1 **Integrating advances in population and evolutionary ecology with**

2 **conservation strategy through long-term studies of red-billed choughs**

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Abstract

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25 1. Conceptual and methodological advances in population and evolutionary ecology are often

26 pursued with the ambition that they will help identify demographic, ecological and genetic

27 constraints on population growth rate (λ), and ultimately facilitate evidence-based

28 conservation. However, such advances are often decoupled from conservation practice,

29 impeding translation of scientific understanding into effective conservation, and of

30 conservation-motivated research into wider conceptual understanding.

31 2. We summarise key outcomes from long-term studies of a red-billed chough (*Pyrrhorcorax*

32 *pyrrhocorax*) population of conservation concern, where we pro-actively aimed to achieve

33 the dual and interacting objectives of advancing population and evolutionary ecology and

34 advancing effective conservation.

35 3. Estimation of means, variances and covariances in key vital rates from individual-based

36 demographic data identified temporal and spatial variation in sub-adult survival as key

37 constraints on λ, and simultaneously provided new insights into how vital rates can vary as

38 functions of demographic structure, natal conditions and parental life-history.

39 4. Targeted analyses showed that first-year survival increased with prey abundance, implying

40 that food limitation may constrain λ. First-year survival then decreased dramatically,

41 threatening population viability and prompting emergency supplementary feeding

42 interventions. Detailed evaluations suggested that the interventions successfully increased

43 first-year survival in some years, and additionally increased adult survival and successful

44 reproduction, thereby feeding back to inform intervention refinements and understanding

45 of complex ecological constraints on λ.

46 5. Genetic analyses revealed novel evidence of expression of a lethal recessive allele, and

47 demonstrated how critically small effective population size can arise, thereby increasing

48   inbreeding and loss of genetic variation. Population viability analyses parameterised with

49   all available demographic and genetic data showed how ecological and genetic constraints

50   can interact to limit population viability, and identified ecological management as of

51   primacy over genetic management to ensure short-term persistence of the focal

52   population.

53   6. This case study demonstrates a full iteration through the sequence of primary science,

54   evidence-based intervention, quantitative evaluation and feedback that is advocated in

55   conservation science but still infrequently achieved. It thereby illustrates how pure science

56   advances informed conservation actions to ensure (short-term) stability of the target

57   population, and how conservation-motivated analyses fed back to advance fundamental

58   understanding of population processes.

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60   **Key words:** Adaptive management; applied ecology; conservation genetics; demography;

61   evidence-based conservation; long-term study; population growth rate; population viability

62   analysis.

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INTRODUCTION

Numerous species are currently experiencing substantial declines or threats to global or local persistence, and are consequently subject to statutory or discretionary species-focussed conservation efforts on international and/or national scales (Hoffmann et al., 2010; Díaz et al., 2015; Eaton et al., 2015). Core principles of conservation science are that such efforts should be evidence-based and iterative, following sequences of i) primary scientific investigation to identify mechanisms causing population declines or threats; ii) design and application of appropriate interventions; and iii) rigorous monitoring and evaluation that can feed back to inform subsequent intervention refinements and also advance wider understanding (Fig. 1, Gillson et al., 2019). Yet, recent reviews suggest that such sequences of concept-driven primary science, intervention, (re-)evaluation and full feedback, and resulting joint application and facilitation of scientific advances, are still infrequently achieved (Cook et al., 2013; Walsh et al., 2014; Toomey et al., 2016; Gillson et al., 2019; Williams et al., 2020).

Any such failures cannot be attributed to a fundamental lack of scientific capability to understand and forecast population dynamics. Rather, recent decades have seen major conceptual and methodological developments in population and evolutionary ecology that facilitate identification of demographic, ecological and genetic mechanisms causing population change, and allow prediction of population outcomes given observed or postulated threats, forms of environmental change or policy-driven interventions. Not least, matrix models and advanced individual-based simulation methodologies allow projection of population growth rate (λ) and persistence given complex age- and/or stage-structure, including estimation of stochastic growth rates (λ_s) in temporally- and/or spatially-varying environments (e.g. Caswell, 2001; Boyce et al., 2006; Bocedi et al., 2014; Lacy & Pollak, 2017).

96   Given estimates of mean vital rates, comprising age- and/or stage-structured reproduction

97   and survival probabilities, matrix models also facilitate prospective elasticity analyses to

98   identify rates in which small changes would have greatest impact on λ (Caswell, 2000, 2001),

99   including 'integrated elasticities' that incorporate vital rate covariation (van Tienderen, 1995).

100   Estimation of among-year variation in vital rates also allows retrospective analyses that

101   identify which rates caused observed variation in λ, thereby identifying actual demographic

102   causes of population change (i.e. 'life table response experiments', Caswell, 2000; Wisdom et

103   al., 2000). Meanwhile, theoretical advances at the interface of population and evolutionary

104   ecology show how age- and/or stage-specific reproductive value can be coupled with

105   demographic variance to estimate effective population size (N_e), and hence evaluate rates of

106   genetic drift and accumulation of inbreeding (Engen et al., 2005, 2007). These objectives

107   reflect growing evidence that genetic constraints associated with small population size,

108   particularly inbreeding and resulting expression of inbreeding depression, can substantially

109   limit λ (Frankham et al., 2014; Bozzuto et al., 2019). Consequently, the need to consider

110   genetic constraints on population persistence alongside ecological constraints is now strongly

111   advocated (Haig et al., 2016; Frankham et al., 2017; Allendorf et al., 2021).

112   Such conceptual developments in population and evolutionary ecology have occurred

113   alongside major statistical and empirical developments which allow theory to be tested and

114   applied in wild populations. Specifically, advanced capture-mark-recapture methods can

115   reduce bias in estimation of vital rates and life-history variation from incomplete data where,

116   as is almost inevitable in wild population studies, not all present individuals are always

117   observed (Nichols & Kendall, 1995; White & Burnham, 1999; Gimenez et al., 2008).

118   Meanwhile, field studies are accumulating sufficient years of individual-based data to allow

119   estimation of vital rate means, variances and covariances, and associations with underlying

120　environmental variation. Comparative demography databases have been compiled, and there

121　are sufficient estimates of key parameters, such as the magnitude of inbreeding depression,

122　to allow broad comparative insights into likely constraints on populations for which direct

123　data are sparse or even completely lacking (e.g. Frankham et al., 2014, 2017; Salguero-Gómez

124　et al., 2016).

125　　　Such theoretical, statistical and empirical advances are often initially pursued within

126　'pure' science programmes, where the primary ambition is conceptual advance rather than

127　direct application. Yet, even pure science programmes commonly invoke explicit or implicit

128　justifications that resulting insights will ultimately facilitate population management and/or

129　conservation. However, in practice, there is a widely acknowledged research-implementation

130　'gap' or 'space', such that new knowledge is not rapidly translated into conservation

131　interventions for threatened populations (Fig. 1, Toomey et al., 2016; Cook & Sgrò, 2017;

132　Dubois et al., 2020; Jarvis et al., 2020). Such gaps are commonly emphasised regarding

133　translation of directly relevant applied research into conservation action (Fig. 1, Arlettaz et

134　al., 2010; Walsh et al., 2014; Taylor et al., 2017). But, there can be further gaps, whereby

135　conceptual and methodological advances achieved at the cutting edges of pure population

136　and evolutionary ecology are not utilised in applied research (Fig. 1). Further, while it is

137　frequently emphasised that conservation interventions should be monitored and evaluated

138　to refine actions, the opportunity for research motivated by application and evaluation to

139　feed right back to advance general conceptual understanding (Fig. 1) is less frequently

140　highlighted or exploited (Cook et al., 2013). Pure and applied science disciplines then do not

141　fully embrace each other, to the likely detriment of both, and to the ultimate conservation

142　objectives.

143 Such divisions have been shown or suggested to persist because research in

144 population and evolutionary ecology versus applied conservation is often undertaken by

145 separate groups and organisations with differing objectives, priorities, capabilities and value

146 systems (Arlettaz et al., 2010; Cook et al., 2013; Walsh et al., 2014; Toomey et al., 2016; Gillson

147 et al., 2019; Roux et al., 2019; Jarvis et al., 2020). This leads to dysfunctional communication,

148 arising partly because concept-led scientific publications by academic researchers are not

149 always accessible, intelligible, or apparently relevant to applied scientists and practitioners

150 (Walsh et al., 2014; Taylor et al., 2017; Fabian et al., 2019). These divisions can be further

151 exacerbated because pure science advances are often achieved using populations or species

152 that are not themselves of current conservation concern but where multi-year observational

153 and/or experimental data can be relatively readily collected. Meanwhile, key data required

154 for advanced demographic and/or genetic analyses often cannot be readily or adequately

155 collected in populations for which conservation action is urgently required, and/or primary

156 publications focus on general concepts and follow editorial policies to deliberately downplay

157 system-specific inferences that could facilitate management.

158 These challenges raise questions regarding the degree to which rapid applications of

159 advances in population and evolutionary ecology are achievable within current professional

160 structures and constraints and how such integration can be improved (Cook et al., 2013;

161 Toomey et al., 2016; Cook & Sgrò 2017; Enquist et al., 2017; Taylor et al., 2017; Jarvis et al.,

162 2020), or else to what degree ultimate conservation application is actually a valid justification

163 for investment in pure science programmes. Reflective case studies that summarise and

164 evaluate efforts at pure-applied integration (Fig. 1), and identify achievements and failures,

165 can then provide useful context and insights to establish and encourage best practice (Arlettaz

166 et al., 2010; Gillson et al., 2019; Williams et al., 2020).

167   Accordingly, we review key outcomes from long-term individual-based research on a

168   red-billed chough (*Pyrrhocorax pyrrhocorax,* hereafter 'chough') population of conservation

169   concern, where we explicitly aimed to achieve the joint, interacting, goals of advancing

170   fundamental scientific understanding and advancing effective conservation (Fig. 1).

171   Specifically, we summarise five research phases that utilised conceptual and methodological

172   advances at the forefronts of population and evolutionary ecology to identify constraints on

173   population size and persistence, and to inform and evaluate resulting conservation

174   interventions (Fig. 2). We thereby highlight how pure science advances contributed to

175   conservation actions and evaluations, and also highlight how research motivated primarily by

176   conservation application fed back to advance conceptual understanding. We summarise the

177   process of pure-applied translation, and highlight remaining challenges in achieving desired

178   conservation outcomes.

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180   **FIELD STUDY AND CONSERVATION CONTEXT**

181   Choughs are corvids that are closely associated with low-intensity pastoral agricultural

182   habitats. They were formerly widespread across the British Isles, but decreased substantially

183   in population size and distribution over the last two centuries (Bignal et al., 1997; Hayhow et

184   al., 2018). Choughs are consequently listed on Annex 1 of the EU Wild Birds Directive and

185   Schedule 1 of the UK Wildlife & Countryside Act, triggering statutory conservation obligations.

186   In particular, NatureScot, the delegated Scottish Government agency, is responsible for

187   safeguarding Scotland's chough population, which is now restricted to the inner Hebridean

188   islands of Islay and Colonsay (Fig. 2, Hayhow et al., 2018). Since choughs are classed as

189   vulnerable and the UK subspecies is amber-listed (Eaton et al., 2015; Stanbury et al., 2017),

190   chough conservation has also been a focus for the Royal Society for the Protection of Birds

191   (RSPB, a non-governmental organisation), including reserve acquisition and management.

192   On Islay, chough research has been ongoing since 1981, including a licensed

193   programme of nest monitoring, individual colour-ringing and resightings run by Scottish

194   Chough Study Group (SCSG, Appendix S2). In brief, adult pairs occupy large territories where

195   they breed once each year during April-June. Nests are traditionally in caves in sea cliffs, but

196   increasingly in farm buildings and custom-built field shelters (Fig. 3, Bignal et al., 1997;

197   Hayhow et al., 2018). The locations of most potential nest sites are consequently known,

198   facilitating demographic monitoring.

199   Each year, a sample of accessible cave and building sites is visited to record breeding

200   success, and chicks are colour-ringed to allow subsequent individual identification (Fig. 3).

201   Nests are usually only visited once per year to minimise disturbance, coinciding with expected

202   chick ringing age (approximately 3-4 weeks post-hatch), but second visits are made if chicks

203   are initially too small. Adults are not caught, again to minimise disturbance. However, survival

204   of colour-ringed fledglings means that ≥60% of adults are now colour-ringed. Adults at

205   accessible and inaccessible nest sites are checked for colour-rings by remote observation

206   (rings readable at ≤300m through a telescope, Fig. 3). Year-round resighting effort in foraging

207   and roosting areas also provides numerous observations of surviving sub-adults.

208   The main demographic monitoring dataset now comprises >2,050 individuals ringed

209   during 1983-2019, with >35,000 subsequent resightings and >1,400 observations of breeding

210   success, allowing estimation of key vital rates that determine λ. Since the population is

211   currently effectively closed with no recent detected immigration or emigration, survival

212   probabilities can be estimated with little or no bias due to emigration, and population

213 dynamics are determined by local demography rather than movements. Yet, while the insular

214 system facilitates demographic analyses, it also fosters inbreeding.

215   Early research focussed on understanding social roosting behaviour (Still, Monaghan

216 & Bignal, 1987) alongside species ecology and life-history (e.g. McCracken et al., 1992;

217 McCracken & Foster, 1994; Bignal et al., 1997; Laiolo et al., 1998). Meanwhile, the number of

218 breeding pairs on Islay decreased from 78 in 1986 to 47 in 1998 (Fig. 2), increasing the urgency

219 to implement evidence-based conservation to reverse the population decline. Accordingly, in

220 2001, efforts commenced to couple the accumulating demographic data with recent

221 conceptual and statistical advances in population and evolutionary ecology to inform

222 conservation strategy (Figs. 1,2).

223

224 **RESEARCH PHASES**

225 **Phase one: Population demography and dynamics**

226 In general, first major steps towards understanding and managing population dynamics are

227 to quantify temporal and spatial (co)variation in vital rates, and identify underlying drivers

228 and impacts on λ. Accordingly, we used demographic data from 1983-2000 to show that

229 among-year variation in mean breeding success (fledglings/breeding attempt) was correlated

230 with variation in weather. Specifically, choughs bred more successfully in springs following

231 warmer previous summers and relatively dry late winters, perhaps reflecting lagged weather

232 effects on invertebrate prey (Reid et al., 2003a). Capture-mark-recapture analyses of ring-

233 resighting data showed that first-year survival probability (i.e. survival from ringing to

234 approximately one year old) also varied substantially among years (Fig. 4), and was strongly

235 positively correlated with population mean breeding success in each cohort's natal year (Reid

236 et al., 2003a). Further, the probability that an individual would survive to recruit to breed

237   (typically age three years), adult lifespan and total lifetime number of offspring fledged were

238   all also positively correlated with mean population breeding success in the natal year, and

239   hence with underlying environmental conditions (Reid et al., 2003a). These analyses, which

240   utilised recent advances in capture-mark-recapture methodologies, provided evidence of

241   strong and long-lasting cohort effects, which had not then been widely demonstrated in wild

242   populations (Lindström, 1999). They also implied strong local environmental influences on

243   overall annual productivity, indicating that long-term legacies of beneficial early-life

244   environmental conditions might substantially influence individual fitness and hence

245   population growth.

246   Further capture-mark-recapture analyses showed that adult survival probability (i.e.

247   survival through each year from age two) was high and varied relatively little among years,

248   while second-year survival probability (i.e. survival from age one to two) was intermediate

249   (Reid et al., 2003a, 2004). Resulting estimates of means, variances and covariances in stage-

250   specific survival and reproductive success allowed parameterisation of matrix models. Here,

251   initial analyses showed that population dynamics were well captured by a four-stage model,

252   comprising first-year, second-year, third-year and adult classes (Reid et al., 2004). Indeed, the

253   modelled population trajectory matched population census data remarkably well, implying

254   that available demographic data allowed unbiased estimation of all key vital rates (Reid et al.,

255   2004). The four-stage model performed well despite evidence that breeding success varied

256   with age within the adult class, including apparent senescence (Reid et al., 2003b, 2004). Since

257   few individuals survived to ages at which vital rates decreased, any senescence scarcely

258   affected annual population mean rates or resulting estimates of λ (Reid et al., 2004). Yet,

259   while they proved non-essential for projecting short-term population dynamics, underlying

260   analyses of age-specific variation provided new conceptual understanding of how interactions

261 among age, reproductive success and longevity, and resulting selective disappearance, can

262 generate actual and apparent senescence through joint cross-sectional (among-individual)

263 and longitudinal (within-individual) variation in age-specific reproductive performance (Reid

264 et al., 2003b).

265   Asymptotic λ, simply estimated as the dominant eigenvalue of the mean projection

266 matrix, was approximately 1, projecting stable population size. However, the approximate

267 stochastic growth rate was $\lambda_s \approx 0.97$, indicating gradual population decline (Reid et al., 2004).

268 This estimate concurred with the observed decrease in population size (Fig. 2), and illustrates

269 the common impact of among-year variation in vital rates in reducing λ (e.g. Boyce et al.,

270 2006; Hilde et al., 2020).

271   As is typical for reduced-dimension matrix models parameterised for species with

272 relatively slow life-histories, prospective analyses indicated that λ was more elastic (i.e.

273 proportionally sensitive) to adult survival probability than to sub-adult (i.e. first-year or

274 second-year) survival probabilities, or to breeding success (Reid et al., 2004). This was also

275 true given integrated elasticities that accounted for covariances among vital rates across

276 years, but the summed elasticity across the sub-adult classes was relatively high (Reid et al.,

277 2004). Further, because sub-adult survival probabilities varied more among years than adult

278 survival probabilities, retrospective 'life table response experiments' showed that first-year,

279 second-year and adult survival contributed similarly to variation in λ, with a major overall

280 contribution from the combined sub-adult class (Reid et al., 2004). These analyses identified

281 that variation in sub-adult survival could play, and had played, a major role in shaping

282 population dynamics. This conclusion broadly concurs with observations from other species

283 with relatively slow life-histories, where juvenile survival also varies substantially among years

284 (e.g. Gaillard et al. 1998). But, still relatively few studies have explicitly quantified vital rate

285   covariation or resulting integrated elasticities, or hence estimated total effects of

286   (co)variation involving juvenile survival on population dynamics (Coulson et al., 2005; Hilde et

287   al., 2020).

288   Fully understanding links among environmental variation, demography and

289   population dynamics requires considering spatial as well as temporal variation in vital rates.

290   Although the total chough-suitable area on Islay is relatively small (<200km^2), it encompasses

291   diverse grassland habitats that are exposed to open Atlantic coasts or more sheltered (Fig. 3),

292   with different underlying geologies, ecologies and pastoral agricultural regimes. We showed

293   that first-year survival probability varied spatially, such that choughs hatched in some areas

294   of Islay were consistently more likely to survive to age one year than choughs hatched in other

295   areas (Reid et al., 2006). This was true even though choughs fledging in all areas typically

296   congregate in communal foraging and roosting areas after fledging, and are no longer

297   associated with their natal territory (Still et al., 1987; Bignal et al., 1997). Our analyses also

298   revealed notably long-lasting associations between an individual's natal area and its adult

299   survival probability. Unexpectedly, natal area explained more variation in annual adult

300   survival than current breeding area (Reid et al., 2006). These analyses further affirmed the

301   long-lasting impacts of natal conditions in driving variation in survival across all life-stages,

302   and hence in λ. They identified key 'source' areas within Islay that were apparently

303   responsible for maintaining population viability, and which differed somewhat from previous

304   conceptions of core chough habitat.

305   The general concept of 'silver-spoon effects', meaning long-term effects of good early-

306   life conditions, is now well-established in ecology and evolutionary biology, including

307   recognition that ultimate effects can differ among ages and subsequent environmental

308   conditions (e.g. Cooper & Kruuk 2018; Pigeon et al., 2019). Yet, such effects are still

309   predominantly considered in relation to temporal (often among-cohort) environmental

310   variation rather than spatial variation (but see van de Pol et al., 2006). Consequently, the

311   possibility that source areas that drive population growth may be missed or erroneously

312   attributed by measuring survival across current inhabitants is still infrequently considered.

313

314   **Phase two: Ecology of sub-adult survival**

315   Overall, the demonstration that sub-adult survival varied temporally and spatially in

316   association with environmental conditions suggested that stochastic population growth rate

317   λ_s, and hence population size, could potentially be effectively increased by increasing mean

318   sub-adult survival and/or reducing frequencies or degrees of poor survival years or locations.

319   This diagnosis prompted new focus on identifying constraints, and potential conservation

320   interventions, that could target sub-adults. While basic sub-adult chough ecology and

321   communal roosting behaviour was already understood (Still et al., 1987; Bignal et al., 1997),

322   we lacked sufficient information on early-life movements, habitat use and ecology to inform

323   targeted conservation interventions.

324   Accordingly, we undertook intensive fieldwork to track two chough cohorts (2006-

325   2007) from fledging through their first year and identify key foraging locations and habitat

326   types (Reid et al., 2009). Meanwhile, we used the accumulating demographic data (1983-

327   2007) to test specific hypotheses regarding the ecological basis of temporal (among-year) and

328   spatial (among-territory) variation in first-year survival probability. We showed that temporal

329   variation was strongly positively correlated with tipulid larvae abundance (Fig. 5, Reid et al.,

330   2008). Tipulids are one major winter food for choughs, and abundance was monitored

331   annually across south-west Scotland (including some sampling sites on Islay) to inform

332   agricultural pest management. Overall, first-year survival probability was higher when

333 choughs fledged following and before winters with high tipulid abundance, and also following

334 relatively warm summers and dry springs. Together, these variables explained up to ~80% of

335 estimated among-year process variation in first-year survival probability (Reid et al., 2008).

336 Our analyses were consequently successful in identifying specific components of early-life

337 environmental variation that could drive first-year survival; such effects are often postulated

338 across diverse bird species but still infrequently rigorously quantified (Maness & Anderson,

339 2013).

340   In contrast, attempts to explain among-territory variation in first-year chough survival

341 probability, and thereby identify determinants of 'source' areas, were less successful. This

342 was partly because data on postulated drivers (e.g. prey abundance, and various forms of land

343 management) were not available on sufficiently small spatial scales (Reid et al., 2008).

344 Nevertheless, the analyses of temporal variation strongly indicated that years of low first-year

345 survival partly reflect early-life food limitation, which could underlie the previously

346 documented long-term cohort effects and impacts on λ (Reid et al., 2003a, 2004, 2008). The

347 attempts to understand variation in first-year survival for applied purposes also advanced

348 general conceptual understanding by revealing that parents with long lifespans systematically

349 produced offspring with low survival probabilities, thereby highlighting how offspring survival

350 can vary as a function of parental life-history strategy (Reid et al., 2010).

351   At this stage, attempts were made to integrate new knowledge of ecological

352 constraints on key vital rates (Reid et al., 2006, 2008, 2009), into conservation action. In 2006,

353 NatureScot added choughs as a qualifying interest for Islay's Gruinart Flats Special Protection

354 Area (SPA), which was already designated due to its internationally important wintering goose

355 populations (Appendix S1). This SPA encompassed key sub-adult chough foraging areas (Reid

356 et al., 2009), and breeding territories that produced fledglings which survived relatively well

357   (Reid et al., 2006, 2008). However, the designation process revealed that high survival

358   probability is not listed as a qualifying criterion in SPA legislation (Appendix S1). There is

359   consequently no legal basis to designate SPAs covering areas that are known to drive

360   population growth by facilitating high survival for any species. This contrasts with clear

361   scientific understanding that λ can be highly sensitive to variation in survival, representing a

362   disconnect between conceptual understanding and conservation legislation. Choughs were

363   consequently added to the Gruinart Flats SPA designation because the focal area qualified by

364   holding >1% of the total UK population (Appendix S1); the desired science-informed

365   designation was therefore achieved through valid but tangential criteria. But, further areas

366   that supported high first-year survival did not contain existing SPAs. Legislative, political and

367   economic constraints were viewed as being too strong to support completely new SPAs, and

368   no such designations were attempted.

369   Management options designed to benefit choughs were also incorporated into the

370   Scottish Rural Development Programme (SRDP) agri-environment scheme (Appendix S1).

371   Since detailed agricultural management data were not available to directly relate to chough

372   demography, SRDP options were designed based on expert knowledge, including from SCSG.

373   They incentivised agricultural practices designed to benefit breeding and sub-adult choughs,

374   for example by adjusting year-round grassland management regimes. There was extensive

375   uptake by farmers in key areas of Islay. However, initial option design and uptake were

376   impeded by constraints on financial incentives due to restrictive definitions of relatively high-

377   value 'in-bye' grassland that did not apply to less favoured agricultural areas of high nature

378   value, and potential conflicts with other conservation-focussed options. This included existing

379   grassland management designed to benefit corncrake (*Crex crex*), which has been highlighted

380   as a successful yet necessarily ongoing agri-environment intervention (Wotton et al., 2015;

381   Green, 2020).

382

383   **Phase three: Emergency intervention and evaluation**

384   While conservation science should ideally pre-emptively prevent catastrophic demographic

385   changes that induce rapid population decline, researchers and practitioners should be alert

386   to unexpected challenges. During efforts to implement appropriate agri-environment options

387   within the SRDP, ongoing chough demographic monitoring revealed a severe decrease in first-

388   year survival probability on Islay, down to approximately 0.1 for cohorts fledged in 2007-2009

389   (Fig. 4) compared to a previous mean of 0.42. Reparameterization of matrix models with such

390   low values projected rapid population decline (λ=0.87, Reid et al., 2004, 2011). Urgent

391   conservation action to maintain sufficiently high sub-adult survival to ensure population

392   persistence was therefore required. This in turn required identification of the timing and

393   causes of increased early-life mortality.

394   This objective was achieved through further analyses of long-term colour-ring-

395   resighting data. Comparisons of monthly survival probabilities for three recent low-survival

396   cohorts (2007-2009) versus earlier cohorts with higher first-year survival (1984-1986, 2005-

397   2006) revealed a new period of low survival through late summer and autumn for the recent

398   cohorts (Fig. 5, Reid et al., 2011). Further observations showed that sub-adult choughs were

399   feeding in atypical areas (e.g. on beaches), and post-mortem examinations of individuals

400   found dead showed emaciation. This further supported previous inferences (Reid et al., 2008)

401   that food shortage was constraining first-year survival and hence λ.

402   These analyses led directly to a targeted emergency supplementary feeding

403   intervention designed to increase post-fledging survival, particularly through late summer

404   and autumn. Starting fully from 2010, restricted quantities of supplementary food were

405   provided almost daily during July-April through each biological year (i.e. excluding the main

406   April-June breeding season) at or near known sub-adult roosting or foraging sites, thereby

407   minimising disruption to natural foraging ecology (Trask et al., 2020). Feeding was designed

408   as a top-up, providing only approximately 15% of a chough's estimated daily energy

409   expenditure (Bignal & Bignal, 2011). High-frequency observations of colour-ringed individuals

410   at feeding sites, currently totalling >95,000 resightings, showed that both sub-adults and

411   adults regularly attended (Fig. 3). We therefore evaluated whether the supplementary

412   feeding intervention was effective in increasing first-year survival (as planned), and/or had

413   collateral (i.e. unplanned) effects on adult survival or breeding success. Since the intervention

414   was implemented as an emergency conservation action, not as randomised, replicated,

415   controlled experiments, we utilised all available data from the intensive year-round

416   demographic monitoring during the intervention period, and from previous baseline

417   monitoring, to draw the best possible inferences.

418   We used multi-state capture-mark-recapture models to simultaneously estimate the

419   proportion of juvenile choughs that attended supplementary feeding sites during defined

420   occasions through the months following fledging, and to estimate survival probability

421   conditional on attendance. These analyses showed that substantial proportions of surviving

422   juveniles (≥70%) typically attended, and that survival probabilities were higher in individuals

423   that attended than those that did not. However, such effects were not evident for all

424   occasions within years, or evident at all in two of eight intervention years when overall annual

425   survival probability was relatively high (Fenn et al., 2021). This implies that intervention

426   efficacy varied with underlying ecological circumstances. Nevertheless, scaling estimated

427   effects up to the population level suggested that the intervention greatly reduced the

428   decrease in population size that was otherwise projected, solely through effects on the target

429   vital rate of first-year survival (Fenn et al., 2021). These positive effects provide further quasi-

430   experimental support for the original inference that food limitation constrained juvenile

431   survival and hence λ. More generally, they show how intervention effects can vary temporally

432   both within and among years, and hence have complex population-level effects (Fenn et al.,

433   2021).

434   While the need to evaluate intervention effects on target individuals is frequently

435   emphasised, evaluations of collateral effects on non-target conspecifics are less commonly

436   attempted or achieved, even though such effects could have substantial positive or negative

437   effects on λ. Accordingly, we estimated effects of supplementary feeding on adult choughs

438   that consistently did or did not attend feeding sites through each non-breeding season. Since

439   adult attendance was structured with respect to territory location, resightings through the

440   eight-year intervention period were coupled with resightings from pre-intervention years to

441   control for spatial environmental variation using before-after-control-intervention (BACI)

442   analyses. Such analyses are widely advocated, especially where formal experiments are

443   impossible, but still relatively rarely implemented (Christie et al., 2019). We showed that

444   adults that attended feeding sites had higher annual survival probabilities, and higher

445   probabilities of successful reproduction, than adults occupying the same territories in

446   previous years, while adults currently occupying other territories did not (Fenn et al., 2020).

447   The estimated increases in adult survival were substantial and, alongside estimated moderate

448   increases in nest success, were almost sufficient to maintain λ close to one and hence

449   maintain population stability (Fenn et al., 2020).

450   These effects on adults were unanticipated in that previous demographic analyses in

451   the chough system had not revealed substantial among-year variation in adult survival

452 probability after accounting for sampling variance, or any recent decrease, and hence had not

453 generated any inference that adults were substantially food limited. Indeed, it is widely

454 expected that adult survival should be buffered from environmental variation in species with

455 relatively slow life-histories (Hilde et al., 2020). Our analyses therefore highlight how

456 implementation and full evaluation of conservation interventions, including collateral as well

457 as planned impacts, can feed back to update understanding of underlying constraints on vital

458 rates and λ (Fig. 1). They should also provide some optimism, since provision of even relatively

459 little supplementary food increased projected population viability. NatureScot consequently

460 extended the supplementary feeding programme to 2022, to allow more time to plan habitat

461 management measures that could provide sustainable natural food (Appendix S1).

462 Together, research phases 1-3 represent a full iteration through the desired process

463 of primary science, intervention, evaluation and feedback to allow refinement of both

464 intervention and fundamental understanding, as advocated but still infrequently achieved in

465 conservation science (Fig. 1; Gillson et al., 2019; Williams et al., 2020).

466

467 **Phase four: Genetic constraints**

468 The emergence of conservation genetics as a major discipline is partly founded on increasing

469 evidence that inbreeding depression can be severe and constrain viability of small populations

470 (Haig et al., 2016; Frankham et al., 2017; Bozzuto et al., 2019; Allendorf et al., 2021).

471 Accordingly, there was increasing concern that genetic constraints might proximately limit λ

472 in Scottish choughs, alongside ecological constraints. Indeed, population genetic analyses

473 based on bespoke microsatellite markers showed strong genetic structure across Scottish and

474 other British and western European chough populations, with particularly low marker

475 diversity in Scotland (Wenzel et al., 2011, 2012). These genetic data support inferences from

476   colour-ring resightings that between-population dispersal and resulting gene flow is currently

477   very infrequent or non-existent, even between the adjacent Islay and Colonsay populations

478   (now 25 years since the last known effective dispersal over only ~10km of sea). Inbreeding

479   must consequently be accumulating.

480   Indeed, observations of blindness in chough chicks provided compelling evidence of

481   negative genetic effects. Individuals' eyes failed to develop properly, with severe corneal

482   opacity analogous to the human genetic disease 'Peters' anomaly' (Fig. 3). Blind chicks could

483   survive to fledging, but inevitably died subsequently. Detailed analyses showed that blindness

484   afflicted exactly 25% of chicks in affected families on average (i.e. families where ≥1 blind

485   chick was observed across years, Trask et al., 2016). This matches the frequency expected if

486   blindness is caused by a single locus recessive allele with Mendelian inheritance, expressed in

487   a homozygous state. While expression of lethal recessive alleles in inbred populations might

488   be expected, in fact there are still very few documented instances in wild populations (Trask

489   et al., 2016). Blindness in Scottish choughs is consequently a textbook example of

490   manifestation of lethal genetic disease in a small wild population of conservation concern

491   (Allendorf et al., 2021).

492   Overall, blindness affected only ~3% of chicks inspected on Islay during 1988-2014.

493   Nevertheless, this frequency implies that the putative underlying recessive allele occurs at a

494   non-trivial frequency of approximately 10%. There are intriguing indications that this may

495   partly reflect overdominance resulting in increased reproductive success of heterozygous

496   carriers; brood sizes in affected families were relatively large, almost compensating for

497   mortality of blind chicks (Trask et al., 2016). Microsatellite-based estimates of relatedness

498   showed that affected families were not more closely related to each other than to unaffected

499   families, implying that the blindness allele is widely distributed in the contemporary

population rather than restricted to a single lineage, and hence may have arisen numerous generations ago (Trask et al., 2016). It would therefore be difficult or impossible to eradicate, for example through selective euthanasia, even if diagnostic genetic markers to identify heterozygous carriers were developed. Since phenotypic expression of blindness is infrequent (requiring homozygosity), it is not currently a major constraint on population-wide first-year survival probability or hence on λ. However, it could be symptomatic of a bigger problem of inbreeding and associated inbreeding depression in survival and/or reproductive success expressed across the population.

To consider this, it is informative to estimate effective population size (N_e), which dictates the rates at which inbreeding will accumulate and genetic variation lost through drift. N_e is defined as the size of an idealized Wright-Fisher population that would experience the same rate of genetic drift as an observed focal population. N_e is commonly substantially smaller than a population's observed census size N_c (i.e. small N_e/N_c ratio) because key Wright-Fisher assumptions of random within-generation mating with a Poisson distribution of effective reproductive success in both sexes are typically violated. However, it remains difficult to quantify N_e, and hence N_e/N_c, in wild populations (Frankham et al., 2014). Recent methods to estimate N_e from individual-based demographic data utilise matrix model estimates of age- or stage-specific reproductive value and concepts of demographic stochasticity and resulting variance, but have rarely been implemented (Engen et al., 2005, 2007). Accordingly, we used the long-term demographic data to apply these methods to estimate N_e for Islay's chough population, giving values of $N_e/N_c \approx 0.2$ and $N_e \approx 30$ (Trask et al., 2017). This value of N_e also broadly concurred with estimates calculated from advanced analyses of microsatellite marker variation (Trask et al., 2017). A value of $N_e \approx 30$ is critically small; smaller than any proposed rule-of-thumb minimum for short-term population viability

524 (Frankham et al., 2014). It implies that inbreeding will accumulate relatively quickly in the

525 continued absence of gene flow.

526   The fact that N_e is small could arguably have been directly and simply inferred from

527 the fact that N_c is small (Fig. 2). However, the explicit estimate of $N_e \approx 30$, coupled with

528 blindness as direct evidence of gene-induced mortality, proved effective and communicable

529 'wake-up calls' that inbreeding and loss of genetic variation is, or soon could be, a non-trivial

530 constraint on viability of the Scottish chough population. Advanced analyses were therefore

531 highly effective in moving genetics onto conservation practitioners' agendas.

532

533 **Phase five: Integration of ecological and genetic threats**

534 The situation where genetic and ecological constraints interact to determine population

535 viability is likely to be commonplace in small populations, raising challenges for conservation

536 practitioners regarding which is the greater constraint and priority for intervention. Major

537 investment in 'ecological management' (e.g. habitat management to increase natural food)

538 would ultimately be ineffective if λ is, or soon will be, primarily constrained by inbreeding. In

539 the absence of natural immigration, 'genetic management' (e.g. population reinforcement

540 through translocations) would then be required to ameliorate inbreeding, at least until

541 natural landscape connectivity with other populations could be restored. But, such

542 translocations would themselves be ineffective if ecology is currently limiting, and survival

543 and/or reproductive success would be too low to maintain $\lambda \geq 1$ even in an outbred population.

544 Investment in each activity could then be futile without investment in the other.

545   This situation applies to the chough system, where research phases 1-4 implied that

546 ecological constraints are currently strongly limiting λ, at least partly through food shortage,

547 but that genetic constraints stemming from inbreeding and small N_e could also be limiting.

548   Consequently, we used individual-based models incorporating inbreeding depression

549   alongside environmental and demographic stochasticity to examine the degrees to which

550   ecological management to improve habitat and increase food abundance, and/or genetic

551   management to reduce inbreeding, could increase λ and ultimately population size (Trask et

552   al., 2019). Models were parameterised using spatially-structured estimates of baseline vital

553   rates from the long-term demographic monitoring (Reid et al., 2004, 2006), and used

554   estimated effects of supplementary feeding as a proxy for how much vital rates could

555   potentially be increased through habitat management (Fenn et al., 2020, 2021; Trask et al.,

556   2020). The population-wide degree of inbreeding was estimated from microsatellite variation.

557   However, since there is currently no tractable way to estimate inbreeding load, a plausible

558   range of values was considered, based on wider literature (Trask et al., 2019). Population

559   viability was simulated across scenarios with no conservation management, ecological

560   management only, genetic management only, or simultaneous ecological and genetic

561   management.

562   These simulations showed that, with no management, population extinction is very

563   likely. Ecological management that achieves the same effect as current supplementary

564   feeding was almost sufficient to maintain short-term population stability (Trask et al., 2019).

565   In contrast, translocations on their own were insufficient, because poor environmental

566   conditions meant individuals died regardless of inbreeding. Ecology was therefore identified

567   as the current primary limiting factor, but accumulating inbreeding still caused medium-term

568   population decline (Trask et al., 2019). Simulations that included both ecological and genetic

569   management gave the best outcome, because successful ecological management improved

570   conditions sufficiently for inbreeding depression to be expressed, which was then alleviated

571   by translocations to reduce inbreeding. These simulations highlighted how ecological and

572 genetic constraints can interact. They imply that joint ecological and genetic management will

573 be necessary to achieve the current conservation objective of maintaining a chough

574 population in Scotland, with ecological management as the primary short-term imperative

575 (Trask et al., 2019). The key requirements for successful conservation, at least in terms of

576 chough biology, are now evident (Trask et al., 2020).

577

578 **DISCUSSION**

579 Investment in population and evolutionary ecology research is often justified by the ambition

580 that resulting advances will ultimately facilitate evidence-based management of populations

581 or species of conservation concern. Yet, the pace of application is often slow (Arlettaz et al.,

582 2010; Walsh et al., 2014; Cook & Sgrò, 2017). Given increasing necessities to reduce

583 biodiversity loss (Díaz et al., 2015) and to justify research funding, increased efforts at rapid

584 scientific integration and translation are required (Cook et al., 2013; Haig et al., 2016; Toomey

585 et al., 2016; Enquist et al., 2017; Dubois et al., 2020; Jarvis et al., 2020). Our case study

586 summarises our pro-active efforts to simultaneously advance population and evolutionary

587 ecology and advance effective conservation of Scottish choughs, and to integrate the two

588 ambitions. Such population-specific reviews have recently been strongly advocated as central

589 to linking fundamental understanding and effective application (Williams et al., 2020), and

590 allow appraisal of which aspects of primary science proved useful, how translation was

591 achieved, and what knowledge gaps and constraints on successful conservation remain (e.g.

592 Arlettaz et al., 2010).

593

594 **Research-application integration**

25

During 2001-2021, we completed one major iteration of the desired sequence of i) rigorous scientific investigation of population ecology, demography and genetics (Reid et al., 2003a,b, 2004, 2006; Trask et al., 2016, 2017) with targeted follow-up investigation of ecological and genetic constraints (Reid et al., 2008, 2009, 2011; Wenzel et al., 2012, 2013; Trask et al., 2017); ii) resulting evidence-based intervention (Bignal & Bignal 2011; Trask et al., 2020), and iii) rigorous quantitative evaluation of efficacy (Trask et al., 2019; Fenn et al., 2020, 2021). This work is now informing full costing and prioritisation of future chough conservation strategy in Scotland, including decisions on increases or cessation of investment in conservation actions, encompassing future agri-environment schemes and translocations (Trask et al., 2020; Appendix S1). Our case study therefore provides examples of how advanced analyses in population and evolutionary ecology contributed to shaping species-focussed conservation actions, enacted through targeted supplementary feeding, SPA designation and agri-environment schemes. Specifically, the underlying science utilised advanced matrix population model analyses, including prospective analyses of integrated elasticities, retrospective analyses of vital rate variation, approximations of stochastic growth rates, and use of stage-specific reproductive values and demographic variances to estimate N_e (Reid et al., 2004; Trask et al., 2017). It also utilised advanced methodologies for analysing capture-mark-recapture data with random effects, time-varying covariates or multiple states (Reid et al., 2003a, 2008; Fenn et al., 2021), estimation of N_e and relatedness from molecular marker data (Trask et al., 2016, 2017, 2019), and population viability analysis (Trask et al., 2019). We also drew on synthetic knowledge of key parameters that we could not directly estimate, namely the magnitude of inbreeding depression (Trask et al., 2019). All these ingredients directly informed inference on what demographic, ecological and genetic constraints are currently limiting λ, and informed resulting conservation and policy actions.

619   These conservation-motivated analyses also generated conceptual insights and

620   leading empirical examples that fed back to advance population and evolutionary ecology.

621   For example, efforts to parameterise fully age-structured matrix models, and to understand

622   observed variation in sub-adult survival, led to new understanding of patterns of age-specific

623   reproductive success, lifelong cohort and spatial effects, and parental effects on offspring

624   survival (Reid et al., 2003a, 2003b, 2006, 2010). Efforts to estimate N_e revealed how high

625   demographic variance can drive small N_e/N_c, and identified which sex-age classes contributed

626   most (Trask et al., 2017). Evaluations of interventions showed how compound effects can

627   scale up to determine population outcomes (Fenn et al., 2000, 2021), and how ecology and

628   genetics can interact to shape population viability (Trask et al., 2019). These general

629   conceptual advances would not have been achieved without the underlying ambition of

630   effective conservation application, and associated fieldwork and funding (Appendix S2).

631

632   **Implementation**

633   It is increasingly emphasised that effective conservation science (Fig. 1) requires pro-active

634   co-working involving diverse researchers, practitioners and wider stakeholders (Arlettaz et

635   al., 2010; Cook et al., 2013; Toomey et al., 2016; Cook & Sgrò 2017; Enquist et al., 2017; Taylor

636   et al., 2017; Roux et al., 2019; Dubois et al., 2020). Such co-working has been central to our

637   project since 2001. Primary science advances were achieved through direct collaboration

638   between academic researchers with expertise in population and evolutionary ecology and

639   life-history variation (JMR, PM), agricultural ecologists (EB, DIMcC) and Islay farmers with

640   outstanding first-hand knowledge of the focal system and associated land management (EB,

641   SB, leading the SCSG). This team has been embedded within the Scottish Chough Forum, a

642   conservation-focussed group set up in 2001 that also includes representatives from

643   NatureScot and RSPB and additional members of SCSG, with meetings that aim to facilitate

644   joint planning, two-way knowledge transfer, policy discussions and advocacy.

645   Considerable effort has gone into pro-active communication and co-production of

646   knowledge involving scientists, policy-makers, conservation practitioners, farmers, land

647   managers, birdwatchers and the wider interested public, thereby crossing traditional

648   boundaries and actual or perceived value systems (e.g. Cook et al., 2013; Toomey et al., 2016;

649   Williams et al., 2020). To fulfil academic objectives, primary scientific papers were

650   strategically published in British Ecological Society journals, targeted at general concept-led

651   international audiences spanning pure and applied ecology (*Journal of Animal Ecology*: Reid

652   et al., 2003a[†],b[‡], 2004, 2006, 2008, 2010; Trask et al., 2016[†], 2017; *Journal of Applied Ecology*:

653   Reid et al., 2011; Trask et al., 2019; Fenn et al., 2020, 2021; total >685 citations, Google

654   Scholar October 2021, Elton prize [‡]winner, [†]highly commended). Yet, while these papers

655   retained some system-specific context, the focus on general conceptual rather than system-

656   specific impact (as required for these BES journals) meant that the full process of pure-applied

657   integration and its application to chough conservation was not previously visible.

658   Rather, while the primary papers were important in establishing scientific credibility,

659   key points were communicated to policy-makers through direct conversations and

660   presentations, accessible 'reader's digest' summaries, and two substantial reports that

661   contain additional policy-relevant information (Reid et al., 2009; Trask et al., 2020). Major

662   knowledge transfer meetings were held on Islay in 2001, 2008 and 2018, the latter two

663   including discussions with local farmers and land managers. Farmers contributed to

664   undertaking supplementary feeding, observations and providing nest sites, constituting direct

665   participation by the local community. Public presentations were delivered on Islay, and at UK-

666   wide ornithology societies. These activities have been broadly successful in reaching diverse

audiences, emphasising the value of plurality in communication and evaluation of scientific outputs (Cook et al., 2013; Walsh et al., 2014; Roux et al., 2019; Williams et al., 2020). Indeed, it is notable that the most-cited primary paper (Reid et al., 2003b, 230 citations October 2021) has become an established general reference regarding cross-sectional versus longitudinal variation in age-specific reproductive success, but was least useful in terms of directly informing conservation action. Meanwhile, papers that provide key evidence underpinning the decade-long supplementary feeding intervention are little cited (Reid et al., 2008, 2011; 28 and 19 citations respectively). As shown elsewhere (e.g. Walsh et al., 2014; Fabian et al., 2019), policy-maker attention was most effectively reached through discussions and targeted reports, which are not particularly valued within academic systems.

All research and policy outcomes for the chough system were critically underpinned by the long-term demographic monitoring (i.e. nest recording, colour-ringing and resightings), further illustrating the immense value of such data for both pure and applied purposes. The chough fieldwork objective has been to obtain sufficient data to estimate temporal and spatial variation in key demographic rates, not to attempt close to complete population marking (as is the ambition in some leading field studies in pure population and evolutionary ecology). The chough system has attributes that facilitate such work, notably that all life-history stages are readily observable within Islay's effectively closed population. Yet, 18 years of data collection (1983-2000) were required even for the initial analyses of vital rate variation (Fig. 2). Such long-term fieldwork is often difficult to fund through either pure or applied streams (Clutton-Brock & Sheldon, 2010; Gillson et al., 2019), inhibiting application of cutting-edge concepts and methods in many systems of conservation concern. In our case, monitoring was achieved on a relatively low budget, encompassing substantial intertwined professional and voluntary effort (summarised in Appendix S2).

691

Limitations and prospects

693 Despite all efforts, the Scottish chough population is still in a perilous state. There were only

694 43 breeding pairs on Islay in 2018 (and 5 on Colonsay). The recently stable population size on

695 Islay (Fig. 2) reflects the ongoing supplementary feeding intervention, which is a positive

696 interim measure but not a long-term solution (Trask et al., 2020). Critical review of the limits

697 of current knowledge and translation is therefore warranted. So far, it has been difficult to

698 incorporate optimal chough management options into the SRDP, or hence facilitate

699 sustainable habitat management. This is partly due to potentially conflicting financial

700 incentives linked to other conservation objectives, and the fact that choughs require complex

701 habitat mosaics that are difficult to provide through simple prescriptive agri-environment

702 measures. There have been insufficient attempts to explicitly link variation in chough

703 demography or invertebrate abundance and availability to agricultural management.

704 Progress here is difficult because data on farm management practices are deemed

705 commercially sensitive and hence not publicly available on small spatial scales, while data on

706 spatio-temporal variation in abundances of diverse invertebrates that choughs of different

707 ages utilise at different times of year have not been systematically collected. Effective year-

708 round monitoring of diverse invertebrate taxa across diverse habitats would be a major

709 challenge, necessitating substantial resources. Any such ambitions cannot be readily achieved

710 through current SRDP programmes, since statutory monitoring of SRDP management focuses

711 on compliance rather than biological impacts, precluding evaluation of efficacy. More

712 targeted farm-specific management agreements and associated biological monitoring in key

713 chough areas may be more effective, and should be considered as the next generations of

714 agri-environment support systems in Scotland are designed. This will in turn require

715   observational, experimental and comparative investigations of effects of agricultural activities

716   such as grazing, silage cutting and livestock treatment regimes, as are now commencing (e.g.

717   MacGillivray et al., 2018; Gilbert et al., 2019; Jonsson et al., 2020; SCSG, unpublished data).

718   Links between changing agricultural practices, chough foraging ecology and parasite burdens

719   should also be investigated, especially given recent observations of substantial intestinal

720   parasites burdens in juvenile choughs (Trask et al., 2020; Fenn et al., 2021). Finally, since early

721   analyses suggested effects of temperature and rainfall on vital rates (Reid et al., 2003a, 2008),

722   potential impacts of climate change should also be projected.

723   Yet, the science base for conserving the Scottish chough population is already

724   unusually strong. The focal geographical area is relatively small and already subject to

725   extensive management through nature reserves and agri-environment schemes, and there

726   are no major conflicts regarding the broad ambition of conserving choughs. The system

727   therefore represents a test case for successful enaction of evidence-based species-focussed

728   conservation (Fig. 1). While policy decisions should of course be taken with appropriate

729   regard for potentially competing societal, economic and ecological priorities, it should be

730   viewed as disappointing if the end point is solely a comprehensive demographic

731   understanding of a population demise.

732

733

747

748 **Conflict of interest**

749 The authors declare no conflict of interest.

750

751 **Author contributions**

752 JMR drafted the current manuscript. All authors contributed to conceptual development and

753 editing and gave final approval for publication. All authors contributed substantially to data

754 collection, analyses and conceptual developments presented in the primary long-term study

755 papers.

756

757 **Data availability**

758 There are no primary data associated with this review manuscript.

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970 **Figures**

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Scientific understanding ⟷ **Effective conservation**

Pure science advances	Applied science advances	Conservation advances	Monitoring & (re)evaluation
• Conceptual advances • Methodological advances • Comparative insights	Causes of population decline or threat	Management & intervention	
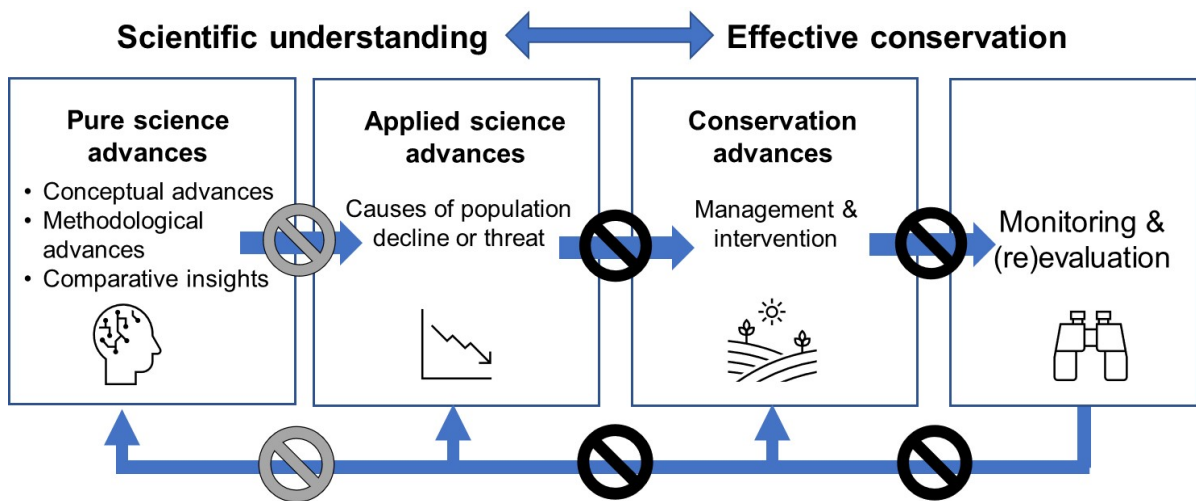
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987 **Figure 2.** (A) Locations of Scotland's remaining chough populations on Islay and Colonsay (red

988 box). (B) Chough population size (number of breeding pairs) on Islay in full census years during

989 1982-2018. Red points denote censuses during a supplementary feeding intervention. (C)

990 Timelines of demographic monitoring and five primary research phases: 1) Population

991 demography and dynamics, 2) Ecology of sub-adult survival, 3) Emergency intervention and

992 evaluation, 4) Genetic constraints, and 5) Integration of ecological and genetic threats.
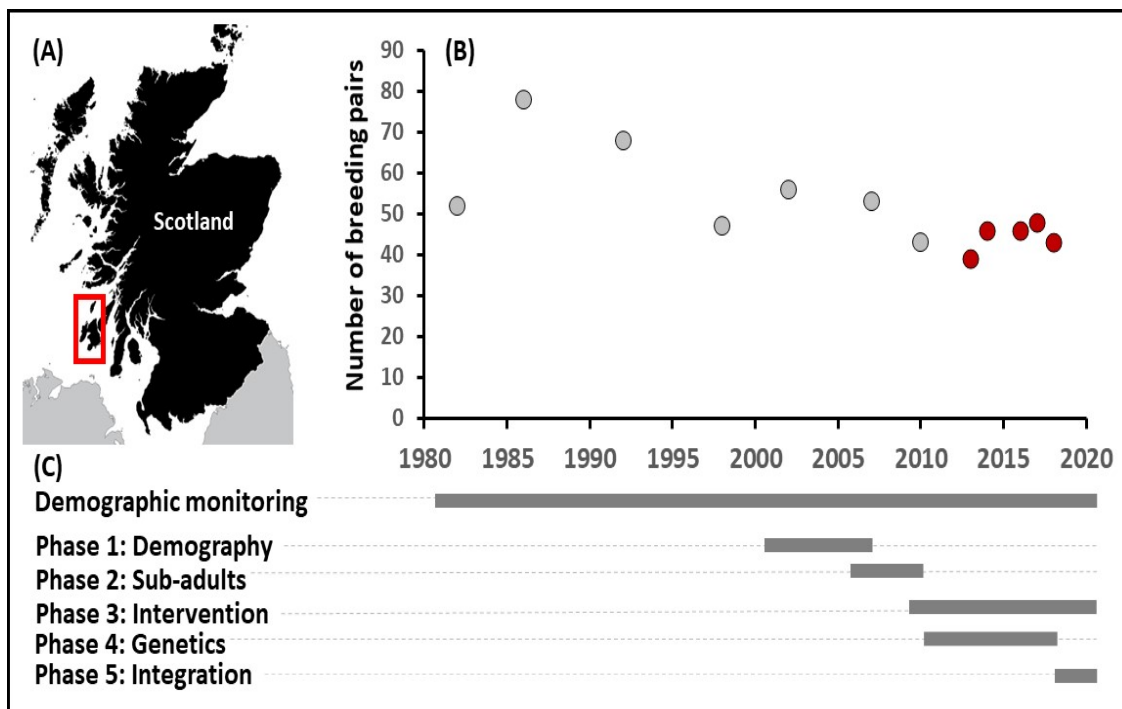
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Figure 3. Examples of chough nest sites in (A) natural sea cave and (B) field shelter built in an inland habitat area, of colour-ringed (C) adult and (D) fledgling, and of (E) choughs attending supplementary feeding, and (F) a blind chick. Photos: (A,B,D,E,F) Scottish Chough Study Group, (C) Gordon Yates.
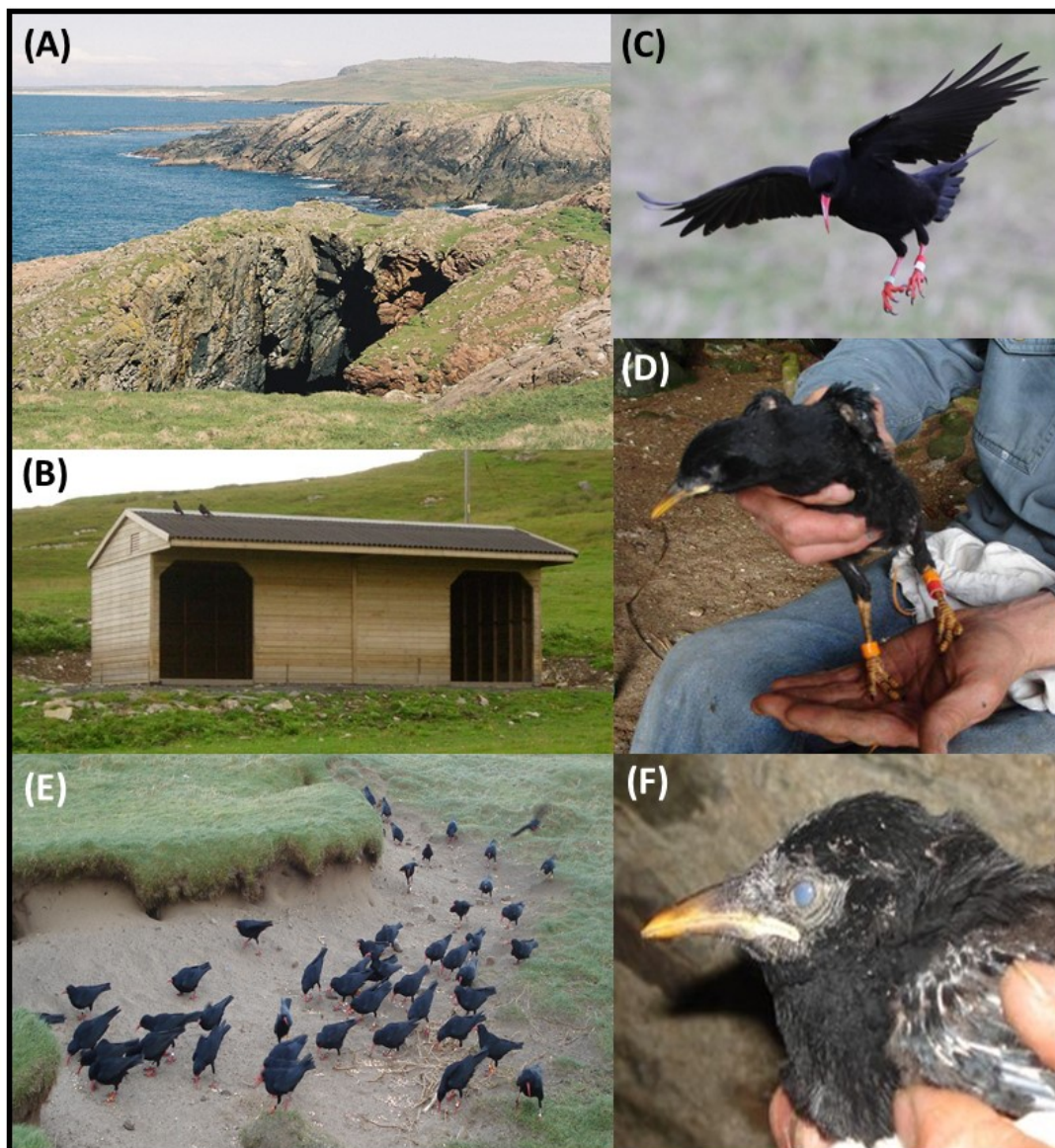
1010 **Figure 4.** Estimated first-year survival probabilities (with 95% confidence intervals). Grey fill

1011 denotes years of baseline demographic monitoring. Blue fill denotes years of intensive

1012 monitoring of sub-adults. Red outline denotes three successive years of very low survival.

1013 Black fill denotes years of supplementary feeding.
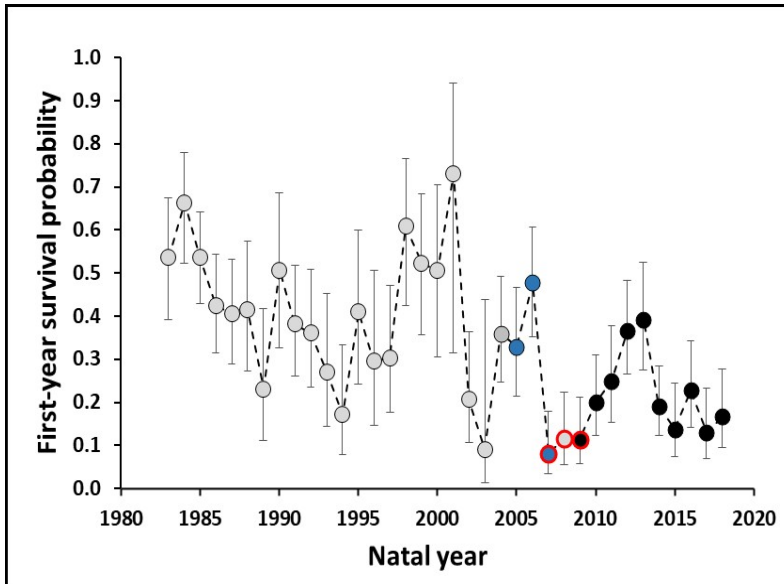
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1026   **Figure 5.** (A) Relationship between first-year chough survival probability and tipulid

1027   abundance (millions/hectare) in the winter before fledging. (B) Monthly survival probabilities

1028   of juvenile choughs fledged in low and high survival cohorts (open and filled symbols

1029   respectively).
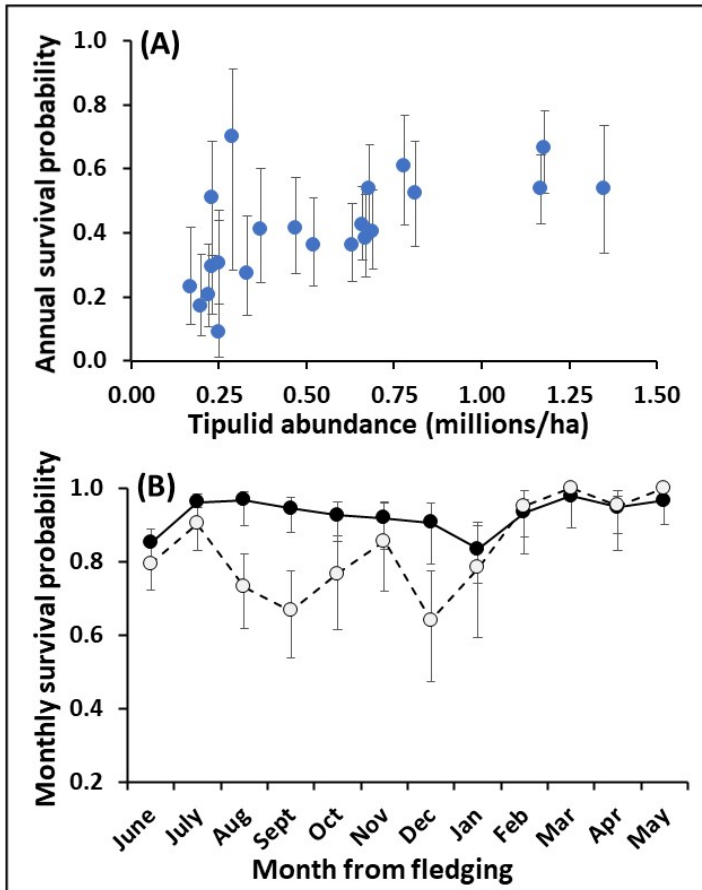
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1 **Supporting Information**

2 **Integrating advances in population and evolutionary ecology with**

3 **conservation strategy through long-term studies of red-billed choughs**

4

5 Jane M. Reid, Eric Bignal, Sue Bignal, Davy I. McCracken, Sarah R. Fenn, Amanda E. Trask &

6 Pat Monaghan

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9 **Appendix S1. Evidence of choughs as a focus for conservation action, agri-**

10 **environment options and designated Special Protection Areas**

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12 [https://www.nature.scot/plants-animals-and-fungi/birds/farmland-and-croftland-](https://www.nature.scot/plants-animals-and-fungi/birds/farmland-and-croftland-birds/chough)

13 [birds/chough](https://www.nature.scot/plants-animals-and-fungi/birds/farmland-and-croftland-birds/chough)

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NatureScot Scotland's Nature Agency
Buidheann Nàdair na h-Alba

Search NatureScot

Chough conservation effective but more action needed
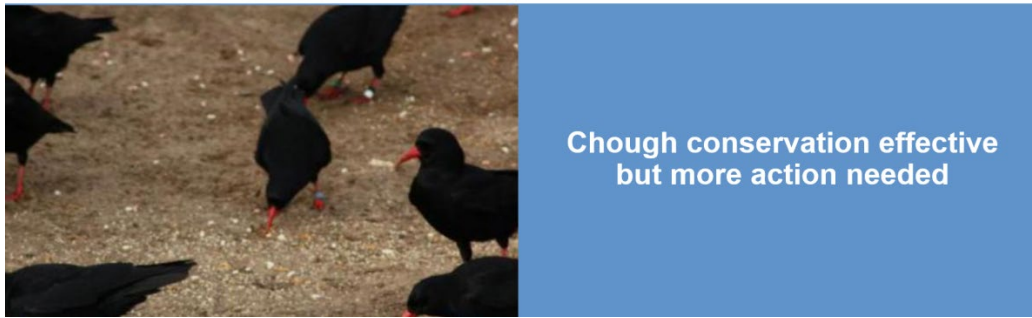
20 **20 November 2020**

21 **Conservation measures to help save the threatened red-billed chough have been effective**
22 **in preventing further large population declines.**

23 A new report published by NatureScot found that supplementary feeding and parasite treatment
24 aimed at preventing chough extinction in Scotland have been successful.

25 NatureScot has now committed to funding the measures for a further two years to support the
26 population, while exploring longer-term recovery options.

27 Red-billed chough in Scotland have declined and are currently restricted to the islands of Islay and
28 Colonsay, where there were fewer than 50 pairs in 2018.

29 The birds are threatened simultaneously by lack of food (affecting first year survival), parasites and
30 low genetic diversity.

31 NatureScot funded an emergency supplementary feeding programme that began in 2010 at multiple
32 sites on Islay with treatment of parasites from 2014, alongside monitoring of the population.

33 The report found that supplementary feeding has successfully increased key demographic rates,
34 including first year survival, and birds treated for parasites recovered after 2-3 days, concluding that
35 the programme was an effective short-term conservation action.

36 However, it adds that in the longer-term, further measures will be needed to stabilise the species,
37 including habitat improvements and reinforcing the population with birds from other UK populations
38 to reduce inbreeding.

39 The detailed analysis in the report has been possible thanks to the tireless and committed long-term
40 monitoring of the population by the Scottish Chough Study Group, RSPB, Aberdeen and Glasgow
41 Universities and SRUC, which began in 1983.

42 NatureScot Ornithologist Dr Jessica Shaw said: "This robust report is the culmination of years of
43 practical and scientific work to prevent the loss of chough from Scotland, with painstaking work by
44 committed individuals on the islands.

45 "It demonstrates that these dedicated efforts have been successful in the short-term, and we're
46 pleased to confirm that NatureScot will continue to fund and support this chough conservation work
47 over the next two years.

48 "The report makes several recommendations for the longer-term, and we will now explore options
49 for the future, in consultation with partners in Scottish Government and the Scottish Chough
50 Forum."

51 **Chough options within the Scottish Rural Development Programme Agri-Environment**

52 **Climate Scheme (2015-2020)**

53 https://www.ruralpayments.org/publicsite/futures/topics/all-schemes/agri-environment-

54   climate-scheme/management-options-and-capital-items/chough-grazing-management/

Scottish Government
Riaghaltas na h-Alba

Rural Payments and Services

Home / All schemes / Agri-Environment Climate Scheme / Management options and capital items

Chough Grazing Management

Date published: 30 March, 2015

Aim

The aim of this option is to benefit chough by providing suitable areas for the birds to forage throughout the year.

Choughs require areas of short grazed grassland, ideally grazed by cattle whose dung supports the insects upon which the birds feed.

Not treating these cattle with Avermectin-based wormers will benefit these insects. This option also allows for an early cut of silage or hay to be taken.

12	Grazed grassland for chough	To benefit chough by providing suitable areas for foraging throughout the year. This Option will provide short cropped grassland, which has not been treated with Avermectin-based products. Grassland must be grazed for all of part of the year by cattle.
17	Mown grassland for chough	To benefit chough by providing suitable areas for the birds to forage. Chough require areas of short grazed grassland to access the insects they feed upon. Delaying shutting off silage or hay fields and cutting them later maximises the amount of spring-grazed pasture for feeding chicks and then provides later aftermath for the fledglings.

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64   **Chough options within the Scottish Rural Development Programme Rural Priorities**

65   **Scheme (2009-2014)**

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78   **Criteria for designating Special Protection Areas**

79   The criteria show that SPAs can be designated on the basis of 'higher breeding success'

80   (stage 2, point 3), but there is no mention of higher survival probability.

81

82   https://jncc.gov.uk/our-work/special-protection-areas-overview/

Stage 1

1. An area is used regularly by 1% or more of the Great Britain (or in Northern Ireland, the all-Ireland) population of a species listed in Annex I of the Birds Directive (79/409/EEC as amended) in any season.
2. An area is used regularly by 1% or more of the biogeographical population of a regularly occurring migratory species (other than those listed in Annex I) in any season.
3. An area is used regularly by over 20,000 waterfowl (waterfowl as defined by the Ramsar Convention) or 20,000 seabirds in any season.
4. An area which meets the requirements of one or more of the Stage 2 guidelines in any season, where the application of Stage 1 guidelines 1, 2 or 3 for a species does not identify an adequate suite of most suitable sites for the conservation of that species.

Stage 2

1. *Population size and density*: Areas holding or supporting more birds than others and/or holding or supporting birds at higher concentrations are favoured for selection.
2. *Species range*: Areas selected for a given species provide as wide a geographic coverage across the species' range as possible.
3. *Breeding success*: Areas of higher breeding success than others are favoured for selection.
4. *History of occupancy*: Areas known to have a longer history of occupation or use by the relevant species are favoured for selection.
5. *Multi-species areas*: Areas holding or supporting the larger number of qualifying species under Article 4 of the Directive are favoured for selection.
6. *Naturalness*: Areas comprising natural or semi-natural habitats are favoured for selection over those which do not.
7. *Severe weather refuges*: Areas used at least once a decade by significant proportions of the biogeographical population of a species in periods of severe weather in any season, and which are vital to the survival of a viable population, are favoured for selection.

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86   **Gruinart Flats Special Protection Area, Islay**

87   https://sitelink.nature.scot/site/8510

88   Choughs are listed as a qualifying interest.

89

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91   # Appendix S2. Summary of study development and major funders and

92   # contributors

93

94   **Long-term demographic monitoring**

95   Long-term demographic studies undertaken with the primary aim of advancing population

96   and evolutionary ecology (e.g. Clutton-Brock & Sheldon, 2010) are commonly predominantly

97   run by university-based academics, although major advances can also be achieved through

98   long-term data collection by 'citizen science' volunteers and their supporting organisations

99   (e.g. Phillimore et al., 2016). The long-term chough demographic monitoring on Islay has

100   been achieved through intertwined professional and voluntary effort, typically involving the

101   same few people. Perhaps unusually, it has involved substantial voluntary effort founded on

102   professional origins (rather than vice versa), but also benefits from considerable

103   professional time funded by diverse academic, governmental and non-governmental

104   organisations. Five PhD students, one undergraduate project student and three

105   postdoctoral researchers have contributed substantially to data collection, undertaken data

106   analyses and led publication.

107

108   Specifically, the current regime of chough demographic monitoring on Islay started in 1980,

109   with an MSc project by Judy Stroud (nee Warnes). EB joined the project in 1981 as part of

110   work undertaken for the UK Nature Conservancy Council (NCC), and started the colour-

111   ringed programme. The work expanded through the 1980s with PhD projects by Elizabeth

112   Still and Clive McKay, supervised by PM and EB and Mike Pienkowski for the NCC. DIMcC

113   then joined through a PhD project, supervised by EB and Garth Foster at the West of

114   Scotland Agricultural College (who also funded the PhD). Since the early 1990s the

115   demographic monitoring has been orchestrated and primarily undertaken by Scottish

116   Chough Study Group (SCSG), led by EB, SB and DIMcC, and licensed by NCC, NCC Scotland,

117   Scottish Natural Heritage (SNH) and now NatureScot. Much of this work has been voluntary,

118   but has been part-funded by NatureScot since 2009, with DIMcC's time supported by

119   Scotland's Rural College (SRUC). Since 2004, additional ring resightings and territory surveys

120   have been undertaken by JMR (part-funded by Royal Society and University of Aberdeen,

121   part voluntary), assisted by AET and SRF (funded by NERC PhD studentships), with logistical

122   support from NatureScot and RSPB. RSPB staff have provided additional data, particularly

123   from RSPB reserves and managed areas on Islay, since 1998.

124

125   Further details of funding sources for each research phase are below, highlighting how

126   advances in population and evolutionary ecology, and in conservation strategy, were jointly

127   achieved through mixtures of pure (i.e. fellowships, studentships, academic time) and

128   applied (governmental and non-governmental organisation contributions) funding, and

129   through programmes designed to combine the two (e.g. UK NERC Connect B programme,

130   CASE student partnerships).

131

211

212   Supporting references

213   Clutton-Brock, T. & Sheldon, B.C. (2010) Individuals and populations: the role of long-term,

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215   *& Evolution*, **25**, 562-573.

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218   *Change Biology*, **22**, 3259–72.

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