or more moved more than 50 km from their natal site, as opposed to 27% of birds of aged 2-3 years, and 20% of 4 year old birds ($\chi^2 = 14.4$, d.f. =2, $P = 0.0007$; Figure 4.6A). This difference between age classes was even more pronounced for Scottish birds, with only 5% of birds aged 5 or more being recovered more than 50 km from their natal sites, as opposed to 36% of birds of aged 2-3 years, and 33% of 4 year old birds ($\chi^2 = 11.8$, d.f. =2, $P = 0.002$; Figure 4.6B). Unsurprisingly, movements of birds aged less than one year were heavily skewed towards the smallest distance band, with 43% of British and Irish birds and 58% of Scottish birds in this age class being recovered within 10 km.

4.4 Discussion

Survival estimates were not attempted for sub-regions of Scotland due to small sample sizes, such that confidence intervals around estimates would likely have been very wide. In addition, recovery probabilities may be non-random with respect to several pertinent factors including cause of death, location of dead birds, age class and even year. For example, in relation to the latter variable, it is notable that recoveries of poisoned and shot birds have become less frequent, in recent decades (Figure 4.2). This might, at least in part, reflect a reduction in the number of birds being illegally killed, which would fit with increases in Raven populations during this time (e.g. Balmer et al. 2013). However, it is also possible that reporting rates for shot and poisoned birds have changed during this time. This means that we should interpret this survival information with caution – particularly because relatively small changes in annual survival rates could have profound consequences for modelled population trajectories.

The findings of this study with respect to survival rates are in keeping with the other published information for ravens and other corvid species. Sæther (1989) compared adult survival estimates derived from ringing data (as our survival rates were) and those deriving from resighting of individually-marked individuals, for a wide taxonomic range of birds, and found that these two methods resulted in very similar estimates, with estimates from colour-marking studies tending to be slightly higher than those derived from ringing recoveries. Sæther (1989) found that body weight explained a high proportion ($r^2 = 0.34$) of species-specific variation in survival, particularly of adult birds. Using the relationship described by Sæther, the mean adult survival rate for species with the weight of a raven (approximately 1.2kg) is 0.77. This is very close to the adult survival rate of 0.8 that we estimated for ravens. The equivalent relationship described by Sæther (1989) for juvenile survival was weaker ($r^2 = 0.15$) but predicts a juvenile survival rate for ravens of 0.44, which is close to our own estimate of 0.5. This paper also reports juvenile survival rates for raven (0.45) and both juvenile and adult survival rates for several other corvid species (jackdaw *Corvus monedula* 0.52 juvenile and 0.61 adult survival; rook *Corvus frugilegus* 0.25 juvenile and 0.79 adult survival; and carrion crow *Corvus corone* 0.44 juvenile and 0.63 adult survival). An independent study of choughs *Pyrrhocorax pyrrhocorax* (Reid et al., 2004) reported a mean adult survival of 0.8 and a mean juvenile survival of 0.43.

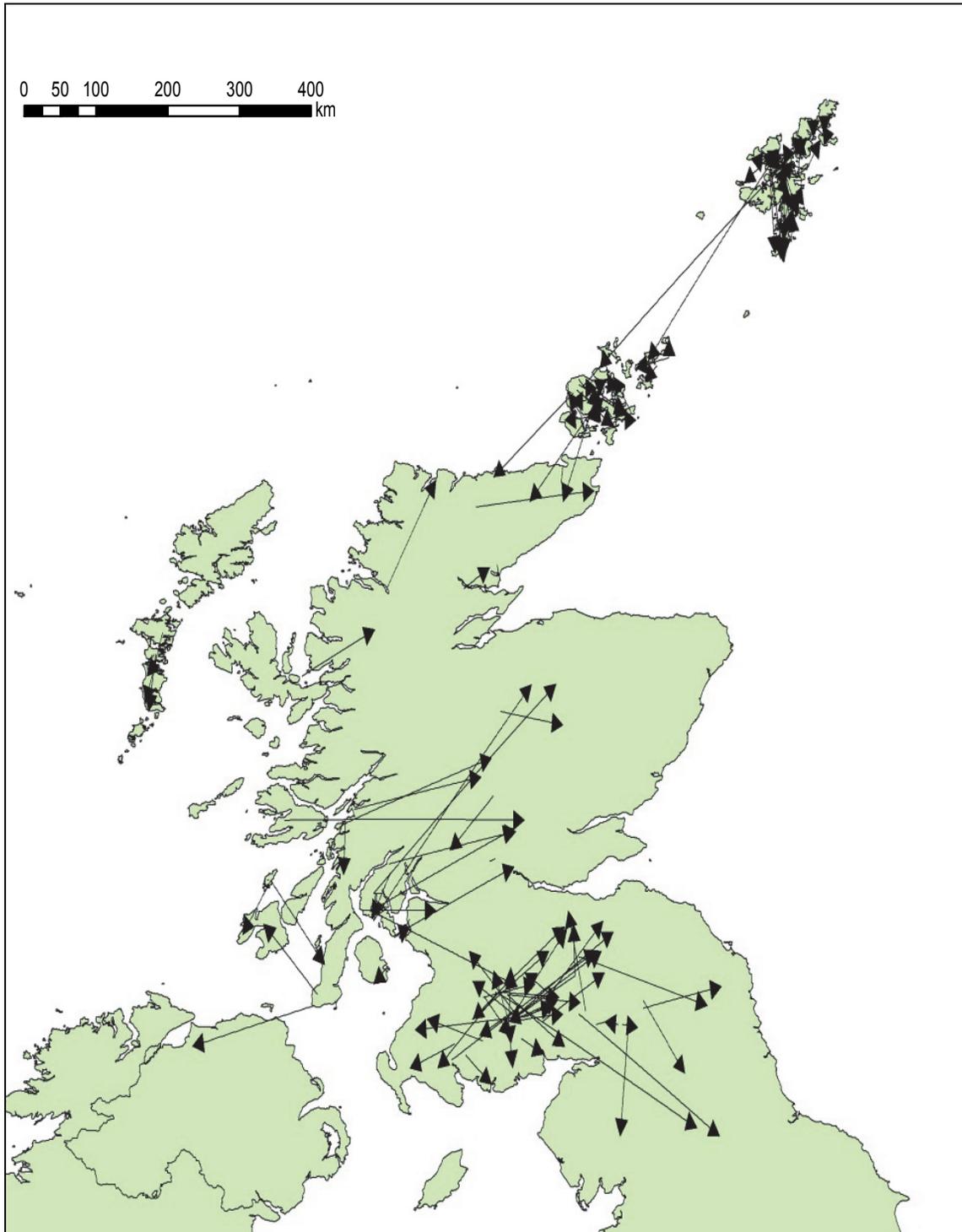


Figure 4.4 Dispersal of ravens ringed in Scotland. Arrows show direction of movement between ringing and recovery.

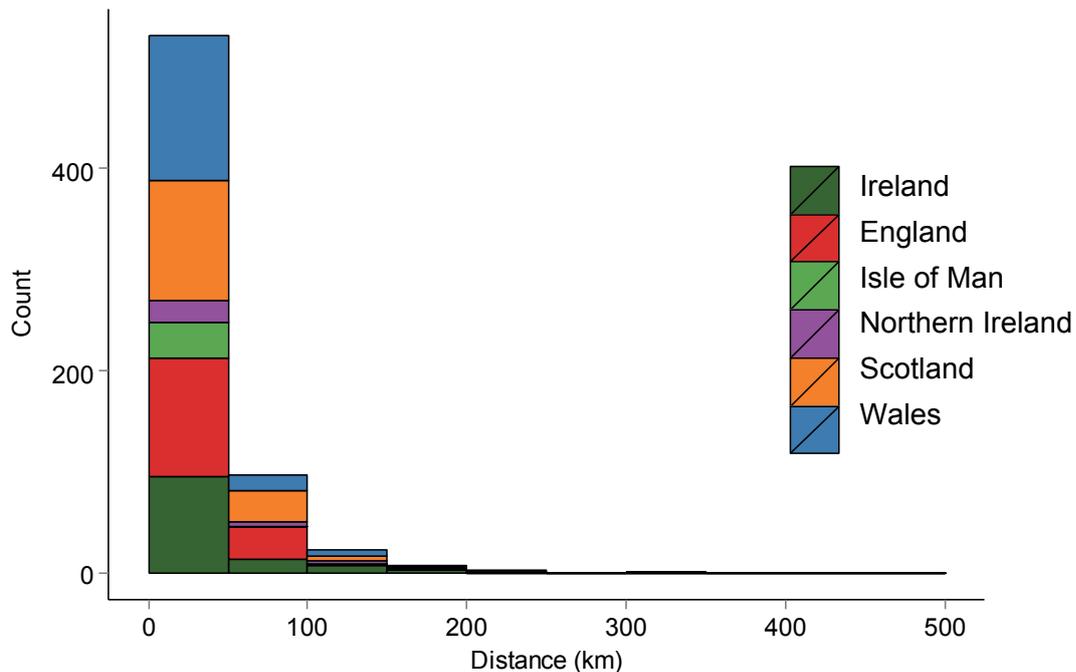


Figure 4.5 Cumulative frequency histogram of distance between ringing as chicks and subsequent ring recovery.

Few of the movements recorded for marked individuals within this population were over distances of more than 100 km. This was particularly the case for birds of breeding age, implying that even if immature ravens can range relatively widely, most ravens that survive to breed are likely to settle on territories within 50 km of the nest from which they fledged. This suggests that 100 km may be a reasonable scale at which to model raven populations as a function of internal processes (survival and productivity) without having to account for the influences of immigration and emigration. Ratcliffe (1997), also using ringing data, reached similar conclusions to about the scale of raven movements. These figures, which are based solely on distances travelled between hatching and death, are broadly in keeping with an entirely independent dataset collected from colour-marked and GPS tagged individuals in alpine populations of raven in Italy, Austria and France, in which the areas used by the majority of individual ravens were equivalent in size to one hectad or less (Loretto *et al.*, 2017).

Another means of examining effective rates of dispersal is achieved by looking at observed range expansion of ravens in some parts of Britain. During the period between the last two Bird Atlas surveys (roughly 1990 to 2010), during which time the British raven population underwent remarkable population growth and range expansion, the maximum recorded linear increase in range (from edge of old range to edge of new range) was about 240 km, in the south of England. This is (very roughly) equivalent to an average increase in range of about 12 km per year. This rate of expansion is consistent with a natal dispersal distance of between 50 km and 100 km. Most ravens do not breed until three years of age, which means that the period between atlases covered about seven generations of ravens. Each generation would have had to travel an average of around 30 km in the direction of expansion. Moreover, considering that dispersing ravens in a newly colonised area are likely to encounter available territories in most directions, there is no reason to suppose that dispersal would always be in the same direction. This means that the new ground occupied by dispersing ravens from one generation to the next might be considerably less than the maximum distance travelled by individual dispersing birds.

It should be noted that our analyses were necessarily based on a relatively small number of ringed and recovered ravens. While these were likely to be broadly representative of ravens in Scotland and the UK, they were not sufficiently numerous to formally test whether or to what extent movements vary within this area (e.g. between different parts of Scotland, or between low and high density breeding populations). Such inter-regional variation in dispersal patterns could have important implications for the consequences of region-specific variation in levels of licencing. For example, if levels of licencing were much higher in one region than in those around it, movements of birds to and from this region could determine the nature of any impact of lethal control on the local population. If dispersal into the region in question resulted in it becoming a population sink, then licencing could also affect raven numbers in nearby regions. During the early 1980s, ravens in north-east Iceland, where levels of human-caused mortality were higher than in other parts of the country, dispersed shorter distances and were recovered at a younger age than ravens in other regions (Skarphéðinsson *et al.* 1990). Such a pattern could come about, without there being any regional differences in dispersal behaviour, if many ravens fledging in regions with high mortality were killed before they had the chance to disperse very far. However, it is also consistent with a population-density mediated effect of lethal control on dispersal behaviour, with juveniles from regions with high breeding success and low mortality being more likely to disperse long distances in search of unoccupied territories.

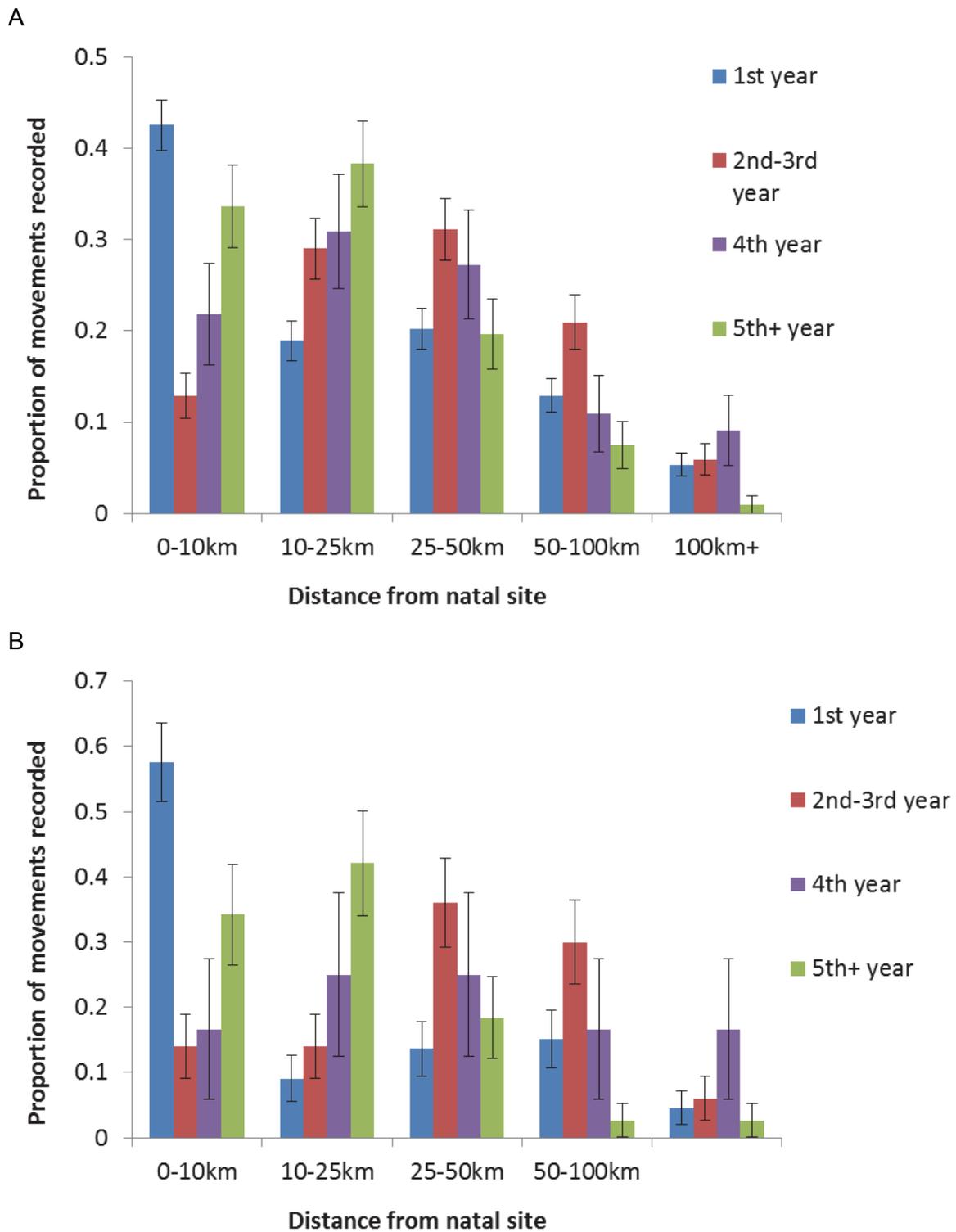


Figure 4.6 Proportional breakdown of dispersal distances according to age class for all recoveries, up to 2015, of ravens ringed as nestlings in a) Britain and Ireland ($n=881$) and b) Scotland ($n=178$). Error bars represent standard errors.

5. ANALYSIS OF PRODUCTIVITY

5.1 Background

Productivity is another crucial component of population growth hence must be estimated to parameterise models. Considering a closed population (one from which individuals do not emigrate, and into which individuals do not immigrate), productivity is balanced against survival to determine the annual surplus (or deficit) of birds. In the context of an open population (one in which changes in numbers can be influenced by birds entering and leaving from other populations), the direction and difference between productivity and mortality determines whether an apparently stable population is a 'source' or a 'sink'. In either case, an understanding of productivity is likely to be at the heart of an assessment of whether a given level of licenced control will be sustainable.

The Scottish Raptor Monitoring Scheme is a rich source of raven productivity information, having gathered 4724 records of raven occupancy and breeding success between 2003 and 2015. While these data do not necessarily represent randomly selected subsets of the Scottish raven population, the spread of data is sufficient to give a useful indication of productivity over large parts of Scotland.

5.2 Methods

In order to assess variation in levels of raven productivity between regions, years and nest site types, we modelled the effect of these variables on overall productivity (the average number of chicks per pair for all – successful and unsuccessful – pairs). Productivity models were specified using a Poisson structure (suitable for integer count data). Data with missing values required by the model (e.g. breeding attempts where outcome or fledged brood size were unknown) were excluded from the analysed dataset. Analysis was carried out using the `glm` (generalised linear model) function in the statistical package R, with selection between candidate models (including different combinations of the three explanatory variables region, year and site type) being carried out using AIC values.

Five regions of Scotland (Figure 5.1) were specified according to 100 km × 100 km grid letter, to fit with the regions for which population densities could be calculated (section 6). From north to south, these were: Northern Isles (letters HP, HU, HT, HY and HZ), North Mainland (letters NC, ND, NH and NM), West (letters NA, NB, NF, NG, NL, NM and NR), East (letters NJ, NK, NO, NT and NU) and South-west (letters NS, NW and NX). Nest site type was specified as a binary variable, distinguishing nests in trees from all other nest site types. This was considered to be important to include in candidate models due to the possibility that tree-nesting ravens may be under-sampled in some parts of Scotland. Such undersampling might arise partly as a result of the people contributing most information on ravens being generally focussed on predominantly cliff and crag nesting birds of prey such as peregrine *Falco peregrinus* and golden eagle *Aquila chrysaetos*, and partly because (at least in some situations) ravens nesting on crags may be more easily detectable than those nesting in conifer plantations.

In order to limit the consideration of productivity to the most current subset of data, and to limit the influence of small sample sizes in some regions during the early years of the SRMS, this analysis was restricted to records from 2009 to 2015. In total, the analysis used 1577 records of raven territories where pairs were found and monitored, and where both breeding success and (in the case of successful attempts) the number of young fledged were recorded. Records of failed breeding attempts were analysed according to the cause of failure assigned to these (to one of the following categories: Deliberate human action, Accidental human disturbance, Weather, Other species, and Intrinsic (failure caused by behaviour or biology of the brood or parents), and whether or not any evidence for cause of failure was included in the record.

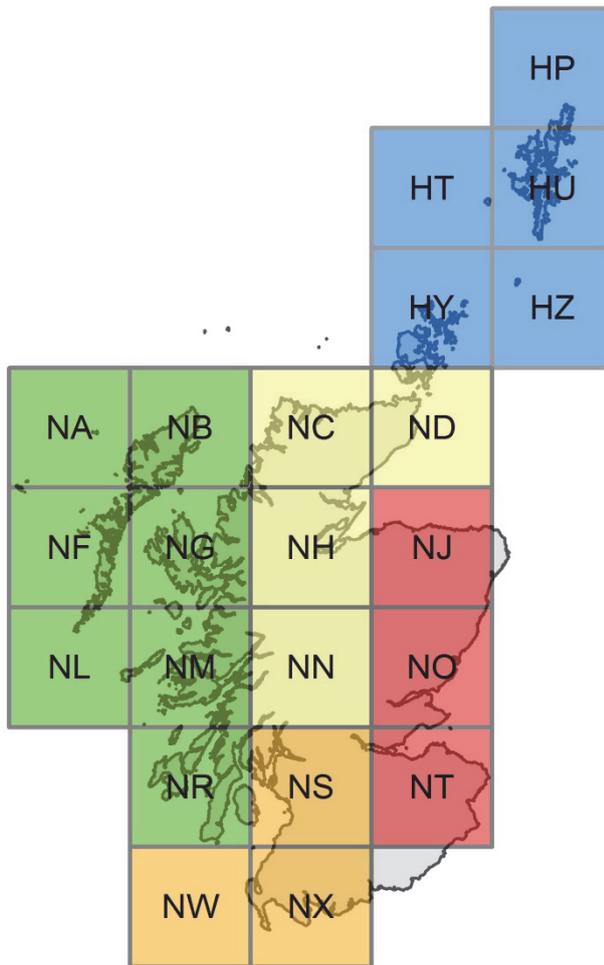


Figure 5.1 Five regions of Scotland used to analyse raven productivity and densities (see Section 6), with OS national grid letters super-imposed. The regions are Northern Isles (blue), Northern mainland (yellow), West (green), East (red) and South-west (orange).

5.3 Results

The average productivity of ravens in Scotland from the period between 2003 and 2015 was 2.35 per territorial pair¹, with substantial variation in rates of breeding success and productivity between different parts of Scotland (Figure 5.2). Of the three explanatory variables considered for inclusion in the model, the only one retained in the final model was region. Year and nest site type explained too little variation to be retained in the final model. Estimates from the final model are shown in Figure 5.3 (more details for this model, as well as for separate models taking binary nest success and size of fledged broods as their response variables, are given in the Annex in Tables 2i.1 – 3 and Figures 2i.1 - 2). The significance of differences between varying levels of the variables was assessed using Tukey’s all-pair comparisons, carried out using the `glht` function in the R package `multcomp`.

¹ Breeding success of nests where large young were recorded was assumed to be similar at nests with unknown fate as at nests where success or failure was recorded. Similarly, fledged brood size at successful nests where number of fledglings was not recorded was assumed to be similar to those nests at which a minimum number of young was recorded.

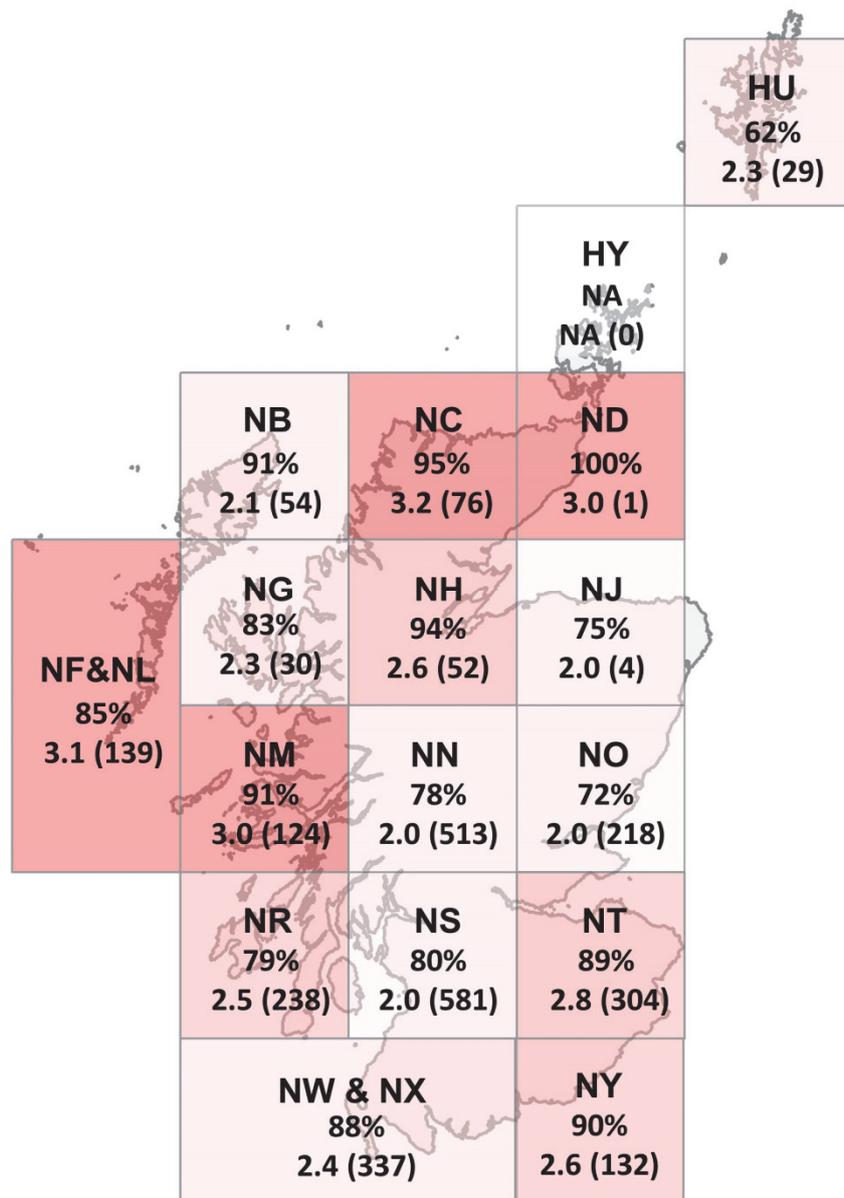


Figure 5.2 Variation in breeding success and productivity of ravens from Scottish Raptor Monitoring Scheme (SRMS) data for different parts of Scotland. For each 100km for which breeding outcomes of raven nesting attempts are recorded in the SRMS, the percentage of attempts successfully fledging young, and the average minimum fledged brood size recorded for breeding attempts with known outcome are given, along with number of breeding attempts with known outcome (in parentheses).

Of 387 records of attempted breeding by ravens known to end in failure (Figure 5.4), a known or suspected cause of failure was identified for 102 records (26%). Twenty-three (22%) of these records were accompanied by information describing observations or additional information that supported the cause of failure assigned by the observer. The most commonly assigned type of failure, accounting for 12% of all records, was deliberate intervention by humans. However, only 17% of these records were accompanied by a description of the evidence supporting this assessment. The proportion of records for which a failure cause was assigned varied non-randomly between the 12 SRMS regions ($\chi^2 = 25.6$, d.f. = 10, $P = 0.001$), ranging from 44% (in Uist) and 40% (in D&G) to 17% (in Central) and 0 (in Lewis & Harris, North-east Scotland and Shetland). Among records for which a failure cause was assigned, there was no significant difference between regions in the proportion of records attributed to deliberate human action ($\chi^2 = 5.8$, d.f. = 10, $P = 0.08$).

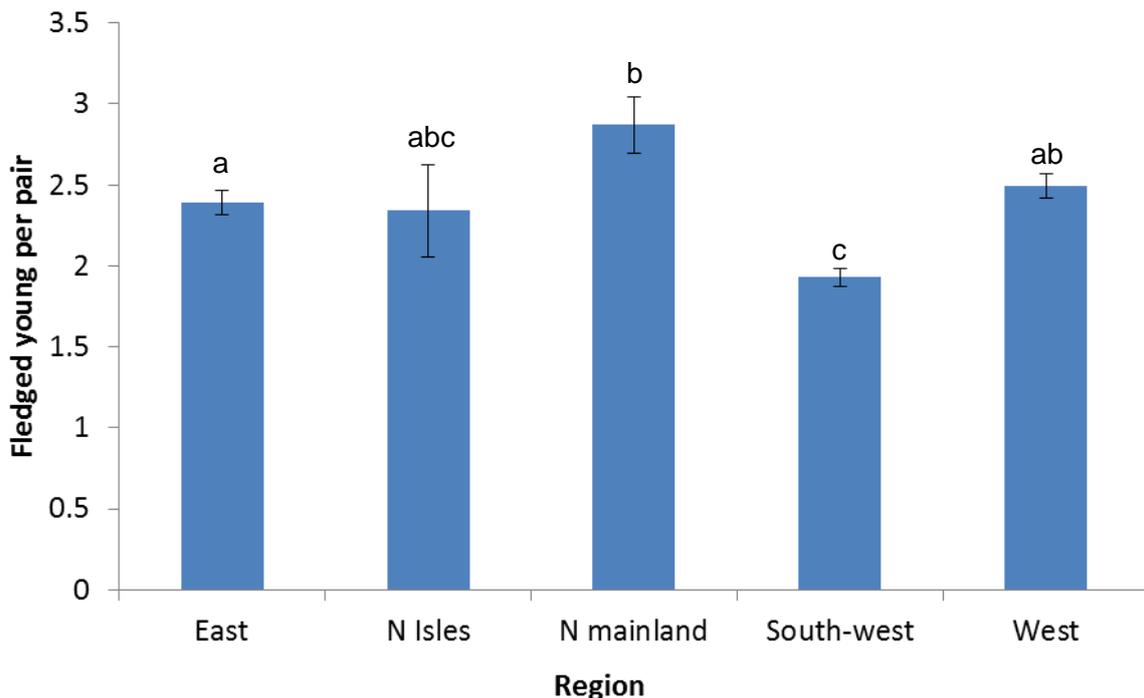


Figure 5.3 Mean level of productivity (young fledged per breeding pair) for ravens in five parts of Scotland between 2003 and 2015. Letters above each bar denote statistical significance – the difference in productivity between regions that share a letter is not statistically significant. Error bars denote standard errors.

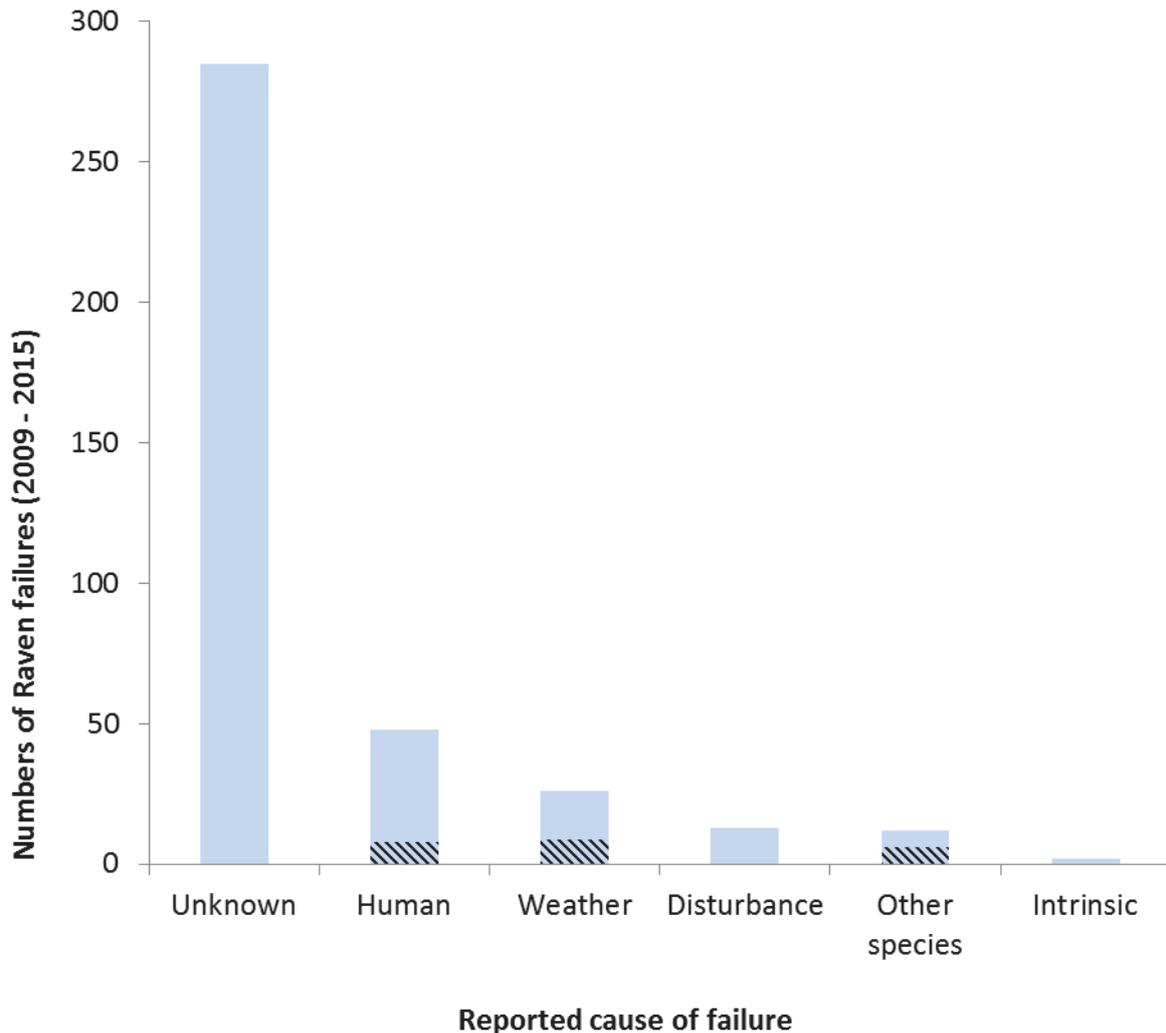


Figure 5.4 Causes of failure for 387 raven breeding attempts reported to the Scottish Raptor Monitoring Scheme between 2009 and 2015 with known, unsuccessful outcome. The category “Human” refers to reports of failure due to deliberate human interventions, whereas “Disturbance” covers accidentally human-induced failures. “Other species” failures are those ascribed to nest competitors and predation or disturbance by other bird species, while “Intrinsic” failures are those attributed to the biology or behaviour of the parent birds. The shaded portion of each bar indicates the number of records for which evidence for the cause of failure was reported.

5.4 Discussion

Productivity estimates for eastern and western populations of raven are very similar, and not significantly different. Both are based on large sample sizes and seem relatively consistent over the time period considered (sufficiently so that the effect of year on overall productivity was not significant). However, productivity in other parts of Scotland was notably different. Productivity in the north and central highland region seems to be higher than some others (including, by a small margin, the east), but the estimate for this region was based on a very small sample. Conversely, the productivity estimate for the south-west was lower than in any other region (this difference being significant with respect to all regions except the Northern Isles), and was based on a larger sample size than the estimate for any other region. Historical levels of productivity reported by Ratcliffe (1997) for different parts of Britain (including three Scottish regions), for variable periods spanning most of the period between 1950 and 2000, are closer to the lower end of this spectrum, ranging between

1.66 and 2.05. This suggests that breeding productivity of ravens (at least at monitored nest sites) has improved since the last century, a trend that might be related to decreased levels of persecution since this time. Exploration of variation in model parameters reflected the scale of these regional differences in productivity, allowing assessment of its significance for population persistence at different levels of licenced control.

Variation in overall productivity can arise from variation in one or both of two properties of breeding attempts: breeding success (the proportion of breeding attempts which successfully fledge one or more young) and the number of chicks fledged from successful broods. Some factors, such as food abundance or poor weather, can influence productivity by acting on both breeding success and fledged brood size (for example, a lack of food could reduce the number of chicks that successful breeders manage to rear to fledging, but could also increase the proportion of breeding attempts that fail completely). However, other factors such as nest predation and destruction or disruption of nesting attempts by humans, are more likely to increase the overall number of breeding failures than to influence the number of chicks reared by successful breeders. The overall regional pattern in productivity described above is influenced by variation in both breeding success and fledged brood size. The highest level of productivity among the five regions was in North mainland, where breeding success was high but fledged brood size similar to most other regions. The lowest level of productivity, on the other hand, was in the South-west, where levels of breeding success were unremarkable but the average size of fledged broods was relatively small. This regional variation may indicate that causes of overall nest failure such as nest predation and persecution are less prevalent in the North mainland region than they are elsewhere. However, as mentioned above, the sample of breeding records from this region was small, and caution is required when interpreting these findings.

Other environmental and demographic factors could give rise to differences in productivity. One such factor that varies broadly between different parts of Scotland, due in large part to the availability of crags and trees, is the type of nest site used. This could affect real productivity (by influencing the security or shelter of the nest site, or associations between availability of different nest site types and landscape-level variation in factors like food availability), but could also influence the effectiveness with which breeding pairs can be located and subsequently monitored. However, SRMS data provide little evidence of any influence of nest site type on overall productivity. Other factors that could influence productivity could themselves be influenced by the demographic consequences of lethal control. These include the age and experience of breeding pairs, which could change if licencing affects the age structure of populations; and also the occurrence and intensity of inter-specific competition. If the number of ravens in more lowland parts of Scotland continues to increase, then competition with other scavenging and predatory species (particularly other corvids and buzzards *Buteo buteo*) could influence the breeding success and productivity of breeding pairs, as well as the effective carrying capacity of these areas for ravens.

The two Raptor Study Group regions that have contributed the fewest data to the SRMS (and, therefore, to this analysis) are Orkney and North-east Scotland. Given that the latter region is one of the few eastern region where there is currently a demand for raven licences, data from this region would have been particularly relevant to these analyses. However, productivity from other regions along the east and west coasts seems to have been relatively homogenous and consistent, so unless ravens in the North-east face very different influences on their reproductive output than other eastern populations, estimates drawn from these data probably represent them adequately.

Where cause of failure information is recorded, failure is most commonly attributed to people. However, we cannot assume that distribution between failure types would be the same for breeding attempts where it is recorded as for those where cause of failure was

unknown. Many contributors of records to the SRMS do not routinely report information about cause of failure, and some may perceive that it is more important to document causes of failures involving human activity, because of concerns about wildlife crime.

The interpretation of regional differences in cause of failure information from SRMS is further complicated by the fact that the greatest source of recorded variation between regions is not cause of failure, but rather whether or not any cause is recorded. In the field, cause of failure may be difficult to establish with certainty for many failed breeding attempts. Moreover, the proportion of records for which evidence for any assumed cause of failure is presented varies considerably between different causes. This variation could reflect differences in the availability of evidence, or differing levels of interest in these causes among contributors. Either way, it means that cause of failure information probably tells us little about differences between regions.

6. ESTIMATION OF BREEDING POPULATION SIZE

6.1 Background

The number of breeding ravens within the regions considered has important implications for the levels of licenced control that could be sustained without impacting adversely on conservation status, however that is defined. For any given level of productivity, the number of breeders determines the overall number of young birds produced each year. Assessments of breeding population density/size are based on the best available information, but contain some uncertainties surrounding the basic information (e.g. the numbers of raven pairs breeding in sites not known to SRMS contributors. However, most of the SRSG fieldworkers who submit large numbers of Raven records maintain a core study area in which they are confident that they find most of the Raven pairs nesting each year. It is much more difficult to estimate numbers of non-breeders within the population (section 7). Although non-breeders may buffer a population against increases in mortality that outstrip productivity, this cannot be sustained in the long-term. Issues of dispersal and non-breeding could be very important in determining impacts of licenced control on breeding populations, particularly if the distribution of licenced control was very patchy.

6.2 Methods

We used densities of breeding ravens recorded in the SRMS (which are available for only a small proportion of Scotland) to calibrate relative abundance of ravens from the Bird Atlas (which is available for the whole country). Densities of breeding ravens were calculated for areas in which the study of this species was thought to be intensive enough to find the majority of pairs. Raven studies were identified using a combination of existing knowledge about long-term contributors of raven data to the SRMS and, using the Geographic Information System software ArcGIS 10.1, by visually identifying clusters of raven records at higher spatial concentrations than in surrounding areas. The main observer (or observers) within these clusters were identified, and minimum convex polygons drawn around all raven records submitted by these observers as well as any other records within 1 km. Many of these polygons included areas within them where raven surveying had been sparse or lacking, so that it was difficult to distinguish between patches of locally low Raven density and patches of low Raven recording effort. We calculated the proportion of each whole and part hectad (10 km × 10 km square) within the polygons that was within 1 km of a recorded raven nest site location. For our estimates of raven breeding density, we only used hectads within which the density of known raven sites was as high (or higher) than the average density for the whole polygon. Within these hectads, we used the maximum number of occupied raven territories recorded in any one year.

In order to understand the relationship between breeding raven density and Bird Atlas-derived relative abundance, both measures were summarised at a relatively coarse resolution. This decision was taken to reflect the likelihood that non-breeding ravens were likely to contribute to the Atlas-derived measure of abundance, which would contribute a considerable level of 'noise' (i.e. unexplained variation) to analyses carried out at finer spatial scales. The majority of recorded raven movements have taken place within distances of 100 km or less (see sections 4 and 7), so it was decided to carry out this analysis at the 100 km scale. For each 100 km × 100 km square in Scotland in which there were five or more hectads contributing information, the maximum number of territories for each of these hectads was summed and divided by the total area of the contributing hectads to give an estimated maximum breeding density. For the same hectads, mean Atlas abundance scores were also summarised at the level of 100 km × 100 km squares. A relationship was fitted between breeding densities and Atlas abundance, and this relationship was used to estimate breeding density for the whole of Scotland, as well as for individual sub-regions defined according to 100 km × 100 km squares. The amount of

variation explained by this relationship was estimated as McFadden's pseudo r-squared, calculated as described by Faraway (2006): $\rho = 1 - (\text{residual deviance} / \text{null deviance})$.

It is likely that many voluntary fieldworkers tend to focus on areas where densities of breeding Ravens are relatively high (at least compared with other nearby areas available to them to study). This, together with the fact that we excluded hectads with locally low densities of recorded Raven pairs, means that our measures of breeding density are likely to have been drawn from areas of locally high Raven abundance. However, this focus on high density areas doesn't compromise the relationship between SRMS and Atlas data, because data from SRMS and from Atlas surveys were taken from the same hectads.

6.3 Results

The relationship between observed densities of occupied raven territories taken from SRMS data and relative abundance for the same areas, taken from Bird Atlas 2007-2011, is shown in Figure 6.1. A logarithmic relationship was fitted to these data, which explained 32% of the variation in SRMS raven densities (Figure 6.1). Using this relationship to predict average raven densities over the whole of Scotland yielded an estimated total population of 3241 pairs (95% C.I. 1035 – 5447 pairs).

For modelling purposes, we needed to estimate representative densities of breeding ravens in Scotland. Because the modelling was at a 100 km scale, we estimated the variation in raven densities at this scale (Figure 6.2). Estimated mean densities (per hectad) for the five regions described in section 5, calculated using the relationship described in Figure 6.1, ranged from 5.91 (± 0.44 S.E.) in the Northern Isles, to 2.12 (± 0.99 S.E.) in eastern areas (Table 6.1).

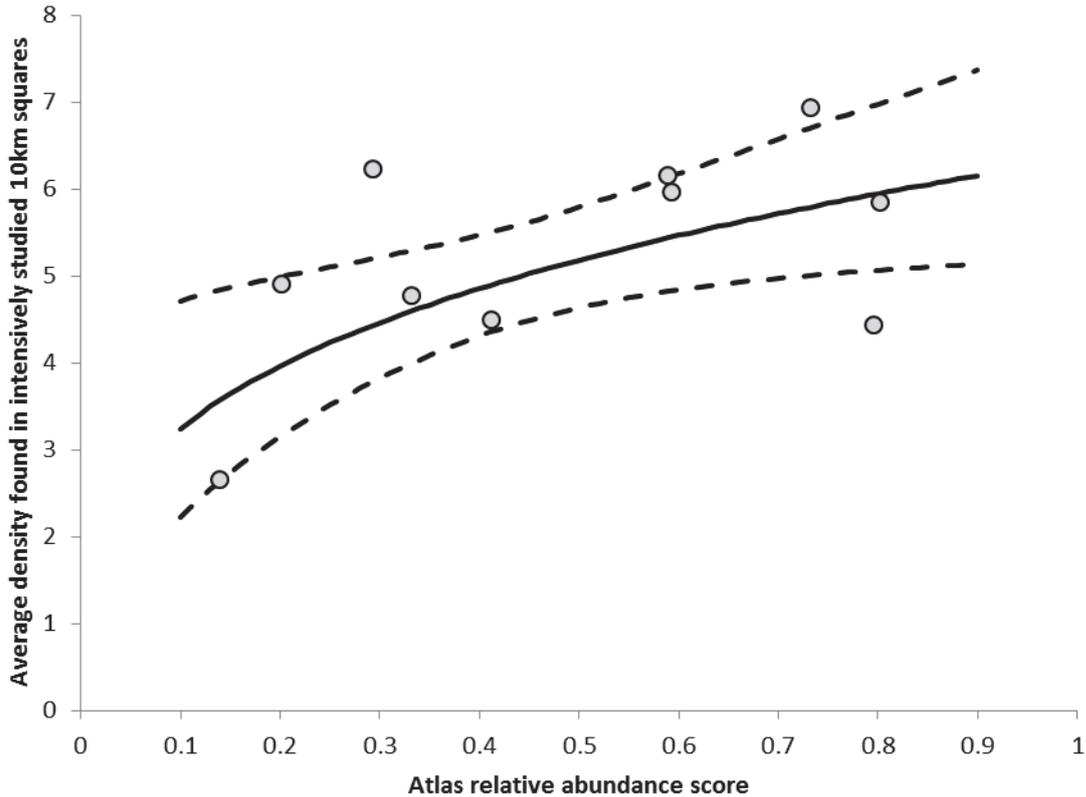


Figure 6.1 Relationship between observed densities (pairs per hectad) of occupied raven territories (SRMS) and relative abundance (Bird Atlas 2007-11) for ten 100 × 100 km squares in Scotland. The Poisson relationship fitted to these data is $\ln(y) = (0.29 \times \ln(x)) - 16.57$, where y = density and x = mean relative abundance. Pseudo R^2 (p) = 0.5, $z_{1,8} = 2.51$, $P = 0.01$. Dashed lines represent upper and lower 95% confidence intervals.

Table 6.1 Estimated mean densities of breeding ravens (pairs per hectad) in five grid-square based regions of Scotland, with standard errors and lower and upper 95% confidence intervals.

	Atlas score	Density	Lower C.I.	Upper C.I.
East	0.09	2.36	1.72	3.25
North Mainland	0.22	4.10	3.33	5.04
Northern Isles	0.83	6.01	5.09	7.09
South-west	0.29	4.42	3.77	5.19
West	0.6	5.46	4.83	6.16
SCOTLAND	0.29	4.31	3.61	5.14

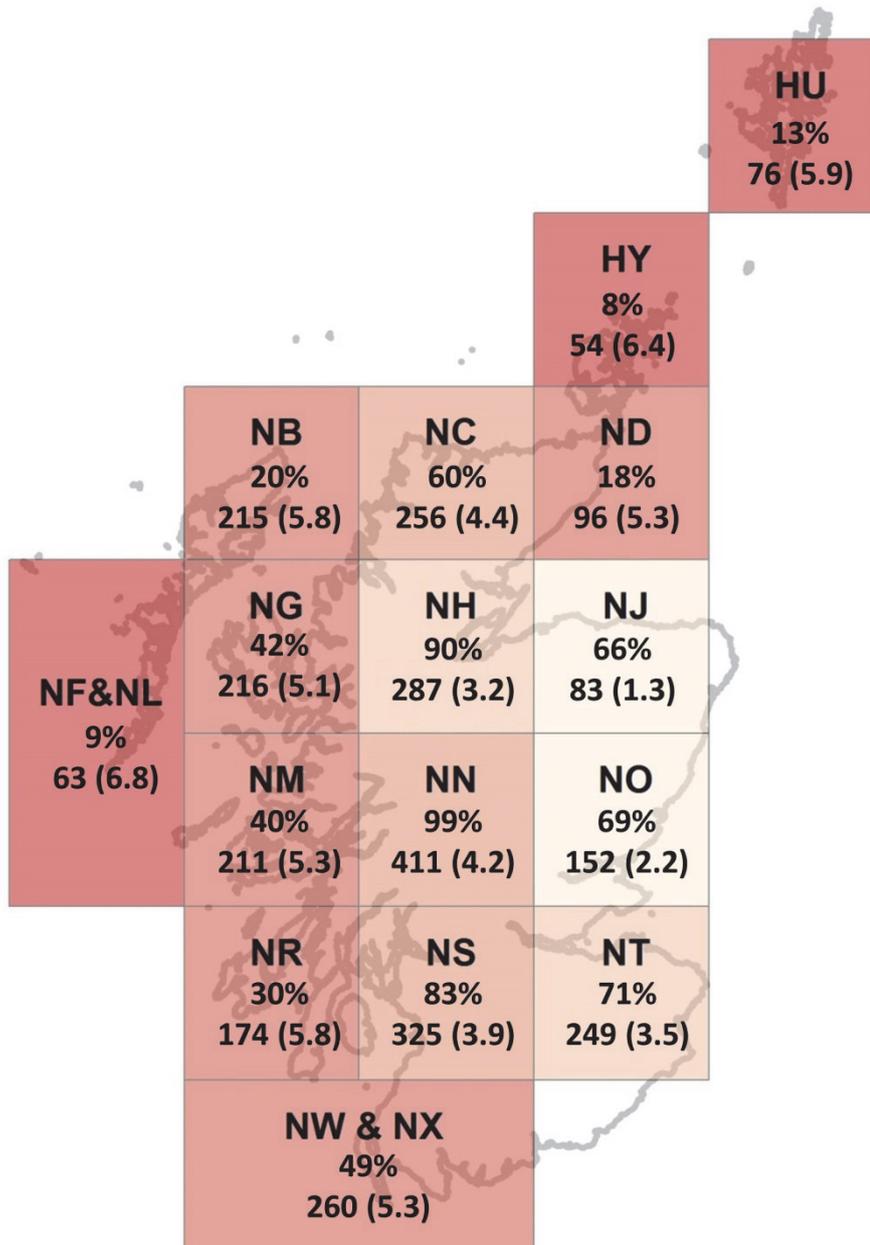


Figure 6.2 Variation in estimated number and density of breeding ravens pairs in 100 km grid squares across Scotland, shaded according to estimated population density. The percentage of the square occupied by land is given, followed by the number of breeding raven pairs estimated for the square, and the density (pairs per hectad) in brackets.

6.4 Discussion

An assumption of this analysis is that the measures of density extracted from SRMS data are accurate and representative. Ideally, we would have used mean densities rather than a maximum as, all other things being equal, these should give the most robust indication of raven breeding density in an area. However, due to variation in survey effort over time and, in particular, how this varied between different SRMS raven study areas, it was decided that maximum abundance in each hectad was likely to provide the best reflection of raven density in most areas.

The decision to restrict our attention to hectads in which the density of raven territories was higher than the mean density in each study area is intended to reduce the risk that information on ravens from some areas contributing to the analysis is incomplete. A consequence of this decision is that areas of genuinely low raven densities where survey effort was high may have been excluded from the analysis. While such a bias would limit the range of variation on which our analysis is based, it would not undermine the validity of this analysis, as the Atlas data with which the SRMS breeding density information was compared were drawn from the same subset of areas.

Other recent estimates of breeding raven numbers in Scotland and the UK vary widely, but can mostly be traced back to two sources. The earliest of these is the *New Atlas of Breeding Birds* (Gibbons *et al.*, 1993), which based its estimate of 7000 pairs for the UK on tetrad counts made during the 1988-1991 Bird Atlas. The Scottish component of this estimate has been placed at 3800 pairs (Park *et al.*, 2005). A slightly later estimate, based largely on expert judgement of breeding numbers and densities in different parts of Scotland, is given by Ratcliffe (1997): a Scotland-specific, much lower figure of 1139 pairs. Ratcliffe (1997) also commented that the earlier estimate was likely to be “wildly optimistic”, pointing to the fact that its authors failed to account for the likelihood that an unknown but potentially large proportion of birds contributing to Atlas survey counts were non-breeders. It is also possible that Ratcliffe’s figure may be too low, however, due to the omission of pairs whose presence was unknown to the raven experts upon whose knowledge the estimate was based (Park *et al.*, 2005; Forrester & Andrews, 2007). If either of these estimates were to be taken at face value to infer the current size of Scotland’s raven population, they would first need to be revised upwards to account for an estimated 40% increase in raven numbers since 1994 (Harris *et al.*, 2016). Updated figures would be 5320 pairs for the estimate based on the Atlas, and 1595 for Ratcliffe’s estimate. The estimate we have produced using SRMS data in conjunction with the most recent Atlas has confidence intervals that coincide closely with the boundaries comprised by these two, disparate estimates. This lends credence to the suggestion that the size of the real breeding population is likely to lie somewhere between these two boundaries. Our central estimate of the population (for Scotland, as well as for the constituent regions) is therefore considered the most reasonable baseline to use in our models.

As discussed in section 4, the majority of recorded raven movements have been relatively local. Nevertheless, immigration and emigration could both play a crucial role in determining how numbers of ravens within any given area vary over time, particularly at smaller scales. For assessing the likely effects of different licencing regimes, however, it is reasonable to assume that the population is effectively closed. If immigration levels were sufficiently high, it is possible that levels of licenced control that our models suggest are unsustainable could be maintained indefinitely. However, a population in such a situation would effectively act as a demographic ‘sink’, making such levels of licenced control unsustainable at the level of the whole population. If, as is likely to be the case, licencing is both operated and assessed at a very localised scale, and levels of licencing vary greatly between regions (see section 8), then movement between areas of different licencing intensities could enable large scale stability across an area comprising smaller scale sources and sinks. However, as discussed above, available data on raven movements suggest that most of these are likely to be at or below the scale of 100 km × 100 km at which our models operate.

7. ANALYSIS OF NON-BREEDING RAVEN NUMBERS

7.1 Background

Most ravens do not breed until the age of three (Ratcliffe, 1997; Hardey *et al.*, 2013) so before they reach this age, they form part of a non-breeding population. However, many authors (e.g. Ratcliffe, 1997, Forrester & Andrews, 2007) have suggested that non-breeding populations typically include birds of breeding age, and that these can (at least in some circumstances) comprise a relatively large proportion of non-breeders. This is in keeping with what is known about peregrines, which have similar breeding dispersion, population stability and (at least up until recently) breeding distribution (Ratcliffe, 1993). Several demographic parameters, including population turnover, age-specific survival and age at first breeding, are better understood for peregrines than for ravens, owing to a recent, long-term study using data from a marked population of breeding peregrines (Smith *et al.*, 2015). This study suggests that, in high density populations, one of the main ways in which population growth is constrained, and peak breeding densities maintained, is through delayed recruitment of reproductively mature birds into the breeding population. In areas with high breeding densities of peregrines, this results in large populations of non-breeders.

Ratcliffe (1997) suggested that the commonly observed phenomenon of rapid re-mating, whereby ravens that lose a partner during the breeding season have been observed to pair up again within a matter of days, implies that (at least in some areas) there must be a surplus of reproductively mature adults without breeding territories. He argues that this surplus is likely to be maintained by the territorial nature of ravens, which can keep densities of territories lower than could theoretically be supported by the available food resources. In the event that licenced control of ravens has an effect that is, in combination with the other existing pressures on raven populations, unsustainable, the size of the non-breeding population is likely to determine how quickly the losses incurred through licencing are translated into a reduction in breeding numbers. It would, therefore, be useful to know the size of non-breeding populations, as it would give regulators an idea of how rapidly populations might be expected to respond to a given level of unsustainable control. There is currently very little information about the size of non-breeding populations, but some large datasets can give us an idea about the occurrence of large flocks, which are thought to be comprised largely of non-breeding birds (Ratcliffe, 1997).

7.2 Methods

The frequency of raven observations with count data submitted to BirdTrack that were pairs or singletons (1-2 birds), small flocks (3-10 birds), moderate flocks (11-50 birds), large flocks (51-100 birds) and very large flocks (>100 birds) was calculated. Bird Atlas timed tetrad data (first hour only, including surveys in both summer and winter) were also summarised in a similar manner. As the group size was not recorded for each observation of ravens, the total number of ravens counted during the first hour of each tetrad was used instead. The frequency of records or surveys including 10 or more ravens in each month was calculated for the whole year for BirdTrack data, and for the months of November to February and April to July for Bird Atlas timed tetrads.

7.3 Results

Observations from both BirdTrack and the Bird Atlas show that, across the whole of Scotland, the vast majority of raven observations relate to small numbers of birds (Figure 7.1). In 98% of 24 428 tetrad surveys in the Atlas where ravens were found, the number of ravens recorded was 10 or fewer. Similarly, out of 22 752 observations of ravens in BirdTrack, 95% are of 10 or fewer individuals. Thus, despite the thoroughly documented propensity for non-breeding ravens to form large flocks, it seems likely that non-breeders spend most of their time in much smaller groups, or even in ones or twos.

Observations of 10 or more ravens were more frequently recorded during winter than during the summer, both in Bird Atlas timed tetrads (Figure 7.2A, $\chi^2 = 54.3$, d.f. = 1, $P < 0.0001$) and in BirdTrack (Figure 7.2B, $\chi^2 = 15.3$, d.f. = 1, $P < 0.0001$).

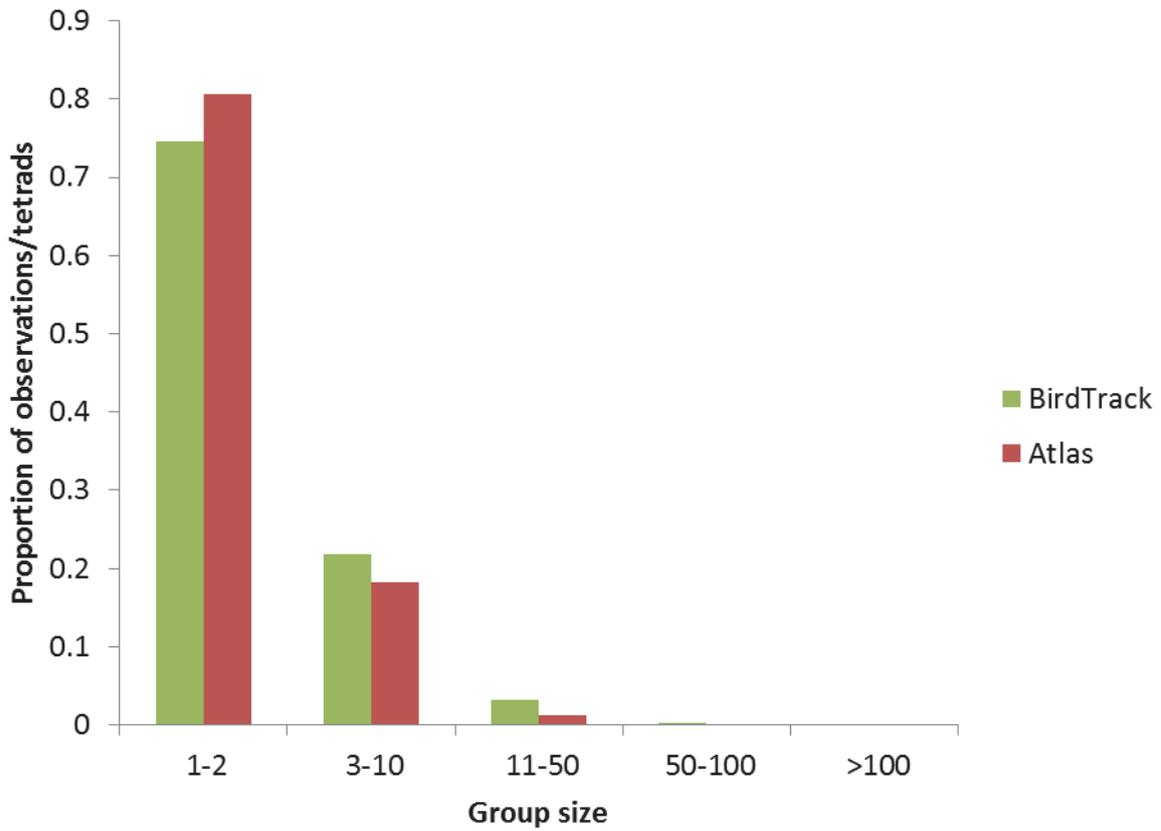
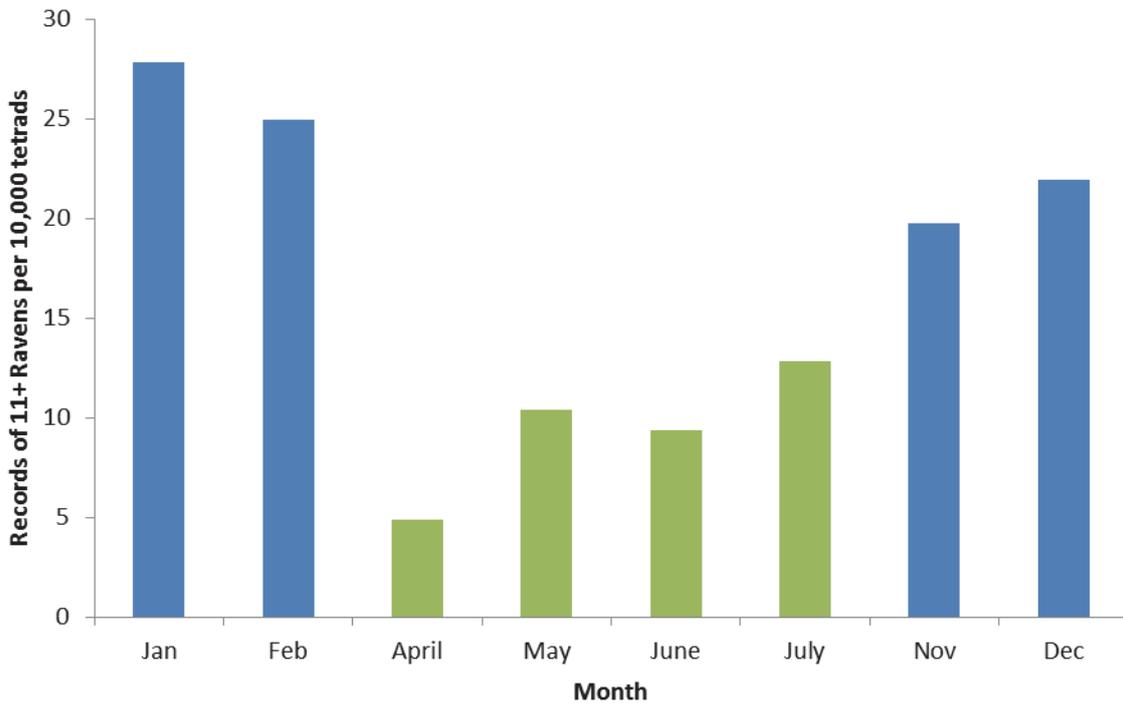


Figure 7.1 The frequency of occurrence of different group sizes for BirdTrack observations and for total numbers seen during timed tetrad Bird Atlas surveys.

A.



B.

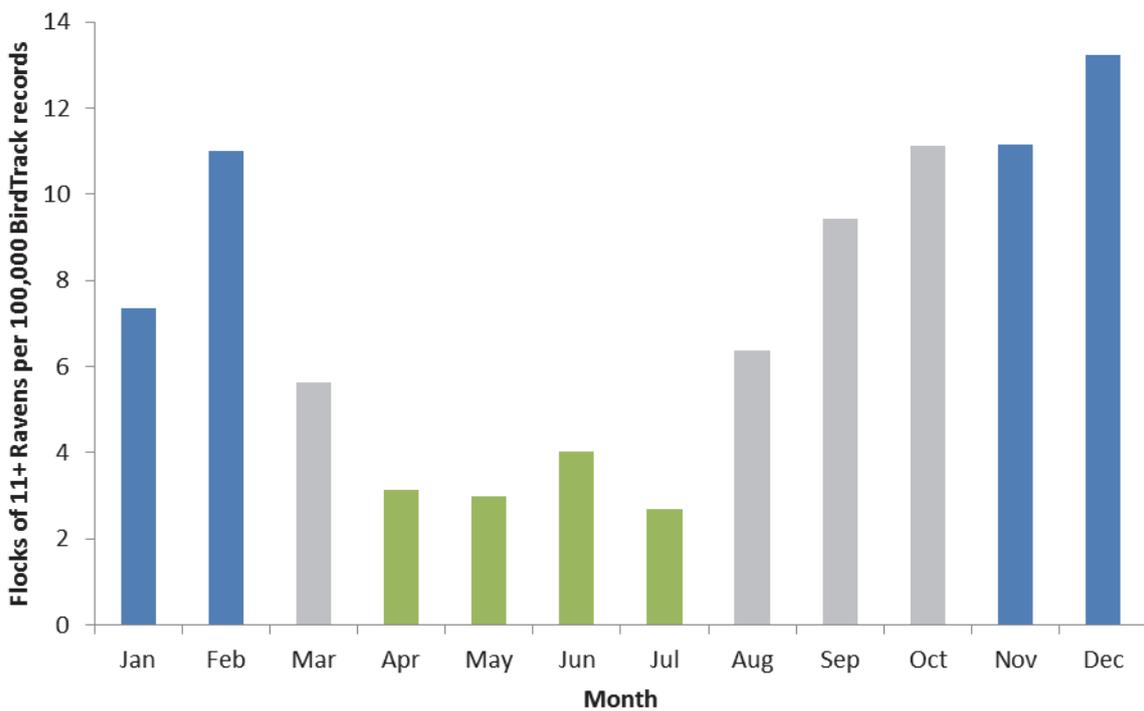


Figure 7.2 Monthly frequency of records with more than ten ravens among A. 182 232 Bird Atlas timed tetrads (number of tetrads per 10 000 with 10 or more ravens recorded) in the 8 months during which these surveys were carried out and B. 4 802 414 BirdTrack records (number of records per 100 000 comprising flocks of more than 10 ravens). Green bars correspond to months during which breeding Bird Atlas surveys were carried out, while blue bars correspond to months during which winter Bird Atlas surveys were carried out.

7.4 Discussion

Large flocks of ravens are thought to comprise mostly non-breeding birds (Ratcliffe, 1997). Moreover, many of these flocks are associated with communal roosts (see below), which are attended almost exclusively by non-breeders; territorial birds invariably return to their territories to roost, even during the winter (Ratcliffe, 1997; Hardey *et al.*, 2013; Mattingley, pers. comm.). Many of the records of large flocks submitted to BirdTrack are accompanied by notes stating that the birds in question were either arriving at, leaving or counted at a roost. Only a few are noted to be flocks of birds foraging together, typically in places where food is available at unusually high levels of abundance, such as at landfill sites. The largest flock sizes recorded were around roosting flocks of around 300 in central Highlands, and 380 on Skye. The limited evidence on raven movements reviewed in section 4 suggests that ravens typically operate within areas of about 10000km² or less. In the absence of any more rigorous information on movements of non-breeding individuals, assuming that these flocks brought birds in from an area with a radius of around 50 km, the size of these flocks imply non-breeding densities of around 5 birds per hectad. However, this figure could be substantially out in either direction, as our assessment of distances travelled by birds in flocks is little better than an educated guess, and we do not know how many non-breeding birds roost outside of these well-known flocks.

Other estimates of non-breeding raven populations are based on similarly imprecise information, typically inferring the numbers of ravens within a large area from maximum counts at communal roosts. Roost counts in four different parts of Argyll range from between 1 and 4 times the number of breeding birds estimated in these areas (ap Reinhallt *et al.*, 2007). Nearby, on the Isle of Islay, Madders & Leckie (1999) estimated that the population of non-breeders (based on counts at a communal roost) varied between 149 and 285 birds, during a period when there were 34 territorial pairs on the island. This would put the ratio of non-breeders to breeders at between 2:1 and 4:1. Other authors (e.g. Ratcliffe, 1997; Forrester & Andrews, 2007) have conservatively estimated that size of non-breeding populations at regional and national scales within Scotland and other parts of the UK is similar to the number of territorial, breeding birds. A recent, large scale study of raven movement and group size in the Austrian Alps, involving 256 non-breeding individuals marked with patagial wing-tags or with GPS tags, estimated that the number of non-breeding individuals using an area of 100 km × 100 km was in the region of “many hundreds if not more than a thousand” birds (Loretto *et al.*, 2017). This could be construed as being equivalent to between 5 and 12 birds per hectad. Assuming similar breeding densities to those found in Scotland, this density of non-breeders would likely be between 1 and 2 times the number of breeders.

As well as the contribution that maximum observed flock sizes can make to our understanding of non-breeding populations, the distribution of observations between flock sizes is also informative. In both surveys, observations of large flock sizes were relatively rare, despite the fact that large flocks would be both more detectable than small numbers of birds (Buckland *et al.*, 2004) and, in the case of BirdTrack, perhaps more likely to be submitted as records. Particularly if non-breeding populations tend to be as large or larger than breeding populations, this implies that non-breeders only spend a small proportion of the time in large flocks, and that many observations of individuals and small groups of birds may well be of non-breeders. This is particularly the case in spring and summer, when the reported occurrence of large flocks is much lower than during the winter.

Both the reality and the perception of raven damage experienced by farmers could be affected by the number of non-breeding ravens around farms. However, the size of the non-breeding population is unlikely to be very important in determining whether (and to what extent) a given level of control would be sustainable. Populations experiencing relatively high levels of population control could be bolstered by immigration of non-breeding ravens

from surrounding areas. However, where maintenance of population size depends on such immigration, the populations in question are sinks, and the levels of control they experience should not be regarded as sustainable. Non-breeders, by definition, do not contribute directly to productivity, and it is the balance of productivity against mortality that determines whether a given level of control is sustainable in the long term without immigration. It is possible that a plentiful supply of non-breeders might contribute to overall productivity levels by allowing losses from the breeding population to be rapidly replaced, so that the impact on breeding output is minimised. However, the robustness of estimates of population size, productivity and survival are all likely to have a much greater influence on our assessments of the impact of different levels of raven population control.

8. EXISTING LEVELS OF LICENCED CONTROL

8.1 Introduction

An assessment of current levels of licenced control, in terms of the number of ravens allowed to be killed under licences issued in the past three years, was carried out to provide useful context in which to discuss the results of the population modelling exercise.

8.2 Methods

Information about licences issued for lethal control of ravens in Scotland was obtained from SNH's Licencing department. This included details of location of the property to which the licence applied, the period during which the licence was valid, the number of ravens allowed to be killed under the terms of the licence, and the licence return (i.e. the number of ravens reported to be killed as a result of the licenced activities).

8.3 Results

Over the three years examined, numbers of licences issued were broadly similar, with 136 licences issued in 2014, 151 in 2015 and 149 in 2016 (Table 8.1). The timing and duration of these licences varied widely, with a typical licence being issued at the start of April and running for three months until the end of June or start of July. The majority of licences issued were for 5 or fewer individual ravens, but a small proportion (10.5%) of licences were for 10 – 20 birds (Figure 8.1). Less than 1% of licences allowed more than 25 birds to be killed, and the highest number of birds allowed to be killed by a single licence was 50. Multiple licences were sometimes issued for a single property in the same year, but the total number of birds licenced for killing never exceeded 50.

The actual number of ravens taken under a licence is often less than the number permitted by the licence. Returns for 2016 indicate that the number of ravens killed was at least 62% (the proportion of allowed take confirmed by licence returns) but no more than 75% (the confirmed take plus the number of ravens allowed to be taken under licences for which no return was received) of the maximum number stipulated on these licences (SNH unpublished data).

The distribution of licenced raven control across Scotland is far from even (Figure 8.2). In most parts of Scotland, licences have allowed an average of less than 1 bird per hectad to be removed each year. However, in three areas in the west of Scotland (NB, NF/NL, and NR) licenced control has permitted an annual take of more than 4 individuals per hectad of land. In one of these areas (NF/NL, corresponding to Uist and Barra), the permitted annual take of ravens has been at an intensity of more than 14.6 per hectad, almost twice as high as in any other square. Variation in average productivity of breeding pairs at the 100km scale (Figure 5.2) was not significantly correlated with variation in licence intensity, whether expressed as (logged) number of ravens permitted to be killed per 100km² of land (Pearson's $r = -0.29$, d.f. = 13, $P = 0.29$), or as (logged) number of ravens permitted to be killed per breeding pair (Pearson's $r = -0.35$, d.f. = 13, $P = 0.20$).

Table 8.1 The total number of individual licences issued for lethal control of ravens in Scotland, and the number of ravens permitted to be killed under the terms of these licences.

All licences	Year		
	2014	2015	2016
Number of licences issued	136	151	149
Ravens licenced to be killed	907	889	901

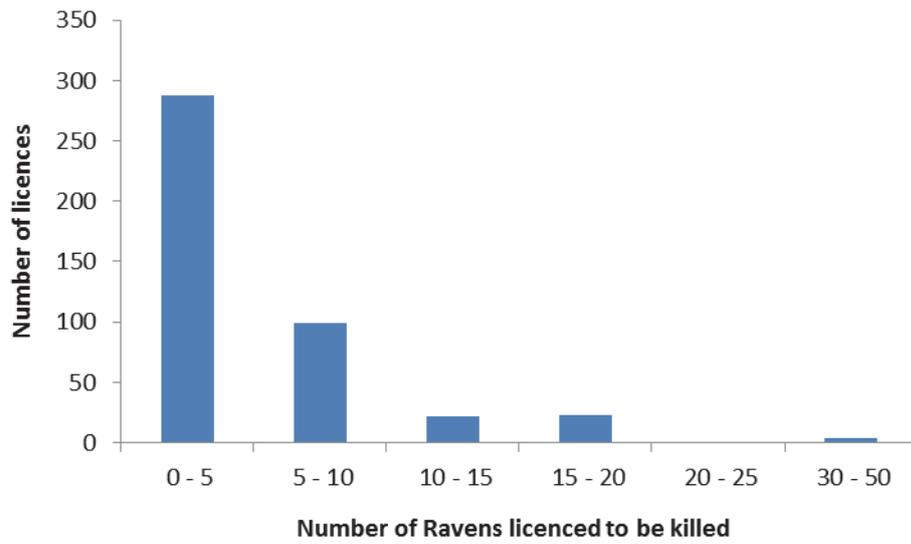


Figure 8.1 Distribution of licences issued for control of ravens between 2014 and 2016 across different levels of control (in terms of numbers of ravens permitted to be taken under the terms of the licence).

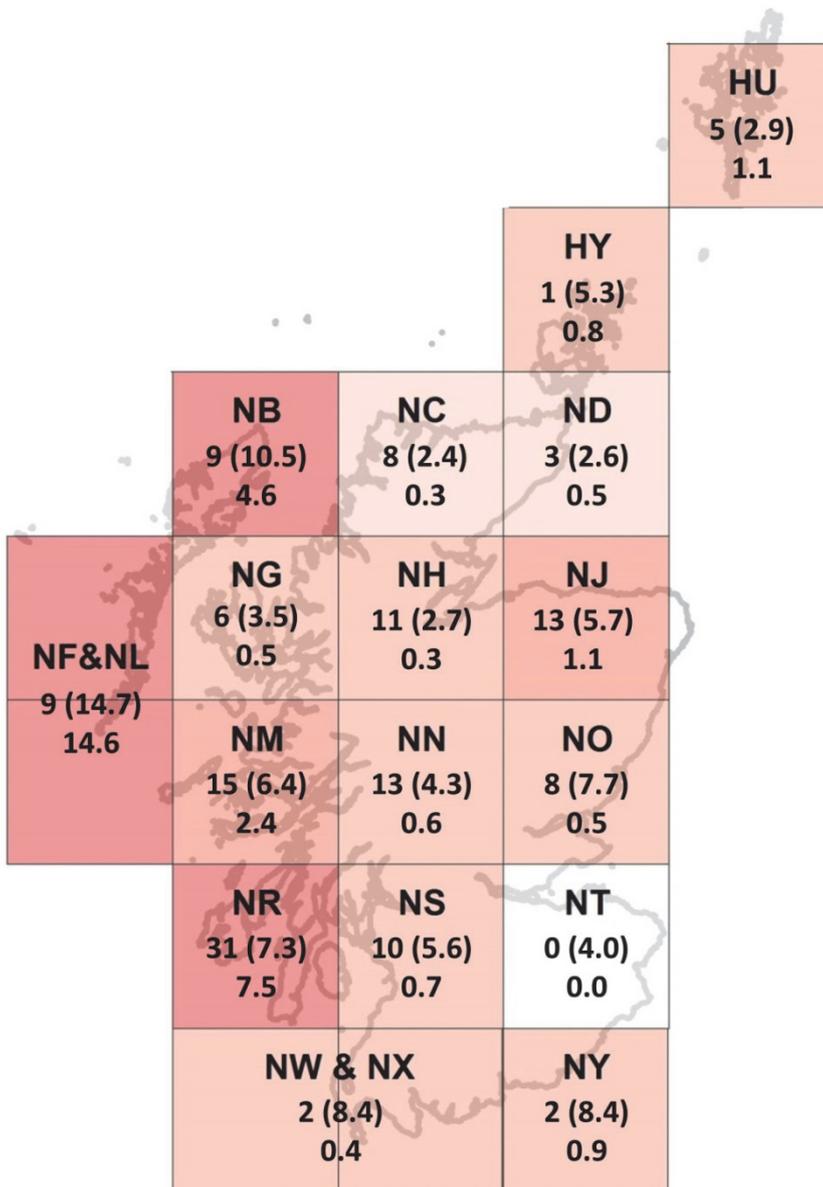


Figure 8.2 Map of Scotland showing 100 km grid squares, shaded according to the intensity of raven control licenced in each square over the past 3 years. The numbers in each square are the average number of licences issued per year, followed in parentheses by the average number of ravens allowed to be killed under each licence. The final figure below these first two numbers is the overall density of licenced control expressed as the average number of individual ravens allowed to be killed annually per hectad of land. For example, the area of land within square NJ is 65.9 hectads, and the average number of ravens allowed to be killed annually under the licences issued within this square is 74, so the intensity of control in this square is $74/65.8 = 1.1$ ravens per hectad. Because they contain less than 1 hectad of land, statistics for licences for NL and NW are combined with neighbouring squares NF and NX, respectively.

8.4 Discussion

Uncertainty about the proportion of ravens allowed to be killed under licence that are actually killed arises from a small proportion of licences for which no return information (stating how many ravens were killed under that licence) is received. However, because licences are typically not granted at properties where returns are outstanding for previous licences, any licence applicants who are keen to control ravens in the long-term have a strong motivation to submit a return. It therefore seems likely that of licences for which returns have not yet been received, a large number would have been nil returns. This would bring the actual proportion of Ravens killed closer to the lower end of the observed range (62%) than the upper end (72%).

Even if licenced takes in all years were at the very upper limits of our uncertainty, levels of licenced control across most of Scotland are relatively low. Assuming breeding densities of around 5 pairs per hectad (similar to those in much of Scotland where raven densities seem relatively stable), and productivity of 2.35 young per breeding pair, levels of control in most 100 km squares are approximately equivalent to between 1% and 10% of annual productivity. However, in a few areas such as the Western Isles and in parts of western Argyll, levels of control are much higher. In some parts of north-east Scotland where the density of licenced raven control is comparable to (or lower than) those in most other parts of the country, it is possible that population densities are too low to sustain these levels of control (Figure 6.2). The population models in the following section explore whether, and in what circumstances, observed levels of licenced control are likely to be sustainable.

9. POPULATION SCENARIOS AND SENSITIVITY ANALYSES

9.1 Background

Population models are widely used tools in wildlife management, both for the conservation of threatened species and for the control of pest species (Akçakaya & Sjögren-Gulve, 2000; Smith *et al.*, 2008; Beissinger & Westphal, 1998). We use Leslie Matrix Models (Caswell, 1978) in order to investigate the extent to which different licensing scenarios may negatively affect local raven populations.

9.1.1 Demographic data

Survival: As described above, analysis of ringing data suggested that the survival rate of adult ravens in 2012 was 0.817 (95% CIs 0.780 – 0.849). Survival rates have increased through time, however, and over the past 20 years have averaged 0.784. The models did not suggest an age-class effect with no clear differences between the survival rates of adult and immature birds. The values from this analysis were consistent with those obtained from another study in the US (Webb *et al.*, 2004) which estimated survival rates of 0.81 for second year birds and 0.83 for third year birds. The latter study also estimated a mean annual survival rate of 0.5 for first year birds, but noted that this was strongly influenced by both proximity of the nest to an anthropogenic food source (nests closer to anthropogenic food sources had higher survival rates) and by when they fledged (early fledging birds had higher survival rates). As an alternative, the study offers a survival rate of 0.28 over the first 33 months (~3 years). This is also consistent with the data presented in Ratcliffe (1997).

Productivity: As described above, productivity data were available from across Scotland for 2003-2015. Over this period, productivity averaged 2.35 chicks nest⁻¹ (range 1.98 – 3.33).

Dispersal: Analyses of ringing data suggest that post-natal dispersal is likely to be modest (most recoveries within 50 km of natal site). Whilst large roosting flocks may contain individuals drawn from a greater distance, without robust data on the numbers of non-breeding birds within a population, this is hard to quantify. Consequently, for simplicity, we consider populations to be closed. The influence of immigration or emigration on the population concerned may be thought of as equivalent to changes in survival whereby emigration reflects a loss of birds from the breeding population and immigration reflects an increase of birds in the population.

Population Size: Based on the analysis of dispersal distances described above, we consider local “populations” of ravens inhabiting areas of 100 km × 100 km. Extrapolation of atlas abundance information suggests that regional breeding densities vary between roughly 2 and 6 pairs per hectad. In western Scotland, where breeding raven populations may be close to carrying capacity, average densities of breeding ravens have been estimated at around 5 pairs per hectad. In eastern Scotland, where raven numbers are thought to be lower than could be supported by these areas, the density of breeding ravens is approximately 2 pairs per hectad, with the lowest density estimated for any 100km square being 1.3 pairs per hectad.

Population Trajectory: Whilst not used in the models themselves, information about the trajectory of the populations concerned is used in order to provide a sense-check and test whether the models are producing realistic results. Data from the latest BBS report (Harris *et al.*, 2016) suggest that between 1995 and 2014, raven populations in Scotland increased by 41%, reflecting an annual growth rate of 1.02. More fine-scale assessments of raven population trends (Sim *et al.*, 2005) found annual growth rates of 1.18 for North East Scotland, 0.975 for the East Flows and 0.991 for Lewis and Harris. However, note that these figures came from upland habitats only and may not be reflective of populations as a whole.

9.2 Population models

Based on the demographic data described above, we considered five scenarios using different combinations of parameters within a Leslie Matrix Model framework. For the first, baseline scenario, we considered the 2012 estimate for adult and immature survival rate of 0.8 obtained from the analysis above, the juvenile survival rate of 0.5 proposed by Webb *et al.* (2004) and the mean productivity rate of 2.35 from the Raptor Monitoring Scheme data. For the second scenario, we used the same values for survival, but reduced productivity to 1.98, the lowest value identified in the raptor monitoring scheme data. For the third scenario, we again considered a productivity rate of 1.98 and a juvenile survival rate of 0.5, but used an adult and immature survival rate of 0.78, reflecting the mean value identified from the analysis of 20 years ringing data described above. For the fourth scenario, we kept the same values for productivity, adult and immature survival but considered a reduced juvenile survival of 0.35. For the fifth scenario, we considered the same values for the survival rates and the mean productivity rate of 2.35. As described above, for the purposes of this analysis, we consider the populations to be closed with no immigration or emigration. The parameters used in all six scenarios are given in Table 9.1.

Table 9.1 Demographic parameters used for six different raven population modelling scenarios. The parameters outlined in red (i.e. from the baseline and low recruit scenarios) are the ones used in the density dependent and capped number of breeders scenarios described below.

	(1) Baseline	(2) Min P	(3) 20 Yr Mean A_s	(4) Low Recruit	(5) Low S_j Mean P
Adult Survival (A_s)	0.8	0.8	0.78	0.78	0.78
Immature Survival (A_i)	0.8	0.8	0.78	0.78	0.78
Juvenile Survival (A_j)	0.5	0.5	0.5	0.35	0.35
Productivity* (P)	2.35	1.98	1.98	1.98	2.35
Growth Rate	1.11	1.07	1.05	0.99	1.02

9.3 Model Structure

The following provides a step by step explanation of how the Leslie Matrix Models were constructed and developed, starting with a basic model with no density dependent regulation and then considering two different mechanisms for regulating numbers of ravens.

9.3.1 Basic model

Starting populations are assumed to contain 1200 breeding birds – equivalent to a breeding density of 6 pairs per hectad within an area of 100 hectads. The population is divided between four different sub-groups: adults (all birds aged 3 years or older), 2 year old birds, 1 year old birds and juveniles. Survival rates differ between these groups as indicated in Table 9.1, with different values for survival of adults (A_s), one and two year old birds (A_i) and juveniles (A_j). In each year of the model, numbers in each of these groups are calculated as follows:

Adults: the sum of two different numbers:

- The number of adults in the previous year multiplied by adult survival A_s
- The number of two year olds in the previous year multiplied by immature survival A_i

Two year olds: the number of one year olds in the previous year multiplied by immature survival A_i

One year olds: the number of juveniles in the previous year multiplied by juvenile survival rate A_j

Juveniles: the number of breeding pairs in the current year (number of adults divided by two) multiplied by the productivity P .

For each iteration (year) of the model, the sequence of events is as follows:

1. Calculate the number of immatures and adults by applying survival rates to cohorts in the previous generation, as described above.
2. Assess population size (before calculating the number of juveniles produced) – this is the number of birds present in the population immediately before breeding.
3. Calculate the number of juveniles by applying the rate of productivity to the number of breeding pairs, as described above.

9.3.2 *Density dependence model*

Under the assumptions of the basic model, growing populations will continue to increase indefinitely and exponentially. In reality, however, population levels of wild birds are constrained by various factors. One such mechanism of constraint is density dependence, operating through a negative relationship between population size and overall growth rate. This relationship is described in greater detail below.

Each iteration of the density dependent model follows the same three steps as outlined for the basic model. However, in each year, survival rates (of all age classes) are modified by density dependence, here assumed to affect survival exclusively. The degree to which survival is affected depends on population size – the larger the population, the lower the survival rates. One plausible mechanism through which such density dependence could operate is food availability, whether all year round or, perhaps more likely, during one or more ‘bottlenecks’. In either case, it makes sense that survival when population size is large (and the average amount of food available to each individual is lower) should be lower than when population size is small (and there is plenty of food to go around). In order to achieve realistic survival rates and densities of breeding adults when the population is stable, maximum allowable survival rates must be higher than those observed in the real populations on which models are based.

9.3.3 *Capped number of breeders model or threshold density dependence*

Under the basic and density dependent models described above, all adults aged 3 or more years contribute to breeding output. However, our knowledge about raven populations suggests that a significant number of adults may not breed. As described in section 7, this could be caused by the territorial nature of breeding ravens, which may limit breeding densities to lower levels than would be permitted either by food resources or by suitable nest sites. An alternative means of constraining modelled population growth, which is consistent with a population including non-breeding adults, and a breeding population limited by territoriality, involves the number of breeders being capped at a realistic density, such as those reported in section 6). If there are more adults than this, the excess adults are non-breeding, and do not contribute to annual productivity. This effectively caps annual productivity, and stabilises the population at a level where the number of individuals lost to annual mortality (of all cohorts) is equal to the number of young produced each year.

The cap on breeders model follows the same three steps as the basic model, but with two separate groups of adults. The number of breeding adults is equal to the cap on breeders or to the total number of adults, whichever is smaller. If the number of adults is greater than the number of breeders, the difference is the number of non-breeding adults. In the absence of any differences in survival rates between breeding and non-breeding adults, the only consequence of this split is the limiting effect it has on productivity. However, in models which incorporate an element of licenced control, the distinction between breeders and non-breeders can have implications for the age distribution of birds killed under licence in scenarios where licenced control is restricted to non-breeders.

9.4 Population growth rates under different scenarios

When applied to a basic (density independent) model, the scenarios listed in Table 9.1 result in population growth rates of between 0.99 and 1.11. Based on the spatial variation in productivity and survival described in the previous sections, the first of these scenarios is a reasonable approximation of the likely growth rates of raven populations in many parts of Scotland (including both east and west coasts) in the absence of regulation by density dependent process. We refer to this as the Baseline model. The fourth scenario reflects the trajectory of a population with survival and productivity at the lower end of what might be observed in Scotland (e.g. adult survival equal to a 20 year average rather than the higher values observed in more recent years; juvenile survival reduced to the lower end of values described for ravens or other corvids; and productivity similar to the region with lowest productivity, namely South-west Scotland). We refer to this scenario as the 'Low Recruitment' model. We explore how the two mechanisms for achieving density dependence described above, as well as different intensities of lethal control, influence population growth for both the 'Baseline' and 'Low Recruitment' models.

9.4.1 Density dependence

The exponential growth observed in the basic model, with baseline parameters, is clearly unrealistic. Consequently, we introduced density dependent regulation of adult survival, considered likely by Ratcliffe (1997). We used a Weibull function (Equation 1) to describe the relationship between population size and adult/immature and juvenile survival (Figure 9.2).

$$S_t = S_{max} \times \exp(-a \times N_{t-1}^b) \quad \text{Equation 1}$$

S is the adult survival rate, **S_{max}** is the biologically plausible maximum value for this parameter, informed by a review of the literature, **N** is the population size, **b** is a shape parameter informed by modelling a range of plausible values and **a** is a scale parameter derived with respect to the shape parameter for known values of **S**. A value of two was selected as a plausible estimate for the shape parameter, **b**. Equation 1 was then rearranged and values of **a** were estimated for adult/immature survival and juvenile survival using estimates of survival and population size at equilibrium. Following this approach, for adult/immature survival **a** was estimated (by visually assessing plots of survival rate against population size) at 4.21×10^{-8} , and for juvenile survival it was estimated at 2.33×10^{-7} .

The density dependent relationship (Figure 9.2) means that, as population size increases, survival rates drop gradually from their maximum values (0.85 for adults/immatures, 0.7 for juveniles) as the population reaches equilibrium (1200 birds). As the population size increases beyond the equilibrium, survival rates drop further, causing the population to return to its size at equilibrium.

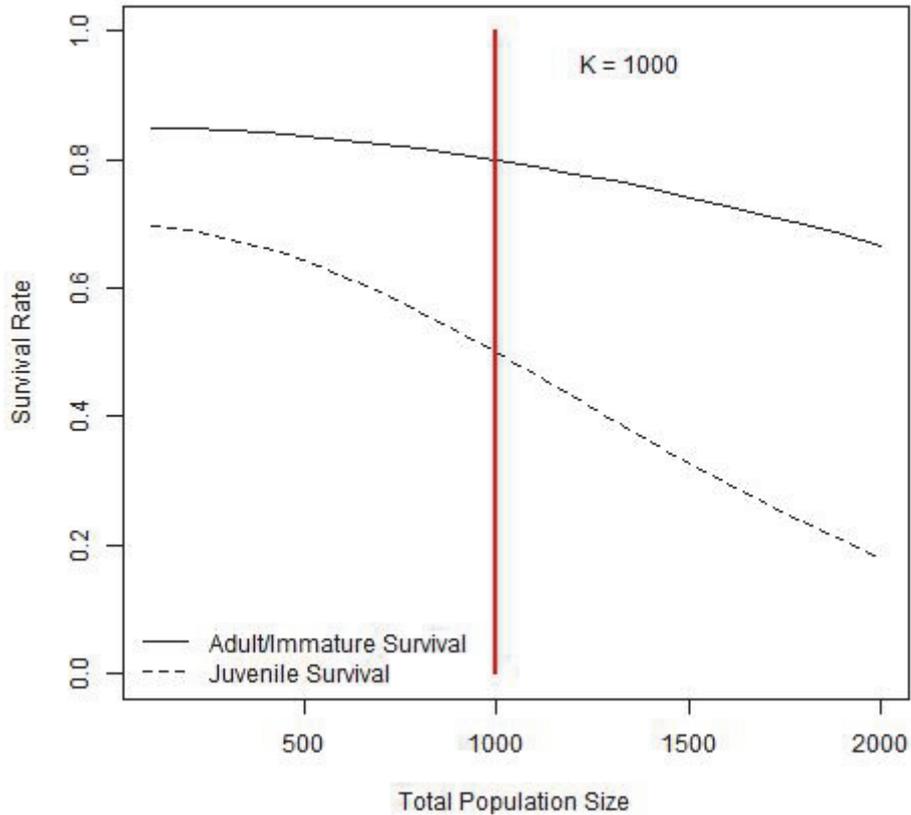


Figure 9.1 Density dependent relationship between population size and adult/immature and juvenile survival rates for ravens.

By introducing density dependence into the models, both the baseline and low recruitment populations remain relatively stable over the 50 years, although the low recruitment population stabilizes at a lower level than the baseline population (Figure 9.3). In these first two models (the basic, density independent model, and the density dependent model), all adult birds are assumed to breed.

9.4.2 Capped number of breeders

As an alternative means of regulating numbers, we considered a cap on the number of breeding adults in the population. Based on previous estimates of population size, we set the cap as 6 breeding pairs per 100 km². Above this level, any additional adult birds enter the non-breeding population, only breeding when vacant territories become available. These models result in the number of breeding adults in the baseline population remaining stable, while the number of breeders in the low recruitment population undergoes a slight decline over the 50 years (Fig. 9.4).

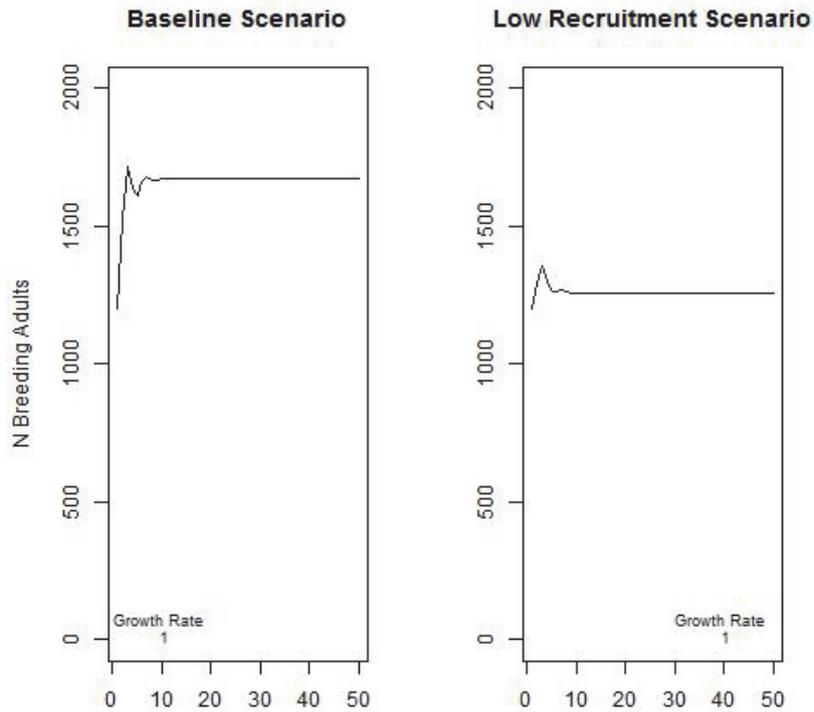


Figure 9.2 Trajectories of Low Recruitment and Baseline populations assuming density dependent regulation of adult survival.

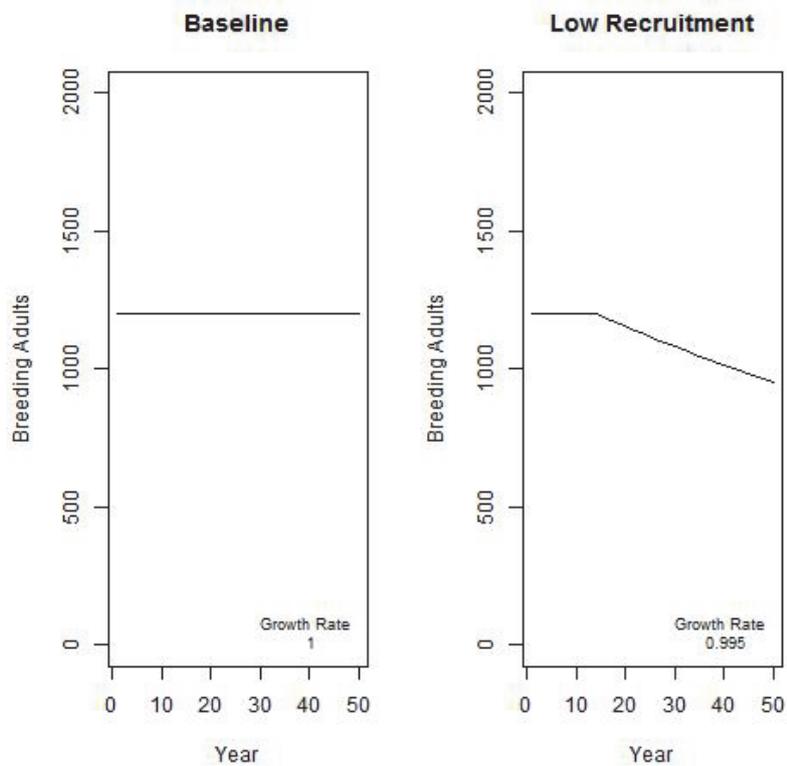


Figure 9.3 Trajectories of Low Recruitment and Baseline populations assuming a cap in the density of breeding adults of 6 pairs per hectad.

9.5 Impact of licenced control

We investigated the impact of licensed control of non-breeders, starting with populations with a stable structure, in the following scenarios:

- Baseline parameters with density dependent survival
- Low Recruitment with density dependent survival
- Baseline parameters with a cap on the number of breeders
- Baseline parameters with a cap on the number of breeders:
 - Basic baseline scenario
 - Control extended to all adults and immatures
 - Expanding (low density) population

Exploration of how control affects raven population trajectories in each of these scenarios helps to illustrate how different understanding and assumptions about the population concerned may influence conclusions about the impact of different levels of licensed control. Ultimately, this will enable us to identify priority knowledge gaps that should be filled in order to reduce levels of modelling uncertainty and thus the level of risk associated with different levels of licensed control.

The effect of lethal control as an abstract concept would be most straightforwardly investigated by scaling levels of control as a proportion of the remaining population (e.g. contrasting scenarios where 0, 5%, 10% etc. of the population was removed each year). In practice, however, implementation of such control would involve monitoring the absolute numbers of ravens in the areas where such limits were being applied (in order to know how many ravens to remove to achieve a given percentage take). Also, importantly, in scenarios where control is intended to be restricted to particular age or breeding categories, such an approach would also require regular assessment of the number of birds within the relevant age categories. Given the current limits of our knowledge of raven numbers and population structure, it is unlikely that such an approach to regulation would be feasible. A more realistic approach to determining the overall take of non-breeding ravens allowed each year is to set an absolute number that is allowed to be taken each year. We consider different levels of licensed control from 0 to 500 individuals per annum. For each model, we present results showing the changes in the number of breeding pairs and non-breeding birds over the 50 year time period considered by these models.

9.5.1 *Density dependence*

In the absence of density dependent processes, the maximum sustainable level of control for the Baseline population was 240 birds per year. Under the Low Recruitment scenario, any level of control resulted in a steepened decline in population size. More details are available in the Annex, in Figures 6.i.1 & 6.i.2.

As expected, incorporating density dependence into the models stabilised the rapidly expanding Baseline population and offset the impact of licensed control on the Low Recruitment population. Under this scenario, the Baseline population was able to sustain the loss of up to 350 non-breeding birds whilst remaining stable (Figure 9.5). The Low Recruitment population was able to remain stable with up to 200 non-breeding birds removed (Figure 9.6). In both cases, similar patterns were repeated for both the breeding and non-breeding birds. However, it should be noted that populations stabilised at different levels depending on the level of control applied.

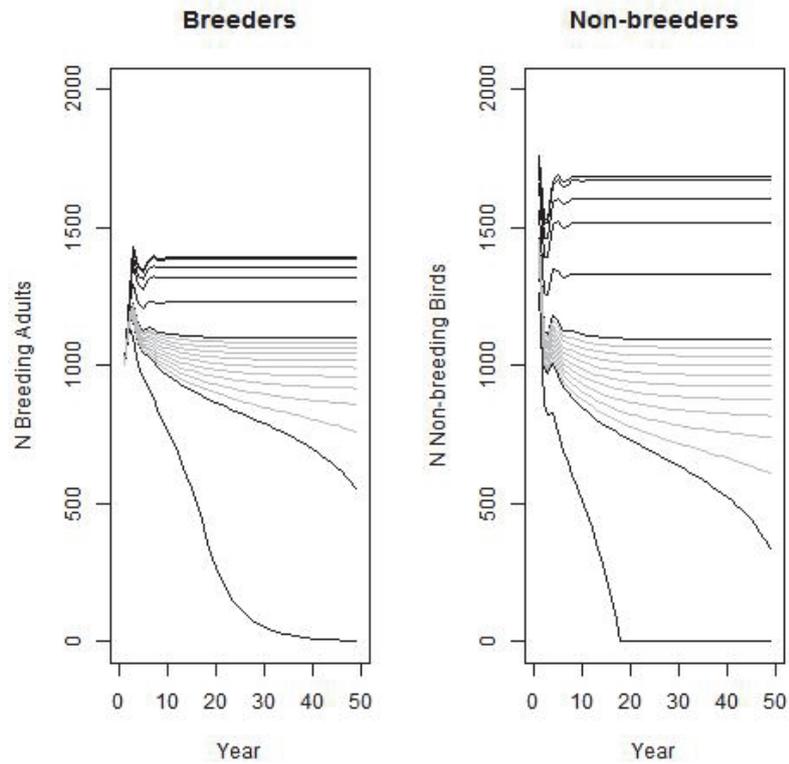


Figure 9.4 Impact of licensed control on the Baseline population, assuming density dependent regulation of survival and that all adult birds breed. From top to bottom, black lines reflect licensed control scenarios of 0, 10, 50, 100, 200, 300, 400 & 500 non-breeding birds removed from the population and grey lines, used to refine estimates on the number of birds that can be sustainably taken, indicate 310, 320, 330, 340, 350, 360, 370, 380 and 390 non-breeding birds removed.

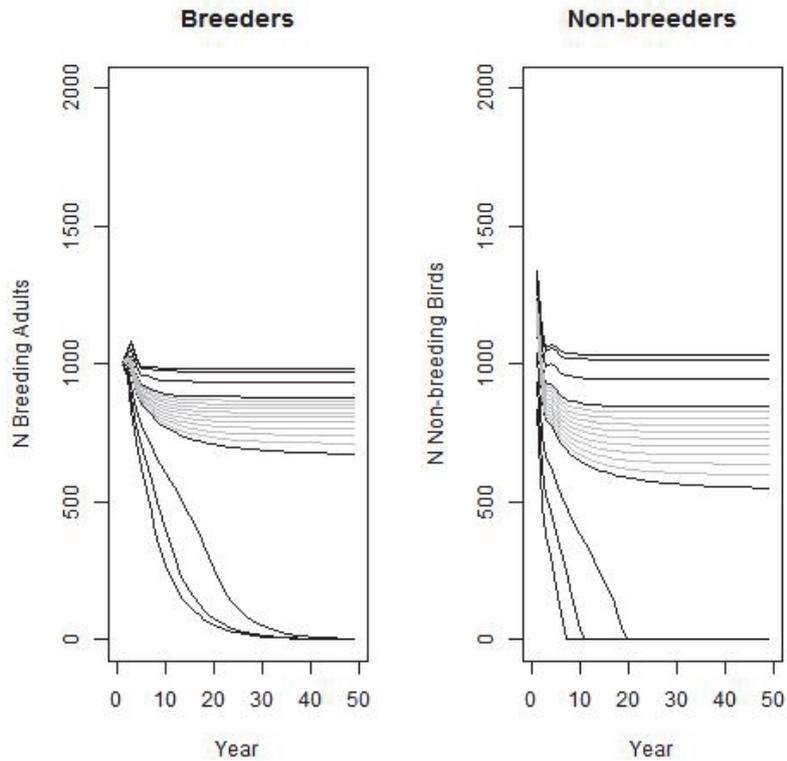


Figure 9.5 Impact of licensed control on the Low Recruitment population, assuming density dependent regulation of adult survival and that all adult birds breed. From top to bottom, black lines reflect licensed control scenarios of 0, 10, 50, 100, 200, 300, 400 & 500 non-breeding birds removed from the population and grey lines, used to refine estimates on the number of birds that can be sustainably taken, indicate 110, 120, 130, 140, 150, 160, 170, 180 and 190 non-breeding birds removed.

9.5.2 Capped number of breeders scenario 1: Baseline scenario

In contrast to the two previous models, this scenario applies a cap on the number of breeding adults in the population and allows any remaining adults to enter the non-breeding population. When territories become available, these birds are then able to enter the breeding population. As with the first model, there are clear differences in how the Baseline and Low Recruitment populations respond to licensed control in this scenario. The Baseline population is maintained at the level of the breeding cap with up to 410 non-breeding birds removed from the population and the number of non-breeding birds in the population stabilised. However, at this level of licensed control, all adults formed part of the breeding population (Figure 9.7). In the Low Recruitment scenario (Figure 9.8), any level of licensed control resulted in an acceleration of the population decline and with 100, or more, non-breeding birds removed from the population it went extinct over the 50 years.

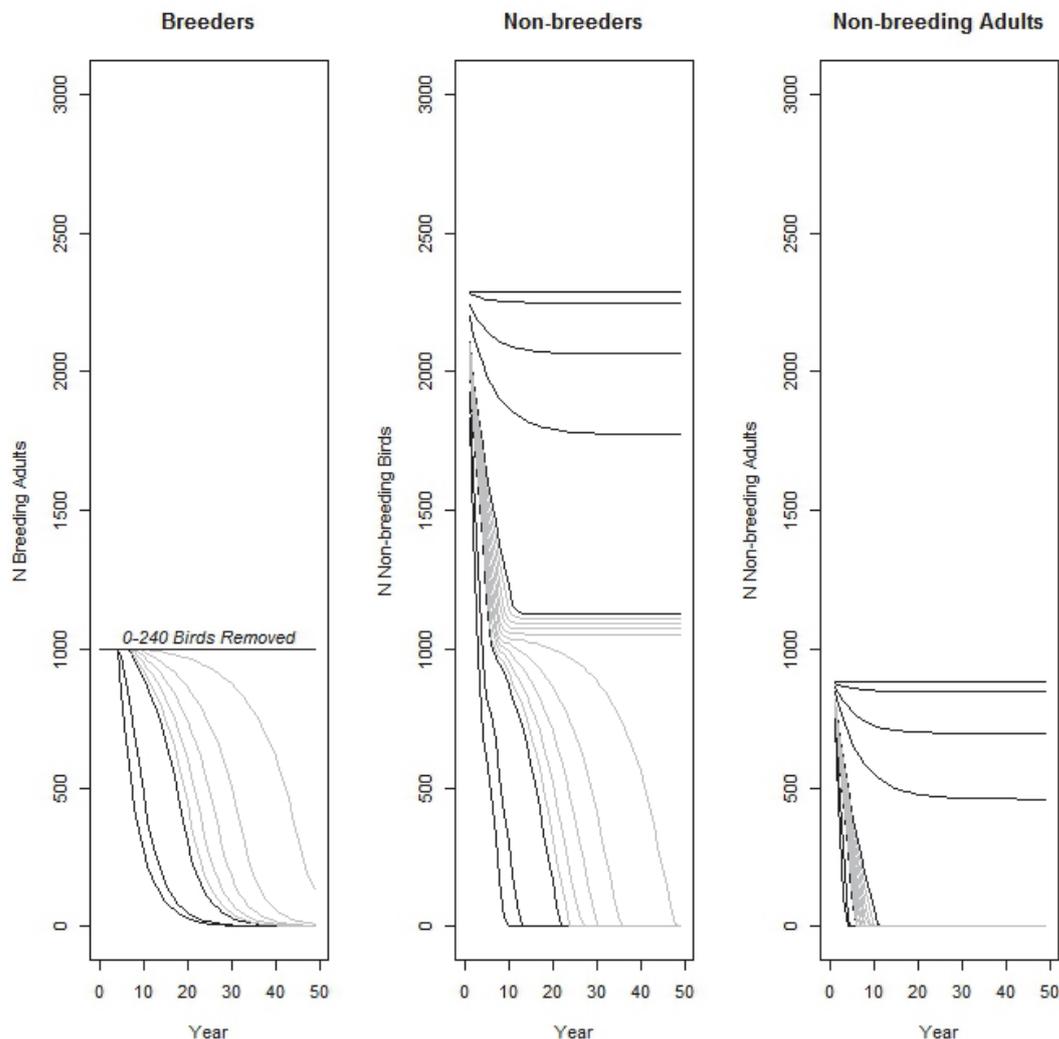


Figure 9.6 Impact of licensed control on the Baseline population, assuming a cap on the number of breeding pairs and that any additional adult birds are part of the non-breeding population. From top to bottom, black lines reflect licensed control scenarios of 0, 10, 50, 100, 200, 300, 400 & 500 non-breeding birds removed from the population and grey lines, used to refine estimates on the number of birds that can be sustainably taken, indicate 210, 210, 230, 240, 250, 260, 270, 280 and 290 non-breeding birds removed. Note, in the graph showing responses in the numbers of breeding adults, the black lines for control scenarios of 10, 50, 100 and 200 birds and the grey lines for scenarios of 210, 220, 230 and 240 birds are not individually discernible from the black line for 0 birds.

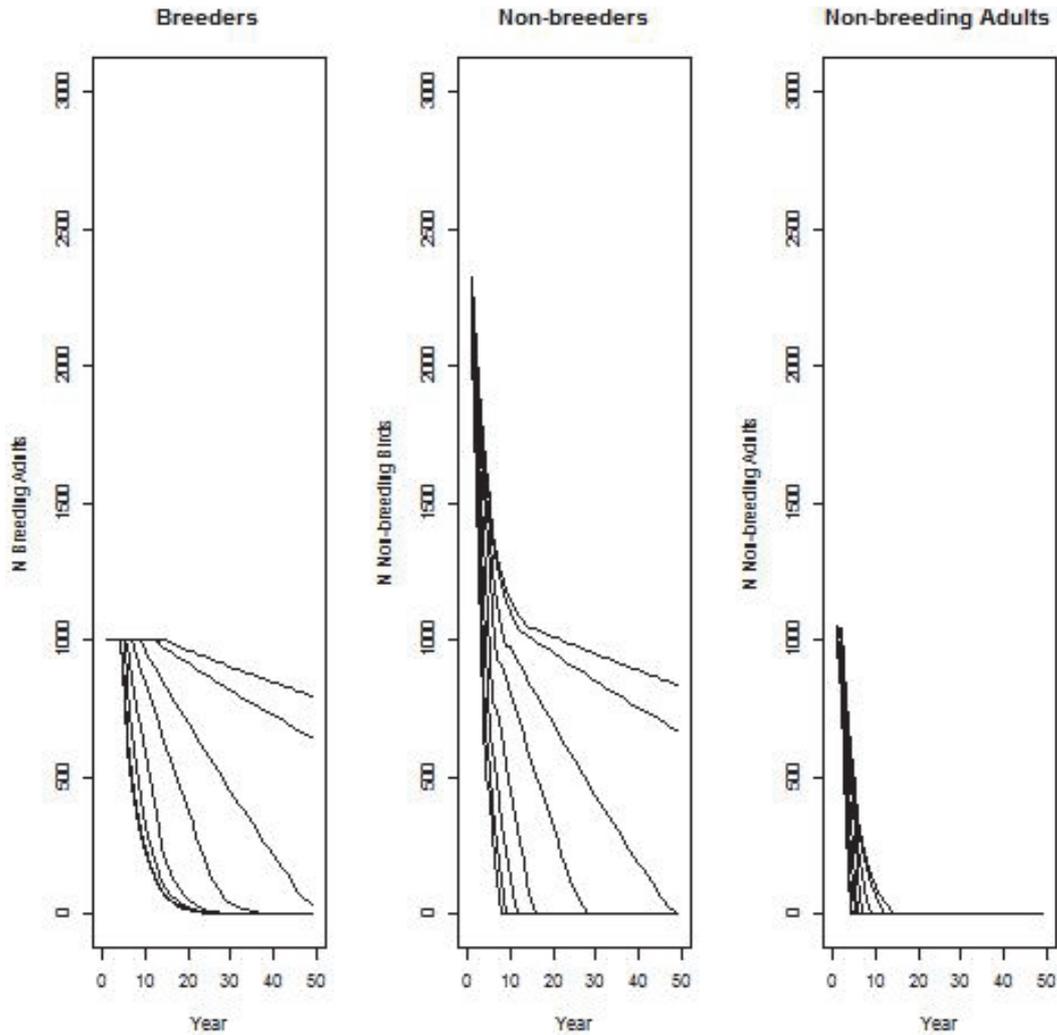


Figure 9.7 Impact of licensed control on the Low Recruitment population, assuming a cap on the number of breeding pairs and that any additional adult birds are part of the non-breeding population. From top to bottom, black lines reflect licensed control scenarios of 0, 10, 50, 100, 200, 300, 400 & 500 non-breeding birds removed from the population.

9.5.3 Capped number of breeders scenario 2: Expanding population

Populations may respond to licensed control differently when they are expanding than when they are at equilibrium. For this reason, we consider a scenario in which a population with the demographic characteristics of the baseline population is still expanding towards its carrying capacity, set by the cap on breeding numbers. In order to understand how population control might affect ravens at densities similar to the lowest we have estimated for Scotland, our starting population is 130 pairs in the 100 km square, which is equivalent to the density estimated for square NJ, in the north-east of Scotland. Under this scenario, the population is able to sustain a substantially lower level of licensed control than is the case when the population is at equilibrium (Figure 9.9). Under this scenario, the population grows to a stable state over 50 years with up to 50 non-breeding birds subject to licensed control, but declines to extinction at levels of control of 60 birds or higher.

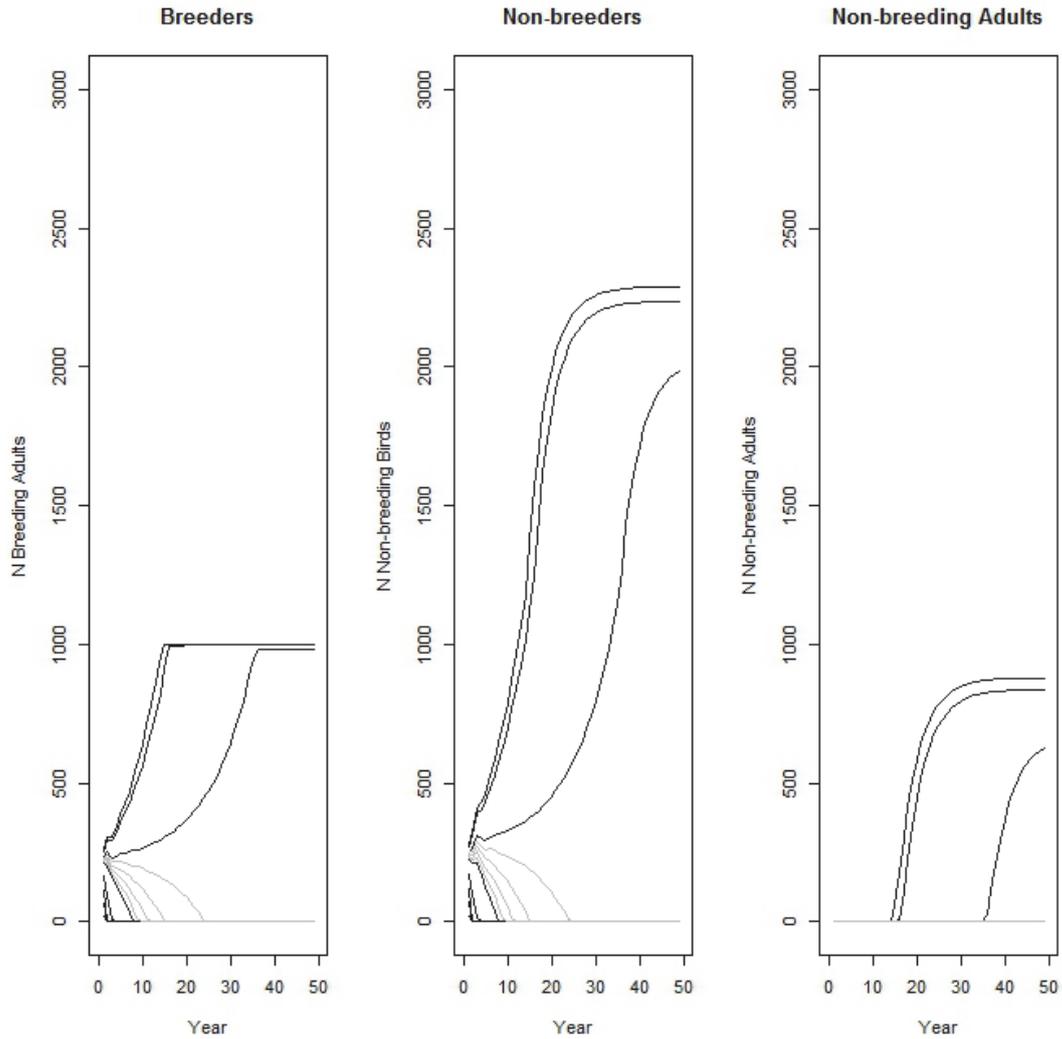


Figure 9.8 Impact of licensed control on an expanding Baseline population, assuming a cap on the number of breeding pairs and that any additional adult birds are part of the non-breeding population. From top to bottom, black lines reflect licensed control scenarios of 0, 10, 50, 100, 200 & 300 non-breeding birds removed from the population. Grey lines, used to refine estimates of the number of birds that can be sustainably taken, indicate 60, 70, 80, & 90 non-breeding birds removed.

9.5.4 Capped number of breeders scenario 3: Breeding adults subject to licenced control

It may be difficult to distinguish between breeding and non-breeding birds, particularly adults. In these circumstances, licensed control may inadvertently get applied to breeding birds. It is important to understand the population level consequences of these errors. As may be expected, for the Baseline population the level of licensed control that can be sustained by the population decreases from 240 (Figure 9.7) to 190 (Figure 9.10).

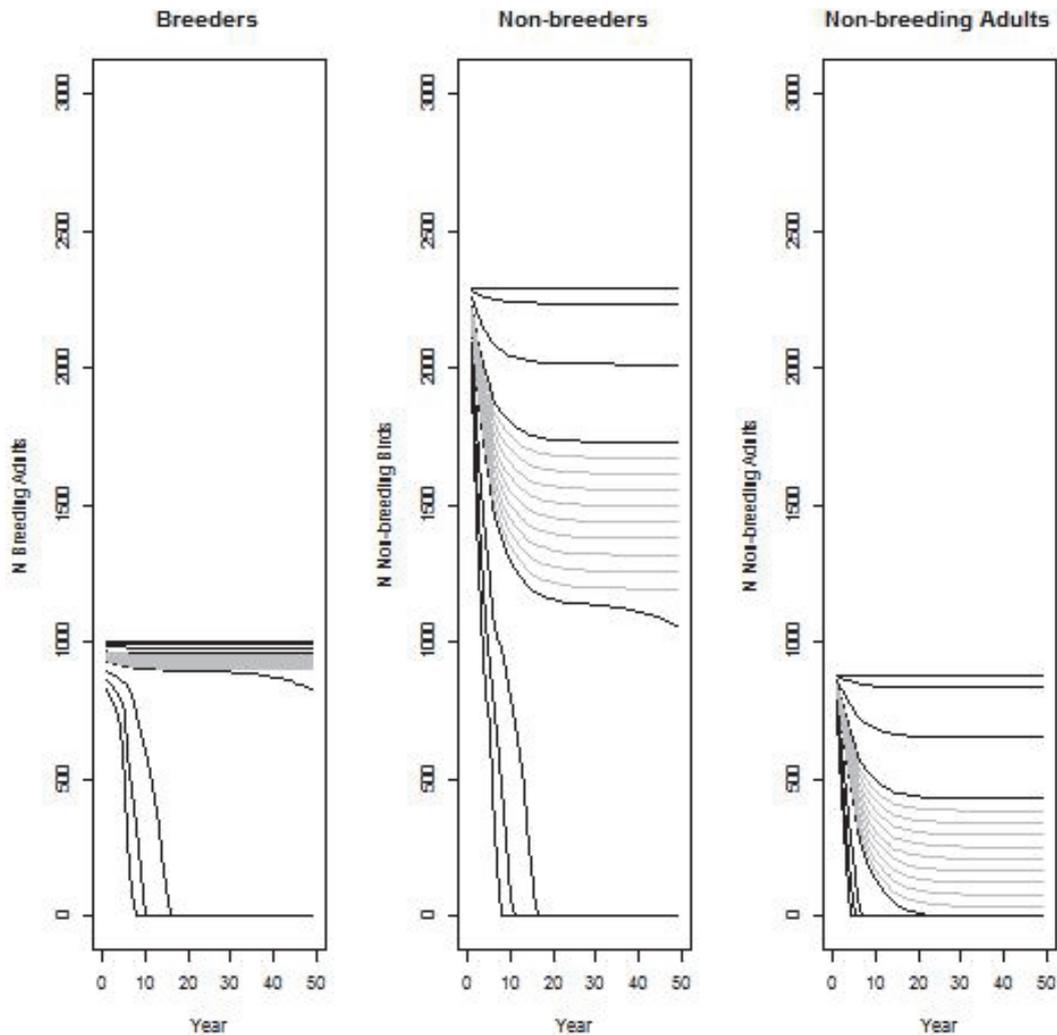


Figure 9.9 Impact of licensed control on the Baseline population, assuming a cap on the number of breeding pairs, that any additional adult birds are part of the non-breeding population, and that breeding adults are also subject to licensed control. From top to bottom, black lines reflect licensed control scenarios of 0, 10, 50, 100, 200, 300, 400 & 500 non-breeding birds removed from the population and grey lines, used to refine estimates on the number of birds that can be sustainably taken, indicate 110, 120, 130, 140, 150, 160, 170, 180 and 190 non-breeding birds removed.

9.6 Sensitivity analysis

The model variants described above differ according to their assumptions about density dependence mechanisms, starting populations, and the demographic groups subject to population control. The implications of these assumptions for our conclusions, and the possibility that real raven populations might depart from these assumptions, are discussed in section 9.7. However, the predictions made by population models are sensitive not only to decisions about model structure, but also to uncertainty in their input parameters (Sæther & Bakke, 2000). This sensitivity may have implications for the conclusions drawn from the outputs and how these are used by decision makers. It is therefore important to determine the parameters to which models are most sensitive, and what implications this sensitivity may have for decisions about sustainable levels of licensed control.

To assess model sensitivity to uncertainty about input parameters, we re-ran the Baseline and Low Recruitment scenarios described above, each with density dependence and capped number of breeders, assuming some level of mis-specification of each demographic parameter in turn, within the following ranges, informed by a review of the literature above:

- Adult survival (-0.20 to +0.05 difference from modelled value);
- Immature survival (-0.20 to +0.05 difference from modelled value);
- Juvenile survival (-0.10 to +0.05 difference from modelled value);
- Productivity (-0.10 to +0.30 difference from modelled value);
- Carrying Capacity/Maximum Density of breeding pairs (-200 to +300 difference from modelled value);
- Density dependent shape parameter (b) (-5 to +5 difference from modelled value).

Model sensitivity may vary in relation the magnitude of the presumed impact (Cook & Robinson, in prep). Consequently, we considered impacts of licensed control of between 0 and 50% of non-breeding birds. We present the results as heatmaps showing the growth rate estimated over the period from year 1 to year 50, and the population size after 50 years for each level of mis-specification and magnitude of impact. If mis-specification of a parameter has no effect on model predictions over the range illustrated by a heatmap, then it will appear as a series of horizontal bands, showing how the output values of the model (in this case growth rate and end population size) respond to variation in intensity of control. The greater the effect that variation in the parameter has on model predictions, the more the orientation of the bands in the heatmap will deviate from the horizontal. Results of the sensitivity analysis are presented for both the baseline and low recruitment populations described above. For the purposes of these sensitivity analyses, we focus on the models with density dependence and a cap on breeding numbers as these are more biologically realistic than the density independent models.

9.6.1 *Density dependence*

Under density dependent regulation, these population models are relatively insensitive to mis-specification of the input parameters. This is because any reduction in population size is compensated for by an increase in adult survival, which helps to stabilise the population. Both the Baseline and Low Recruitment populations seem to show similar sensitivity to mis-specification of input parameters (Figures 9.11 – 9.14). In addition to sensitivity to adult survival, these models are also sensitive to the parameters describing the density dependent relationship between population size and adult survival. Sensitivity to mis-specification of some of the input parameters, including survival rates and population density, varies in relation to the level of licensed control being considered.

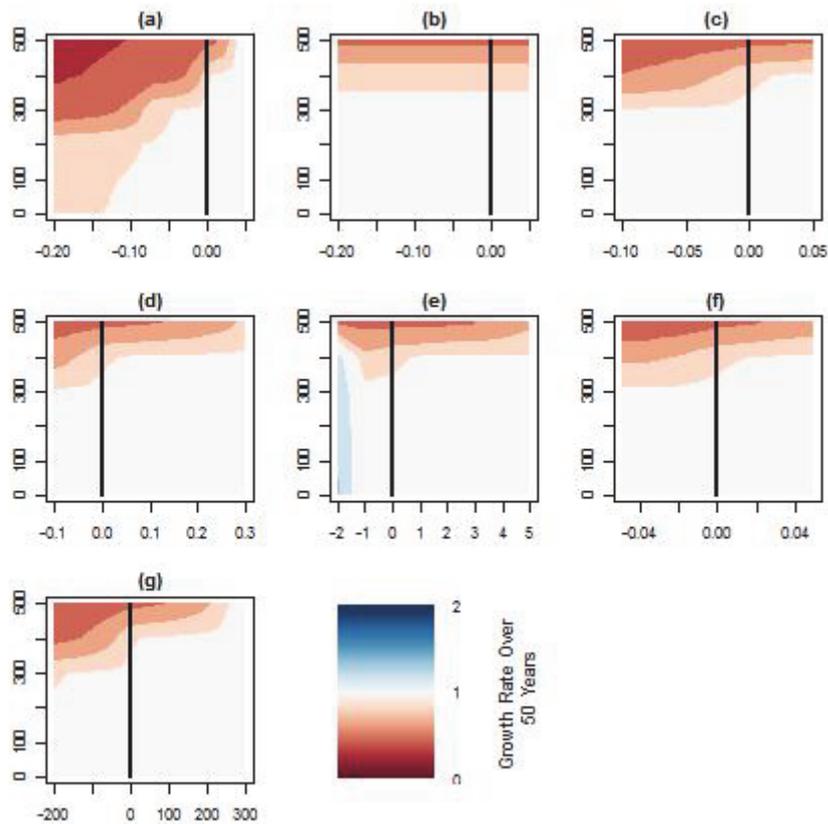


Figure 9.10 Sensitivity of population growth rates derived from density dependent models of different levels of licensed control of the Baseline population to mis-specification of (a) adult survival rate; (b) immature survival rate; (c) juvenile survival rate; (d) productivity; (e) density dependent shape parameter; (f) maximum allowable adult survival rate and (g) population carrying capacity. Black lines indicate parameter estimates used in original models.

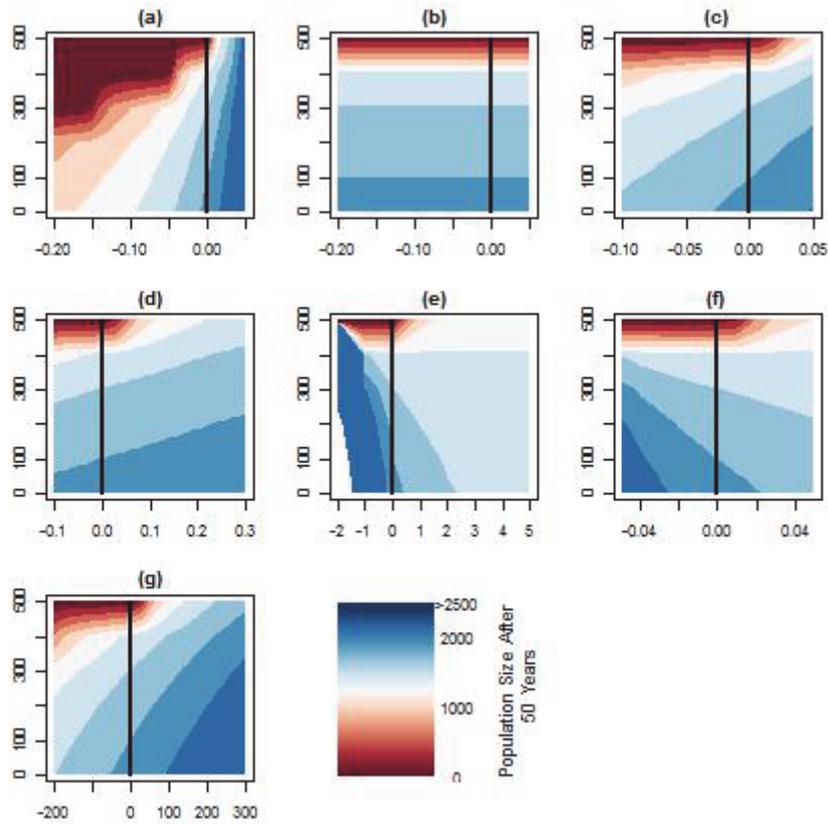


Figure 9.11 Sensitivity of population size after 50 years derived from density dependent models of different levels of licensed control of the Baseline population to mis-specification of (a) adult survival rate; (b) immature survival rate; (c) juvenile survival rate; (d) productivity; (e) density dependent shape parameter; (f) maximum allowable adult survival rate and (g) population carrying capacity. Black lines indicate parameter estimates used in original models.

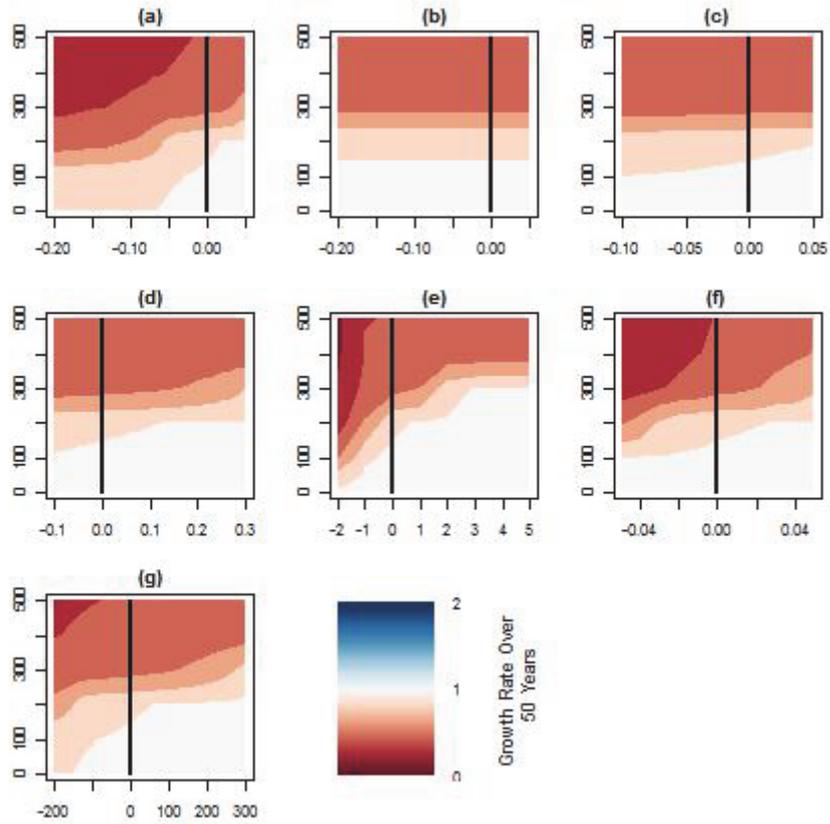


Figure 9.12 Sensitivity of population growth rates derived from density dependent models of different levels of licensed control of the Low Recruitment raven population to mis-specification of (a) adult survival rate; (b) immature survival rate; (c) juvenile survival rate; (d) productivity; (e) density dependent shape parameter; (f) maximum allowable adult survival rate and (g) population carrying capacity. Black lines indicate parameter estimates used in original models.

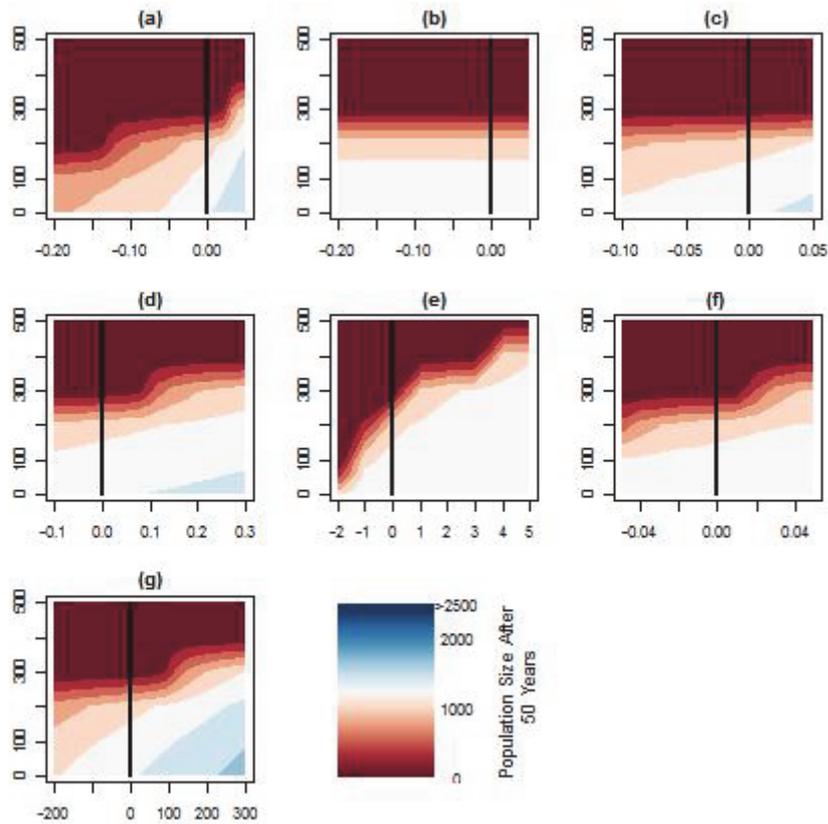


Figure 9.13 Sensitivity of population size after 50 years derived from density dependent models of different levels of licensed control of the Low Recruitment raven population to mis-specification of (a) adult survival rate; (b) immature survival rate; (c) juvenile survival rate; (d) productivity; (e) density dependent shape parameter; (f) maximum allowable adult survival rate and (g) population carrying capacity. Black lines indicate parameter estimates used in original models.

9.6.2 Capped number of breeders

The heatmaps suggest that the Baseline population may be more sensitive to mis-specification of the size of the cap on breeding numbers than is the case for the Low Recruitment population (Figures 9.15 – 9.18). Sensitivity of the models to individual parameters show similar patterns to those described previously, with population growth rate and end population size particularly sensitive to mis-specification of adult survival.

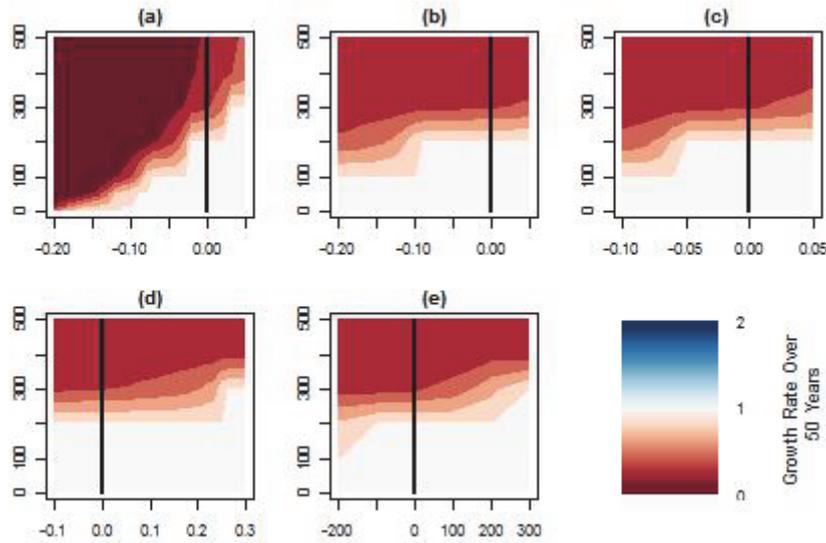


Figure 9.14 Sensitivity of population growth rates derived from models with a cap on the size of the breeding population and different levels of licensed control of the Baseline population to mis-specification of (a) adult survival rate; (b) immature survival rate; (c) juvenile survival rate; (d) productivity and (e) population carrying capacity (cap on breeding numbers). Black lines indicate parameter estimates used in original models.

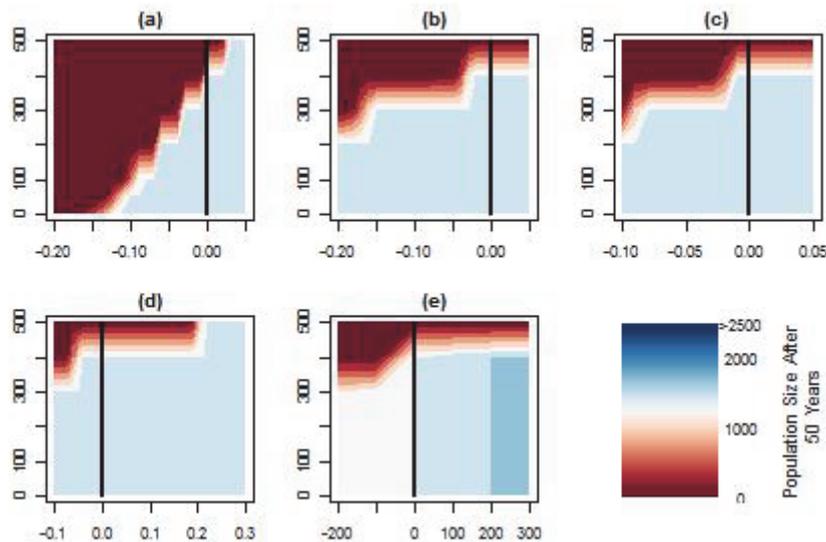


Figure 9.15 Sensitivity of population size after 50 years derived from models with a cap on the size of the breeding population and different levels of licensed control of the Baseline population to mis-specification of (a) adult survival rate; (b) immature survival rate; (c) juvenile survival rate; (d) productivity and (e) population carrying capacity (cap on breeding numbers). Black lines indicate parameter estimates used in original models.

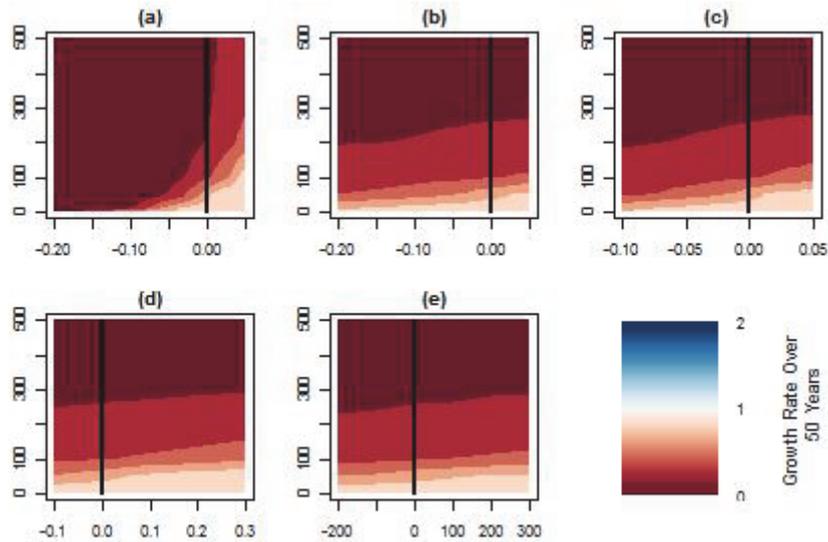


Figure 9.16 Sensitivity of population growth rates derived from models with a cap on the size of the breeding population and different levels of licensed control of the Low Recruitment population to mis-specification of (a) adult survival rate; (b) immature survival rate; (c) juvenile survival rate; (d) productivity and (e) population carrying capacity (cap on breeding numbers). Black lines indicate parameter estimates used in original models.

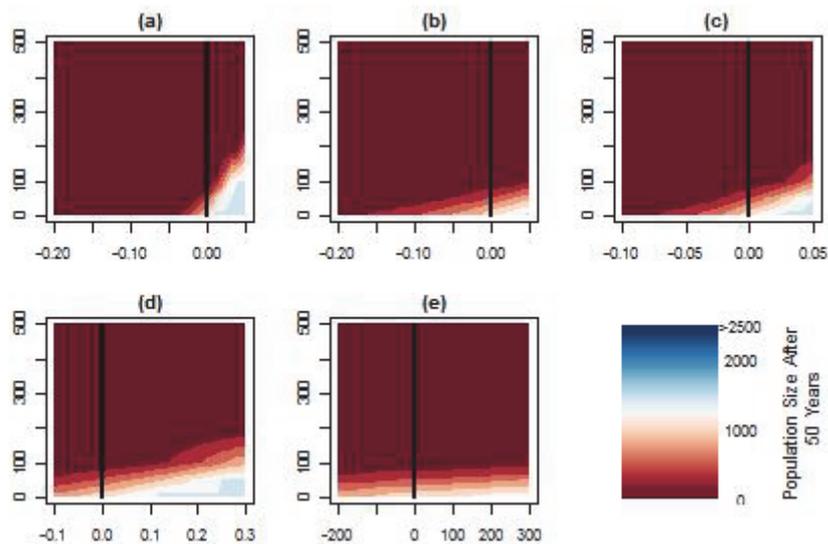


Figure 9.17 Sensitivity of population size after 50 years derived from models with a cap on the size of the breeding population and different levels of licensed control of the Low Recruitment population to mis-specification of (a) adult survival rate; (b) immature survival rate; (c) juvenile survival rate; (d) productivity and (e) population carrying capacity (cap on breeding numbers). Black lines indicate parameter estimates used in original models.

9.6.3 Capped number of breeders, expanding population

The heatmaps show that the Baseline population may be more sensitive to mis-specification of the size of the cap on breeding numbers than is the case for the Low Recruitment population (Figures 9.15 – 9.18). Sensitivity of the models to individual parameters show similar patterns to those described previously, with population growth rate and end population size particularly sensitive to mis-specification of adult survival.

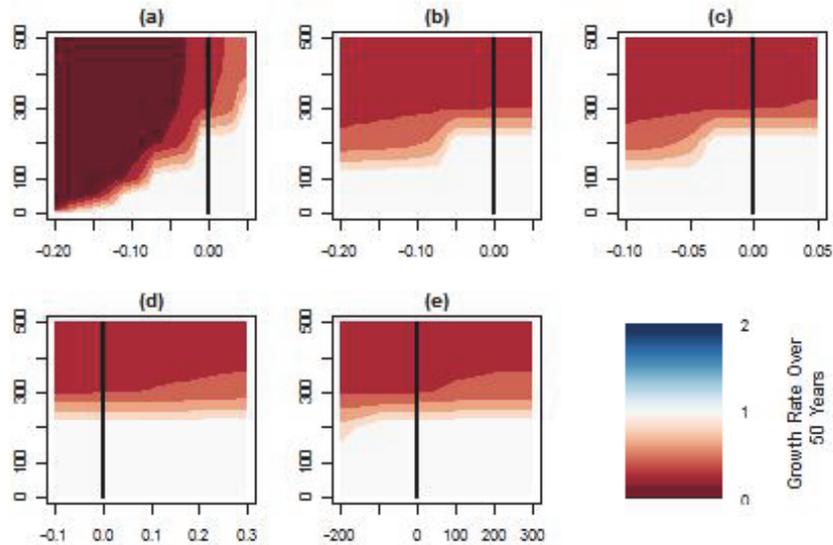


Figure 9.18 Sensitivity of population growth rates derived from models with a cap on the size of the breeding population and different levels of licensed control of an expanding (low density) population to mis-specification of (a) adult survival rate; (b) immature survival rate; (c) juvenile survival rate; (d) productivity and (e) population carrying capacity (cap on breeding numbers). Black lines indicate parameter estimates used in original models.

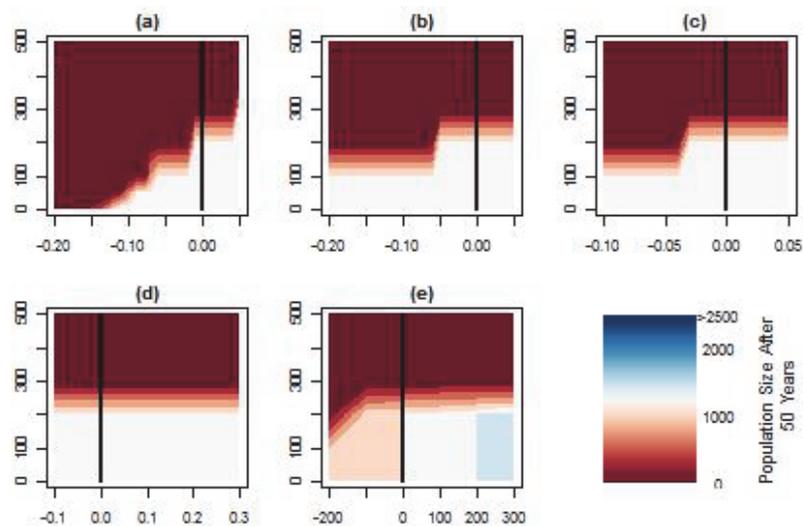


Figure 9.19 Sensitivity of population size after 50 years derived from models with a cap on the size of the breeding population and different levels of licensed control of an expanding (low density) population to mis-specification of (a) adult survival rate; (b) immature survival rate; (c) juvenile survival rate; (d) productivity and (e) population carrying capacity (cap on breeding numbers). Black lines indicate parameter estimates used in original models.

9.7 Discussion

9.7.1 Sustainable harvest levels

The modelling demonstrates that the level of lethal control that can be sustained by a population varies considerably in relation to the process by which the population is regulated (Table 9.2). The two main regulation processes considered were density dependence in survival and a cap on the number of breeders. The strong territoriality observed in ravens (Ratcliffe, 1997) and the likelihood that non-breeding adults make up a large proportion of non-breeders in many raven populations (section 7), suggest that a cap on the number of breeders is likely to limit raven population productivity in many areas. However, it is entirely plausible that the 'background' mortality rates we have documented, and which we use in our models, are shaped by density dependent processes. Raven population size could be regulated by both processes in tandem, with the relative importance of each depending on population status, as well as other environmental factors such as availability of food, severity of winters etc. However, for the purpose of considering the effects of licencing, we suggest that the most conservative approach is to assume that populations are limited primarily through a limit on the number of birds that can breed, and not to assume that survival rates will respond positively to a decrease in population density.

Under this assumption, the number of ravens that can be sustainably removed each year, with population parameters set at levels that reflect our best understanding for ravens over the majority of Scotland, would be around 240 non-breeding birds per 10 000km² (Table 9.2). However, under alternative scenarios, for example where a population was still expanding, or where there is a risk of adult birds being caught up by the licensed control, the number of non-breeding birds that could be removed from the population was substantially reduced (Table 9.2). It is also important to consider the sensitivity of our models to current levels of uncertainty in the input parameters (see below).

It should be pointed out that 'sustainable' in this context does not mean that a given level of harvesting has no impact. Under scenarios where population productivity is controlled exclusively by a cap on the number of breeders, sustainable levels of licenced control have a negligible impact on the number of breeders. However, when considering non-breeders as well as breeders, all situations in which even small numbers of birds are removed from the population result in a decrease in the size of the overall population. Our use of the word sustainable refers to the 'harvest' of ravens under a given licencing regime. If the same number of ravens can be removed from the population every year without detrimental effects on the numbers of breeders, we describe it as sustainable.

In our models even low levels of licenced control reduce end population size because we have assumed that mortality arising from licenced control is entirely additive to 'background' causes of mortality. That is to say, we assumed that the licenced removal of birds from the population does not alter survival probability for the remaining birds. If at least a component of what we are calling background mortality arises from density-dependent processes, or if susceptibility to shooting by licence holders is positively correlated with 'background' survival probability, then mortality from licenced control is likely to be (at least partly) compensated for by a reduced level of mortality from other causes. This means that our approach is precautionary, and our estimates of sustainable levels of licenced control may, in this regard, be slightly conservative.

Another assumption that may affect our findings is that levels of licensed take remain constant over long periods of time. As well as possible changes in the number of ravens permitted to be killed, the number actually killed under licence may also be affected by other factors. These might include the size of the raven population, the levels of damage to livestock sustained and perceived by farmers, and the behaviour and distribution of ravens.

All of these factors could, themselves, be influenced by levels of control, raising the possibility of a feedback loop between intensity of control and some of its consequences, so that licensing demand itself is 'density dependent'. In situations where this is the case, demand levels for licences (and, therefore, take of ravens) could fall in response to decreased raven numbers. This means that the idea of one level of licencing being set and maintained over a long period of time, as assumed in our models, is not necessarily realistic. It seems likely that Raven numbers in some parts of Scotland can be limited by un-licensed killing or interference with breeding attempts by humans (Ratcliffe 1997; Forrester & Andrews 2007). Changes in the levels of licenced control could interact with the nature and effects of illegal Raven control in ways that could make the outcomes of these changes for Raven populations harder to predict.

In most parts of Scotland, levels of control over the past 3 years have been well below the maximum sustainable levels indicated by these models. However, in some parts of western Scotland, control has been licenced at or above the highest levels that current knowledge suggest to be sustainable. In at least one area (Uist), levels of licenced control over the past three years (and for several years before this) have been high enough to outweigh expected productivity from breeding pairs in this area. Raven numbers on Uist do not appear to have declined markedly during most of this period (Andrew Stevenson pers. comm.), suggesting that either there is a discrepancy between the estimates of raven survival or productivity used in the models and those applying to ravens on Uist (see below), or that raven numbers in this region are being bolstered by immigration. In this regard, it should be noted that our estimates of raven movements are based on too small a dataset to examine regional variation in dispersal. We do not have large enough samples of birds recovered on Uist or ringed in north-west Scotland from which to assess any exchange movements (Figs 4.1 and 4.4). In Iceland, dispersal of Ravens in the early 1980s, during a period of intense population control, varied significantly between different regions, and appeared to be related to factors such as population density, breeding success, and levels of control. Among the factors that may have contributed to patterns of immigration and movement in the Outer Hebrides, as well several other parts of western Scotland, is the presence of large, landfill dumps. Until the 2000s, many of these included food waste in their remit. The last large landfill with food waste in the Outer Hebrides that remains in operation (at the time of writing), and which still attracts large numbers of Ravens, is near Stornaway on the Isle of Lewis (Andrew Stevenson pers. comm.). High value food resources can attract ravens from hundreds of kilometres away (e.g. Loretto *et al.* 2017), and could result in immigration of non-breeding ravens from surrounding areas with lower levels of population control.

If recent levels of population control on Uist (or elsewhere in Scotland) have not affected the numbers of ravens observed in this area, it may be that control has been, from a literal perspective, sustainable. However, if this sustainability depends on immigration of ravens from other areas, the population may be acting as a sink, and levels of control on Uist could be affecting populations in other areas. It would, therefore, be desirable to closely monitor raven populations, not only in areas with relatively high levels of population control but also in surrounding regions. This would enable any responses in breeding numbers/output of these populations to be flagged and acted upon swiftly.

Levels of licenced population control reported in the east of Scotland (Figure 8.2) are well under the level of 2.4 birds per hectad estimated as being sustainable for most of Scotland. However, the 100 km square with the highest level of licencing in this region (1.1 birds per hectad) also has the lowest estimated breeding population density (1.3 pairs per hectad). At such low densities, a licenced take of just 0.6 birds per hectad could be enough to cause population decline and (in the absence of immigration) local extinction (Figure 9.9). Moreover, considering that the raven population in this area is still in a colonising phase, with many suitable areas for territories unoccupied and territorial turnover high (Mick Marquiss pers. comm.), the estimate of pair density, based as it is on atlas data, may include newly

established pairs or even immigrant non-breeders dispersing into the area. If this were the case, both the productivity of ravens in this area and the maximum sustainable level of harvesting that the population could tolerate would be less than we have estimated. However, although the raven population in the north-east of Scotland is small, its size, like that of the population on Uist, has remained relatively stable in recent years (Challis *et al.* 2015, Marquiss pers. comm.). This supports the idea that the role of immigration in maintaining populations in these areas is greater than suggested by levels of dispersal observed in the wider population. If this is the case, the role of licenced control in limiting population size or suppressing population growth rates may play out at a wider scale than the 100km square level we have considered here. This raises the possibility that levels of control in one area could have consequences for raven population size that are felt most in other areas. In order to establish whether this is the case, more information is needed on dispersal of ravens between different areas, and how this relates to variation in levels of licenced population control.

9.7.2 *Model sensitivity*

It is important to emphasise that estimates relating to levels of sustainable harvest must be interpreted in the context of the degree of uncertainty around the relevant population parameters and model structure. As Figures 9.11 – 9.18 show, varying the values of these parameters, within the likely range of uncertainty around them, can have profound consequences for population trajectories. In particular, conclusions about sustainable levels of removal are very sensitive to variation in levels of adult survival. Under a baseline scenario, with productivity limited by a cap on the number of breeders, if levels of adult survival were 10% lower than we have estimated, the level of sustainable take would drop to less than half the level we currently predict.

Given this sensitivity to input parameters, it is important to treat the suggested sustainable levels of control as indicative rather than definitive. We report the consequences for model outputs of varying the number of ravens controlled by as few as 10 individuals, in order to assist in making comparisons between different models and scenarios. This does not imply that our confidence in all the relevant input parameters justifies using this level of precision to determine exactly how many ravens could be removed before negative consequences were expected. Furthermore, our analyses suggest that the sensitivity of the models to mis-specification of demographic parameters can be affected by the levels of population control being considered. This is particularly important in situations where model sensitivity is positively related to levels of control (Cook & Robinson, in prep). In such cases it is particularly important to be confident about the demographic parameters used in models to project population level changes.

It is important to consider sensitivity in the context of our uncertainty about the various model parameters. The parameter to which model outcomes are most sensitive, within the range of variation we tested, is adult survival. However, our confidence in our estimates of this parameter, at least for ravens from those parts of Scotland where good numbers of ravens have been ringed, is relatively high – the lower 95% confidence limit being only 2% lower than the values we used in our models. There is a possibility that survival in some parts of Scotland from where data are sparse, such as the north-east, could be lower than elsewhere – particularly if one or more causes of mortality was more prevalent there. Low reproductive success, and high territory turnover and mortality of raptors have been associated with some upland areas in Scotland managed for red grouse, among them areas in the north-east with low densities of raven. The sensitivity heatmap suggests relatively little response of population growth rates or end population size to this level of variation in adult survival. In contrast, although the models are less sensitive to variation in survival rates of other age classes, or breeding density, our uncertainty about these (particularly in relation to breeding

density, for which the confidence limits around our estimates are relatively large) may actually have more important implications for our estimates of sustainable levels of control.

Sensitivities to parameter mis-specification are much greater when population size is regulated through a cap on the number of breeding pairs than when survival is density dependent. This makes sense, as the density dependent relationship allows compensation for significant changes in population size, such as might result from mis-specification of demographic parameters, by altering the adult survival rate in order to stabilise the population. These results suggest that assuming that populations are limited primarily by a cap on breeders, as we suggest above, is a more precautionary approach. If density dependent models are used to represent raven populations, predictions arising from them are likely to be sensitive to assumptions about the parameters describing the shape of the density dependent relationship. It would therefore be important to ensure that this function is parameterised properly; an improved understanding of the relationship between population size and adult survival in the raven would be required.

Table 9.2 Impact of licensed control on key model scenarios over 50 years. Starting population and population size at 50 years both refer to the numbers of breeders – all other immature and non-breeding adults are included in the number of non-breeders.

Population parameters	Growth regulation	Control	Starting state	Starting population	Maximum stable take	No. Adults at 50 years	No. Non-Breeders at 50 years
Baseline	Cap on breeders	Non-breeders only	Equilibrium	1000	240	1000	1053
Baseline	Density dependent	Non-breeders only	Equilibrium	1000	350	992	923
Low recruitment	Density dependent	Non-breeders only	Equilibrium	1000	200	673	550
Baseline	Cap on breeders	All adults and immatures	Equilibrium	1000	190	1000	1289
Baseline	Cap on breeders	Non-breeders only	Expanding	260	50	1000	1970

9.7.3 Conclusions

Our analyses suggest that, in much of Scotland, raven populations could sustain levels of licencing of around 200 individuals per area of 100 km × 100 km. However, in order to ensure that licenced control is sustainable, lower limits should be set in situations where productivity or survival are known or suspected to be lower than the average values used in our analysis, where raven numbers have not yet reached carrying capacity, in areas where this carrying capacity is lower, or where control might affect both breeding and non-breeding birds.

The accuracy of this assessment depends on our estimates of survival and productivity being correct. Our conclusions about the sustainability of different licencing levels are particularly sensitive to variation in survival, particularly that of adult ravens. Current survival estimates are based entirely on information from birds ringed as chicks and recovered after death. There is a risk that conclusions drawn from such a dataset, particularly as related to survival of young birds, could be affected by biases associated with the effect of age class, location or cause of death on the probability of recovery.

The evidence base for making recommendations about licenced control of ravens would be improved by better information on survival rates. Two possible strategies would be to trap and ring more raven adults (allowing better estimates of survival, and generating additional

valuable information from live re-traps of ringed birds) and to carry out colour-marking studies (allowing information on the survival and movements of individual ravens to be collected without the need for birds to be recaptured or recovered after death). Colour-marking would have the additional advantage of enabling identification of individual birds in areas used by ravens for foraging, breeding and roosting. This could yield much better information about the numbers, breeding status and movements of ravens causing damage to livestock, which in turn could greatly help in assessing and improving the effectiveness of licencing strategies.

Even if our estimates of survival and productivity are currently accurate, they might change in the future, in response to changes in licencing or to other environmental factors. This could, potentially, alter the levels of control that can currently be tolerated by raven populations. It is therefore important to maintain and, where possible, enhance current monitoring of raven populations. Particularly important is the annual monitoring of ravens collated by the SRMS, most of which is carried out by members of the Scottish Raptor Study Group. As well as helping to assess and refine the findings of the current study, information from the SRMS will be invaluable in enabling the detection of changes over time in both the productivity and, size of raven populations. In the event that levels of removal become unsustainable, our findings indicate that any resulting decline in population is likely to take place over a period of decades. There should, therefore, be the opportunity for information from the SRMS to be used to detect changes in population size in areas where control is being carried out, in time to allow assessment and, if appropriate, alteration of licencing regulation. Several, ongoing improvements to the SRMS aim to increase the availability and quality of information about survey effort, which will improve the accuracy and comparability of information about population density. These include an online recording system, collection of information from SRMS contributors about current and historical levels of survey effort, and a new recording scheme for widespread raptors called Raptor Patch which is currently being trialled (see <http://raptormonitoring.org/getting-involved/raptor-patch>).

Regulation of licences currently requires the majority of lethal control to be carried out at the locations where damage to livestock is experienced or anticipated. Current thinking is that most of this damage is being inflicted by non-breeding ravens, and that the individuals killed under licence are therefore likely to be mostly non-breeders. Our models indicate that, in a scenario where breeding adults are subject to licenced control at similar rates to non-breeders, the number of individuals that could be sustainably killed will be reduced. Finding out more about the movements and behaviour of breeding and non-breeding ravens would not only tell us more about the likely effects of different licencing levels, but would also provide insights into how effective different licencing options might be.

Future assessments of the likely effects of licencing would benefit from increased understanding of the movements and behaviour of individual ravens. In particular, information on regional variation in movements of ravens between fledging and breeding would help us to understand where, and to what extent, apparently stable populations are being maintained by immigration. As mentioned above, colour-marking could help to improve our knowledge of raven movements over the long-term. A more intensive approach that could yield detailed information in a relatively short period of time is remote-tracking, using GPS-satellite tags or a similar technology. The information generated by GPS, in particular, would also shed light on several other aspects of raven ecology that could be of interest and value to those interested in conserving and managing ravens, including: the ranging behaviour of territorial ravens, and whether this varies between different parts of Scotland; the circumstances in which, and extent to which, ravens in different parts of Scotland cause damage to livestock; and whether the majority of this damage is caused by particular individuals or demographic groups of ravens and, if so, how their life stage, movements and behaviour compare to those of other ravens.

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ANNEX 1: DISPERSAL AND SURVIVAL

Included below are graphs illustrating more of the survival models summarised in Table 4.1, and maps showing dispersal of ravens ringed in parts of Britain and Ireland other than Scotland.

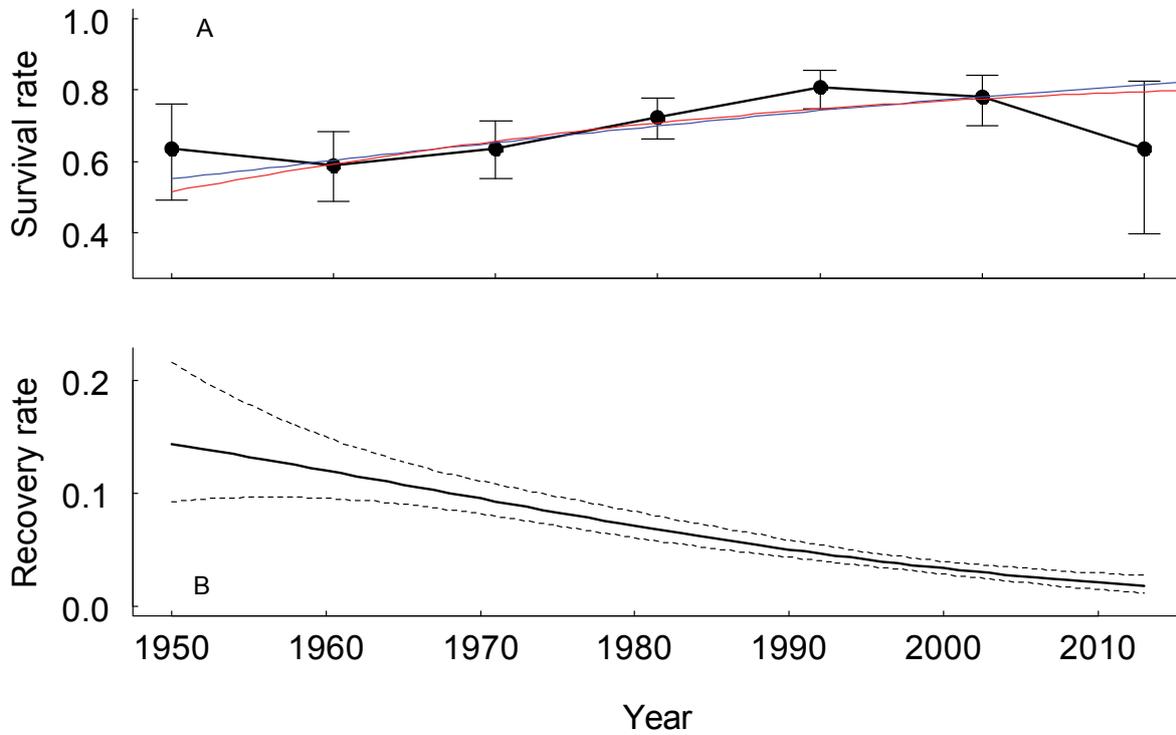


Figure 1i. 1 A. The survival rates of British ravens 1950-2013; modelled in 10 year blocks (model 3, black line and 95% confidence interval), modelled as a linear function (model 1, red line), and modelled as a quadratic function (model 4, blue line). B. The recovery rate of rings from British ravens 1950-2013 modelled as a quadratic function.

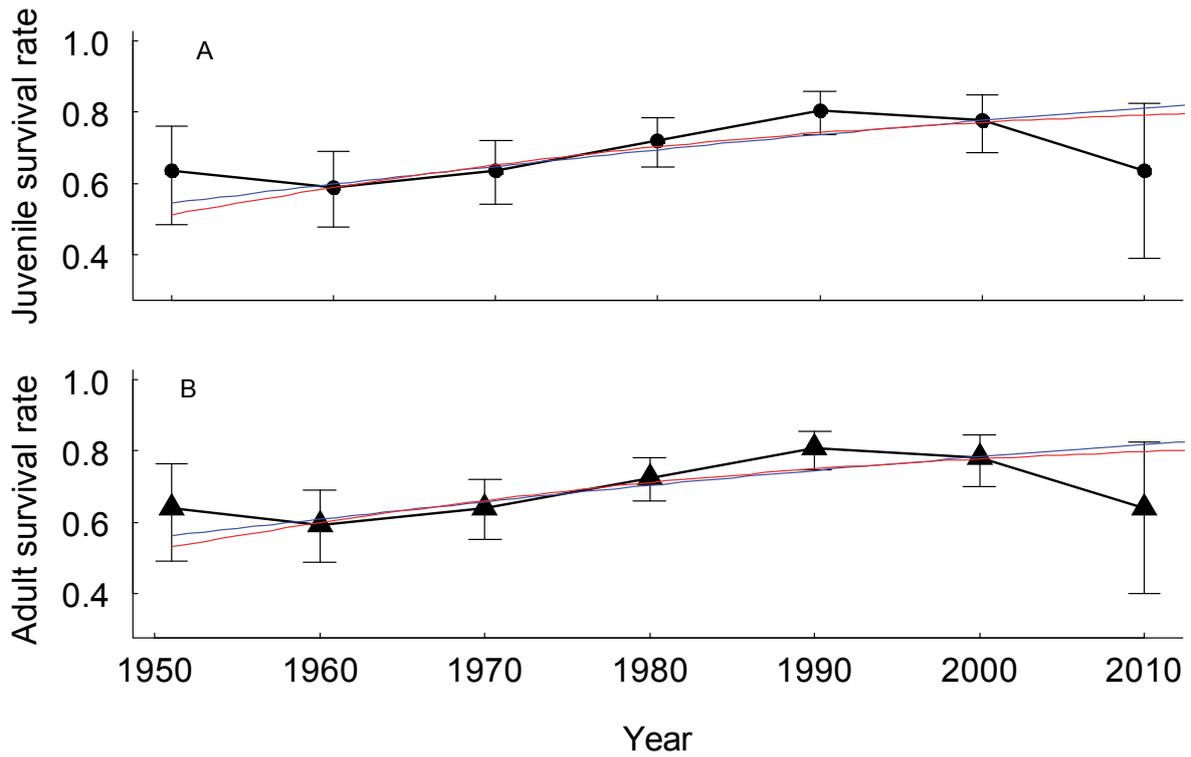


Figure 1i. 2 A. The survival rates of juvenile British ravens 1950-2013; modelled in 10 year blocks with an additive relationship between the age classes (model 6, black line and 95% confidence interval), modelled as a linear function with an additive relationship between the age classes (model 5, red line), and modelled as a quadratic function with an additive relationship between the age classes (model 7, blue line). B. The survival rates of British ravens older than age one, model structures as detailed for plot A

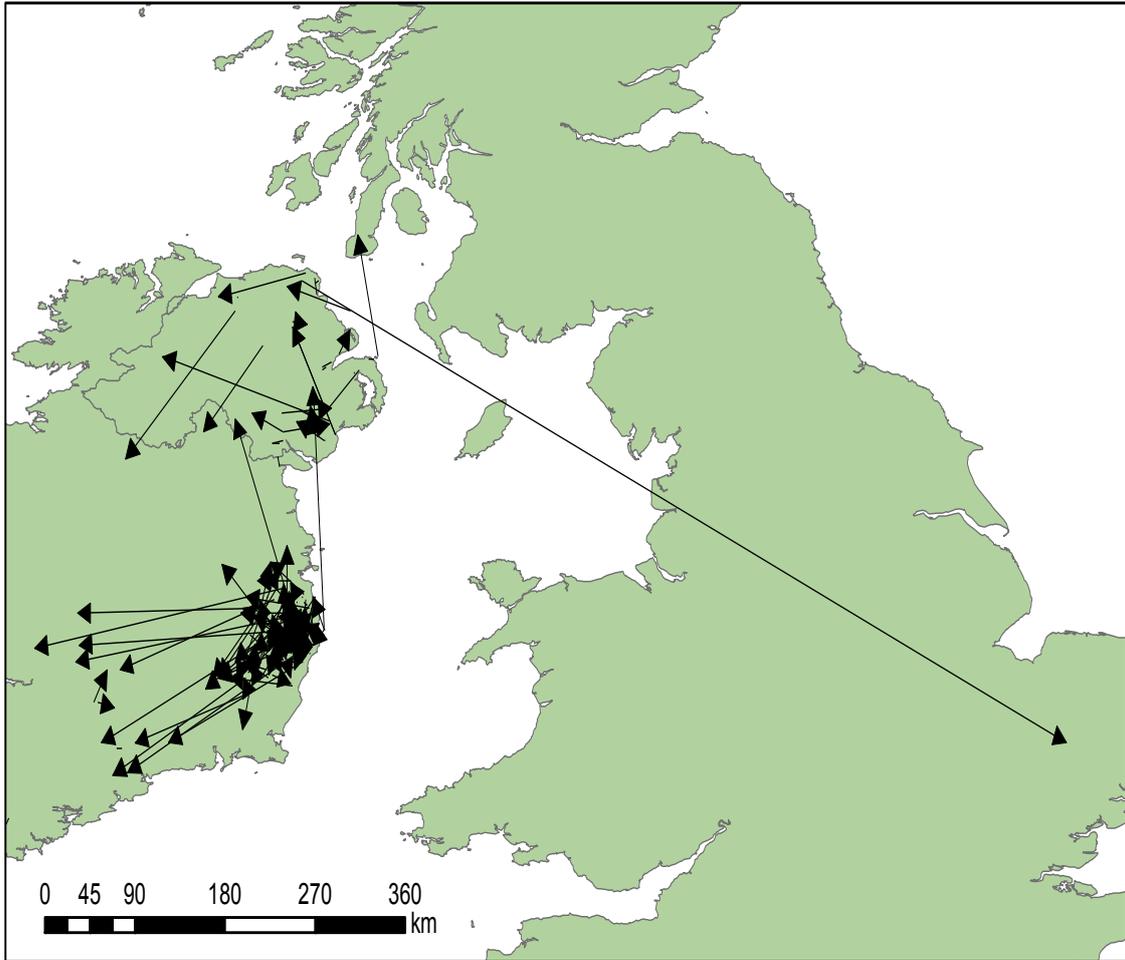


Figure 1i. 3 Dispersal of ravens ringed in Eire and Northern Ireland. Arrows show direction of movement between ringing and recovery.

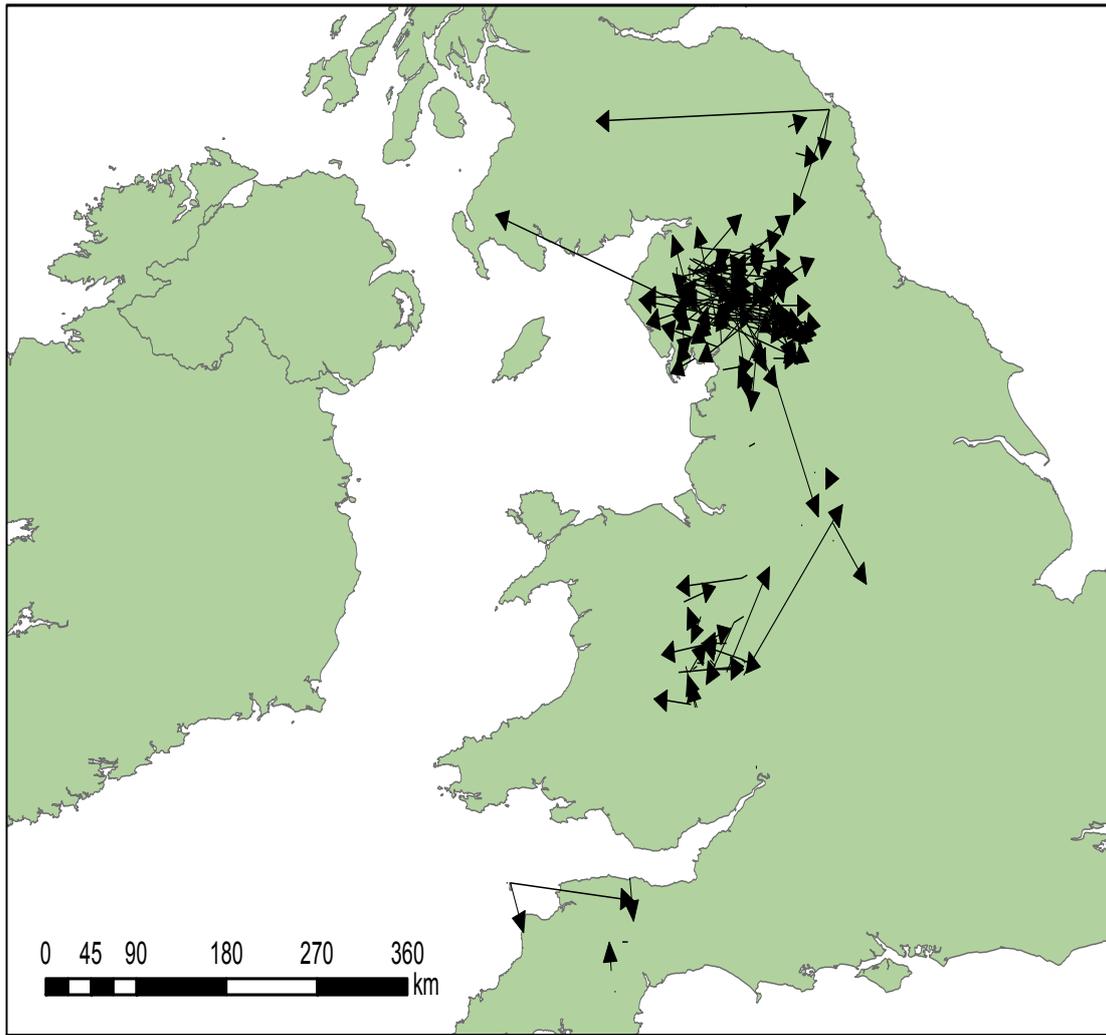


Figure 1i. 4 Dispersal of ravens ringed in England. Arrows show direction of movement between ringing and recovery.

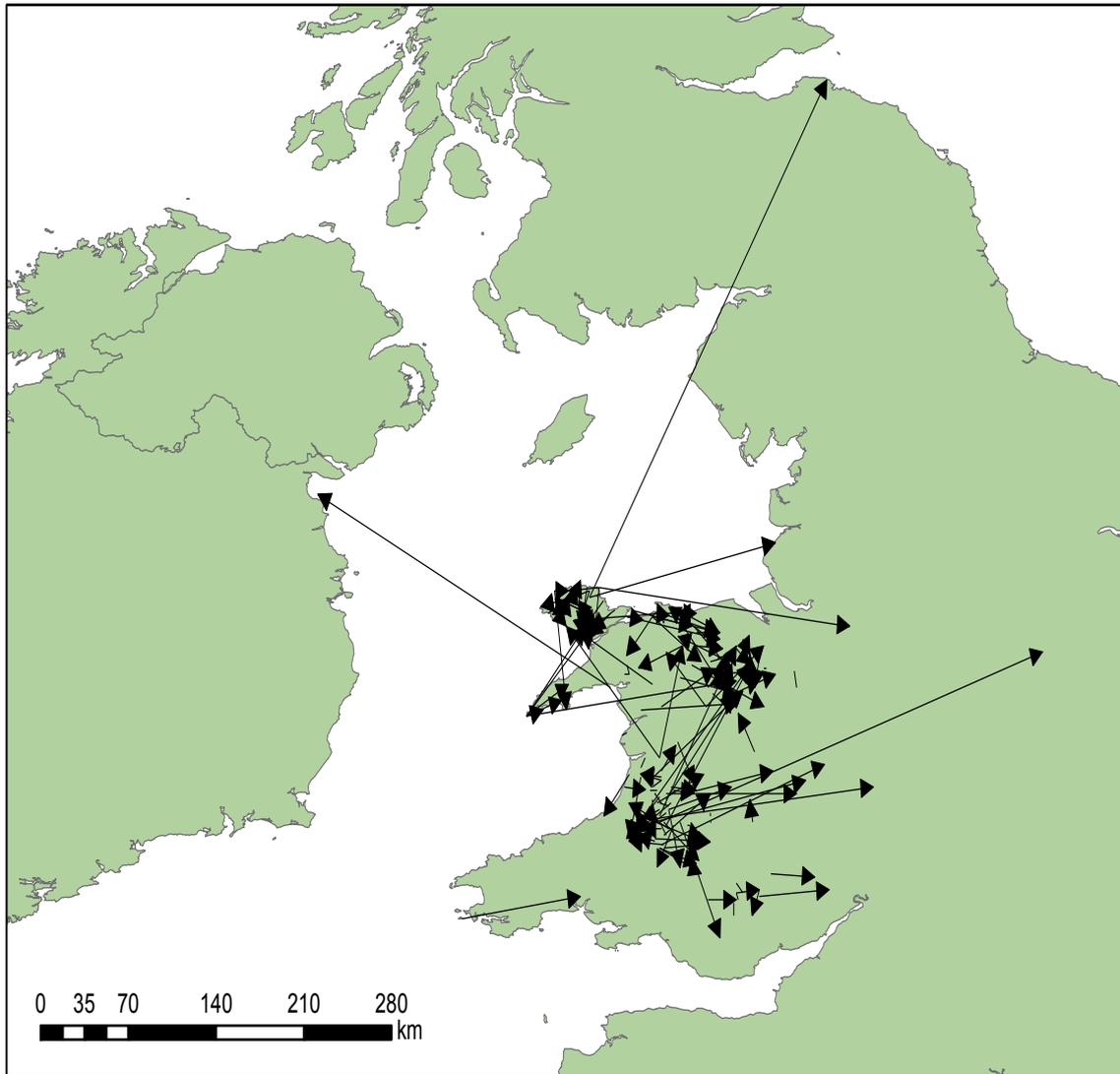


Figure 1i. 5 Dispersal of ravens ringed in Wales. Arrows show direction of movement between ringing and recovery.

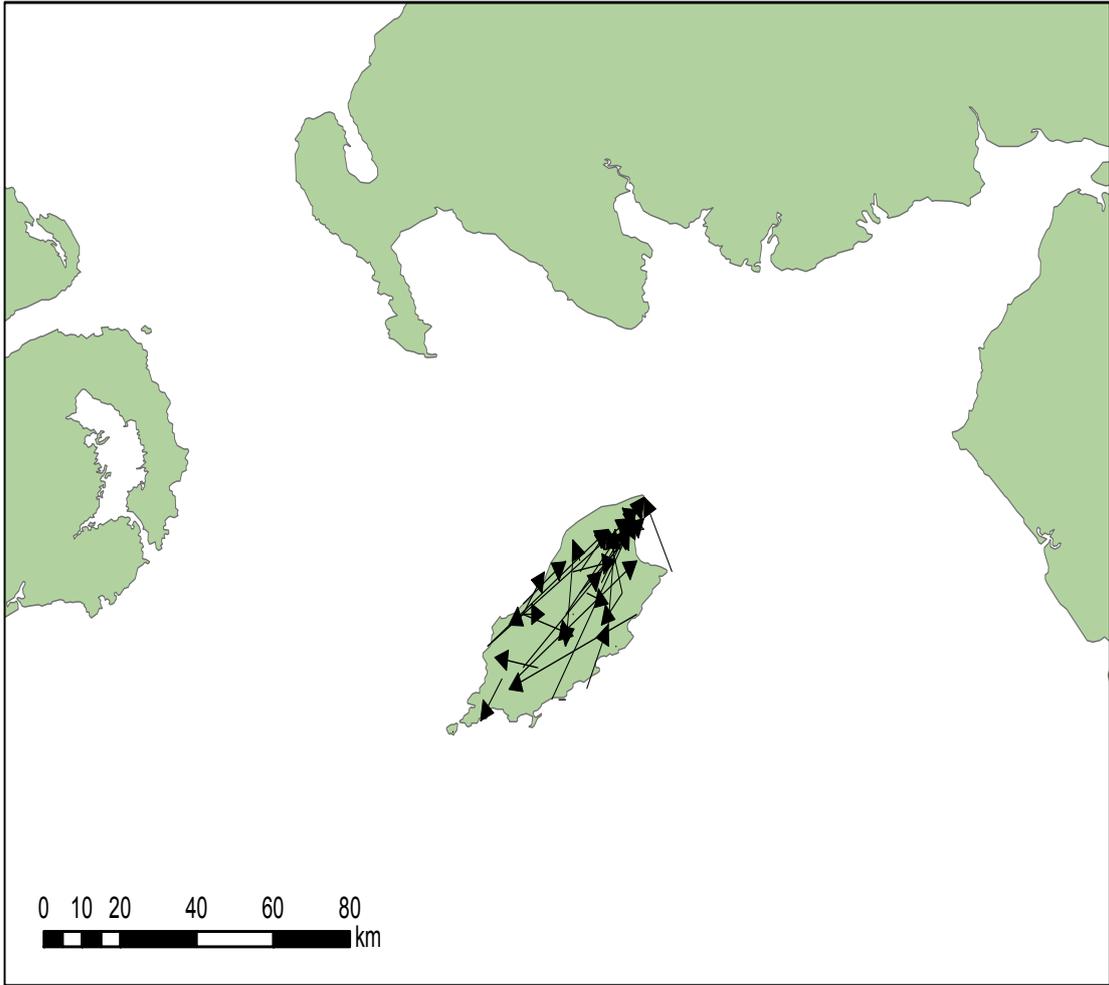


Figure 1i. 6 Dispersal of ravens ringed on the Isle of Man. Arrows show direction of movement between ringing and recovery.

ANNEX 2: PRODUCTIVITY

Included below are details of three generalised linear models, which have as their response variables binary nest success (proportion of breeding attempts resulting in fledging), fledged brood size, and overall productivity (number of young fledged per breeding pair). There are also graphs illustrating the size and significance of the differences in these metrics between different parts of Scotland.

Table 2i. 1 Model estimates and predicted breeding success (proportion of breeding pairs successfully fledging one or more young), \pm standard error, for each of five regions of Scotland. Null deviance = 1278.2, residual deviance = 1254.5, d.f. = 1430, AIC = 1264.5.

Area	Model estimate	z value	P value	Success	No. records
East (intercept)	1.49 \pm 0.14	10.911	<0.0001	0.82 \pm 0.02	399
Northern Isles	-0.90 \pm 0.42	-2.155	0.0312	0.64 \pm 0.09	29
North Mainland	1.88 \pm 0.60	3.121	0.0018	0.97 \pm 0.02	94
South-west	0.09 \pm 0.18	0.486	0.6268	0.83 \pm 0.02	609
West	0.24 \pm 0.20	1.234	0.2172	0.85 \pm 0.02	446

Table 2i. 2 Model estimates and predicted fledged brood sizes (number of young fledged per successful pair), \pm standard error, for each of five regions of Scotland. Null deviance = 634.7, residual deviance = 585.0, d.f. = 1195, AIC = 3950.9.

Area	Model estimate	z value	P value	Fledged brood	No. records
East (intercept)	1.09 \pm 0.03	32.044	<0.0001	2.97 \pm 0.10	399
Northern Isles	0.24 \pm 0.13	1.913	0.056	3.77 \pm 0.46	29
North Mainland	0.02 \pm 0.07	0.309	0.7569	3.03 \pm 0.19	94
South-west	-0.24 \pm 0.05	-5.32	<0.0001	2.33 \pm 0.07	609
West	0.01 \pm 0.05	-0.136	0.89	2.95 \pm 0.10	446

Table 2i. 3 Model estimates and predicted productivity values (number of young fledged per breeding pair), \pm standard error, for each of five regions of Scotland. Null deviance = 19746, residual deviance = 1915.4, d.f. = 4,1572, AIC = 5620.1.

Area	Model estimate	z value	P value	Productivity	No. records
East (intercept)	0.87 \pm 0.03	26.92	<0.0001	2.39 \pm 0.08	399
Northern Isles	-0.02 \pm 0.13	-0.16	0.877	2.34 \pm 0.28	29
North Mainland	0.18 \pm 0.07	2.66	0.008	2.87 \pm 0.17	94
South-west	-0.22 \pm 0.04	-4.96	<0.0001	1.93 \pm 0.06	609
West	0.04 \pm 0.04	0.93	0.353	2.49 \pm 0.07	446

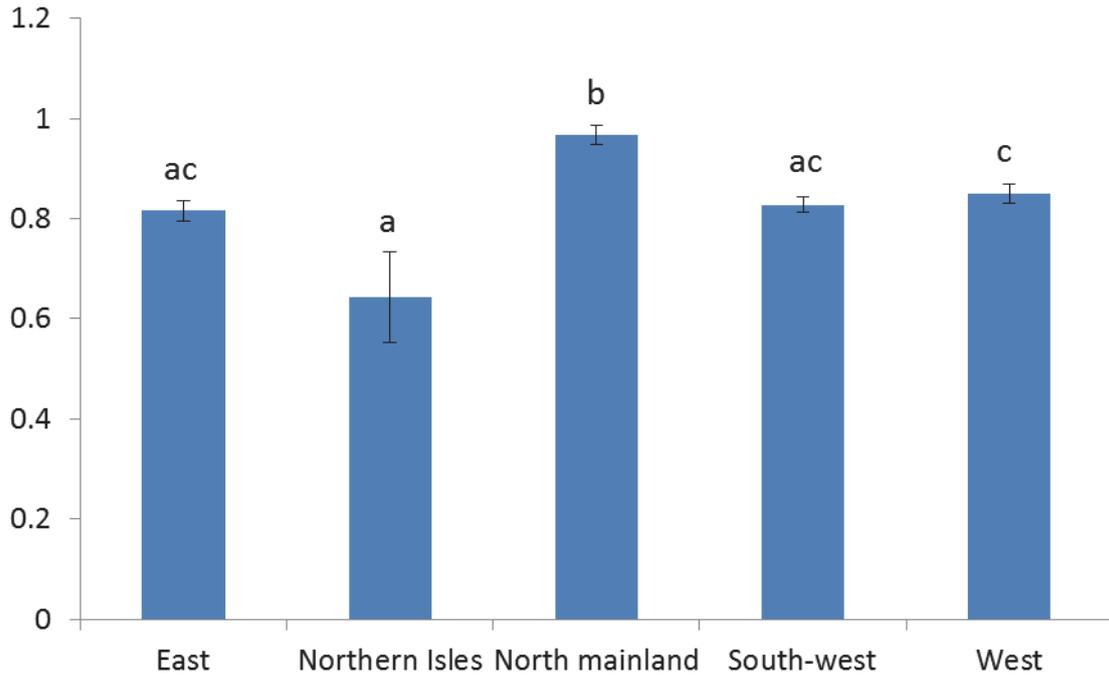


Figure 2i. 1 Mean success (proportion of breeding pairs successfully fledging one or more young) for ravens in five parts of Scotland. Letters above each bar denote statistical significance – the difference in productivity between regions that share a letter is not statistically significant. Error bars denote standard errors.

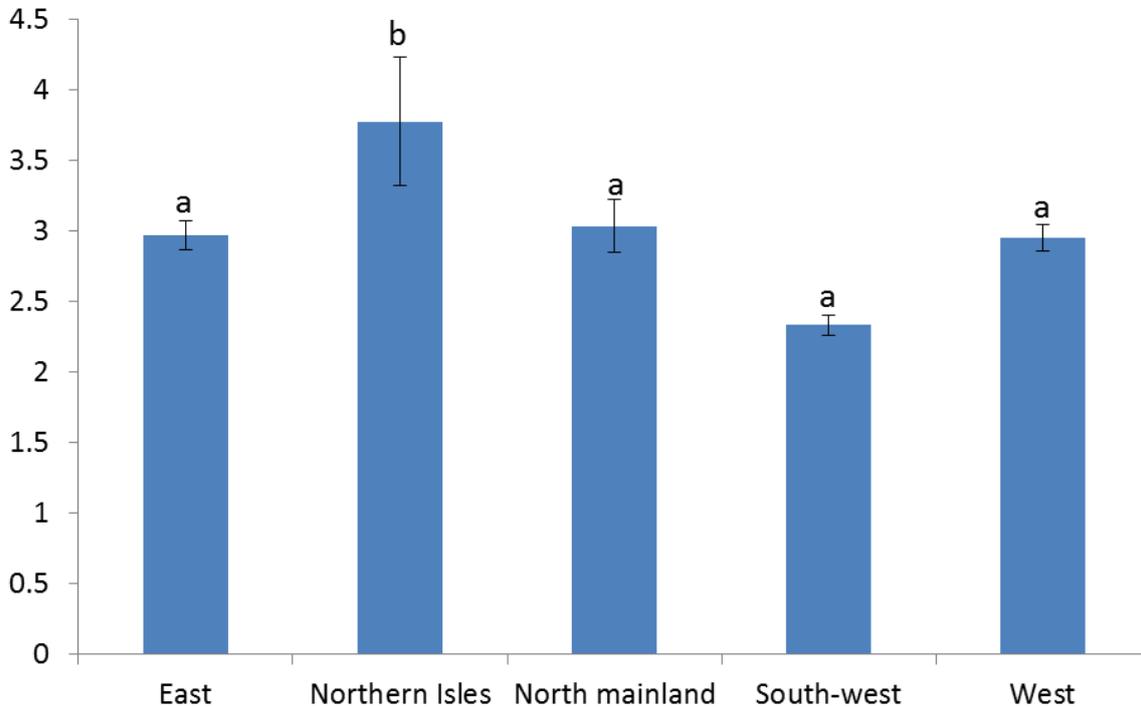


Figure 2i. 2 Mean fledged brood size for ravens in five parts of Scotland. Letters above each bar denote statistical significance – the difference in productivity between regions that share a letter is not statistically significant. Error bars denote standard errors.

ANNEX 3: POPULATION SCENARIOS AND SENSITIVITY ANALYSES

More detail is provided here on population trajectories of birds under density independent scenarios.

Density Independence

The impact of the different licensed control scenarios varied between the Baseline and Low Recruitment populations. In the growing Baseline population, with no density dependent regulation of adult survival, the population continued to expand rapidly with up to 230 non-breeding birds removed from the population (Figure 3i.1). In contrast, in the Low Recruitment population, removal of non-breeding birds prompted the population to decline, and with more than 200 non-breeding birds removed the population went extinct after 50 years (Figure 3i.2). In both cases, similar patterns were repeated for both the breeding and non-breeding birds.

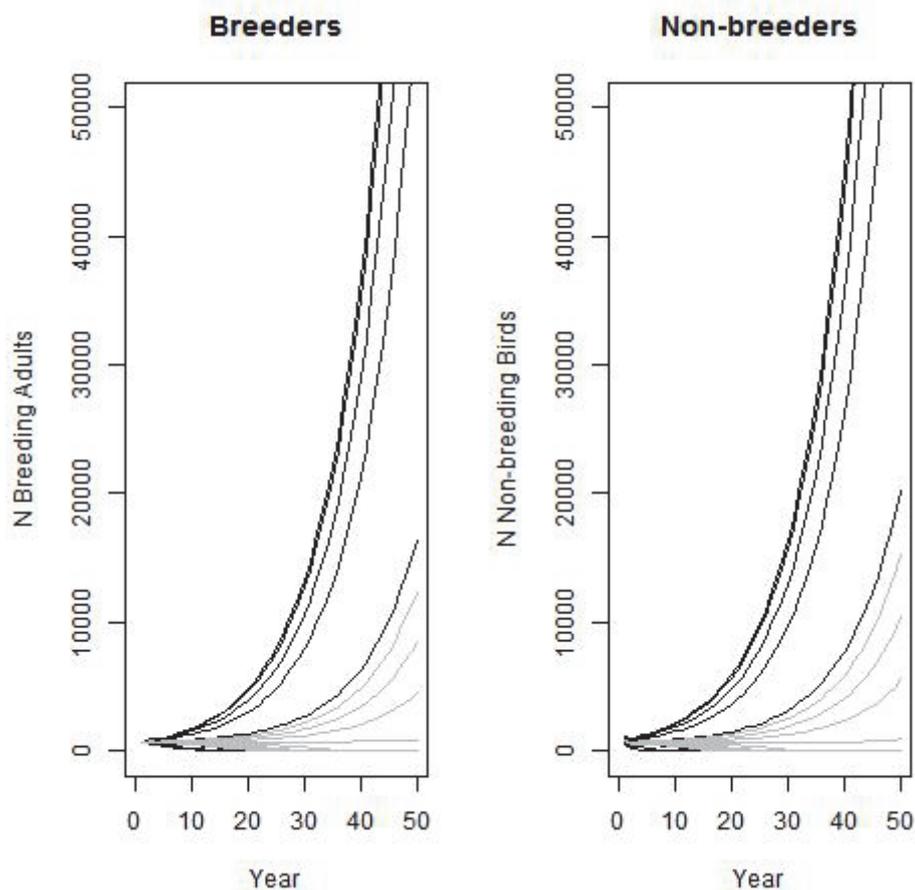


Figure 3i. 3 Impact of licensed control on the Baseline population, assuming no density dependent regulation of adult survival and that all adult birds breed. From top to bottom, black lines reflect licensed control scenarios of 0, 10, 50, 100, 200, 300, 400 & 500 non-breeding birds culled and grey lines, used to refine estimates on the number of birds that can be sustainably culled, indicate 210, 220, 230, 240, 250, 260, 270, 280 and 290 non-breeding birds culled.

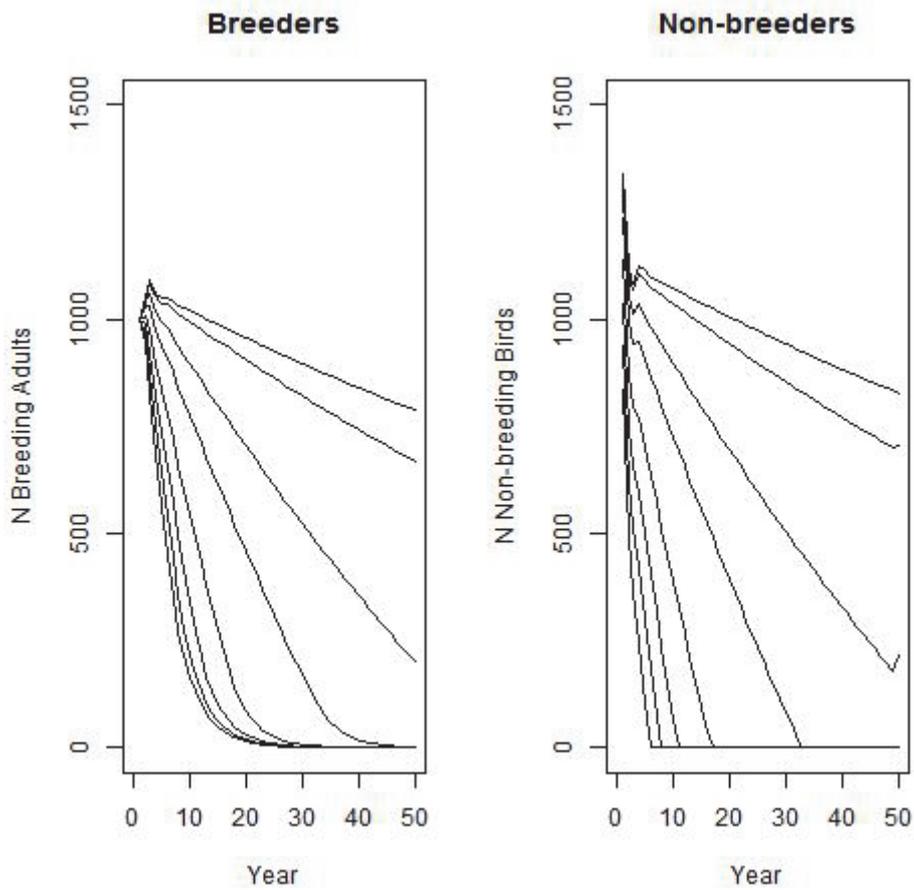


Figure 3i. 4 Impact of licensed control on the Low Recruitment population, assuming no density dependent regulation of adult survival and that all adult birds breed. From top to bottom, lines reflect licensed control scenarios of 0, 10, 50, 100, 200, 300, 400 and 500 non-breeding birds culled.

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