



Llywodraeth Cynulliad Cymru  
Welsh Assembly Government  
CORFF NODDEDIG SPONSORED BODY



Cyngor Cefn Gwlad Cymru  
Countryside Council for Wales

## **Hen harrier population studies in Wales**

**D. Philip Whitfield & Alan H. Fielding**

**CCW Contract Science No. 879**

© CCGC/CCW 2009

You may reproduce this document free of charge for non-commercial and internal business purposes in any format or medium, provided that you do so accurately, acknowledging both the source and Countryside Council for Wales's copyright, and do not use it in a misleading context.

This is a report of research commissioned by the Countryside Council for Wales. However, the views and recommendations presented in this report are not necessarily those of the Council and should, therefore, not be attributed to the Countryside Council for Wales.

**Report series:** CCW Contract Science  
**Report number:** 879  
**Publication date:** April 2009  
**Contract number:** FC 73-01-542  
**Contractor:** Natural Research (Projects) Ltd  
**Contract Manager:** Dr S.C. Whitehead  
**Title:** **Hen harrier population studies in Wales**  
**Author(s):** **D.P. Whitfield & A.H. Fielding**  
**Restrictions:** None

**Distribution list (core):**

CCW HQ Library, Bangor	National Library of Wales
CCW North Region Library, Mold	British Library
CCW North Region Library, Bangor	Welsh Assembly Government Library
CCW S&E Region Library, Cardiff	Joint Nature Conservation Committee Library
CCW S&E Region Library, Llandrindod	Scottish Natural Heritage Library
CCW West Region Library, Aberystwyth	Natural England Library

**Distribution list (others):**

Dr Siân Whitehead, CCW Bangor  
Arfon Hughes, CCW North Region  
Bethan Beech, CCW North Region  
Fiona Evans, CCW North Region  
RSPB Cymru, Maes y Ffynnon, Bangor  
Ian Spence, Wales Raptor Study Group  
Keith Offord, Wales Raptor Study Group  
Pete Roberts, Wales Raptor Study Group  
Ian Evans, Wales Raptor Study Group  
Iolo Williams, Wales Raptor Study Group

**Recommended citation for this volume:**

Whitfield, D.P. & Fielding, A.H. 2009 Hen harrier population studies in Wales. CCW Contract Science Report No: 879, 42pp, CCW, Bangor.

**CONTENTS**

	Page
List of Figures .....	iii
List of Tables .....	iv
Crynodeb Gweithredol .....	vi
Executive Summary .....	ix
Introduction .....	1
Project Objectives .....	1
Metapopulation dynamics .....	1
Recommendations for future work and monitoring methods .....	2
Methods .....	3
Source material .....	3
Field methods .....	3
Study areas .....	3
Harrier survey .....	4
Nest visits .....	4
Resightings of tagged birds and male traits .....	5
Weather data .....	6
Analysis .....	6
Breeding statistics .....	6
Age at first breeding .....	6
Dispersal and survival of full grown birds .....	7
Population modelling .....	8
Results .....	10
Population abundance .....	10
Breeding statistics and productivity .....	10
Breeding failure .....	12
Sex ratio at fledging .....	16
Replacement clutches .....	17
Polygyny .....	18
Age at first breeding .....	19
Dispersal .....	20
Natal dispersal .....	20
Breeding dispersal .....	22
Survival of full-grown birds .....	23

**CONTENTS (continued)**

	Page
Population modelling .....	26
Discussion .....	27
Recommendations for future work and monitoring methods .....	30
Principles and surveillance goals .....	30
Favourable condition of the Welsh harrier population .....	31
Potential monitoring methods .....	32
Recommended future monitoring methods .....	33
Acknowledgements .....	36
References .....	37
Appendix 1: Source Material .....	42

## LIST OF FIGURES

**Fig. 1.** *10 km grid squares in Wales with potentially suitable habitat for breeding hen harriers, as identified during the 2004 national survey (Sim et al. 2007).*

**Fig 2.** *Locations of Berwyn (to the east) and Migneint (to the west) SPAs in north Wales.*

**Fig. 3.** *Annual estimates of the number of female hen harriers occupying a territory in Wales.*

**Fig. 4.** *Annual estimates of mean ( $\pm$  SD) clutch size of hen harriers in Wales, with the three year moving average (red line).*

**Fig. 5.** *Annual estimates of breeding productivity (fledglings per breeding attempt) of hen harriers in Wales, and the three year moving average (thin line).*

**Fig. 6.** *Annual estimates of the number of hen harrier breeding failures where human interference was implicated, expressed per breeding attempt.*

**Fig. 7.** *Annual estimates of the number of hen harrier breeding failures where predation (usually by fox) was implicated, expressed per breeding attempt.*

**Fig. 8.** *Frequency histogram for natal dispersal distance in Welsh female hen harriers, classed in 5 km bins. The single record over 35 km involved a c180 km dispersal to a breeding site in northern England.*

**Fig. 9.** *Compass directions of natal dispersal movements in 14 Welsh male and female hen harriers (measured from natal to breeding site).*

## LIST OF TABLES

**Table 1.** *Annual estimates of fledging rate (number of fledglings per breeding attempt: see Whitfield et al. 2008a), and fecundity rates used in (female-only) Leslie matrix Model 1 and Model 2, after correction for sex ratio at fledging and empirical 'observed' breeding replacement rates (Model 1) and assumed correction for observed and unobserved breeding replacement clutches (Model 2): see text for details.*

**Table 2.** *Descriptive statistics for measures of breeding performance in Welsh hen harriers by time period: Y per attempt = fledglings per breeding attempt, Y per attempt eggs = fledglings per attempt when egg-laying recorded, Y per success attempt = fledglings per successful attempt, Prop attempt lay = proportion of breeding attempts for which egg-laying recorded, Prop attempts success = proportion of all breeding attempts which were successful, Prop eggs success = proportion of breeding attempts for which egg-laying recorded which were also successful. Results of t-tests contrasting the two periods 1986-1996 and 1997-2004 are also presented.*

**Table 3.** *Number of breeding attempts 1990-1995 which were recorded as being on ground which was managed by gamekeepers (= gamekeeper) or not managed by gamekeepers (= no gamekeeper) and numbers of these breeding attempts which were recorded as having failed due to predation or having failed due to human interference.*

**Table 4.** *Annual estimates of numbers of hen harriers fledged in Wales, the number of fledglings which were wing-tagged, and the numbers of tagged birds which were female (F) and male (M): estimated proportions of fledged birds of each sex which were tagged are given in parentheses. \* For 1990-1995 numbers of each sex which fledged was estimated by  $(F \text{ or } M) \text{ tagged} + (N \text{ fledged} - N \text{ tagged})/2$ : if the resulting calculations gave 0.5 of a bird to each sex, then 1 was assigned to males and 0 to females to reflect the apparent sex bias in tagged birds. Values for 1996-2004 are observed samples. \*\* Totals for all years include numbers observed in tagged birds from 1990-1995, and not from overall annual estimates in those years.*

**Table 5.** *Estimated numbers of: territorial females, nesting attempts, individual females which nested, and nesting attempts which were relay (replacement) attempts.*

**Table 6.** *Numbers of territories where male pairing status was judged and numbers of males considered monogamous (paired with one female) and polygynous (paired with more than one female: in all cases, two). Totals are broken down for years when estimates of survival were derived and for all years when pairing status data were available, and values in brackets are percentages.*

**Table 7.** *Age of first recorded breeding for six wing-tagged males and eighteen wing-tagged females. Proportions are shown in parentheses. \* A bird with the same cohort tags (not individually identified) occurred at the same site in the preceding year, so this bird likely first bred at age 2 years. \*\* Does not include a bird identified as breeding in England when three years old.*

**Table 8.** *Numbers of territorial paired males which were aged on plumage and numbers which were classed as having grey 'adult' plumage or as having brown 'subadult' plumage. Grey plumaged birds were assumed to be at least two year old (at least third calendar year) and brown plumaged birds were assumed to be one year old (second calendar year). Grey birds included 'saddleback' males with some brown mantle feathers and sometimes with brown tail feathers, which were assumed to be two year old (third calendar year). Brown (or 'ringtail') males often had some grey in the plumage. Displaying and apparently unpaired birds known or considered to be male were not included.*

**Table 9.** *Numbers of hen harriers which were wing tagged 1990-1995 and known or presumed to have fledged, according to sex and parts of the study area (see Offord (2002) for divisions of Berwyn and Migneint SPAs). Numbers of tagged birds fledged does not include three males (one each in 1991, 1993 and 1995) which were tagged but found dead before fledging.*

**Table 10.** *Natal dispersal in relation to the two main breeding areas of Welsh hen harriers, Berwyn and Migneint. \* Includes one bird originating at a site north of Migneint. \*\* Includes one bird breeding at a site north of Migneint.*

**Table 11.** *Matrices for a) females and b) males showing for each cohort of wing-tagged birds the numbers which fledged (in bold) and which were subsequently resighted on the breeding grounds in each year. Cells were left blank when it was not possible from available information to attribute any resightings or lack thereof to a particular cohort. \* = minimum number of birds. Resightings of birds in the non-breeding season did not alter the values for numbers of birds known to be alive in each breeding season, largely because sightings of known individuals were few after a birds' first winter.*

**Table 12.** *Minimum numbers of birds checked for wing tags in relation to the estimated number of territorial birds as a basis for estimating the annual proportion of birds which were checked for tags. The estimated number of tagged birds which was missed was derived from:  $C = (B/A - B) - N$  birds known to have been missed at breeding age (because seen in a subsequent year: see Table 11). \* For males due to 0 observed tags in some years, annual estimates could not be derived and so an overall estimate was obtained using summed values for the years 1992-1995 (1991 excluded as males first breed at age 2 and 1990 was first year of nestling tagging). Note that for males this exercise does not account for those cases of known polygyny (Table 6). Higher proportions of territorial birds may have been checked because records of tagged birds exceeded those given here (hence disparities with Table 11), although at least some of these records did not apparently involve breeding birds.*

## CRYNODEB GWEITHREDOL

1. Mae'r adroddiad hwn yn disgrifio ymchwiliadau i ddemograffeg a dymameg poblogaethau bodaod tinwyn *Circus cyaneus* yng Nghymru. Roedd yr ymchwiliadau'n seiliedig ar ddata hanesyddol o arolygon poblogaeth, ymweliadau â nythod a rhaglen dagio adenydd cywion a gynhaliwyd ym 1990-1995.
2. Ychydig o samplau oedd ar gael er mwyn amcangyfrif nifer o werthoedd paramedrau demograffig drwy ail-weld adar â'u hadenydd wedi'u tagio. Roedd hyn yn anorfod gan fod y 'boblogaeth' yng Nghymru'n gymharol fach a chan na chafodd cymaint o waith coladu cofnodion ail-weld adar ei wneud ar ôl i'r tagio ddod i ben ym 1995.
3. Roedd 'poblogaeth' bodaod tinwyn Cymru'n ymddangos yn gymharol sefydlog mewn tua 24 o diriogaethau a ddefnyddid ganddynt am gyfran helaeth o'r 1980au hwyr a'r 1990au, ac roedd ar gynnydd ar ôl y flwyddyn 2000. Yn ôl y cyfrifiad diweddaraf sydd ar gael, a gynhaliwyd yn 2006, roedd tua 45 o diriogaethau'n cael eu defnyddio gan fodaod tinwyn.
4. Casglwyd yr amcangyfrifon o gynhyrchiant bridio a llwyddiant wrth fridio dros nifer o flynyddoedd, ac roeddent yn weddol debyg i'r amcangyfrifon a oedd wedi'u cyhoeddi cyn hynny. Roedd y cyfnod o gynnydd yn y boblogaeth, a ddechreuodd yn y 1990au hwyr, yn gysylltiedig â chynnydd mewn cynhyrchiant bridio. Roedd nifer yr wyau mewn un eisteddiad ar ei isaf pan oedd y boblogaeth ar gynnydd, ac mae hynny'n awgrymu nad yw'r bwyd a oedd ar gael cyn dodwy'n debygol o fod yn gyfrifol am y cynnydd a welwyd yn ddiweddar yn nifer yr adar magu.
5. Ysglyfaethu (gan lwynogod coch) ac ymyrraeth dyn oedd y rhesymau a gofnodwyd amlaf dros fethiant i fridio. Roedd yr ymyrraeth yn gysylltiedig â nythod ar y ddaear lle cyflogid ciperiaid, ond ymddengys bod hynny wedi dod i ben ar ôl y 1990au hwyr, a gwelwyd cynnydd mewn cynhyrchiant ac yn nifer y poblogaethau. Nid oedd yn ymddangos bod unrhyw gysylltiad rhwng ysglyfaethu a phresenoldeb neu absenoldeb ciperiaid.
6. Dangosodd dadansoddiadau amlamrywedd fod cyfraniadau annibynnol nifer o baramedrau eglurhaol i amrywiad y gellid ei egluro mewn cynhyrchiant bridio fel a ganlyn: ymyrraeth dyn (40.5%), tymheredd uchaf mis Mai (36.9%), tymheredd isaf mis Ebrill (15.5%), nifer yr wyau mewn eisteddiad (5.1%) ac ysglyfaethu (2.0%). Dangosodd dadansoddiadau fod cydberthynas arwyddocaol rhwng cynhyrchiant bridio ac ymyrraeth dyn (negyddol) a thymheredd mis Mai (cadarnhaol). Felly, gellid priodoli'r cynnydd a welwyd yn ddiweddar mewn cynhyrchiant bridio gan mwyaf i lai o ymyrraeth gan ddyn (ciperiaid gan mwyaf yn ôl pob golwg) a thywydd cynhesach tua diwedd y gwanwyn.
7. Dangosodd achosion o ail-weld adar â'u hadenydd wedi'u tagio fod yr oed canolrifol ar gyfer magu am y tro cyntaf yn flwydd ar gyfer benywod a dwyflwydd ar gyfer gwrywod. Cadarnhaodd plu gwrywod magu mai ychydig o wrywod oedd yn magu yn ystod eu blwyddyn gyntaf. Ymddengys nad yw amlweddogrwydd (un gwryw yn paru gyda nifer o fenywod) yn gyffredin.
8. Roedd gwasgariad genedigol (symudiad rhwng safle genedigol a safle bridio cyntaf) yn fwy na gwasgariad bridio (symudiad rhwng safleoedd bridio olynol). Roedd y pellter gwasgariad genedigol canolrifol oddeutu 18 km mewn benywod, ac nid oedd unrhyw gyfyngiadau amlwg ar symudiadau rhwng y ddwy brif ardal fridio yng Nghymru, sef y Berwyn a'r Migneint. Roedd yn ymddangos bod rhywfaint o wasgaru i ardaloedd y tu

hwnt i Gymru, ond mae'n debyg nad oedd llawer o hynny. Roedd y pellter gwasgaru ar gyfer gwrywod yn llai nag ar gyfer benywod, er mai ychydig o wrywod wedi'u tagio oedd wedi cael eu hail-weld. Mae'n debyg bod hyn oherwydd ei bod yn anodd i wylwyr weld tagiau ar wrywod.

9. Roedd yr amcangyfrifon o oroesiad ymddangosiadol ( $\approx$  gwir oroesiad + allfudiad net) o reidrwydd yn syml, ond yn achos benywod roeddent yn dangos gwerthoedd tebyg i amcangyfrifon a gyhoeddwyd mewn rhannau eraill o'r Deyrnas Unedig. Amcangyfrifid bod cyfraddau goroesiad blynyddol benywod yn 0.362 ar gyfer y blynyddoedd cyntaf ac yn 0.774 ar gyfer adar hŷn.
10. Yn dilyn hynny defnyddiodd matricesau Leslie penderfynedig (rhagamcanu poblogaeth) a modelau poblogaeth ULM stocastig fesurau paramedrau demograffig deilliadol i ragfynegi niferoedd yr adar magu, er mwyn eu cymharu â nifer yr adar magu a welwyd. Roedd y modelau'n ymwneud â menywod yn unig, gan ei bod yn anodd cael gwerthoedd paramedrau dibynadwy ar gyfer gwrywod. Roedd rhagamcanion y modelau'n cyfateb yn dda i nifer yr adar magu a welwyd a'u newid yn ystod cyfnod yr astudiaeth, ac yn dangos bod amcangyfrifon y paramedrau'n ddibynadwy. O fewn ystod y mesurau demograffig empirig, ni ddiflannodd poblogaeth y bodaod tinwyn a fodelwyd yng Nghymru mewn unrhyw un o'r efelychiadau stocastig.
11. Dangosodd mesurau hyblygrwydd mai cyfraddau goroesi oedd y paramedrau demograffig a allai gael y dylanwad mwyaf ar nifer yr adar magu. Roedd y gyfradd atgenhedlu yn cael ychydig bach mwy o ddylanwad ar nifer yr adar magu nag mewn adar ysglyfaethus mwy, yn unol â'r disgwyl, ac awgrymodd y modelau y gellir egluro'r cynnydd a welwyd yn ddiweddar yn nifer y bodaod tinwyn yng Nghymru yn gyfan gwbl drwy gyfeirio at y cynnydd mewn cynhyrchiant bridio. Felly, mae'n debyg mai canlyniad diwedd ymddangosiadol ymyrraeth dyn, a thywydd cynhesach yn y gwanwyn yn cynyddu cynhyrchiant cywion, yw'r cynnydd a welwyd yn ddiweddar ym mhoblogaeth bodaod tinwyn Cymru.
12. Tynnir sylw at asesiad a wnaethpwyd yn ddiweddar o statws cadwraeth bodaod tinwyn yng Nghymru (Fielding et al. 2008). O'r tri maen prawf er mwyn barnu 'cyflwr ffafriol', cafodd un ei basio (cyfradd atgenhedlu) a methwyd dau (% defnyddio cynefin addas a dwysedd bridio). Mae Fielding et al. (2008) a'r astudiaeth bresennol yn nodi y dylai'r boblogaeth yng Nghymru basio'r tri maen prawf yn y dyfodol, yn y tymor canolig, os bydd y tueddiadau a welwyd yn ddiweddar yn parhau. Mae'r astudiaeth bresennol yn cadarnhau y dylai'r targed sylfaenol ar gyfer cynhyrchiant bridio blynyddol cyfartalog fod yn 1.2 cyw ar gyfer pob pâr sy'n defnyddio tiriogaeth.
13. Nodir blaenoriaethau ar gyfer gwaith monitro yn y dyfodol sy'n darparu amcangyfrifon o faint a dosbarthiad y boblogaeth fridio ac, yn ail, yn cadw golwg ar y paramedrau demograffig sy'n cael y dylanwad mwyaf ar faint poblogaeth. Nid ydym yn rhoi pwyslais cryf ar sicrhau bod cadw llygad ar oroesiad yn cael mwy o flaenoriaeth na chadw llygad ar atgenhedliad. Mae'r potensial gan oroesiad i gael mwy o ddylanwad ond, heb erledigaeth, ymddengys nad yw mor newidiol â chyfradd atgenhedlu, sydd mewn astudiaethau achos yn y DU yn ddiweddar wedi cael cryn dipyn o effaith ar dueddiadau ym mhoblogaeth bodaod tinwyn.
14. Mae dulliau monitro'n cael eu hystyried a'u hadolygu. Mae'r dulliau 'sylfaenol' sydd y tu ôl i'r astudiaeth bresennol yn darparu ar gyfer mesur, a thrwy hynny fonitro, niferoedd bridio a dosbarthiad, a chyfraddau atgenhedlu. Argymhellir bod y dulliau hyn yn dal i

gael eu gweithredu yn y dyfodol, a bod ymgais yn cael ei gwneud i gynnal cyfrifiad llawn bob tair blynedd o leiaf.

15. Bydd angen mwy o adnoddau er mwyn monitro goroesiad a gwasgariad, ac mae dau fath o ddull ar gael: mae un yn defnyddio tagiau unigol allanol ac mae'r llall yn defnyddio tagiau unigol mewnol (DNA). Disgrifir cryfderau a gwendidau sawl math o dag allanol: tag adeinbilen, tag radio a thag PIT. Mae'n ymddangos mai tagiau adeinbilen yw'r dewis sy'n cael ei ffafrio. Mae gan dagiau DNA nifer o fanteision o'u cymharu â thagiau adeinbilen, er enghraifft, nid ydynt mor fewnwithiol, maent yn barhaol, gellir eu hymgorffori'n rhwydd mewn gwaith monitro 'sylfaenol', a gellir storio samplau nes bydd eu hangen. Anfantais y tagiau hyn yw'r costau dadansoddi, ac mae'n bosibl bod mwy o anawsterau gyda'r dull wrth drin bodaod tinwyn nag wrth drin rhai rhywogaethau eraill o adar ysglyfaethus.
16. Nid oes bygythiad amlwg ar hyn o bryd i oroesiad bodaod tinwyn Cymru, ond mae'n syniad da monitro'u goroesiad gan y gallai'r sefyllfa newid yn y dyfodol. Nid yw tagiau adeinbilen yn ddelfrydol ar gyfer strategaeth fonitro benagored. Mae tagiau DNA yn fwy addas ond dim ond os gellir datrys diffygion posibl ar gyfer bodaod tinwyn. Yn y pen draw, yr adnoddau sydd ar gael fydd yn pennu a ddylid monitro goroesiad ai peidio a sut y dylid gwneud hynny.

## EXECUTIVE SUMMARY

1. This report describes investigations into the demography and population dynamics of Welsh hen harriers *Circus cyaneus*, using historical data from population surveys, nest visits, and a programme of wing tagging nestlings in 1990-1995.
2. Sample sizes for estimation of several demographic parameter values through resightings of wing tagged were limited, inevitably with a relatively small Welsh 'population' and because collation of resighting records declined after tagging stopped in 1995.
3. The Welsh harrier 'population' appeared to be relatively stable at around 24 occupied territories for much of the late 1980s and 1990s, before increasing in the 2000s. The latest available census, in 2006, estimated 45 occupied territories.
4. Estimates of breeding productivity and breeding success were derived across several years and were largely similar to previously published estimates. The period of population expansion, starting in the late 1990s, was associated with increased breeding productivity. Clutch size was lowest when the population was expanding suggesting pre-laying food availability was unlikely to explain the recent increase in the number of breeding birds.
5. Predation (largely by red foxes) and human interference were the most commonly recorded causes of breeding failure. Interference was associated with nests on ground where gamekeepers were employed, but appeared to cease in the late 1990s onwards, concomitant with an increase in both productivity and population abundance. Predation appeared to show no association with the presence or absence of gamekeepers.
6. Multivariate analyses indicated that the independent contributions of several explanatory parameters to explained variation in breeding productivity were as follows: human interference (40.5 %), maximum May temperature (36.9%), minimum April temperature (15.5 %), clutch size (5.1 %) and predation (2.0 %). Analyses illustrated that breeding productivity was significantly correlated with human interference (negatively) and May temperature (positively). Thus, the recent increase in breeding productivity was largely due to reduced human interference (apparently mostly by gamekeepers) and warmer weather in late spring.
7. Resightings of wing tagged birds showed median age of first breeding was one year old for females and two year old for males. Plumage of breeding males confirmed that few males first bred in their first year. Polygyny (one male paired with several females) was apparently unusual.
8. Natal dispersal (movement between natal site and first breeding site) was greater than breeding dispersal (movement between successive breeding sites). Median natal dispersal distance was around 18 km in females, with no obvious restrictions on movement between the two main Welsh breeding areas, Berwyn and Migneint. Some dispersal apparently involved areas beyond Wales, but was probably minimal. Dispersal distance for males was lower than for females, though there were relatively few resightings of tagged males. This was probably a result of the difficulty in observers seeing tags on males.
9. Estimates of apparent survival ( $\approx$  true survival + net emigration) were necessarily crude, but for females indicated values similar to published estimates elsewhere in the UK.

Female annual survival rates were estimated at 0.362 for first-years and 0.774 for older birds.

10. Deterministic Leslie (population projection) matrices and stochastic ULM population models then used derived measures of demographic parameters to predict numbers of breeding birds, for comparison with observed numbers of breeding birds. Models were female-only, due to difficulty in obtaining some reliable parameter values for males. Model predictions provided a good match to observed numbers of breeding birds and their change over the study period, indicating parameter estimates were reliable. Within the range of empirically derived demographic measures, the modelled Welsh harrier population did not become extinct in any of the stochastic simulations.
11. Derivation of elasticity measures showed that survival rates were potentially the most influential demographic parameters on numbers of breeding birds. Reproductive rate was comparatively more influential on numbers of breeding birds than in larger raptors, as expected, and modelling suggested that the recent increase in Welsh harrier numbers can be explained entirely by increased breeding productivity. Therefore, the recent increase in the Welsh harrier population is probably a result of the apparent cessation of human interference and warmer spring weather increasing the production of fledglings.
12. A recent assessment of the conservation status of Welsh hen harriers (Fielding et al. 2008) is highlighted. Of the three criteria to judge 'favourable condition', one was passed (reproductive rate) and two were failed (% occupation of suitable habitat and breeding density). Fielding et al. (2008) and the present study point out that if recent trends continue the Welsh population should pass all three criteria in the medium term future. The present study confirms that a minimum target for average annual breeding productivity should be 1.2 fledglings per pair occupying a territory.
13. Priorities for future monitoring are identified which provide estimates of size and distribution of the breeding population and, secondarily, surveillance of the demographic parameters which are most influential on population abundance. We do not place a strong emphasis on survival surveillance having a higher priority than reproduction surveillance. Survival potentially has a greater potential influence but, in the absence of persecution, appears to be less variable than reproductive rate which in recent UK case studies has markedly affected hen harrier population trends.
14. Monitoring methods are considered and reviewed. The 'basic' methods behind the present study provide for measuring, and thereby monitoring, breeding numbers and distribution, and reproductive rates. It is recommended that these methods are continued in the future, with a full census being attempted at least every three years.
15. More resources will be needed to monitor survival and dispersal, and two types of methods are available: one involves external individual tags and the other utilises internal individual (DNA) tags. Strengths and weaknesses are described for several types of external tags: patagial wing tags, radio tags and PIT tags. Patagial wing tags are seen to be the preferred option. DNA tags have several advantages over patagial wing tags, notably that they are less invasive, permanent, can be incorporated easily into 'basic' monitoring, and samples can be stored until needed. Their disadvantage is in cost of analysis and the method may have more difficulties for harriers than some other raptor species.

16. There is no obvious current threat to Welsh harrier survival, although monitoring survival is desirable as it may change in the future. Patagial wing tags are not ideally suited to an open-ended monitoring strategy. DNA tags are better-suited but only if potential shortcomings for harriers can be resolved. Ultimately, the decision on whether and how survival should be monitored is dictated by resources.

## 1 INTRODUCTION

Hen harrier *Circus cyaneus* is listed on Annex 1 of the EC Birds Directive, red-listed at the UK and Welsh level (Gregory et al. 2002, Thorpe & Young 2003), and is a WAG Species of Principle Importance for Conservation of Biological Diversity (Section 42, Natural Environment & Rural Communities Act 2006). Ongoing surveys in Wales provide good data on population status within the three core breeding areas (two of which are Special Protection Areas (SPAs) for the species: Berwyn and Migneint-Dduallt), but there are apparently sparse data on bird movements and the relationship between the core areas, and with other breeding and non-breeding populations in other parts of the species' UK range. For a species that is rare, very localised, and dependent on good quality upland habitats, an understanding of metapopulation dynamics is fundamental to the adequate management of designated sites, and the wider landscape.

The present project was designed to review and use available data to increase understanding of the metapopulation dynamics of Welsh harriers and, on the basis of review, recommend further study and methods which may increase understanding still further. In particular, these recommendations refer to methods by which the population could be monitored in the future.

## 2 PROJECT OBJECTIVES

The objectives of the project specification are as follows:

- To review the existing data on population dynamics of hen harriers in Wales, with emphasis on the role of birds within the SPAs, in order to gain an understanding of the current status and prospects of Welsh harriers.
- To review methods which could be employed to monitor the population dynamics of Welsh harriers and recommend future approaches.

### 2.1 Metapopulation dynamics

1. What is the extent of breeding interchange in birds within Wales and between Wales and the rest of the UK?
2. Are there any marked patterns in breeding and/or natal dispersal?
3. Can any Welsh breeding sites be identified as sources or sinks?
4. Which population parameters are most influential on the status of Welsh harriers?
5. What are the future prospects of the hen harrier in Wales?

The first question refers to establishing the extent to which the group of birds which breed in Wales can be considered as a metapopulation, and so primarily refers to dispersal. The second, related, question requires quantification of natal and breeding dispersal within the Welsh 'metapopulation'. Question 3 effectively requires a quantification of the (meta)population dynamics of Welsh breeding harriers, because populations can be sources or sinks due to each of the key component demographic parameters. The fourth question requires assessment of potential environmental influences on harrier demographics and also an analysis of the role of different demographic parameters on population trends. Finally, the report considers, based on the most recent demographic data and population-trend available, what the future may hold for the hen harrier in Wales.

Most material relating to the first project objective has been accepted for publication in the peer-reviewed literature (Whitfield et al. 2008a, Fielding et al. in press), and so this report has had to accommodate issues pertaining to copyright and duplication concerning these publications. Nevertheless, the report does contain some material which was not appropriate for the peer-

reviewed papers. On the other hand the peer-reviewed papers should be referred to as complementary material that contains detail not presented here.

## **2.2 Recommendations for future work and monitoring methods**

A number of field methods are available to measure and, thereby monitor, the various parameters which contribute to understanding the dynamics of the Welsh harrier population. These include documenting breeding attempts, revisiting breeding attempts to record their fate (e.g. failed and cause of failure, or number fledged), ringing, wing-tagging, and the use of DNA “fingerprinting”, drawn from several potential sources of DNA, to use as ‘markers’ of individuals’ presence/absence. These methods are reviewed in terms of their value, efficacy, and cost-benefits in light of the current schemes already in place. The results of this review are contained in a final section (section 6) of this report.

### 3 METHODS

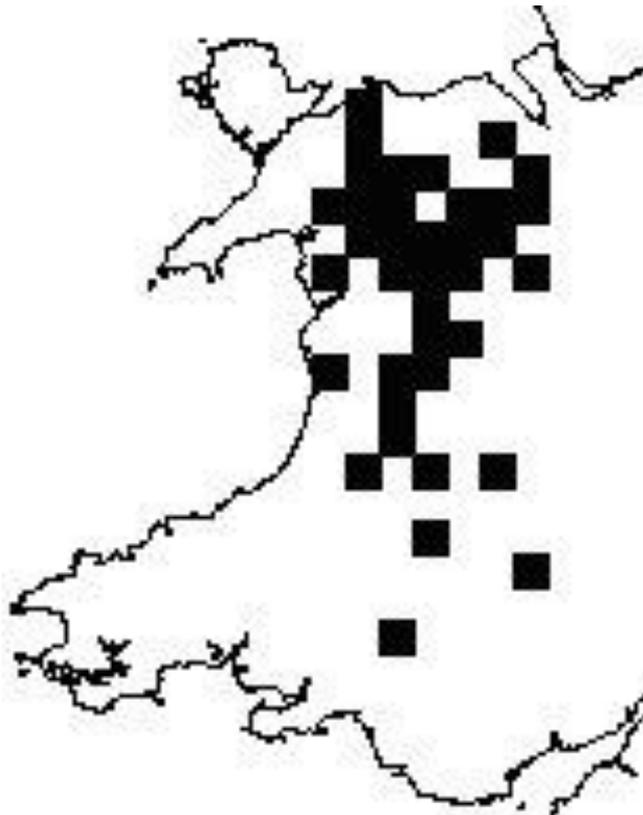
#### 3.1 Source material

Several source materials were collated and subjected to review and cross-validation; these are detailed in Appendix 1. Essentially, the available material involved the results of a programme of wing-tagging nestlings conducted 1990-1995, which was part of a wider UK programme (Etheridge et al. 1997), and the results of population monitoring and nest visits 1975-2006 (with effort becoming coordinated and attempting to cover all potential breeding areas from 1986 onwards). Data review for the two SPAs, Berwyn and Migneint, was undertaken by Offord (2002) and this information was supplemented by reports, nest record forms, and a collation of available nest record data by Andy Young, RSPB Wales.

#### 3.2 Field methods

##### 3.2.1 Study areas

The study was carried out in all potentially suitable upland habitats in Wales (Fig. 1), with particular emphasis on the main breeding areas, represented by the boundaries of the Berwyn and Migneint SPAs in north Wales (Fig. 2). Berwyn and Migneint were divided into three components (north, central, south) for the purposes of some analyses (Offord (2002) gives details of divisions). Studies were conducted from 1975 – 2006 (with occasional records from the late 1950s), although coordinated attempts to cover all potentially suitable breeding areas were not made until 1986.



**Fig. 1.** 10 km grid squares in Wales with potentially suitable habitat for breeding hen harriers, as identified during the 2004 national survey (Sim et al. 2007).



**Fig 2.** Locations of Berwyn (to the east) and Migneint (to the west) SPAs in north Wales.

### **3.2.2 Harrier survey**

From April to early August, areas of moorland and conifer forest plantations were searched for signs of breeding hen harriers and nests were located whenever possible, following methods outlined elsewhere (Bibby & Etheridge 1993, Sim et al. 2001, 2007). A territory was considered to be occupied if a pair was seen with any of the following traits:

- Display ('skydancing' or territorial aggression), or;
- Agitated behaviour (mobbing or alarm calling), or;
- Food 'pass' or carrying food, or;
- Any evidence of breeding (nest building, nest, eggs and/or chicks, remains of eggs or chicks)

A male and female seen together in potential breeding habitat, birds hunting or a single male or single female engaged in 'courtship' display (skydancing), were not considered evidence of occupation.

In 1990-1995 and at most occupied territories in subsequent years observers recorded several features of the territory, including a broad vegetation classification (heather moorland, young forest, thicket forest, mature forest) and whether the territory occurred on an estate which employed a gamekeeper or not (obtained during the process of gaining access permission).

### **3.2.3 Nest visits**

Once located, nests were typically visited and checked at intervals of 1 – 3 weeks to obtain information on the progress and fate of breeding attempts. At each visit the number of eggs and chicks in the nest, and the presence and behaviour of harrier parents were recorded. Whenever possible egg length and breadth were measured to 0.1 mm with dial callipers and egg mass was measured to 0.1g with a Pesola spring balance (although these data were not used in the present studies).

Observers recorded whether a breeding attempt was considered to be a replacement (relay) on the basis of timing of breeding, and if an attempt had failed and a new attempt was initiated nearby coincidentally. Such estimations in the field, sometimes without the benefit of appropriate information (Etheridge et al. 1997), should probably be regarded as minimal but can be refined with information on the timing of breeding (Etheridge et al. 1997). However, annual samples sizes for first egg dates in Welsh harriers were too small (between three and 15) to incorporate any annual variation in first egg dates and, hence, to estimate replacement attempts reliably. Our analyses involving changes in breeding productivity (reported in detail by Whitfield et al. 2008a) therefore primarily utilised the more reliable metric, number of breeding attempts.

When a breeding attempt failed, the contents of the nest were recorded and an area immediately around the nest was searched for evidence of the cause of failure. Broken eggshells with bill holes were taken to be evidence of egg predation by a bird, probably a crow *Corvus corone*. Partially eaten remains or ‘chewed’ feathers of the incubating female and/or nestlings were assumed to be evidence of predation by a mammal, whereas cleanly plucked feathers were assumed to be evidence of predation by a raptor. Any corroborative evidence of the predator involved, such as faeces, hair, feathers or distinctive scent, was also recorded. An empty nest or with eggshell fragments was considered to have failed for unknown reasons. Human interference or disturbance was implicated in failure if there was any evidence of a human having visited the nest around the time of failure; such evidence included footprints, vehicle tracks, shot parent harrier, trampled vegetation or nest contents, material tied to vegetation surrounding the nest (as a presumed marker) or other items left behind, such as wrappers or cigarette ends. A nest without any corroborative evidence for a cause of failure (e.g. an empty nest) was considered to have failed for unknown reasons.

When nestlings were 23 – 28 d old, they were sexed on iris colour (Balfour 1970), measured and ringed. Between 1990 and 1995 as many young as possible were marked with two patagial wing tags made from flexible PVC-covered nylon fabric, attached by nylon pins and washers. Colours of tags denoted sex and year of marking, and a letter or number painted on each tag provided unique identification.

Most nests with nestlings were visited around the time of fledgling to determine the number of fledglings produced. In the absence of any visits around fledging age, all nestlings were assumed to have fledged if they had reached ringing age.

### **3.2.4 Resightings of tagged birds and male traits**

All harriers were checked for wing tags in each of the years 1990 – 1997; such efforts in subsequent years were either lower or coordination of sightings was lower and in 1997 records of female resightings were usually by cohort rather than by individual. Presence or absence of tags, colours and, whenever possible, letter or number were recorded. Since letters and numbers were more difficult to record than colours, several resightings could only determine sex and year in which the bird had been marked.

Males were classed as either in first-year (second calendar year) or in adult (at least second-year or third calendar year) plumage according to having predominantly brown upperparts or grey and white upperparts respectively. Males recorded as having ‘saddleback’ plumage (grey upperparts with patches of brown feathers in the mantle and scapulars) and/or predominantly grey with brown in the tail were probably second-year birds and so were considered adults (Cramp & Simmons 1980, Bildstein 1988). Females could not be aged on plumage in the field.

Observers noted the occurrence of polygyny (one male paired with more than one female) when an individual male was obviously associated with more than one territory-occupying female (e.g.

seen to deliver food to more than one female). As no dedicated efforts were made to record polygyny, however (see Amar et al. (2005) for example), consequent estimates of polygyny occurrence should be regarded as minima and, likely, underestimates.

### **3.2.5 Weather data**

Meteorological Office weather data from 1980 to 2004 were obtained for Bala (52.9 N, 03.6 W), the town between Berwyn and Migneint SPAs. Monthly averages of daily records were compiled for April, May, June and July (approximating pre-laying, laying and incubation, and chick-rearing elements of the harrier breeding season) for maximum temperature and minimum temperature and, for rainfall, monthly total. Temperature data were missing for Bala in some months and so we used a fuller dataset from Valley, Anglesey (53.3 N, 04.5 W) about 60 km northwest of Migneint SPA, to complete the Bala data using predictive linear regressions: Bala max temp =  $-1.567 + (1.109 * \text{Valley max temp})$  ( $R^2 = 0.966$ ,  $n = 82$ ); Bala min temp =  $-2.968 + (1.061 * \text{Valley min temp})$  ( $R^2 = 0.967$ ,  $n = 82$ ).

## **3.3 Analysis**

### **3.3.1 Breeding statistics**

Clutch size was taken to be the number of eggs in a nest which had not increased since the previous nest visit or the recorded number of eggs in a nest that was probably at least half way through incubation.

In analyses involving examinations of reproductive output, as noted earlier (section 3.2.3), we did not account for replacement clutches. Breeding success was expressed as the number of fledglings produced per successful breeding attempt (an attempt in which at least one young was fledged) and breeding productivity was expressed as the number of fledglings per breeding attempt, including those from replacement attempts. We also calculated the proportion of breeding attempts for which egg-laying was recorded: this parameter will include genuine failures of females to lay eggs (a common feature in several raptor species: Newton 1979) and will also include recorded breeding attempts when failure occurred after egg-laying but egg-laying was not discovered.

In population modelling it was more important to account for replacement clutches (in both reproductive rates and number of females in the population), and this is described in more detail in the relevant section (3.3.4).

### **3.3.2 Age at first breeding**

The age when birds were first recorded breeding was available for six cohorts of birds (1990 – 1995) but the distributions of first observed breeding were effectively curtailed by insufficient resighting information after 1997. The effect of this curtailment will have been to prevent increasingly the detection of birds' first breeding when older for increasingly later cohorts so that, for example, birds first breeding when three years old from the (final) 1995 cohort would not have been recorded. This bias can be corrected for by, for example, estimating proportions of first breeding age using log-linear GLM models, with cohort and age effect as factors, and by comparing the proportions of birds breeding at age 2 – 5 years with those at 1 year old from natural logs of the coefficients of age effects (Etheridge et al. 1997). However, when few birds from the earliest cohorts were first recorded breeding at three years old or later (see Results), and when the main purpose of deriving values for this population parameter was to apply a modal or median value in population models (see also Etheridge et al. (1997) and Arroyo et al. (2002), for example), we felt that no correction of the likely small bias was necessary.

### 3.3.3 *Dispersal and survival of full grown birds*

Following Greenwood & Harvey (1982) we took natal dispersal to be the movement from the natal nest site to the nest site where breeding or territory occupation first took place, natal dispersal distance and direction being the straight line (Euclidian) distance and eight-point compass direction respectively from natal to breeding sites. Breeding dispersal was the movement between breeding/occupied sites in successive years, with dispersal distance measured as a straight line (Euclidian distance) between sites.

Dispersal was documented by appropriate records of the location of resightings of tagged birds. Documentation of dispersal required a higher level of tagged bird identification than for survival or (to a lesser degree) age of first breeding, since individually unique, and not just cohort, tag characteristics needed recording. Hence, available sample sizes reported for dispersal differed from those for other demographic parameters, such as survival, for example.

Estimates of survival utilised the results of the wing tagging programme. This inevitably involved small sample sizes. Survival estimates were made without the aid of statistical methods which attempt to account for dispersal and missed resightings (so that,  $N$  individuals resighted  $\neq$   $N$  individuals surviving), such as those described by Rothery (1985) and included within the program MARK (White & Burnham 1999). Resultant survival estimates, therefore, should be regarded as minima. Since sample sizes were small (as the Welsh harrier population is small), inevitably this would have resulted in extremely wide confidence limit/variance estimates of survival with, for example, use of MARK. Hence, statistical error/variance estimation was not deemed appropriate, given the project objective of estimating a set of demographic parameter estimates that were useful as judged by their performance in explaining the observed population changes.

In other words, our objective was to produce a model of the Welsh harrier population based on demographic parameter estimates whose performance we judged on how well they fitted the (independent) observed changes in the numbers of breeding birds. Consequently, borrowing from the terms of Altman & Royston (2000) we wished to produce a ‘clinically’ valid model, which was robust (or ‘useful’) in the sense that it provided an independent explanation of changes in the number of birds attempting to breed over time so that its fit was within reasonable observed limits. As Altman & Royston (2000) point out, the purpose of modelling is to produce a model which is actually independently useful when applied in practical circumstances, and ‘statistically valid’ methods are not always the best means to this end. In the present case it was obvious that due to small sample sizes a ‘statistically valid’ approach (e.g. via MARK) would have produced wholly unrealistic limits to survival estimates and so would not have been ‘clinically’ useful or satisfied the fundamental point of the modelling process. (Subsequent use of MARK with the Welsh harrier data confirmed these suppositions.)

Hence, apparent survival (= true survival – + ‘losses’ due to dispersal and ‘missed’ resightings) was estimated by constructing a simple cohort-based matrix for each sex (see Results: section 4.9) logging, in successive years (matrix columns) and for each cohort (matrix rows), the numbers of birds marked and minimum numbers of birds resighted. If a bird marked in year  $x$  was first seen in year  $x + 3$ , for example, then it was assumed to have been alive in years  $x + 1$  and  $x + 2$ .

For females, due to a shortage of specific tag resighting reports after 1995, we used only data from the 1990 – 1993 cohorts ( $N = 58$  birds tagged). For males, resighting rates were substantially lower than for females and generated ‘survival’ rates which, on face value and, after exploratory modelling, suggested that either there was a problem in observers seeing wing-tags on males, or that a substantial proportion of the male population was immigrant because

wing-tag sightings produced implausibly low survival rates. With no substantial subsidiary evidence for the latter possibility, the former explanation seemed most likely, as it was documented more thoroughly in a contemporaneous wing-tagging study of Scottish hen harriers (Etheridge et al. 1997, B. Etheridge pers. comm.). Therefore, we used only demographic data for females in population modelling.

Although we had greater confidence in resightings of tagged females, several factors potentially led to the underestimation of apparent survival rates in females, including dispersal beyond the study area limits (Baker et al. 1995), tag loss and missed resightings through not all birds being checked. Tag loss can probably be discounted as a serious bias because no birds were reported with only one tag, suggesting tag loss was minimal in influence. The extent of a potential bias resulting from incomplete census of the Welsh population for resightings can be crudely examined, at least for those years when tagging took place, from estimates of the proportion of birds which were checked for tags with reference to the number of tagged birds which were seen amongst checked birds. Hence, for period x:

$C = (B/A - B) - N$  birds known to have been missed in period x (because potentially available to be seen but only seen after period x), where

C = estimated number of tagged birds missed,

B = N tagged territorial birds seen, and

A = proportion of territorial birds checked for tags..... [equation 1]

### **3.3.4 Population modelling**

Initially, we employed both deterministic and stochastic Leslie (population projection) matrices (Caswell 2001) for females. Exploratory results were very similar between the two approaches and as empirical annual values of reproduction were available for many years we chose deterministic final models. Start conditions were assigned initially according to empirical parameter values or perturbations based on potential value variation, utilising the program POPTOOLS 2.6.9 (Hood 2002). POPTOOLS was also used to explore the relative importance of different demographic parameters on population growth through their elasticities (e.g. de Kroon et al. 2000, Heppell et al. 2000). Elasticity explores the effect of a proportional change in a contributory arc (= vital rate = demographic parameter in the transition matrix) on population growth rate, lambda, where the natural log of lambda = r, the intrinsic rate of increase and lambda is the equivalent of  $R_0$ , or net birth rate per individual (when lambda = 1, r = 0,  $R_0 = 1$  and a population is stable). Because the elasticities of a transition matrix sum to unity, they can be interpreted as the relative contributions of the matrix transitions to population growth i.e. the relative influence of proportional changes in different demographic parameters on population change and abundance. For derivation of elasticities we used a fixed fecundity rate of 0.75 female fledglings per territorial female (approximately the mean empirical rate as used in Leslie modelling) as survival rates were also fixed (see later).

As a starting point in our models we took an empirical breeding population in 1988 of 24 breeding females which had produced 12 female offspring. In setting the demographic parameter values for our models we generically assumed annual survival rates across all years of 0.362 for first-year birds (year 0 – 1) and 0.774 for older birds (year 1+), and that all birds first bred in their first year (see Results). In Model 1, for fecundity rates 1990 – 2004 we took empirical annual measures of fledgling rate (fledglings per breeding attempt: Whitfield et al. 2008a) x proportion of fledglings which were female (see Results) x mean attempts per female per year (1.08, 1990 – 1996; 1.04, 1997 – 2004). For 1989 fecundity rate we took the empirical fledgling rate x mean proportion of fledglings which were female 1990 – 1996 (0.466) x 1.08; and for fecundity rate 2005 onwards we used mean fledgling rate 1997 – 2004 (1.853) x mean

proportion of fledglings which were female 1997 – 2004 (0.47) x 1.04. In Model 2, we used revised correction factors for replacement attempts because in our first model we used field-observed values (1.08 or 1.04) and knew that these likely did not account for all replacements (Etheridge et al. 1997). As we could not calculate the rate of replacements using Etheridge et al.'s (1997) method, we simply used an approximate measure from Etheridge et al. (1997: Table 8, p. 1093) with a reduced rate 1997 onwards to reflect the higher breeding success then, and hence lower probability of replacement (1.2, 1989 – 1996; 1.1, 1997 onwards). Fecundity rates used in the two models are given in Table 1. (Justification for derivation and the use of all demographic parameter measures can be found in the Results section.) For both Model 1 and 2, outputs were predicted number of breeding (territorial) females per year.

A simplified three-stage stochastic model (ages 0 - 1, 1 - 2 and 2+) was also run in the ULM population modelling software (v4.0: Legendre & Clobert 1995). Survival rates were 0.362 for ages 0 - 1 and 0.774 for older birds, and fecundity rates were identical to those described in Table 1 (Model 1). In the Monte Carlo simulations (N = 1000), noise was added to each population parameter by sampling from beta distributions with means equal to Model 1 annual fecundity rates (Table 1) and equal to 0.362 or 0.774 for survival rates, and a standard deviation equal to 10% of the parameter values. An extinction threshold was set at 10 individuals (age 1+ females) i.e. we conservatively assumed that if the breeding population fell below 10 females it was liable to go extinct.

We modelled population predictions between 1988 and 2012 in all models. Our start-year was determined by when a full census of the Welsh population was first attempted (Whitfield et al. 2008a) and our end-date was determined, somewhat arbitrarily, by when we judged that population abundance estimates could be reasonably projected to the future, considering that the extent of suitable habitat for Harriers in Wales is relatively limited compared to other parts of the UK (Sim et al. 2007).

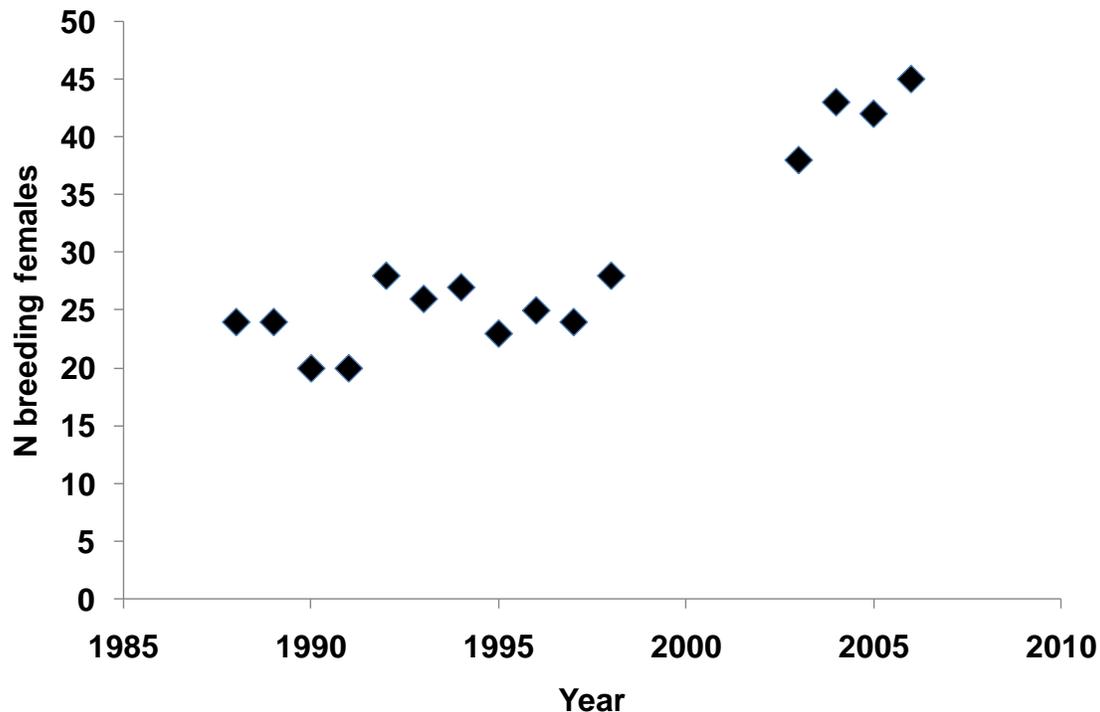
**Table 1.** Annual estimates of fledging rate (number of fledglings per breeding attempt: see Whitfield et al. 2008a), and fecundity rates used in (female-only) Leslie matrix Model 1 and Model 2, after correction for sex ratio at fledging and empirical 'observed' breeding replacement rates (Model 1) and assumed correction for observed and unobserved breeding replacement clutches (Model 2): see text for details.

Fledging				Fledging			
Year	rate	Model 1	Model 2	Year	rate	Model 1	Model 2
1989	0.71	0.36	0.40	2001	2.13	0.95	1.00
1990	1.25	0.74	0.82	2002	2.11	0.83	0.88
1991	1.80	0.94	1.04	2003	2.22	1.33	1.41
1992	1.96	0.75	0.83	2004	1.45	0.89	0.94
1993	1.42	0.90	1.00	2005	1.85	0.91	0.96
1994	0.85	0.25	0.27	2006	1.85	0.91	0.96
1995	0.83	0.48	0.53	2007	1.85	0.91	0.96
1996	1.04	0.56	0.62	2008	1.85	0.91	0.96
1997	1.29	0.55	0.58	2009	1.85	0.91	0.96
1998	1.93	1.29	1.37	2010	1.85	0.91	0.96
1999	1.79	0.93	0.98	2011	1.85	0.91	0.96
2000	1.91	0.47	0.49	2012	1.85	0.91	0.96

## 4 RESULTS

### 4.1 Population abundance

The results suggested that through the 1990s the Welsh harrier population was more or less stable at around 24 occupied territories with numbers having increased subsequently (Fig. 3).



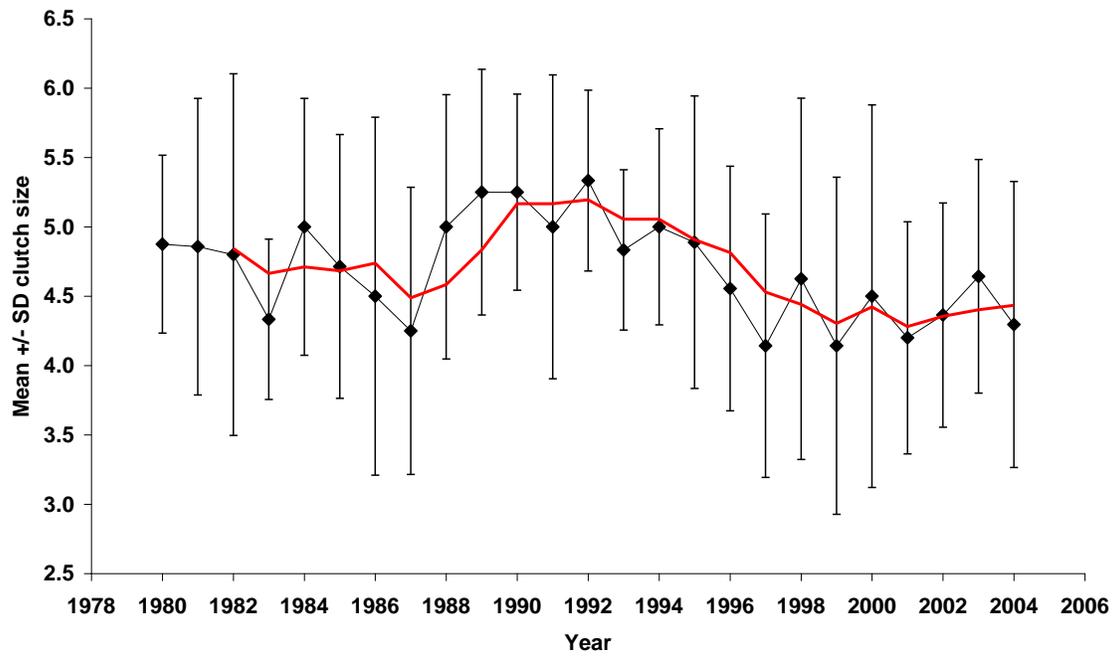
**Fig. 3.** Annual estimates of the number of female hen harriers occupying a territory in Wales.

### 4.2 Breeding statistics and productivity

Clutch size showed temporal trends across the study period, being highest in the late 1980s – early 1990s before falling to the lowest observed levels in the late 1990s – early 2000s (Fig. 4). Mean  $\pm$  SD clutch size was  $4.69 \pm 0.97$  (1980 – 2004,  $n = 236$ ),  $4.93 \pm 0.89$  (stable low population: 1986 – 1996,  $n = 106$ ,  $CV = 18\%$ ) and  $4.36 \pm 1.00$  (increasing higher population: 1997 – 2004,  $n = 92$ ,  $CV = 23\%$ ). Whitfield et al. (2008a) found no significant correlations between annual mean clutch size and annual measures of monthly weather variables.

Interestingly, the recent period of apparent population expansion since the late 1990s (Fig. 3) and recent increase in breeding productivity (Fig. 5) was accompanied by a period of relatively low clutch size (Fig. 4). Clutch size can be an indicator of pre-laying food availability in harriers (Simmons et al. 1986, Salamolard et al. 2000, Redpath et al. 2001, 2002a, Amar et al. 2003) and so this suggested that the increase in breeding

productivity was unlikely to be explained by increases in pre-laying food availability. Whitfield et al. (2008a) confirmed that clutch size had relatively little influence on breeding productivity (see later)



**Fig. 4.** Annual estimates of mean ( $\pm$  SD) clutch size of hen harriers in Wales, with the three year moving average (red line).

Summarised descriptive statistics for measures of reproduction are given in Table 2. Most measures of reproductive output were greater during 1997-2004, the period when the population was increasing (Fig. 3), than in 1986-1996, when the population was more-or-less stable (Table 2; Fig. 5).

**Table 2.** Descriptive statistics for measures of breeding performance in Welsh hen harriers by time period: *Y per attempt* = fledglings per breeding attempt, *Y per attempt eggs* = fledglings per attempt when egg-laying recorded, *Y per success attempt* = fledglings per successful attempt, *Prop attempt lay* = proportion of breeding attempts for which egg-laying recorded, *Prop attempts success* = proportion of all breeding attempts which were successful, *Prop eggs success* = proportion of breeding attempts for which egg-laying recorded which were also successful. Results of *t*-tests contrasting the two periods 1986-1996 and 1997-2004 are also presented.

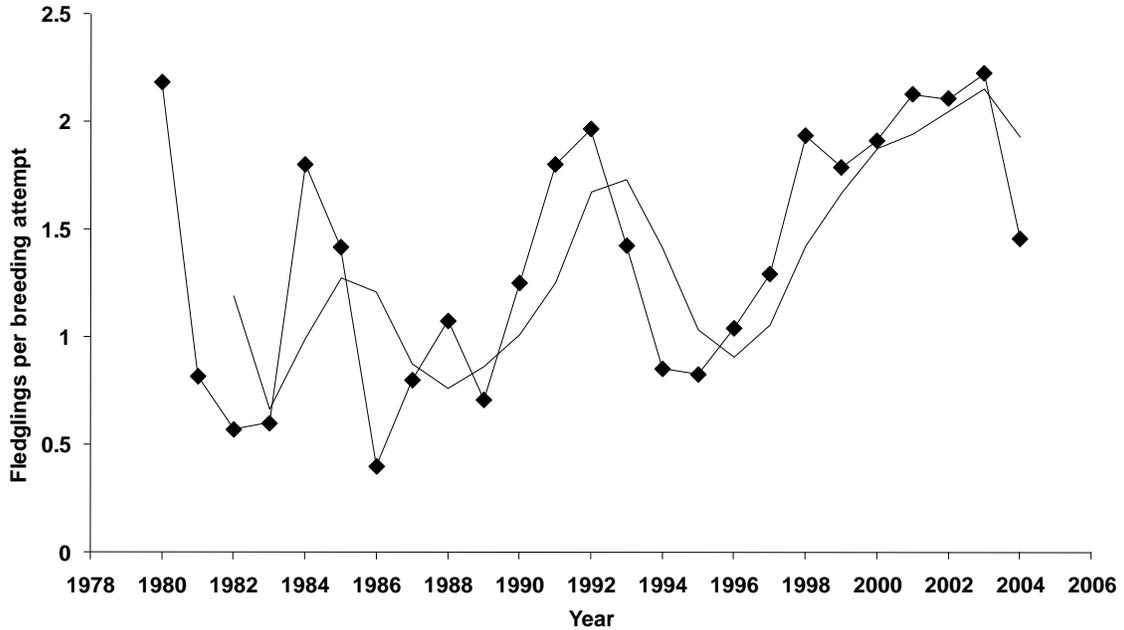
Period	Statistic	Y per attempt	Y per attempt eggs	Y per success attempt	Prop attempt lay	Prop attempts success	Prop eggs success
1986-1996	Mean	1.10	1.93	3.30	0.65	0.33	0.50
	SD	0.47	0.61	0.46	0.10	0.12	0.15
1997-2004	Mean	1.85	2.42	3.08	0.83	0.60	0.73
	SD	0.33	0.56	0.35	0.07	0.09	0.13
	t	-3.84	-1.54	1.09	-4.48	-5.42	-3.37
	P	0.001	0.143	0.290	<0.001	<0.001	0.004
1986-2004	Mean	1.42	2.14	3.21	0.73	0.44	0.60
	SD	0.56	0.70	0.43	0.12	0.17	0.18

### 4.3 Breeding failure

There were 87 documented nest failures where a cause of failure was not attributed (typically the nest was found empty). Of 86 failed attempts where a cause of failure was attributed, 51 nest losses were due to predation (including 20 to red fox, two to carrion crow and one to a raptor), 25 losses to human interference, five losses to eggs failing to hatch, four losses to nest desertion, and one to starvation of chicks. Hence, the two main attributed causes of breeding failure if eggs were laid were predation (usually by red fox *Vulpes vulpes*) and human interference (evidence varying from, for instance, shot female, trampled chicks in the nest, nest kicked out over surroundings, bootprints surrounding nest, and gamekeeper in possession of chicks).

Failure attributed to interference in the years 1990-1995 was significantly more likely to occur on ground where a gamekeeper was employed than on ground where no gamekeeper was employed (Fisher's Exact Test,  $P = 0.025$ : Table 3). There was no significant difference between recorded instances of predation at nests on ground managed by gamekeepers and at nests where a gamekeeper was not employed (Fisher's Exact Test,  $P = 0.478$ : Table 3). The latter result was unexpected, as gamekeepers were presumed to have controlled foxes; the finding suggests that fox control either did not occur or was not effective. Either way, it suggests that any failures due to interference on

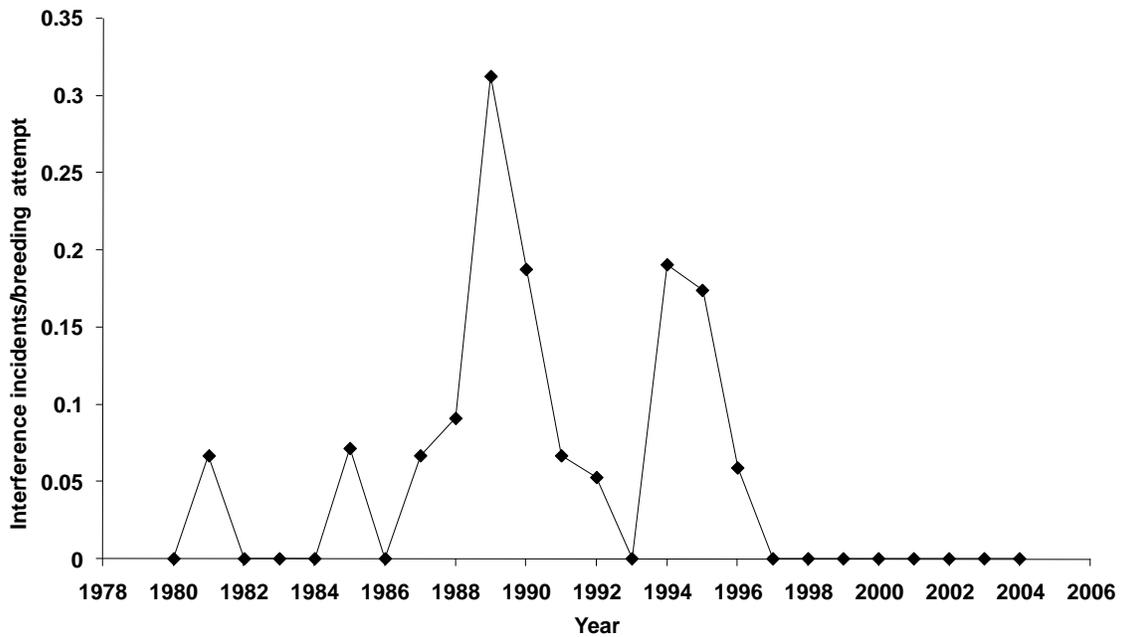
ground managed by gamekeepers were probably not compensated for by reduced losses to fox predation.



**Fig. 5.** Annual estimates of breeding productivity (fledglings per breeding attempt) of hen harriers in Wales, and the three year moving average (thin line).

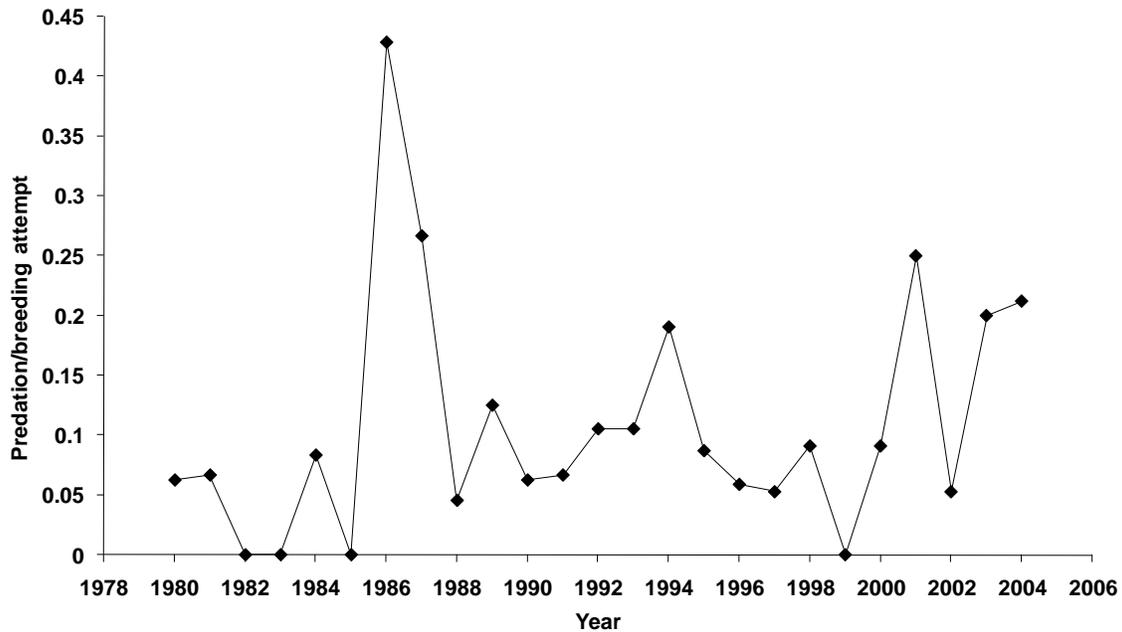
**Table 3.** Number of breeding attempts 1990-1995 which were recorded as being on ground which was managed by gamekeepers (= gamekeeper) or not managed by gamekeepers (= no gamekeeper) and numbers of these breeding attempts which were recorded as having failed due to predation or having failed due to human interference.

	Gamekeeper	No gamekeeper
Breeding attempts	58	39
Failure due to predation	6	2
Failure due to interference	9	0



**Fig. 6.** Annual estimates of the number of hen harrier breeding failures where human interference was implicated, expressed per breeding attempt.

Using a simple index of interference intensity (attributed failures to interference per breeding attempt) suggested that interference was greatest in the late 1980s and early 1990s, with peaks in 1989 and 1994, with a notable lack of any evidence of interference from 1997 to 2004 (Fig. 6). Interestingly, these changes appeared to be at least crudely reflected in changes in harrier productivity, especially the association of increasing productivity from the late 1990s onwards with a lack of interference (Fig. 5). This also coincided with an increasing population (Fig. 3).



**Fig. 7.** Annual estimates of the number of hen harrier breeding failures where predation (usually by fox) was implicated, expressed per breeding attempt.

No obvious annual changes were apparent in an index of predation intensity (attributed failures due to predation per breeding attempt), apart from a marked peak in 1986 and 1987. There does not appear to have been any marked change in the occurrence of predation as a cause of failure during the period 1997 – 2004 when interference apparently stopped and harrier productivity and harrier population increased (Fig. 7).

These simple exploratory considerations were followed up by Whitfield et al. (2008a), which provide details of multivariate analyses that also incorporated climatic data, on these apparent influences on Welsh harrier breeding success. Whitfield et al. (2008a) used hierarchical partitioning in preference to variable selection in a Generalized Linear Model (GLM) (Chevan & Sutherland 1991, MacNally 2000, Fielding 2007) to calculate the independent contributions of each explanatory parameter to explained variation in breeding productivity: human interference (40.5 %), maximum May temperature (36.9 %), minimum April temperature (15.5 %), clutch size (5.1 %) and predation (2.0 %). These results confirmed the GLM analyses in the relative roles of the explanatory variables' influence on harrier breeding productivity

This paper illustrated that a negative effect of human interference (apparently largely or exclusively on areas managed for grouse shooting, until recent cessation), and a positive effect of May temperature, were most influential on variation in harrier breeding productivity. This study also quantified, for the first time, that cessation of persecution can result in a marked improvement in hen harrier reproductive output. Nest predation by red foxes had no effect on variation in breeding productivity and there was no evidence that control of fox numbers by gamekeepers compensated for their depression of

productivity through destroying harrier nests. These analyses also indicated that gamekeepers probably destroyed an unknown number of nests before they were discovered. The recent increase in the breeding productivity of Welsh harriers has probably been influential in the recent recovery of the Welsh harrier population and has apparently been due to a combination of cessation of human interference and warmer May temperatures.

#### **4.4 Sex ratio at fledging**

During the period of the wing-tagging programme, 1990-1995, when most information on nestlings and fledglings was collected, there was a bias towards males in the sex ratio of fledglings (0.55 fledglings were male, or a ratio of 1:1.21 females to males) although this was not significantly different from 1:1 ( $X^2_{(1)} = 0.73$ ,  $P = 0.393$ ) (Table 4). Available data from later years suggested a bias towards females, so that across all years the sex ratio at fledging was about even (1:1.01) (Table 4).

**Table 4.** Annual estimates of numbers of hen harriers fledged in Wales, the number of fledglings which were wing-tagged, and the numbers of tagged birds which were female (F) and male (M): estimated proportions of fledged birds of each sex which were tagged are given in parentheses. \* For 1990-1995 numbers of each sex which fledged was estimated by  $(F \text{ or } M) \text{ tagged} + (N \text{ fledged} - N \text{ tagged})/2$ : if the resulting calculations gave 0.5 of a bird to each sex, then 1 was assigned to males and 0 to females to reflect the apparent sex bias in tagged birds. Values for 1996-2004 are observed samples. \*\* Totals for all years include numbers observed in tagged birds from 1990-1995, and not from overall annual estimates in those years.

Year	N fledged	N tagged	F fledged*	F tagged	M fledged*	M tagged
1990	25	11	13	6 (0.46)	12	5 (0.42)
1991	36	27	17	13 (0.76)	19	14 (0.74)
1992	55	51	20	18 (0.90)	35	33 (0.94)
1993	37	36	21	21 (1.00)	16	15 (0.94)
1994	23	15	8	4 (0.50)	15	11 (0.73)
1995	19	15	10	8 (0.80)	9	7 (0.78)
1990-1995	195	155	89	70 (0.79)	106	85 (0.80)
1996			4		4	
1997			1		3	
1998			8		2	
2003			14		10	
2004			15		9	
1996-2004			42		28	
All years**			112		113	

#### 4.5 Replacement clutches

An estimated 6.7% of all 105 nesting attempts 1991 – 1996 were relays (Table 5), suggesting overall that each laying female made 1.07 attempts per year, although as also noted previously this should be regarded as a minimum estimate.

**Table 5.** Estimated numbers of: territorial females, nesting attempts, individual females which nested, and nesting attempts which were relay (replacement) attempts.

Year	N territorial F	N nesting attempts	N laying F	N relays
1991	20	17	17	0
1992	28	22	21	1
1993	26	17	15	2
1994	27	18	18	0
1995	23	14	13	1
1996	25	17	14	3
Total	149	105	98	7

#### 4.6 Polygyny

Records of polygyny were relatively uncommon, with less than 3% of males being paired polygynously, with a maximum of two females (Table 6). However, methods which are appropriate to identifying polygyny in unmarked males (e.g. Amar et al. 2005) were not used in the present study, and so it was highly likely that the incidence of polygyny was underestimated. This tends to be confirmed by the circumstances when polygyny was recorded, in that at least two of the three recorded cases of polygyny involved distinctively plumaged ‘saddleback’ males.

As ‘harems’ of polygynous hen harrier males are geographically clustered (e.g. Picozzi 1984b, Amar et al. 2005) it may be interesting for a future analysis to examine the occupation of Welsh territories in each year and to look for such geographical clusters at an appropriate scale. The present study could not undertake such analyses as many grid references of nest locations were not available. Whilst not all territories in clusters will necessarily involve polygynous males, such an exercise, in combination with examination of timed observation records at relevant territories, may provide a maximum indication of polygyny, bearing in mind that harems of over two females appear to be rare on the UK mainland (Etheridge et al. 1997, Amar et al. 2005).

**Table 6.** *Numbers of territories where male pairing status was judged and numbers of males considered monogamous (paired with one female) and polygynous (paired with more than one female: in all cases, two). Totals are broken down for years when estimates of survival were derived and for all years when pairing status data were available, and values in brackets are percentages.*

Year	N territories	N monogamous	N polygynous
1989	15	15	0
1990	17	17	0
1991	13	13	0
1992	21	15	3
1993	18	18	0
1994	24	24	0
1995	23	23	0
Sub-total 1989-1995 (% of males)	131	125 (97.66)	3 (2.34)
1997	8	8	0
1998	8	8	0
2003	14	12	1
2004	13	13	0
Total all years (% of males)	174	166 (97.67)	4 (2.35)

#### 4.7 Age at first breeding

Results from wing tagging on age of first recorded breeding or occupation of a territory revealed relatively small sample sizes, especially for males (Table 7). It was apparent, however, that most females first bred when in their first year and most males first bred in their second year.

**Table 7.** *Age of first recorded breeding for six wing-tagged males and eighteen wing-tagged females. Proportions are shown in parentheses. \* A bird with the same cohort tags (not individually identified) occurred at the same site in the preceding year, so this bird likely first bred at age 2 years. \*\* Does not include a bird identified as breeding in England when three years old.*

Sex	Age in years			Mean	Median
	1	2	3		
Male	0	5 (0.83)	1 (0.17)*	2.17	2
Female	13 (0.72)	4 (0.22)	1 (0.06)**	1.33	1

Age of breeding males, or at least the occurrence of males breeding when in their first year, could also be estimated from the frequency of brown plumaged birds in paired males occupying territories. Such brown plumaged birds, in their first year, only accounted for about 1% of all breeding males (Table 8).

If numbers of polygynous males were greater than estimations in Table 8, as seems likely, and if adult males are more likely to be polygynous than first year males (e.g. Picozzi 1984a, Amar et al. 2005) then some adult males will have been ‘double counted’, inflating their apparent contribution to the territorial paired male population. Nevertheless, even accepting this likely bias in the results, it was apparent that male hen harriers in Wales rarely paired and occupied a territory in their first year, confirming the results from the wing tagged birds.

**Table 8.** *Numbers of territorial paired males which were aged on plumage and numbers which were classed as having grey ‘adult’ plumage or as having brown ‘subadult’ plumage. Grey plumaged birds were assumed to be at least two year old (at least third calendar year) and brown plumaged birds were assumed to be one year old (second calendar year). Grey birds included ‘saddleback’ males with some brown mantle feathers and sometimes with brown tail feathers, which were assumed to be two year old (third calendar year). Brown (or ‘ringtail’) males often had some grey in the plumage. Displaying and apparently unpaired birds known or considered to be male were not included.*

Year	Grey	Brown	N aged
1990	5	0	5
1991	11	0	11
1992	16	0	16
1993	18	0	18
1994	25	0	25
1995	22	1	23
Total	97	1	98
%	99.0	1.0	

## 4.8 Dispersal

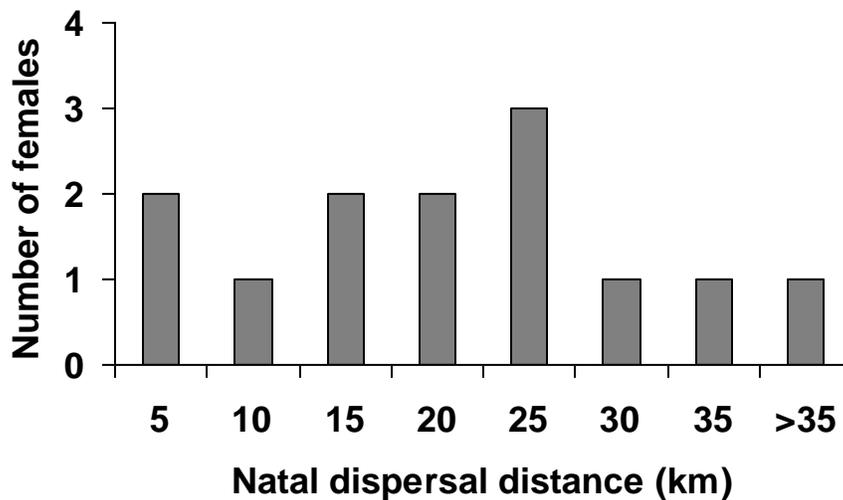
A total of 70 female and 85 male fledgling harriers were wing tagged, with slightly more males tagged on Berwyn than Migneint (Table 9).

### 4.8.1 *Natal dispersal*

Median natal dispersal distance was 18.4 km (N = 13, inter-quartile range 7.6 – 22.6 km) for females (Fig. 8) and 12.1 km (N = 3) for males. The furthest movement recorded, and the only observation of a Welsh bird breeding outside Wales, was of a 1990 female breeding in northern England in 1993. A female which had been tagged at Langholm, southwest Scotland was seen in Wales during spring 1997 although there was no evidence that she bred. A first-year male tagged as a nestling in Argyll southwest Scotland was present for one day in early May 1993, and was thought to be on passage.

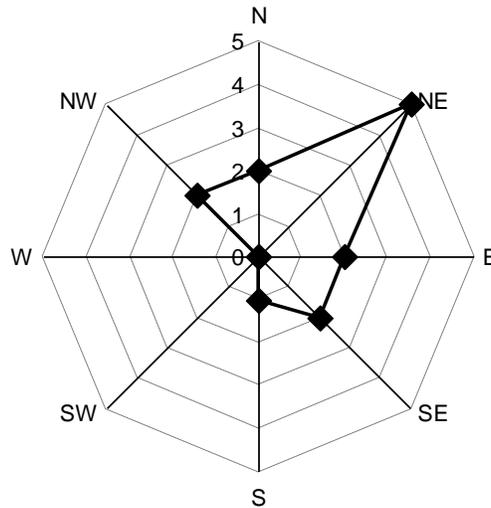
**Table 9.** Numbers of hen harriers which were wing tagged 1990-1995 and known or presumed to have fledged, according to sex and parts of the study area (see Offord (2002) for divisions of Berwyn and Migneint SPAs). Numbers of tagged birds fledged does not include three males (one each in 1991, 1993 and 1995) which were tagged but found dead before fledging.

Area	N wing-tagged fledglings	
	Females	Males
North Berwyn	7	17
Central Berwyn	9	13
South Berwyn	12	16
North Migneint	26	22
Mid Migneint	0	0
South Migneint	0	0
Wales, elsewhere	16	17



**Fig. 8.** Frequency histogram for natal dispersal distance in Welsh female hen harriers, classed in 5 km bins. The single record over 35 km involved a c180 km dispersal to a breeding site in northern England.

An apparent propensity for natal dispersal towards the northeast (Fig. 9) probably reflected the geography of fledgling origin in relation to suitable breeding habitat, rather than any innate bias in dispersal direction.



**Fig. 9.** *Compass directions of natal dispersal movements in 14 Welsh male and female hen harriers (measured from natal to breeding site).*

Although sample sizes were small, considering the two SPAs, Berwyn and Migneint, most natal dispersal movements occurred within the respective SPA. Nevertheless, dispersal was not restricted in occurrence to within a SPA (Table 10). Although more sophisticated analyses of observed dispersal in relation to the expectation of intra- and inter- SPA movements may be warranted, it was apparent that natal dispersal generated connectivity between the two SPAs so that effectively harriers (notably, females) probably considered the SPAs to be part of the same breeding area. This is perhaps not surprising when the boundaries of the SPAs are only c. 6 – 17 km apart. It would also probably be safe to assume that, at least so far as females were concerned, the same consideration applied to Wales as a whole.

**Table 10.** *Natal dispersal in relation to the two main breeding areas of Welsh hen harriers, Berwyn and Migneint. \* Includes one bird originating at a site north of Migneint. \*\* Includes one bird breeding at a site north of Migneint.*

Natal area	Breeding area	N females	N males
Berwyn	Berwyn	3	1
Berwyn	Migneint	1	0
Migneint	Migneint	3	1**
Migneint	Berwyn	3*	1*

**4.8.2 Breeding dispersal**

Breeding dispersal (N consecutive years = 10 for females and 1 for males) was a median of 0.0 km and involved six records of birds returning to the same site and five movements

of 1.0, 3.2, 19.7, 32.0 and 38.0 km between years. Insufficient data were available to examine any effects (e.g. breeding success) on breeding dispersal.

#### 4.9 Survival of full-grown birds

Sample sizes of resightings were low for wing tagged birds and, as noted in Methods, further compromised to a degree by a reduction in reporting rate in years after tagging ceased. From matrices constructed for each sex documenting, by cohort and year, resightings of wing tagged birds, minimum apparent annual survival for females was 0.293 in their first year (i.e. until breeding age) and 0.774 in subsequent years (i.e. at breeding age) (N = 58 birds and N = 31 bird-years available, respectively) (Table 11). From equation 1 (section 3.3.3) it was apparent that between 1991 and 1995 four resightings of tagged females may have been missed (Table 12). If all these were simplistically assumed to refer to first year birds (probably an unrealistic assumption, because the resultant increase in number of tagged first year birds would have also required a larger pool of older birds which were not seen subsequently), the first year female survival would have been 0.362.

Minimum apparent survival for males was 0.071 in their first two years (i.e. until breeding age) and 0.625 annually in subsequent years (i.e. at breeding age) (Table 11). Fewer resightings of males were estimated to have been missed within Wales, with only a single resighting missed in five years (Table 12). Since polygyny was probably underestimated (section 4.6), the proportion of territorial birds checked for tags (A, in equation 1) will also have been underestimated and thus the estimated number of tagged birds missed within Wales was probably a negligible influence, at least for those cohorts where it could be estimated. No changes in apparent male survival estimates were therefore justified on this basis. Exploratory modelling using these low survival estimates caused the male population to rapidly decline to zero, in sharp contrast to observations.

The apparently low resighting rate of Welsh males at breeding age (and thus very low apparent pre-breeding survival) could be due to several factors:

1. Tagged birds were not representative of the wider male population
2. Tag loss
3. Low proportion of breeding males checked for tags or tags were not readily visible (i.e. tagged birds were missed by observers)
4. Low male pre-breeding survival
5. High male natal dispersal (and therefore emigration)

**Table 11.** *Matrices for a) females and b) males showing for each cohort of wing-tagged birds the numbers which fledged (in bold) and which were subsequently resighted on the breeding grounds in each year. Cells were left blank when it was not possible from available information to attribute any resightings or lack thereof to a particular cohort. \* = minimum number of birds. Resightings of birds in the non-breeding season did not alter the values for numbers of birds known to be alive in each breeding season, largely because sightings of known individuals were few after a birds' first winter.*

a) Females

1990	1991	1992	1993	1994	1995	1996	1997	1998
<b>6</b>	2	2	3	2	1			
	<b>13</b>	0	0	1	1			
		<b>18</b>	7	7	3			
			<b>21</b>	6	4	1*		
				<b>4</b>	0			
					<b>8</b>		1*	

b) Males

1990	1991	1992	1993	1994	1995	1996	1997	1998
<b>5</b>	0	0	0	0	0	0		
	<b>14</b>	1	1	1	0	0		
		<b>33</b>	5	1	1	0		
			<b>15</b>	0	2	1		
				<b>11</b>	0	1	1	
					<b>7</b>	0	1	1

The influence of the first two potential factors can be readily dismissed (Table 4; tag loss was very low, as judged by the number of birds seen with only one tag). In the absence of immigration, low male pre-breeding survival should potentially lead to a severe shortage of males, which in turn should have the following consequences: a) reduction of age of first breeding, and b) high degree of polygyny. With no substantial subsidiary evidence for these possibilities (Tables 6-8) or for emigration, the third explanation seemed most likely. This was documented more thoroughly in a contemporaneous wing-tagging study of Scottish hen harriers (Etheridge et al. 1997, B. Etheridge pers. comm.). In other words, for some reason possibly related to their plumage colour or that they are seen less frequently around nests than females, patagial wing tags on male harriers are relatively difficult for observers to see. As noted earlier, this observation bias excluded males from population modelling.

**Table 12.** *Minimum numbers of birds checked for wing tags in relation to the estimated number of territorial birds as a basis for estimating the annual proportion of birds which were checked for tags. The estimated number of tagged birds which was missed was derived from:  $C = (B/A - B) - N$  birds known to have been missed at breeding age (because seen in a subsequent year: see Table 11). \* For males due to 0 observed tags in some years, annual estimates could not be derived and so an overall estimate was obtained using summed values for the years 1992-1995 (1991 excluded as males first breed at age 2 and 1990 was first year of nestling tagging). Note that for males this exercise does not account for those cases of known polygyny (Table 6). Higher proportions of territorial birds may have been checked because records of tagged birds exceeded those given here (hence disparities with Table 11), although at least some of these records did not apparently involve breeding birds.*

Year	N territorial pairs	N nest records	N birds checked		Proportion of territorial birds checked (A)		N tagged birds observed (B)		Estimated N tagged birds missed (C)	
			M	F	M	F	M	F	M	F
1991	20	13	11	11	0.55	0.55	0	2		1
1992	28	18	16	18	0.57	0.64	0	2		1
1993	26	18	18	17	0.69	0.65	1	9		2
1994	27	26	25	26	0.93	0.96	2	14		0
1995	23	25	23	22	1.00	0.96	2	11		0
All	124	100	93	94	0.75	0.76	5	38	1*	4

#### 4.10 Population modelling

Both Leslie Models 1 and 2 produced predictions which were similar to those of the observed breeding female population, matching the observed stability in numbers in the 1990s and the observed population increase in the 2000s. Judging from the performance of the models the ‘empirical’ correction for replacement breeding attempts was slightly too low (Model 1) and the ‘assumed’ correction was too high (Model 2), and Model 1 should probably be (conservatively) favoured. Mean (SE) Model 1 population growth rates ( $\lambda$ ) were 1.056 (0.040) for 1989 – 2004 and 1.006 (0.030) for 1989 – 1997. With mean population growth rate for 2008 – 2012 of 1.078 from Model 1, the number of territorial female Harriers was predicted to reach 69 in 2012 (observed estimate was 45 females in 2006). Most of the elasticity in the population projection matrices was in the first and second year survival rates, with reproductive rates making relatively low potential contributions to population growth rate, highlighting that survival rates were *potentially* most influential on population growth.

In the ULM stochastic model, predictions were virtually identical to those from the Leslie matrix modelling. The population growth rate of the mean population across 1000 simulations was 1.061 (SE = 0.0002) and the mean scaled population structure was 0.459 (age 0-1), 0.155 (age 1-2) and 0.386 (age 2+). Elasticity values were identical to those from the Leslie matrix modelling, albeit summed over the age classes. None of the simulated populations decreased below the extinction threshold (10 females), indicating that with the observed survival and fecundity rates, under the imposed stochasticity rules, there was nil probability of extinction. Expected remaining lifespans were 2.66 years (SD = 2.76) for stage 0 individuals (age 0-1 years), 4.17 years (SD = 3.57) for stage 1 individuals (1-2 years) and 4.10 years (SD = 3.56) for stage 2 birds (2+ years).

Full details of the results of the population modelling are given by Fielding et al. (in press).

## 5 DISCUSSION

The Welsh hen harrier population has increased over the last twenty years and this is associated with an increase in their breeding productivity. The population expansion can be explained entirely by the improvement in breeding productivity, despite survival rates in young full-grown birds being potentially the most influential demographic parameters in harrier population abundance. The population modelling inferred that there has been no recent change in female survival rates, even though we could only estimate survival during the 1990s. Whitfield et al. (2008a) note that the increase in productivity was not related to an increase in clutch size, rather it was associated with an increased proportion of breeding females laying eggs combined with a general, but noisy, increase in the average number of young fledged. The main factors that seemed to explain the variation in productivity were a negative effect of recorded human interference (and its cessation after 1997) and a gradual increase in the maximum May temperature. Whitfield et al. (2008a) also point out that the apparent recent increase in the proportion of females laying eggs was probably because in several instances territorial females were recorded but nesting attempts were destroyed by humans before they were found by observers.

Gamekeepers employed to manage grouse moor were probably largely or entirely responsible for breeding failures due to human interference, as indicated by both indirect evidence, in that human interference was only recorded on ground managed by gamekeepers, and by direct evidence, in that gamekeepers were implicated or confirmed as responsible for breeding failure due to interference (e.g. found in possession of harrier nestlings). The absence of any difference between recorded instances of predation at nests on ground managed by gamekeepers and at nests where a gamekeeper was not employed was unexpected, because gamekeepers were presumed to have controlled foxes (Hudson 1992). This finding suggested that fox control either did not occur or was not effective and further implied that harrier breeding failures due to interference on ground managed by gamekeepers were probably not compensated for by reduced losses to fox predation (see also Green & Etheridge 1999) as did the absence of any marked increase in predation when interference and grouse moor management waned.

Thus, the improved fortune of the Welsh harrier population is substantially explicable by the apparent cessation of human interference from 1997 onwards (coming towards the end of a steady decline in the number of red grouse shot: Offord 2002). This effectively provided an experiment which confirmed its influence on harrier breeding productivity in that breeding productivity was markedly higher after interference ceased.

Several interesting inferences stem from this key finding. The first is that while interference was spatially restricted by occurring only on a part of Berwyn (Offord 2002), one of two main breeding sites, it was sufficient to prevent the Welsh harrier population from realising its full potential by stabilising breeding numbers below the likely carrying capacity. Secondly, although we did not formally consider population sources and sinks in our analyses, the implication was that when interference was occurring, given the strength of its apparent influence, it was probably creating an 'ecological trap' (Delibes et al. 2001) within the Berwyn. Thirdly, despite there being records of interference involving the killing of adult birds, these were apparently isolated incidents, as analysis suggested that interference primarily involved the destruction of nest contents.

Although constrained by small sample sizes our estimates of several demographic parameters of Welsh harriers were similar to or consistent with those from other studies elsewhere. Etheridge et al. (1997) reported a bias towards males in fledglings during a large study of Scottish harriers (1 female : 1.09 males). According to Hughes & Williamson (1991) the typical situation in Wales is for a slight bias towards male fledglings. This was confirmed by the present study for Wales in

the 1990s, when the most complete surveys took place, although more females were apparently produced in later years. The sex ratio of fledglings on Orkney changed significantly temporally, from a greater proportion of females in the 1950s and early 1960s to a greater proportion of males during the 1970s and early 1980s (Picozzi 1984b).

Fledgling sex ratio can vary in space and time because it is apparent that harriers can vary the sex ratio of their offspring in response to several potential factors, such as population characteristics, food abundance or other influences on the probability of offspring recruitment. For instance, Millon & Bretagnolle (2005) showed that fledgling sex ratio varied between populations of vole specialist Montagu's harriers *Circus pygargus* in western France, and whatever the population, relatively more male offspring were produced during peak years of the vole cycle but also during poor years. Their results suggested that sex ratio analyses should take into account life history characteristics, and more generally, spatial-temporal environmental variations. Arroyo (2002), working on the same species in Spain, where vole specialisation did not occur, found that fledgling sex ratio variation was related to estimates of food availability during the pre-laying period, with more females produced in years of higher food availability. This variation was related to the probability that females, but not males, were recruited to the breeding population and were recruited at younger ages, if fledged in good food years. Her results differed from others on the same species (cf Millon & Bretagnolle 2005): geographical variation in observed sex ratio might be explained by differences between populations in factors influencing age of first breeding or other demographic variables. In the present study, a period of more male hen harrier offspring was apparently associated with a period of relatively good food availability (as indexed by clutch size) whereas more females were produced when clutch size suggested food availability was lower.

Simmons (1988) has suggested that polygyny in his study population of northern harriers (the North American *hudsonicus* subspecies of the hen harrier) was more likely related to food abundance than adult sex ratio (i.e. a shortage of males), and Hamerstrom et al. (1985) also found that polygyny in northern harriers increased when prey supply was greater, so that overall about 27% of males were polygynous. Most research points to a bias towards females in adult sex ratio of hen (northern) harriers (e.g. Picozzi 1984b, Hamerstrom et al. 1985, Simmons 1988). The results of food supplementation experiments on hen harriers (Redpath et al. 2001, Amar & Redpath 2002) were consistent with polygynous pairing being predisposed by the adult sex ratio but that breeding was influenced by food abundance. Amar et al. (2003) recently recorded that 22 % of hen harrier males were polygynous at Langholm southwest Scotland and 17 % were polygynous on Orkney (a reduction in historical rates: Amar et al. 2005, Picozzi 1984a). 75% and 88% of territorial males and 48% and 100% of territorial females bred on Orkney and Langholm, respectively (Amar et al. 2003). In both studies, however, there were factors potentially associated with a predisposition towards polygyny: a biased sex ratio on Orkney and a rapidly expanding population on Langholm. Rates of polygyny in most other areas of Scotland do not appear to be so high (Etheridge et al. 1997, B. Etheridge, pers.comm.). While polygyny was undoubtedly under recorded in Wales, and more realistic estimates are desirable, it is perhaps unlikely that they were as high as those documented elsewhere by Amar et al. (2003).

The finding that in Wales most females probably first bred in their first year and most males probably first bred in their second year is similar to an earlier study in Scotland (Etheridge et al. 1997). Hamerstrom et al. (1985) suggested that in their study of Wisconsin northern harriers most females first bred in their first year but most males first bred in their second year. In Montagu's harriers a first breeding age of two and three years was assumed for females and males respectively (Arroyo et al. 2002). Salamolard et al. (2000) noted that in western France, Montagu's harriers are specialist predators of voles and respond numerically to changes in vole abundance. Yearling females accounted for 1.7 – 6 % of the breeding population in years of

increasing vole numbers, but reached 19 – 30 % in peak vole years, and fell to 0 % when vole abundance was lowest. A similar situation of changes in subadult breeding (in both males and females) has been described for the northern harrier in populations which also seemed to specialise on voles (Hamerstrom et al. 1985, Simmons et al. 1986). In Scottish hen harriers, breeding males in first-year (brown) plumage were more common on grouse moor (5.6% of males), than on other moorland (0.6%) and conifer forest (1.0%), differences which were attributed to higher male mortality (and thus a greater shortage of adult males) on grouse moors (Etheridge et al. 1997).

In Scotland, median natal dispersal distance in female harriers was 10 km and 51 km for birds hatched on moorland and conifer forest respectively, and it was 38 km, 14 km and 150 km for males originating on grouse moor, other moorland and conifer forest, respectively, with much lower sample sizes than for females (Etheridge et al. 1997): the larger dispersal distances of males approached statistical significance. Median breeding dispersal distance was 0.7 km, with no difference between the sexes. The present study had limited sample sizes for dispersal estimates but suggested that in Wales natal dispersal was about 18 km in females. The lower distance estimated from wing-tagged males was probably an artefact of a very small sample size. However, similar to Scottish birds, breeding dispersal appeared to be much lower than natal dispersal in Welsh harriers. Adult Montagu's harriers also show high fidelity to breeding sites in western France (Salamolard et al. 2000), but exhibit very low natal philopatry (> 15% of fledglings disperse > 50 km) and only 5% return to the natal area with the majority not settling in their natal colony. In western France 9 -27% (depending on cohort) of fledglings were seen subsequently, and in central Spain 12-16% of fledglings were seen subsequently (Arroyo et al. 2002). Thus dispersal in both hen and Montagu's harriers seems to occur primarily before the first breeding attempt.

Within Wales, there was obvious connectivity between different breeding sites through natal dispersal. Our study further suggested that based on dispersal distances the Welsh Hen Harrier population probably has low linkage with other breeding areas in the British Isles and that, at least currently and for females, is more-or-less 'closed' and, to assess long-term viability, does not require population models with geographically-explicit linkage (Kauffman et al. 2004). If the population continues to expand, as predicted, then through density-dependent dispersal (Matthysen 2005) this is liable to change and emigration through natal dispersal may become more frequent, allowing Wales to be a source of colonists for other unoccupied habitat in southern Britain (Potts 1998).

The Welsh female survival rate estimates were similar to those which have been estimated on Orkney (first year 0.33, adult 0.877: Rothery 1985) and on 'other moorland' elsewhere in Scotland (first year 0.361, adult 0.778: Etheridge et al. (1997). For males on Orkney estimated survival to two years old was 0.13 and adult survival rate was 0.72. In the widespread Scottish study, too few wing-tagged males were resighted as breeding birds to estimate survival (Etheridge et al. 1997). Likely reasons for the low resighting rates were given as the greater difficulty in reading wing-tags on males and that long distance natal dispersal may occur more often for males. Number of observations which could be used in estimating natal dispersal distance in Etheridge et al.'s study was 108 for females and 18 for males. A similar though less marked imbalance between resightings of females and males was evident in the present Welsh study, although far fewer resightings were documented overall. Nevertheless, the results from Wales did serve to confirm the finding from Scotland that tags on male hen harriers were probably more difficult to see than tags on females; this was despite different tag colours being employed in the two areas.

Although survival rates are potentially most influential on the size of a breeding hen harrier population, the changes in the abundance of Welsh harriers have been driven primarily by changes in reproductive output. Reproductive rates of Welsh harriers before 1997, and before the apparent cessation of human interference (Whitfield et al. 2008a), were just sufficient to maintain a stable population ( $\lambda$  values were just above 1), and resulted in no estimated risk of extinction. The implication of this result is that provided mean annual breeding productivity does not drop below the rate observed in this period (0.61 female fledglings per territorial female) then, with caveats on maintenance of survival rates and available habitat, Wales should continue to support a viable Hen Harrier population. In the continued absence of human interference and availability of suitable habitat, and assuming survival rates change little, however, the recent breeding productivity is clearly more than sufficient to maintain a population which is not reliant on the species' fortunes in other breeding areas. These results are consistent with the wider conclusions of Fielding et al. (2008), and their implications for management and monitoring are discussed in more detail in section 6.

## **6 RECOMMENDATIONS FOR FUTURE WORK AND MONITORING METHODS**

### **6.1 Principles and surveillance goals**

The results of our analyses using data available up to 2006 suggested that the future of the Welsh hen harrier population is encouraging given that the main source of adverse influence (human interference, primarily through the activities of some grouse shooting interests) has apparently stopped, and that the recent trend towards warmer springs has been beneficial for harriers.

Katzner et al. (2007) have highlighted the importance of monitoring programmes being designed appropriately according to demographic parameters if they are to be effective in detecting change in populations and their dynamics. Future monitoring efforts for Welsh harriers should be guided primarily by the need to provide estimates of size and distribution of the breeding population and, secondarily, surveillance of the demographic parameters which are most influential on population abundance. In practice, if budgets for surveillance are limited, effort should concentrate on those measures which are most likely to change. As such budgets may vary temporally and are presently unknown, the approach we have adopted is to propose a prioritised 'wish list for surveillance', as follows:

1. Number of occupied territories and distribution
2. Survival rates
3. Reproductive rates
4. Immigration/emigration through dispersal

The top priority is to estimate the number of occupied territories and distribution. Our reasoning for subsequent prioritisation is based on the fact that in hen harrier populations survival rates are potentially the most influential parameters (section 4.10, Fielding et al. in press). As recent studies of raptors have emphasised, monitoring survival (though difficult) incorporates valuable information in identifying threats and causes of population change (Whitfield et al. 2004a, Katzner et al. 2006, Kenward et al. 2007). However, the difference in potential influence of survival and reproduction is not as marked in harriers as in other species (e.g. large eagles: Whitfield et al. 2004a, Katzner et al. 2006) with higher survival rates and lower reproductive rates (Heppell et al. 2000). In the absence of persecution on the breeding grounds affecting survival rates, estimates from different breeding areas of the UK are similar (this study, Fielding et al. 2008) despite birds having different non-breeding areas (Etheridge & Summers 2006). One caveat to this similarity is that estimates from Scotland and Wales were collected during the

same period (Etheridge et al. 1997, this study), although the present study suggested that average survival rates of Welsh birds have probably not changed markedly over the course of the 20 year study period. And as the present study has also noted, reproductive rates can in practice be strongly influential on hen harrier population trends (see also Amar et al. 2003, 2005). We therefore do not place a strong emphasis on survival surveillance having a higher priority than reproduction surveillance.

Finally, although immigration and emigration can be powerful but under-appreciated factors in population dynamics (Clobert et al. 2001) we have given them the lowest priority for monitoring. This is because their effect in the medium term for Welsh harriers does not appear to be substantial, according to the present study, since the population is probably more-or-less closed. We also highlighted earlier, nevertheless, that this situation may change in the longer term.

## 6.2 Favourable condition of the Welsh harrier population

Watson & Whitfield (2002), using information from the EU Directives on Wild Birds, and Habitats and Species, introduced the overarching concept of ‘favourable condition’ to assess whether the three elements of a conservation strategy<sup>1</sup> for a species or regional population are effective. The concept indicates that “conservation status of a species means the sum of the influences acting on the species concerned that may affect the long-term distribution and abundance of its populations” and that “the conservation status will be taken as ‘favourable’ when:

- Population dynamics data on the species concerned indicate that it is maintaining itself on a long-term basis as a viable component of its natural habitats, and
- The natural range of the species is neither being reduced nor is likely to be reduced for the foreseeable future, and
- There is, and will probably continue to be, a sufficiently large habitat to maintain its populations on a long-term basis.”

This concept, and its implementation, has been developed in detail for the golden eagle, which involved setting criteria (or ‘tests’) to assess favourable condition (= conservation status) (Whitfield et al. 2006a, 2008b). Fielding et al. (2008) proposed three criteria for national and regional ‘favourable condition’ targets for hen harriers:

1. A minimum of 1.2 young fledged per pair
2. At least 50 % of apparently suitable habitat occupied
3. A density threshold of 2.12 pairs per 100 km<sup>2</sup>

As noted in previous sections, with the empirically derived survival rates for Welsh birds, the first criterion is consistent with the reproductive rate observed during the period of Welsh population stability. In recent years the Welsh population readily ‘passes’ the first criterion, but according to Fielding et al. (2008) fails criteria 2 and 3. As also noted by Fielding et al. (2008), however, and is apparent from the present study, hen harriers in Wales are recovering well and should pass these criteria in the medium term, if recent population trends continue.

The study of Fielding et al (2008) therefore provides further justification for continued monitoring of the Welsh harrier population. It also applies a framework concerning those aspects of population demographics which deserve to be monitored in the future and on which conservation status can be assessed. A minimum target for future monitoring should be an average annual breeding productivity rate of 1.2 fledglings per pair occupying a territory. Note

---

<sup>1</sup> Species protection, site protection, and conservation in the wider environment.

that this rate does not refer to breeding attempts but to numbers of birds (i.e. breeding attempts after correcting for replacements).

### 6.3 Potential monitoring methods

The basic methods behind the present study (sections 3.2.2 and 3.2.3), and as described also by Sim et al. (2001, 2007) and Hardey et al. (2006), provide for measuring, and thereby monitoring, breeding numbers and distribution, and reproductive rates. Several refinements involving collecting additional data through nest visits and handling or recording of nest contents are possible under the basic methods, which have fortunately been largely followed in Wales, and these are considered in more detail in the next sub-section.

Estimating survival and dispersal rates demands more intensive methods, and involves mark-recapture (or mark-resighting) of individuals. Although not mutually exclusive, this requires:

- Intervention to mark birds externally for visual (e.g. patagial wing tags: this study, and Etheridge et al. 1997), telemetric (e.g. radio tags: Kenward et al. 1999) or PIT (Passive Integrated Transponder) tag (e.g. Wright 2003, M. McGrady et al. unpubl. data: [http://www.natural-research.org/projects/pereguine\\_pit.htm](http://www.natural-research.org/projects/pereguine_pit.htm)) identification<sup>2</sup>.
- Techniques which can utilise ‘internal’ markers of individual identification in the form of DNA ‘fingerprinting’ (e.g. Wink et al. 1999, Marsden et al. 2003, Rudnick et al. 2005, Kenward et al. 2007). Several sources for DNA extraction are possible (Horváth et al. 2005, Harvey et al. 2006). For example, Natural Research is currently using moulted feathers (for breeding adults), ‘blood feathers’ and buccal swabs (for nestlings) in projects examining survival and turnover in golden eagle *Aquila chrysaetos*, white-tailed eagle *Haliaeetus albicilla* and northern goshawk *Accipiter gentilis* (<http://www.natural-research.org/index.htm>).

There are advantages and disadvantages to each of these two suites of methods. ‘External marking’ is field labour intensive. This is particularly so for radio telemetry, although the objective in the present situation would be simply to document presence/absence of marked birds (and not necessarily to use tags to estimate ranging behaviour or other movements, for example). Satellite tags can be readily dismissed because their cost would be prohibitively expensive, sample sizes would therefore be too small, and other cheaper methods could deliver the same results. The same considerations argue against VHF tags, even though they are substantially cheaper than satellite tags.

Compared to patagial wing tags and PIT tags, radio tags are more time consuming to fit, and to serve a long term (lifetime) function would arguably require greater intervention to fit. They are probably also less reliable, in terms of tag loss or failure, than patagial wing tags. Perhaps their sole advantage over patagial tags, with the monitoring objectives, would be for males because the apparent difficulty that observers have in seeing patagial wing tags on males would be obviated. Whether this outweighs their disadvantages and could justify their deployment, however, is highly debateable.

PIT tags are less invasive than patagial tags but are effectively more expensive because they require ‘readers’ to be placed at nests to log a bird’s ‘microchip identity’. The necessity of a reader to record ‘resightings’ restricts the method to those fieldworkers with access to one, and this can therefore potentially restrict geographical application. The effort and time to collect resightings are also greater with PIT tags although, once a network of recorders with readers is established PIT tagging is arguably more conducive to long-term monitoring. Since recording resightings with PIT tags requires active nests, the time available to collect data is shorter than

---

<sup>2</sup> We have discounted standard BTO rings as an effective tool to quantify survival and dispersal.

for patagial tags and some records may be missed due to breeding failure. With potentially high failure rates in harriers this may give patagial tags an overall advantage.

Thus, the favoured option for an external marking method would be patagial wing tags, on balance. In any new programme deploying patagial wing tags it would be important to appreciate that, for their full value to be realised, efforts to identify tagged birds should continue several years after the last birds were tagged.

An advantage of ‘DNA tags’ over patagial wing tags is that they are less field labour intensive because they require no special training or licence, and less time to collect marking-resighting data. Essentially, little extra field effort is required over-and-above the basic methods used for monitoring occupied territories, distribution and breeding productivity. Unlike patagial tags, DNA tags are permanent and do not affect survival or recapture rates. DNA tags can probably be incorporated more easily in to long term monitoring than patagial tags, which are more likely to produce ‘snapshot’ survival estimates, because effort (and costs) to derive estimates is more ‘front-loaded’ in the field; DNA tag data can be stored on an on-going basis until there is a need (or funds) for analysis. DNA tags are also less intrusive for the birds, if moulted feathers, blood feathers or buccal swabs are used to collect samples for DNA extraction. For individual identification, DNA samples must be genotyped at microsatellite loci (e.g. Rudnick et al. 2005), and suitable loci for hen harrier have not been published, but they have recently been developed (R. McEwing pers. comm.).

Equipment and preparatory time costs for collection of data are probably comparable between DNA tags (e.g. buffer solutions and sample tubes) and patagial wing tags. The disadvantage of DNA methods compared to patagial wing tags is that data are more expensive to process. This expense consists of initial sample collation after receipt from fieldworkers, and subsequent DNA extraction, genotyping and analysis. Currently the approximate costs after collation are about £20 - £25 per sample, although they vary according to number of samples being processed, and will probably decrease with time.

Preliminary results from a pilot study using moulted feathers as a source of DNA tags to estimate annual adult survival of harriers in the Uists, NW Scotland (Natural Research & Haworth Conservation unpubl. data) has shown that cast feathers around nests were far less frequent than in other species, even for females, and male feathers were very rarely found (P. Haworth & R. Reid pers. comm.). This would tend to restrict the utility of DNA tags in estimating survival. Parentage (and therefore its change over time) garnered from DNA of nestlings, however, can be used to estimate parental survival (Wink et al. 1999) but this obviously limits survival estimates to successful breeders. This would equate, on average, to about half of the Welsh population (Table 2) and may provide a biased sample if, for example, survival and breeding success co-vary or breeding success is age-dependent. More studies are probably required to test the DNA tagging method with harriers

#### **6.4 Recommended future monitoring methods**

Given the prioritisation documented in preceding sub-sections, it is essential that existing monitoring efforts are continued, especially when, with the likelihood of an expanding population, new breeding sites will probably be colonised. Detecting new breeding sites in an expanding population inevitably involves more effort than simply re-visiting established sites, and so this additional effort should not be under-estimated. Obviously, therefore, attempting a census (full coverage of all breeding attempts) of the Welsh population is less costly than a survey (partial coverage of a sample). With a six-year cycle for government to report to the EU on harrier populations, we would suggest that a full census should be attempted at least every three years, preferably more frequently.

Annually, we would recommend that, consistent with previous practice in Wales, the following parameters should continue to be recorded (see section 3.2 for definitions) along with dates of all site visits:

- Number and location of occupied territories
- Number and location of breeding attempts
- Notes which document whether a breeding attempt may be a replacement
- Clutch and egg size
- Cause (and timing) of breeding failure
- Brood size
- Sex of nestlings
- Number (and sex) of fledglings
- Mating status of male (monogamous or polygynous)
- Plumage type ( $\approx$  age) of male

The last measure, as alluded to earlier, may provide an indirect warning signal of reduced adult male survival (Balbontín et al. 2003, Ferrer et al. 2003, Whitfield et al. 2004b, Katzner et al. 2007). In this respect, we would emphasise that in recording whether first-year males are involved in a breeding attempt and/or occupied territory that the long-standing criteria for territory occupancy followed by raptor workers in Wales continue to be followed. In national surveys a single male ‘skydancing’ has been classed as evidence of an occupied territory (Sim et al. 2001, 2007). As discussed by Whitfield et al. (2006b) a more stringent criterion ignores a single displaying male. This was employed ‘traditionally’ by Welsh raptor workers and followed by the present study, and seems more appropriate to document genuine breeding site occupancy (Whitfield et al. 2006b).

There is currently no obvious threat to adult survival of Welsh harriers, and the recent status of the population also argues for no urgent immediate need for new relevant information on survival. Another consideration is that, with knowledge of population trends and reproductive rates (which should continue to be monitored) any downward departure from predicted population estimates with given survival rates and empirically derived (observed) reproductive rates has to infer a ‘problem’ with either the given survival rates and/or emigration (Whitfield et al. 2006a, 2008b). This would not, of course, identify which age-specific survival rate was ‘deficient’ and hence problematic. Neither would records of the age of male breeders (see above). And survival rates may, of course, change in the future due to an unanticipated threat.

Ideally, monitoring survival (and dispersal) is clearly desirable (section 6.1). With an objective of detecting a potential unanticipated future change in survival, patagial wing tagging is arguably not best placed when it is field labour intensive (‘front loaded’ on resource/funding requirements) and imposes a mildly invasive procedure on birds. It is not ideally suited to a long term protocol with no obvious requirement or end in sight.

DNA tags would serve this purpose better: samples could be stored until a need for analysis, implicated by other methods, was implicated. This would also allow a more rapid and useful identification of the potential survival problem (Kenward et al. 2007) than instigating a patagial wing tag study once the problem was implicated. As we have highlighted in the preceding section, however, using DNA tags in harriers is not free of difficulties and shortcomings. Further explorations of the practical utility of DNA tags in harriers are needed. Moreover, the UK is fortunate in that most raptor monitoring effort is undertaken by highly skilled and experienced volunteers. Retaining DNA samples collected by volunteers, without any short-term prospect of

analysis results, would not provide much in the way of encouragement or feedback on return rates of individual harriers, in contrast to patagial wing tags.

Ultimately, the decision as to whether and how survival should be monitored is dictated by resources. Hence, definitive recommendations on monitoring protocols are limited not only by incomplete knowledge of practical utility of a potentially valuable tool (DNA tagging) but also, critically, of available resources and what funds would be required over and above the substantial efforts already being contributed by skilled volunteers to maintain the 'basic' monitoring.

## **7 ACKNOWLEDGEMENTS**

Foremost, we would like to thank the many dedicated and skilled fieldworkers who collected the data on which this report is based and who have contributed enormously to knowledge of hen harrier ecology in Wales. For efforts in collating Welsh harrier monitoring efforts we thank Keith Offord, Reg Thorpe, Iolo Williams and, most recently and especially with regard to the present study, Andy Young. Brian Etheridge was extremely helpful (as always) in providing data on resightings and knowledge of harrier ecology. Andy Young (RSPB) and Siân Whitehead were also of great assistance in providing previously reported data and invaluable discussion. Harrier field studies in Wales have been funded by CCW, RSPB and the voluntary contributions of raptor workers.

## 8 REFERENCES

- Altman, D.G. & Royston, P. 2000. What do we mean by validating a prognostic model? *Statistics in Medicine* 19, 453-473.
- Amar, A. 2001. *Determining the Cause of the Hen Harrier Decline on Orkney*. Unpublished PhD thesis, University of Aberdeen, UK.
- Amar, A. & Redpath, S.M. 2002. Determining the cause of the hen harrier decline on the Orkney Islands: an experimental test of two hypotheses. *Animal Conservation* 5, 21-28.
- Amar, A., Redpath, S. & Thirgood, S. 2003. Evidence for food limitation in the declining hen harrier population on the Orkney Islands, Scotland. *Biological Conservation* 111, 377-384.
- Amar, A., Picozzi, N., Meek, E.R., Redpath, S.M. & Lambin, X. 2005. Decline of the Orkney hen harrier *Circus cyaneus* population: do changes to demographic parameters and mating system fit a declining food hypothesis? *Bird Study* 52, 18-24.
- Arroyo, B.E. 2002. Fledgling sex ratio variation and future reproduction probability in Montagu's Harrier, *Circus pygargus*. *Behavioral Ecology & Sociobiology* 52, 109-116.
- Arroyo, B., Garcia, J.T. & Bretagnolle, V. 2002. Conservation of the Montagu's harrier (*Circus pygargus*) in agricultural areas. *Animal Conservation* 5, 283-290.
- Baker, M., Nur, N. & Geupel, G.R. 1995. Correcting biased estimates of dispersal and survival due to limited study area: theory and an application using wrentits. *Condor* 97, 663-674.
- Balbontín, J., Penteriani, V. & Ferrer, M. 2003. Variations in the age of mates as an early warning signal of changes in population trends? The case of Bonelli's eagle in Andalusia. *Biological Conservation* 109, 417-423.
- Balfour, E. 1970. Iris colour in the hen harrier. *Bird Study* 17, 47.
- Bibby, C.J. & Etheridge, B. 1993. Status of the Hen Harrier *Circus cyaneus* in Scotland in 1988/89. *Bird Study* 40, 1-11.
- Bildstein, K. L. 1988. Northern harrier. In: *Handbook of North American Birds. vol. 4 Diurnal Raptors (Part 1)*, R.S. Palmer (ed.), pp. 251-303. Yale University Press, New Haven, Connecticut, USA.
- Caswell, H. 2001. *Matrix Population Models: Construction, Analysis and Interpretation*. Sinauer Associates, Sunderland, MA, USA.
- Chevan, A. & Sutherland, M. 1991. Hierarchical partitioning. *American Statistician* 45, 90-96.
- Clobert, J., Danchin, E., Dhondt, A.A. & Nichols, J. (eds) 2001. *Dispersal: Causes, Consequences and Mechanisms of Dispersal at the Individual, Population and Community Level*. Oxford University Press, Oxford, UK.
- Cramp, S. & Simmons, K.E.L. (eds.) 1980. *The Birds of the Western Palearctic*. Vol. 2. Oxford University Press, Oxford.
- de Kroon, H., van Groenendael, J. & Ehrlén, J. 2000. Elasticities: a review of methods and model limitations. *Ecology* 81, 607-618.

- Delibes, M., Gaona, P. & Ferreras, P. 2001. Effects of an attractive sink leading into maladaptive habitat selection. *American Naturalist* 158, 277-285.
- Etheridge, B. & Summers, R.W. 2006. Movements of British hen harriers *Circus cyaneus* outside the breeding season. *Ringing & Migration* 23, 6-14.
- Etheridge, B., Summers, R.W. & Green R.E. 1997. The effects of illegal killing and destruction of nests by humans on the population dynamics of the hen harrier *Circus cyaneus* in Scotland. *Journal of Applied Ecology* 34, 1081-1105.
- Ferrer, M., Penteriani, V., Balbontín, J. & Pandolfi, M. 2003. The proportion of immature breeders as a reliable early warning signal of population decline: evidence from the Spanish Imperial Eagle in Doñana. *Biological Conservation* 114, 463-466.
- Fielding, A.H. 2007. *Cluster and Classification Techniques for the Biosciences*. Cambridge University Press, Cambridge.
- Fielding, A., Haworth, P., Whitfield, P. & McLeod, D. 2008. *Raptor Species Conservation Frameworks: Hen Harrier Framework Progress Report – Phase 1*. Unpublished Report from Haworth Conservation to Scottish Natural Heritage.
- Fielding, A.H., Whitfield, D.P. & Whitehead, S. In press. Population dynamics of the Hen Harrier *Circus cyaneus* in Wales. *Bird Study*
- Green, R.E. & Etheridge, B. 1999. Breeding success of the hen harrier *Circus cyaneus* in relation to the distribution of grouse moors and the red fox *Vulpes vulpes*. *Journal of Applied Ecology* 36, 472-483.
- Greenwood, P.J. & Harvey, P.H. 1982. The natal and breeding dispersal of birds. *Annual Review of Ecology and Systematics* 13, 1-21.
- Gregory, R.D., Wilkinson, N.I., Noble, D.G., Robinson, J.A., Brown, A.F., Hughes, J., Proctor, D.A., Gibbons, D.W. & Galbraith, C.A. 2002. The population status of birds in the United Kingdom, Channel Islands and Isle of Man: an analysis of conservation concern 2002-2007. *British Birds* 95, 410-450.
- Hamerstrom, F., Hamerstrom, F.N. & Burke, C. 1985. Effect of voles on mating systems in a central Wisconsin population of harriers. *Wilson Bulletin* 97, 332-346.
- Hardey, J., Crick, H.Q.P., Wernham, C.V., Riley, H.T., Etheridge, B. & Thompson, D.B.A. 2006. *Raptors: a Field Guide to Survey and Monitoring*. The Stationery Office, Edinburgh, UK.
- Harvey, M.G., Bonter, D.N., Stenzler, L.M. & Lovette, I.J. 2006. A comparison of plucked feathers versus blood samples as DNA sources for molecular sexing. *Journal of Field Ornithology* 77, 136-140.
- Heppell, S.S., Caswell, H. & Crowder, L.B. 2000. Life history and elasticity patterns: perturbation analysis for species with minimal demographic data. *Ecology* 81, 654-665.
- Hood, G. M. 2000. *PopTools - Software for the Analysis of Ecological Models*. Version 2.5.5. <http://www.cse.csiro.au/poptools>

- Horváth, M.B., Martínez-Cruz, B., Negro, J.J., Kalmár, L. & Godoy, J.A. 2005. An overlooked DNA source for non-invasive genetic analysis in birds. *Journal of Avian Biology* 36, 84-88.
- Hudson, P.J. 1992. *Grouse in Space and Time: the Population Biology of a Managed Gamebird*. Game Conservancy Trust, Fordingbridge.
- Hughes, B. & Williamson, I. 1991. *Hen Harriers in Wales 1991*. Unpublished report from RSPB to CCW.
- Kenward, R. E., Marcström, V. & Karlbom, M. 1999. Demographic estimates from radio-tagging: models of age-specific survival and breeding in the goshawk. *Journal of Animal Ecology* 68, 1020–1033.
- Kenward, R., Katzner, T., Wink, M., Marcström, V., Walls, S., Karlbom, M., Pfeffer, R., Bragin, E., Hodder, K. & Levin, A. 2007. Rapid sustainability modeling for raptors by radiotagging and DNA-fingerprinting. *Journal of Wildlife Management* 71, 238-245.
- Katzner, T., Bragin, E. & Milner-Gullard, E.J. 2006. Modelling populations of long-lived birds of prey for conservation: a study of imperial eagles (*Aquila heliaca*) in Kazakhstan. *Biological Conservation* 132, 322-335.
- Katzner, T., Milner-Gullard, E.J. & Bragin, E. 2007. Using modeling to improve monitoring of structured populations: are we collecting the right data? *Conservation Biology* 21, 241-252.
- Kauffman, M.J., Pollack, J.F. & Walton, B. 2004. Spatial structure, dispersal, and management of a recovering raptor population. *American Naturalist* 164: 582-587.
- Legendre, S. & Clobert, J. 1995. ULM, a software for conservation and evolutionary biologists. *Journal of Applied Statistics* 22, 817-834.
- MacNally, R. 2000. Regression and model-building in conservation biology, biogeography and ecology: the distinction between – and reconciliation of – ‘predictive’ and ‘explanatory’ models. *Biodiversity and Conservation* 9, 655-671.
- Marsden, A., Rebecca, G.W. & Parkin, D.T. 2003. A non-invasive technique for monitoring raptor populations using genetic profiling: a case study using merlin (*Falco columbarius*). In: Thompson, D.B.A., Redpath, S., Fielding, A.H., Marquiss, M., Galbraith, C.A. (Eds.), *Birds of Prey in a Changing Environment*, pp. 209-213. The Stationery Office, Edinburgh, UK.
- Matthysen, E. 2005. Density-dependent dispersal in birds and mammals. *Ecography* 28, 403-416.
- Millon, A. & Bretagnolle, V. 2005. Nonlinear and population-specific offspring sex ratios in relation to high variation in prey abundance. *Oikos* 108, 535-543.
- Newton, I. 1979. *Population Ecology of Raptors*. Poyser, Berkhamstead, UK.
- Offord, K. 2002. *Review of Raptor Data on Berwyn and Migneint-Dduallt SPAs*. CCW Contract Science Report 479.
- Picozzi, N. 1984a. Breeding biology of polygynous hen harriers *Circus c. cyaneus* in Orkney. *Ornis Scandinavica* 15, 1-10.

- Picozzi, N. 1984b. Sex ratio, survival and territorial behaviour of polygynous hen harriers *Circus c. cyaneus* in Orkney. *Ibis* 126, 356-365.
- Potts, G.R. 1998. Global dispersion of nesting hen harriers (*Circus cyaneus*): implications for grouse moors in the UK. *Ibis* 140, 76-88.
- Redpath, S.M., Thirgood, S.J. & Leckie, F.M. 2001. Does supplementary feeding reduce predation of red grouse by hen harriers? *Journal of Applied Ecology* 38, 1157-1168.
- Redpath, S.M., Thirgood, S.J. & Clarke, R. 2002a. Field Vole *Microtus agrestis* abundance and Hen Harrier *Circus cyaneus* diet and breeding in Scotland. *Ibis* 144, E33-E38.
- Redpath, S.M., Arroyo, B.E., Etheridge, B., Leckie, F., Bowman, K. & Thirgood, S.J. 2002b. Temperature and hen harrier productivity: from local mechanisms to geographical patterns. *Ecography* 25, 533-540.
- Rothery, P. 1985. Estimation of age-specific survival of hen harriers (*Circus c. cyaneus*) in Orkney. In: *Statistics in Ornithology*, North, P.M. & Morgan, B.J.T. (eds.), pp. 341-355. Springer-Verlag, Berlin, Germany.
- Rudnick, J.A., Katzner, T.E., Bragin, E.A., Rhodes, E. & DeWoody, J.A. 2005. Using naturally shed feathers for individual identification, genetic parentage analyses and population monitoring in an endangered eastern imperial eagle (*Aquila heliaca*) population from Kazakhstan. *Molecular Ecology* 14, 2959-2967.
- Salamolard, M., Butet, A., Leroux, A. & Bretagnolle, V. 2000. Responses of an avian predator to variations in prey density at a temperate latitude. *Ecology* 81, 2428-2441.
- Sim, I.M.W., Gibbons, D.W., Bainbridge, I.P. & Mattingley, W.A. 2001. Status of the Hen Harrier *Circus cyaneus* in the UK and Isle of Man in 1998. *Bird Study* 48, 341-353.
- Sim, I.M.W., Dillon, I.A., Eaton, M.A., Etheridge, B., Lindley, P., Riley, H., Saunders, R., Sharpe, C. & Tickner, M. 2007. Status of the Hen Harrier *Circus cyaneus* in the UK and the Isle of Man in 2004, and a comparison with the 1988/89 and 1998 surveys. *Bird Study* 54, 256-267.
- Simmons, R.E. 1988. Food and the deceptive acquisition of mates by polygynous male harriers. *Behavioural Ecology & Sociobiology* 23, 83-92.
- Simmons, R.E. 2000. *Harriers of the World: Their Behaviour and Ecology*. Oxford University Press, Oxford.
- Simmons, R., Barnard, P., MacWhirter, B. & Hansen, G.L. 1986. The influence of microtines on polygyny, productivity, age, and provisioning of breeding Northern Harriers: a 5-year study. *Canadian Journal of Zoology* 64, 2447-2456.
- Simmons, R.E., Barnard, P.E. & Smith, P.C. 1987. Reproductive behaviour of *Circus cyaneus* in North America and Europe: a comparison. *Ornis Scandinavica* 18, 33-41.
- Thorpe, R.I. & Young, A. 2003. *The population status of birds in Wales: an analysis of conservation concern: 2002-2007*. RSPB Cymru, Cardiff.
- Watson, J. & Whitfield, P. 2002. A conservation framework for the golden eagle *Aquila chrysaetos* in Scotland. *Journal of Raptor Research* 36 (1 Supplement), 41-49.

- White, G.C. & Burnham, K.P. 1999. Program MARK: Survival estimation from populations of marked animals. *Bird Study* 46 Supplement, 120-138.
- Whitfield, D.P., Fielding, A.H., McLeod, D.R.A. & Haworth, P.F. 2004a. Modelling the effects of persecution on the population dynamics of golden eagles in Scotland. *Biological Conservation* 119, 319-333.
- Whitfield, D.P., Fielding, A.H., McLeod, D.R.A. & Haworth, P.F. 2004b. The effects of persecution on age of breeding and territory occupation in golden eagles in Scotland. *Biological Conservation* 118, 249-259.
- Whitfield, D.P., Fielding, A.H., McLeod, D.R.A., Haworth, P.F. & Watson, J. 2006a. A conservation framework for the golden eagle in Scotland: refining condition targets and assessment of constraint influence. *Biological Conservation* 130, 465-480.
- Whitfield, D.P., McLeod, D.R.A., Haworth, P.F. & Fielding, A.H. 2006b. *Scoping assessment for a conservation framework for the hen harrier*. Report to SNH under contract no. 15367.
- Whitfield, D.P., Fielding, A.H. & Whitehead, S. 2008a. Long-term increase in the fecundity of hen harriers *Circus cyaneus* in Wales is explained by reduced human interference and warmer weather. *Animal Conservation* 11, 144-152.
- Whitfield, D.P., Fielding, A.H., McLeod, D.R.A. & Haworth, P.F. 2008b. *A Conservation Framework for the Golden Eagle: Implications for Conservation and Management in Scotland*. Scottish Natural Heritage Commissioned Report No. 193. Scottish Natural Heritage, Battleby, UK.
- Wink, M., Staudter, H., Bragin, Y., Pfeffer, R. & Kenward, R. 1999. The use of DNA-fingerprinting to estimate survival rates in the saker falcon. *Journal of Ornithology* 140, 481-489.
- Wright, P. A. 2003. Recruitment, site fidelity, and dispersal of merlins *Falco columbarius* from the southeast Yorkshire Dales, England. *Ringing & Migration* 21, 227-233.

## **APPENDIX 1: SOURCE MATERIAL**

Held by Brian Etheridge, RSPB Scotland, Inverness:  
Tagging & ringing record forms 1991-1995  
Tagged bird sightings return forms 1991-1995

Held by RSPB Wales & CCW:  
Hen harrier nest record forms 1990-1995  
RSPB/CCW 'Hen harriers in Wales' annual reports 1991 – 1994  
'Hen Harriers / Bod Tinwen 1996' summary sheet  
Berwyn 'Hen harriers' annual reports 1989 – 1998 (excluding 1991), 2003 and 2004  
Hen harrier nest records 1960s to 2006 compiled by Andy Young, RSPB Wales, in Excel

Offord, K. 2002. *Review of Raptor Data on Berwyn and Migneint-Dduallt SPAs*. CCW Contract Science Report 479.