1   **Collateral benefits of targeted supplementary feeding on demography and growth rate**

2   **of a threatened population.**

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Abstract:

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21   1. Effective evidence-based conservation requires full quantification of the impacts of

22   targeted management interventions on focal populations. Such impacts may extend

23   beyond target individuals to also affect demographic rates of non-target conspecifics

24   (e.g. different age classes). However, such collateral (i.e. unplanned) impacts are

25   rarely evaluated, despite their potential to substantially alter conservation outcomes.

26   Subsequent management decisions may then be poorly informed or erroneous.

27   2. We used 15 years of individual-based demographic data in a "before-after control-

28   impact" (BACI) analysis to quantify collateral demographic impacts of a targeted

29   multi-year supplementary feeding programme designed to increase sub-adult survival

30   and hence viability of a small, threatened red-billed chough (*Pyrrhocorax*

31   *pyrrhocorax*) population. Specifically, we assessed whether the intervention also

32   affected adult survival and reproductive success, and whether such collateral effects

33   were themselves sufficient to stabilise population size and hence achieve short-term

34   conservation aims.

35   3. The probabilities of adult survival and successful reproduction increased substantially

36   between the "before-feeding" and "during-feeding" periods in those choughs

37   associated with supplementary feeding, but not otherwise. Overall breeding success

38   (i.e. number of chicks fledged per occupied territory) also tended to increase, even

39   though brood sizes did not increase. These relationships, which were detectible only

40   through BACI analyses, suggest that supplementary feeding targeted at sub-adults had

41   unplanned positive impacts on adult demographic rates.

42   4. Deterministic matrix models designed to project population growth demonstrate that

43   these estimated collateral effects were sufficient to make a substantial contribution to

44   increasing population growth rate and achieving short-term population stability.

45   5. *Synthesis and applications*: Our results indicate substantial positive collateral impacts

46   of a targeted supplementary feeding intervention on population viability, despite no *a*

47   *priori* expectation that the non-target adults were food-limited. This case-study

48   illustrates how thorough assessment of collateral impacts of targeted interventions can

49   affect assessment of short-term efficacy and reveal new opportunities for future

50   interventions, thereby informing subsequent management decisions.

51

55

INTRODUCTION

Pro-active conservation of threatened populations and species should ideally be enacted through cycles of evidence-based design, implementation and (re-)evaluation of targeted management interventions (Salafsky, Margoluis, Redford, & Robinson, 2002; Sutherland, Pullin, Dolman, & Knight, 2004). However, even when evidence-based interventions can be designed and implemented, evaluation is often incomplete, impeding effective and responsive management policy.

Not least, efficacy is typically evaluated solely in terms of impacts on target individuals and demographic rates during management periods. Yet, interventions may have collateral (i.e. unplanned) side-effects on non-target conspecific individuals or demographic rates (e.g. Carrete, Donázar, & Margalida, 2006; Isaksson, Wallander, & Larsson, 2007), including carry-over effects that last into subsequent seasons (e.g. Harrison, Blount, Inger, Norris, & Bearhop, 2011; O'Connor & Cooke, 2015; Ruffino, Salo, Koivisto, Banks, & Korpimäki, 2014). Such effects could potentially enhance, impair or even reverse intended management impacts on population growth rate (λ), and thereby alter conservation success. Quantifying such effects could also reveal previously unknown constraints on demography, thereby opening new routes to successful management.

Yet, rigorous assessments of both direct and collateral impacts are often hindered because formal randomised controlled experiments cannot be implemented. This is particularly likely for small, threatened, populations where experiments may be inappropriate, or emergency interventions were rapidly implemented to ameliorate critical threats to viability. Apparent effects of management may then be confounded with correlated environmental variation, especially when underlying demography differs between managed and unmanaged areas (Mahlum, Cote, Wiersma, Pennell, & Adams, 2018). In such cases, before-after-control-impact (BACI) analyses, which use pre-intervention differences between

81   unmanaged and managed areas as baselines to evaluate post- and/or during-intervention

82   differences, are a relatively robust method for evaluating management effects (Christie et al.,

83   2019; Mahlum et al., 2018; Smokorowski & Randall, 2017). Multi-year monitoring of

84   marked individuals is then valuable in facilitating evaluation of baseline demography, and in

85   assessing effects of interventions that are not uniformly experienced (Badia-Boher et al.,

86   2019; Oro, Margalida, Carrete, Heredia, & Donázar, 2008). However, individual-based, time-

87   controlled evaluations of collateral effects of conservation interventions on conspecifics are

88   still rarely achieved. Furthermore, estimated demographic effects are often assumed to

89   translate straightforwardly into altered population viability (e.g. Tollington et al., 2018). Yet,

90   since λ is not equally sensitive to all vital rates, the degree to which demographic responses

91   to interventions affect λ should be explicitly evaluated through population models (e.g. Oro

92   et al., 2008; Trask et al., 2019).

93   One common intervention to facilitate the recovery of threatened and declining

94   populations is supplementary feeding. Since natural food limitation often restricts individual

95   survival and/or reproductive success (Ferrer, Morandini, Baguena, & Newton, 2017; Nagy &

96   Holmes, 2005), supplementary feeding is expected to increase λ (Boutin, 1990; Robb,

97   McDonald, Chamberlain, & Bearhop, 2008), representing a rapid and tangible strategy to

98   temporarily maintain populations. Indeed, there is rigorous evidence that supplementary

99   feeding successfully aided recovery of priority species, including kakapo (*Strigops*

100   *habroptilus,* Clout & Craig, 1995), Spanish imperial eagle (*Aquila adalberti*, González,

101   Margalida, Sánchez, & Oria, 2006; Ferrer et al., 2017) and bearded vulture (*Gypaetus*

102   *barbatus*, Ferrer et al., 2017).

103   However, the assumption that supplementary feeding is beneficial is not always

104   critically assessed, and potential costs, and/or additional collateral benefits through non-target

105   individuals, are rarely considered (Cortés-Avizanda et al., 2016; Ewen, Walker, Canessa, &

106   Groombridge, 2014; Martínez-Abraín & Oro, 2013; Schoech et al., 2008). Some studies

107   showed little or no effect of supplementary feeding on target populations (Oppel et al., 2016;

108   Sim, Wilkinson, Scridel, Anderson, & Roos, 2015; Todd, Poulin, Wellicome, & Brigham,

109   2003); such interventions then waste conservation resources. Supplementary feeding has also

110   been linked to unintended negative consequences, including skewed offspring sex ratios

111   (Clout, Elliott, & Robertson, 2002; but see Ferrer, Newton & Pandolfi, 2009), and reduced

112   productivity of current and future generations (Carrete et al., 2006, Crates et al., 2016;

113   Harrison et al., 2010; Plummer, Bearhop, Leech, Chamberlain, & Blount, 2013; Zanette,

114   Clinchy, & Sung, 2009). Supplementary feeding programmes should therefore be carefully

115   designed to address specific ecological and demographic constraints on focal populations,

116   and subsequently monitored to quantify collateral as well as intended effects.

117   One population subject to targeted conservation-driven supplementary feeding is the

118   small, threatened, red-billed chough (*Pyrrhocorax pyrrhocorax*; hereafter choughs)

119   population on Islay, Scotland. Choughs are a UK and European conservation priority species

120   (Schedule 1 Wildlife and Countryside Act 1981, Annex 1 EU Birds Directive), which have

121   experienced substantial population declines, attributed partly to changing pastoral agriculture

122   and livestock grazing practices (Bignal, Bignal, & McCracken, 1997). Islay's chough

123   population decreased substantially during 1986-2007, from ~95 to ~55 breeding pairs

124   (Monaghan, Bignal, Bignal, Easterbee, & McKay, 1989; Reid et al., 2009). Furthermore, a

125   drastic decrease in first-year survival probability from ~0.42 to ~0.10 during 2007-2009

126   threatened population viability (projected $\lambda \approx 0.87$, Reid et al., 2011). This decrease in first-

127   year survival was attributed to low food availability in late summer and autumn, with no

128   evident decrease in adult survival or reproductive success (Reid et al., 2008, 2009, 2011).

129   Consequently, a targeted supplementary feeding programme was implemented during eight

130   non-breeding seasons (2010-2018) to try to increase sub-adult survival and prevent

131   population extinction (Bignal & Bignal, 2011). However, observations showed that many

132   adults (i.e. non-target individuals) also regularly utilised supplementary food. Supplementary

133   feeding might therefore have additional consequences for population viability through

134   unplanned effects on adult survival, to which λ is highly sensitive (Reid, Bignal, Bignal,

135   McCracken, & Monaghan, 2004), or on subsequent reproductive success. Full assessment of

136   the efficacy of the supplementary feeding intervention, and evidence-based decisions

137   regarding continuation or cessation, requires rigorous evaluation of such collateral effects.

138   Accordingly, we used 15 years of intensive ring-resighting and nest monitoring data

139   to quantify non-target demographic effects of a non-breeding season supplementary feeding

140   programme implemented to increase sub-adult survival. Specifically, we used BACI analyses

141   to test whether supplementary feeding was associated with increased adult survival and

142   reproductive success, even though there was no *a priori* (i.e. pre-intervention) expectation

143   that these key life-history stages were food limited. We then parameterised matrix population

144   models to explicitly evaluate the extent to which the observed adult effects were sufficient in

145   themselves to stabilise population size (i.e. λ=1) and hence achieve the short-term

146   conservation objective irrespective of any effect on the target demographic of sub-adult

147   survival.

148

149   **MATERIALS AND METHODS**

150   **Study system and supplementary feeding**

151   Islay's chough population has been intensively monitored since 1983 (Bignal et al.,

152   1987; Reid, Bignal, Bignal, McCracken, & Monaghan, 2003, 2004; Reid et al., 2008). Adult

153   pairs hold large (>1km^2) territories, in which they typically attempt to breed each year from

154   age three, with little subsequent breeding dispersal (Bignal et al., 1997; Reid et al., 2003).

155 Adults can occupy their territories year-round, or move to communal feeding and roosting

156 areas during the non-breeding season (Appendix 1). During 2003-2018, an extensive sample

157 (≥80%) of territories was monitored (mean 36.0±5.3SD occupying pairs per year), and the

158 occurrence of a potentially breeding adult pair and the number of offspring reaching fledging

159 age were recorded (grand mean 2.1±1.5SD fledglings/pair). During a single licenced nest

160 visit per year, offspring were marked with unique colour-ring combinations allowing

161 subsequent identification of known-age sub-adults and adults. Intensive resighting effort

162 across Islay during 2003-2018 resulted in very high adult annual resighting probability

163 (P≥0.98).

164   A restricted quantity of supplementary food (estimated to provide roughly 15% of

165 individual daily energy requirement, Bignal & Bignal, 2011) was provided daily at up to

166 three sites (Appendix 1) during the non-breeding season (typically late-June to mid-April)

167 2010-2018. No food was provided during the main breeding season (late-April to early-June).

168 Supplementary feeding protocols were designed to target sub-adults by providing food at key

169 sub-adult foraging and roosting locations (Bignal & Bignal, 2011; Appendix 1). Identities of

170 colour-ringed individuals attending supplementary feeding were regularly recorded.

171 Resightings from feeding sites and elsewhere on Islay (total: >92,000 observations) were

172 used to identify individual adults (aged ≥3 years) that did and did not use the supplementary

173 food. These observations showed that food usage varied substantially among individuals;

174 generally, individual adults either frequently and regularly attended feeding, or never or very

175 infrequently attended (Appendices 1 and 4). Accordingly, each colour-ringed adult was

176 assigned as "fed" or "unfed" for each non-breeding season (Appendix 1).

177

BACI framework

178

179   Since supplementary feeding was implemented as an emergency conservation

180 intervention, not as a controlled randomised experiment, we used BACI analyses to estimate

181 effects on adult survival and reproductive success. This approach requires definition of

182 "control" and "impact" units of comparison that are consistent across the "before" and "after"

183 (or "during") intervention periods (Fig. 1, Smith, 2002). Initial data inspection showed that

184 adult choughs assigned as "fed" and "unfed" during supplementary feeding years generally

185 inhabited territories in certain regions of Islay, generating spatial structuring of occupied

186 territories in relation to non-breeding season food use (shown in Appendix 1). We therefore

187 used this evident spatial structure to define the required BACI units. Specifically, we defined

188 proxy "areas" representing territories used by "fed" or "unfed" adults during the

189 supplementary feeding years (hereafter "area-fed" and "area-unfed", respectively; Appendix

190 1). We then defined the four BACI groups as choughs inhabiting "area-fed" or "area-unfed"

191 in the "before" or "during" supplementary feeding years (hereafter "time-periods", Fig. 1).

192 Supplementary feeding impacts were then estimated by quantifying the relative difference in

193 demographic rates between the "before" and "during" feeding time-periods in "area-fed"

194 versus "area-unfed" (i.e. an area by time-period interaction, Fig. 1). As for all BACI analyses,

195 interpretation relies on an assumption that the focal treatment is responsible for any observed

196 difference in relative demographic performance between control ("area-unfed") and impact

197 ("area-fed") groups over time (i.e. between the "before" and "during" time-periods).

198 Interpretation does not require any further assumptions about underlying variation in habitat

199 quality between defined areas; the analyses average over such variation. In a few cases,

200 assignment to "area-fed" or "area-unfed" did not fully match an individual's observed status

201 as fed or unfed, or feeding state was less clear (Appendix 4). However, additional analyses

202 showed that altering these few assignments did not substantially alter results or key

203 conclusions (Appendix 4).

204

Statistical analysis

206   BACI analyses used 15 years of intensive ring-resighting and nest monitoring data;

207 primarily 7 years before the supplementary feeding programme (2003-2004 to 2009-2010;

208 hereafter "period-before"), and 8 years during it (2010-2011 to 2017-2018; hereafter "period-

209 during", Appendix 1). Generalised linear mixed models (GLMMs) were fitted to estimate

210 interacting effects of area and time-period on annual adult survival probability and annual

211 reproductive success (Fig. 1). Annual survival was defined as whether or not an individual

212 survived from one May to the next (binary variable). Since previous mark-recapture analyses

213 showed that annual resighting probability was ≥ 0.98, it was not necessary to control for low

214 or variable detection. Overall breeding success (sometimes termed "productivity", e.g. Ferrer

215 et al., 2017) was defined as the number of offspring reaching fledging age per territory

216 occupied by an adult pair (range 0-5 offspring, where zero values represent attempts that

217 failed, or rarely, instances of no evident breeding attempt). We additionally partitioned

218 overall breeding success into two components: nest success, defined as whether or not ≥ 1

219 fledgling was produced on each territory (binary variable), and conditional brood size,

220 defined as the number of fledglings produced conditional on nest success (i.e. where ≥ 1

221 fledgling was produced). All three measures of reproductive success refer to the breeding

222 season immediately following each over-winter season of supplementary feeding. Since

223 individuals were assigned to "area-fed" versus "area-unfed" at the start of the non-breeding

224 season following territory establishment (typically aged ≥ 3 years), current analyses of

225 reproductive success consider individuals aged ≥ 4 years (all should be capable of breeding).

226   GLMMs used either binomial (survival, nest success) or Poisson (conditional brood

227   size, overall breeding success) error structures, with logit or log link function, respectively.

228   The BACI groups "area" and "time-period" were modelled as fixed effects, with random year

229   and individual identity effects to account for non-independence of observations within years,

230   and of individuals across years. Potential age effects were controlled by including mean-

231   centred linear effects in all models (mean age=6.32 years; alternative age formulations gave

232   similar conclusions, Appendix 2). ANOVAs were used to test whether variation in survival or

233   the three measures of reproduction was significantly better explained when including the area

234   by time-period interaction than with additive effects only.

235   Main analyses were restricted to colour-ringed adults so that age effects could be

236   controlled. As the Islay population is isolated from other UK chough populations, and there

237   are no recent observations of permanent emigration, estimates of local "apparent survival"

238   can be interpreted as true survival. Since previous analyses showed that annual survival

239   probability did not differ between sexes (Reid et al., 2003), and exploratory analyses

240   suggested no difference in the current dataset, effects of sex on survival were not considered

241   further. However, since a paired male and female could both be colour-ringed and would

242   have identical observed reproductive success in a given year, reproductive success was

243   primarily analysed separately for each sex to avoid data replication (Appendix 3). Individual

244   sex was inferred from breeding behaviour (female incubation, with male provisioning; Bignal

245   et al., 1997). Most adults were of known sex (female 49.0%, male 43.9%), but colour-ringed

246   individuals of unknown sex (7.2%) were excluded from reproductive success analyses.

247   Additional models, that considered reproductive success of fed versus unfed pairs rather than

248   individuals, and hence maximised sample sizes but excluded age effects, yielded similar

249   results (Appendix 3).

250   Models were fitted in R 3.4.3 (R Core Team, 2019) using the "glmer" function from

251   the lme4 package (Bates, Mächler, Bolker, & Walker, 2015) with the bobyqa optimizer to

252   assist model convergence by increasing the maximum iterations. Model estimates were back-

253   transformed onto the observed scale for presentation. Full model summaries are in

254   Appendices 2 and 3, sample sizes are in Table 1.

255

256   **Population projection models**

257   To evaluate the potential consequences of collateral effects of supplementary feeding

258   for λ, and hence likely population viability, we analysed pre-breeding census, birth-pulse,

259   stage-structured deterministic matrix projection models. Four models were parameterised,

260   using adult survival probability and reproductive success estimated for the four BACI groups

261   (full details in Appendix 5). Given the current objective of explicitly evaluating collateral

262   impacts of supplementary feeding on λ through adult survival and reproductive success, all

263   other demographic rates were set to constant baseline values (Appendix 5). Deterministic λ

264   was calculated as the dominant eigenvalue of each projection matrix. Associated 95%

265   confidence intervals (95%CIs) were calculated by sampling 10,000 times from distributions

266   of adult survival and reproductive success reflecting estimates and 95%CIs from the BACI

267   analyses (Appendix 5). To estimate overall λ for period-during, we estimated the proportion

268   of adults classed as fed in 2015-2017 (Appendix 1) and calculated a weighted value of λ

269   across the values estimated for the fed and unfed areas.

270

271   **RESULTS**

272   **Adult survival**

273   Supplementary feeding status and area were assigned for 161 colour-ringed adult

274   choughs alive during 2003-2018 (period-before only 56, period-during only 69, both periods

275   36). Of 105 individuals alive in period-during, 69 were primarily assigned as fed and 36 as

276   unfed (Appendix 1). In total, there were 627 annual survival observations of the 161 adults

277   (mean per individual: 3.9±2.8SD; Table 1).

278   Variation in annual adult survival was significantly explained by the area by time-

279   period interaction (Fig. 2, p=0.01; Appendix 2). In "area-fed", survival increased

280   substantially between time-periods from an initially low value, by approximately 0.14 (Fig.

281   2). Meanwhile, in "area-unfed", survival decreased slightly, by approximately 0.03 (Fig. 2).

282   Survival also decreased with increasing age (latent scale β=-0.06±0.03SE, p=0.05).

283

284   **Reproductive success**

285   Since information on reproduction was not recorded for all colour-ringed individuals

286   in all years, the dataset comprised 414 observations of 109 known sex individuals (alive in

287   period-before only 35, period-during only 50, both periods 24, mean observations per

288   individual: 3.8±2.4SD; Table 1).

289   Variation in female nest success (i.e. success versus failure to produce ≥1 fledged

290   offspring) was significantly explained by the area by time-period interaction (Fig. 3b; p=0.03,

291   Appendix 2). Nest success increased in "area-fed" between time-periods by approximately

292   0.15, but decreased in "area-unfed" by approximately 0.14 (Fig. 3b). For male nest success

293   the interaction was marginally non-significant (Fig. 3a; p=0.07, Appendix 2), but success was

294   estimated to decrease in "area-unfed" between time-periods, by approximately 0.27.

295   Consequently, the estimated relative difference in nest success between areas across time-

296   periods was substantial (approximately 0.3) in both sexes.

297   Variation in conditional brood size (i.e. number of fledglings given ≥ 1 fledgling

298   produced) was not significantly explained by the area by time-period interaction for either

299   sex (males: $p=0.44$; females: $p=0.63$; Table S3). Conditional brood size remained similar in

300   "area-fed" and "area-unfed" between time-periods in both sexes (Fig. 3c,d).

301   Consequently, for overall breeding success (i.e. number of fledglings produced at

302   each occupied territory), the area by time-period interaction was borderline significant in

303   males ($Z=2.0$, $p=0.05$) but not females ($Z=1.2$, $p=0.24$, Appendix 2). However, the estimated

304   effects are biologically substantial. Mean overall breeding success increased very slightly

305   between time-periods in "area-fed", but tended to decrease in "area-unfed" (Fig. 3e,f).

306   Together, this resulted in total differences between areas and time-periods of 0.91 fledglings

307   for males and 0.57 fledglings for females (Appendix 4). Furthermore, these estimates are

308   generally slightly conservative compared to those from additional models with slightly

309   different assignments of individuals to areas (Appendix 4).

310   Nest success, conditional brood size and overall breeding success did not vary with

311   individual age across the current datasets (linear latent scale estimates $\pm$SE: nest success:

312   males $\beta=-0.03\pm0.07$, $p=0.71$, females $\beta=0.10\pm0.07$, $p=0.13$; conditional brood size: males β

313     $=0.00\pm0.02$, $p=0.85$, females $\beta=0.00\pm0.02$, $p=0.82$; overall breeding success: males $\beta=-$

314   0.004 ± 0.02, $p=0.81$, females $\beta=0.02\pm0.02$, $p=0.42$; Appendix 2).

315

316   **Population projection models**

317   Matrix projection models using female reproductive success estimates show that λ

318   significantly increased in "area-fed" between period-before and period-during, from 0.86

319 (95%CI 0.81-0.91) to 0.99 (95%CI 0.94-1.03), but tended to decrease in "area-unfed" from

320 1.00 (95%CI 0.95-1.05) to 0.96 (95%CI 0.91-1.00) (Fig. 4). Models using male or pair-level

321 reproductive success estimates gave quantitatively similar results (Fig. 4, Appendix 5).

322   During 2015-2017, an average of 69% of adults were estimated to be fed (Appendix

323 1). Weighting λ for the "area-fed" and "area-unfed" values for period-during by this

324 proportion gave point estimates of overall-λ of 0.95 and 0.96 using female and male

325 reproductive success, respectively.

326

327 **DISCUSSION**

328   Quantifying collateral impacts of targeted conservation interventions on non-target

329 individuals within focal populations should be integral to evidence-based management, but is

330 rarely achieved. We used multi-year BACI analyses to infer that a supplementary feeding

331 programme designed to target sub-adult choughs within a threatened population apparently

332 had major additional benefits through collateral effects on adult survival and probability of

333 successful breeding. Projection models show that these estimated effects alone would

334 substantially increase population growth rate (λ) towards the desired outcome of population

335 stability.

336   The substantial relative increase in adult survival between the defined fed and unfed

337 areas across time-periods suggests a strong positive effect of supplementary feeding, given

338 standard BACI assumptions. The evidence for effects on reproductive success was more

339 nuanced: there was a substantial relative increase in nest success between "area-fed" and

340 "area-unfed" across time-periods, but no increase in conditional brood size. Consequently,

341 overall breeding success of choughs in the "area-fed" group remained constant or increased

342 very slightly, compared to decreases elsewhere. The estimated biological effects were

343 substantial, yet only marginally statistically significant when estimated across known-age

344 males and not statistically significant across known-age females. This may partly reflect that

345 BACI analyses can have low power given relatively small sample sizes and substantial

346 environmental noise, and may consequently estimate moderate true effects as non-significant

347 (Christie et al., 2019). Since choughs are year-round monogamous (Bignal et al., 1997),

348 differences between estimated reproductive success of known-age females and males likely

349 primarily represent sampling variance.

350   Inference of supplementary feeding effects from non-experimental data relies on the

351 BACI approach, and different conclusions would have been drawn had we not considered the

352 before-feeding demographic baseline. Specifically, a direct "control-impact" comparison

353 would have shown similar adult survival in "area-unfed" (0.84, 95%CI 0.77-0.89) and "area-

354 fed" (0.87, 95%CI 0.81-0.91) in period-during, implying little or no feeding effect. But this

355 misses the substantial increase in survival in "area-fed" between time-periods, where survival

356 was previously substantially lower ("area-fed" in period-before 0.73, 95%CI 0.65-0.80,

357 versus "area-unfed" 0.87, 95%CI 0.79-0.92). Many studies of demographic impacts of

358 conservation interventions are restricted to control-impact comparisons only, with no baseline

359 pre-intervention data available (Christie et al., 2019). Further, supplementary feeding studies

360 are commonly short (e.g. 1-2 years, Brommer et al., 2004; Sim et al., 2015), and have limited

361 capability to account for background environmental variability. For example, short-term

362 interventions may coincide with periods of naturally high food availability (Ruffino et al.,

363 2014; Sim et al., 2015; Todd et al., 2003), which may negate the need for individuals to use

364 supplementary food, and thereby reduce differences between fed and unfed groups.

365 Furthermore, many studies assess supplementary feeding based on comparisons between

366 groups that were or were not provided with food, without data on actual food use to inform

367 the validity of assumed groupings. In practice, supplementary food may not be equally used

368   by all individuals (Crates et al., 2016; Newey, Allison, Thirgood, Smith, & Graham, 2010;

369   Maggs et al., 2019; Tollington et al., 2018). In our study, regular and frequent observations of

370   food use, general location use and territory occupancy of colour-ringed individuals allowed

371   definition of proxy "areas" for supplementary feeding impact, and previous demographic

372   monitoring provided data from choughs inhabiting the same areas in pre-feeding years. Our

373   study therefore illustrates how collection of long-term, individual-based demographic data

374   can contribute to understanding effects of conservation management (Badia-Boher et al.,

375   2019; Oppel et al., 2016).

376   Adult survival and reproductive success are key demographic rates which can

377   strongly affect λ. They must consequently be considered when evaluating the overall

378   population consequences of any management intervention, particularly for longer-lived

379   species that might experience interventions over multiple years. Our matrix projection models

380   show that the inferred positive effects of supplementary feeding on adult survival and nest

381   success translate into increases in λ that alone make substantial progress towards achieving

382   population stability irrespective of any positive impact on the original target demographic of

383   sub-adult survival. This occurred even though only ~70% of adults regularly used

384   supplementary food. Alongside short-term efficacy of the current supplementary feeding

385   intervention, these results suggest new longer-term routes to increasing λ. Although there was

386   no evidence of declines in adult survival or reproductive success during 1983-2010 (Reid et

387   al., 2009), the apparent collateral effects of supplementary feeding imply that (some) adults

388   were also food-limited through all or part of the non-breeding season while in communal

389   areas. Since supplementary feeding overlapped with the start of the breeding season in April,

390   feeding may directly reduce early nest failure (and hence increase overall nest success), but

391   there was no detectable carry-over effect on conditional brood size after the seasonal end of

392   supplementary feeding. Overall, the estimated effects on adult survival and nest success are

393 notably large, especially since the quantity of supplementary food provided was highly

394 restricted rather than *ad lib* (to minimise risk of artificial food dependency; Bignal & Bignal,

395 2011). Future conservation interventions for Islay's choughs should therefore aim to increase

396 food abundance and/or availability for all life-history stages, ideally through effective habitat

397 management.

398   While there was no *a priori* expectation that adult survival would differ between

399 "area-fed" and "area-unfed" before feeding started, there was in fact a clear difference (Fig.

400 2). Survival of choughs in "area-fed" during period-before was low compared to those in

401 "area-unfed" and estimates from other British populations (Johnstone, Mucklow, Cross,

402 Lock, & Carter, 2011; Reid et al., 2009). One possible interpretation of this is that "area-fed",

403 and/or choughs inhabiting "area-fed", were originally of lower quality than "area-unfed".

404 Analyses of other conservation supplementary feeding programmes found that feeding is

405 particularly beneficial when habitat quality varies, and food can be targeted at individuals

406 which will benefit most (e.g. Ferrer et al., 2017). Indeed, response to supplementary feeding

407 often depends on territory quality, with individuals on low quality territories responding

408 relatively more strongly than individuals on high quality territories (Ferrer et al., 2017;

409 González et al., 2006). This highlights the value of spatially-optimised conservation

410 interventions. However, our results imply that expanding the current supplementary feeding

411 programme to other areas of Islay may do little to further improve adult chough survival

412 across the whole population, since choughs in "area-unfed" already have high survival rates.

413 Therefore, survival in unfed areas may not be improved sufficiently by feeding to warrant

414 extra cost. Indeed, during the current feeding programme, adult survival in "area-fed" only

415 increased to similar levels as in "area-unfed", suggesting that adult survival may now be near

416 its maximum. However, if underlying habitat quality in currently unfed areas continues to

417   decline, further supplementary feeding may be warranted. Adult survival should therefore be

418   closely monitored to inform future management decisions.

419   Implementing management based on current knowledge, while simultaneously

420   evaluating efficacy, is especially valuable where populations are at imminent risk of decline

421   towards extinction (e.g. Ferrer, Newton & Muriel, 2013). Our analyses suggest that the

422   current supplementary feeding programme has important demographic and population-level

423   benefits, without even considering impacts on the original target demographic (sub-adult

424   survival). Quantifying effects on sub-adult survival and recruitment is itself a major

425   challenge. The BACI approach is not readily applicable because sub-adults are more mobile,

426   and resighting probabilities are lower, meaning that individuals cannot be readily assigned to

427   discrete fed and unfed "areas". However, multi-state models that quantify survival and

428   movements over finer temporal and spatial scales indicate effects are also positive, at least in

429   some years (Fenn et al., unpublished data). Therefore, our results, and the observation that

430   population size has been approximately stable since 2014, imply that supplementary feeding

431   has been an effective intervention to prevent a rapid population decline. Stochastic population

432   viability analyses, which also considered genetic effects, consequently estimated substantial

433   positive effects on population viability (Trask et al., 2019).

434   Nonetheless, supplementary feeding is not a sustainable or desirable long-term

435   solution to remedy constraints on natural food availability. Rather, the underlying causes of

436   food shortage now need to be addressed through longer-term management (e.g. habitat

437   restoration, Schoech et al., 2008; Weidman & Litvaitis, 2011). Choughs can feed on diverse

438   invertebrates, and plants, at different times of year (Kerbiriou & Julliard, 2007; MacGillivray,

439   Gilbert, & McKay, 2018). However, changes in traditional pastoral agriculture and livestock

440   grazing have likely reduced invertebrate abundance and availability (Bignal et al., 1997).

441   Improvements would ideally be achieved through agri-environmental schemes, including

442   livestock and grassland management initiatives that promote spatial and temporal diversity,

443   abundance and availability of invertebrates. Finding long-term strategies to improve habitat

444   quality on Islay, particularly of sand dune systems known to be important for both sub-adult

445   and adult choughs, while also addressing known genetic threats (Trask et al., 2019), is

446   imperative to ensure long-term population viability.

447

448   **Authors contributions**

449   All authors contributed to conceptual development. S.R.F. and J.M.R. devised the

450   analyses. S.R.F. undertook analyses. E.M.B. undertook supplementary feeding and collected

451   data, with contributions from D.I.M., J.M.R, S.R.F and A.E.T. S.R.F. and J.M.R led

452   manuscript writing, with input and final approval from all authors.

453

464

465 **Data accessibility**

466 Data available via Dryad Digital Repository upon manuscript acceptance.

467

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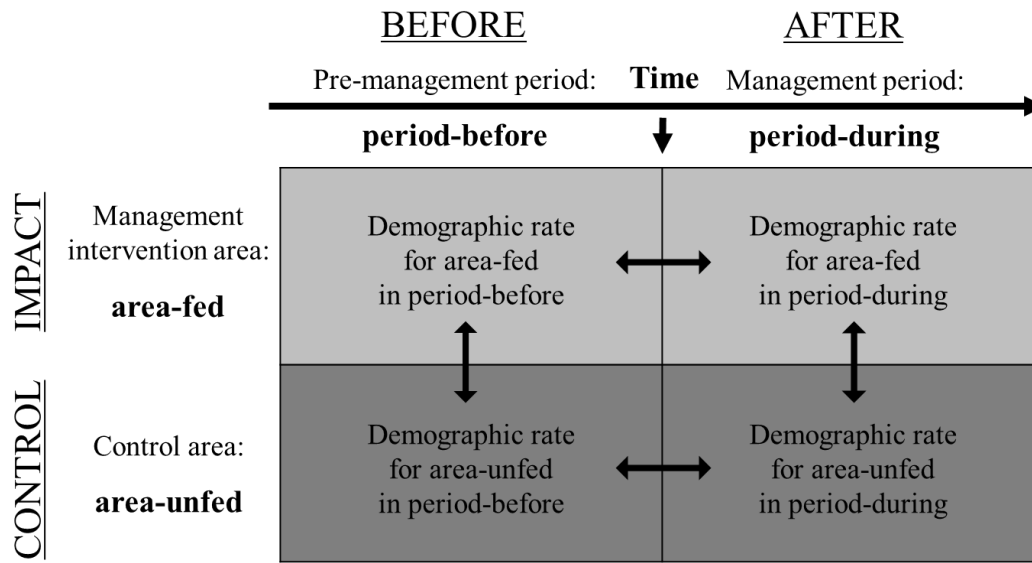
696

697 **Figure 1: Representation of the before-after control-impact (BACI) framework used to**

698 **estimate effects of supplementary feeding on chough demographic rates. Comparisons**

699 **(arrows) can be made between "control" and "impact" groups (here, "area-unfed" and**

700 **"area-fed", respectively) in the "before" and "after" (or "during") time-periods (here,**

701 **period-before and period-during, respectively), and within groups across periods. A**

702 **significant area by time-period interaction, wherein focal demographic rates increase in**

703 **"area-fed" more than "area-unfed" between period-before and period-during, would**

704 **suggest a positive effect of the management intervention.**

705

706 **Table 1: Summary of sample sizes in each BACI group for adult survival and measures**

707 **of male and female reproductive success (RS). Reproductive success: (1) nest success**

708 **and overall breeding success, (2) conditional brood size. Sample size (n): number of**

709 **datapoints (number of individual adults); mean observations per individual: $\bar{x}\pm$SD.**

Demographic rate	Area-period							
	Fed-before		Fed-during		Unfed-before		Unfed-during	
	n	$\bar{x}\pm$SD	n	$\bar{x}\pm$SD	n	$\bar{x}\pm$SD	n	$\bar{x}\pm$SD
Survival	148(59)	2.5±1.8	222(63)	3.5±2.2	117(34)	3.4±2.2	140(44)	3.2±2.2
Male RS-1	43(18)	2.4±1.3	82(23)	3.6±1.7	33(11)	3.0±1.9	30(13)	2.3±1.9
Female RS-1	41(19)	2.2±2.0	94(23)	4.1±2.3	36(11)	3.3±1.9	55(15)	3.7±1.9
Male RS-2	33(18)	1.8±1.2	65(21)	3.1±1.9	29(11)	2.6±1.9	21(9)	2.3±2.2
Female RS-2	26(14)	1.9±1.5	73(20)	3.7±2.3	32(9)	3.6±1.6	42(15)	2.8±2.0

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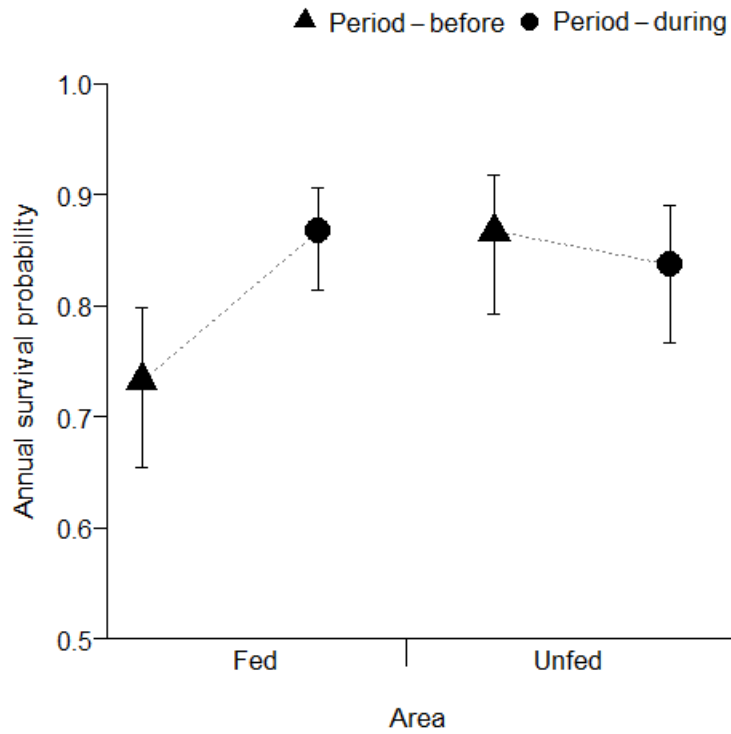
Figure 2: Estimated annual survival probability (with 95% confidence intervals) of adult choughs by area and time-period. Triangles and circles denote period-before and period-during supplementary feeding respectively, in "area-fed" and "area-unfed". Dotted lines aid visualisation of between-period changes within each area.

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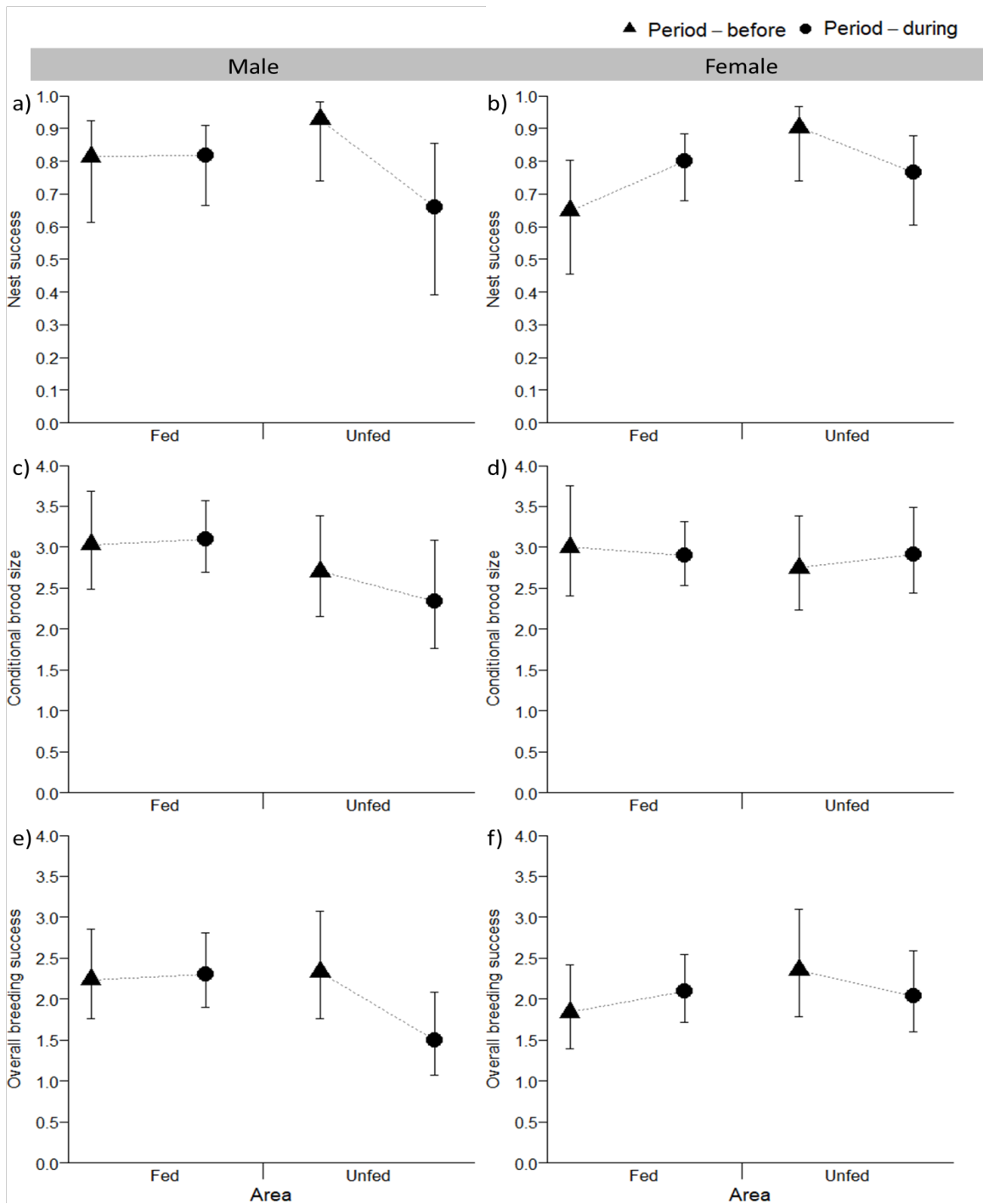
719　**Figure 3: Estimated measures of reproductive success (with 95% confidence intervals)**

720　**of adult choughs: (a & b) nest success, (c & d) brood size conditional on nest success and**

721　**(e & f) overall breeding success, estimated from colour-ringed (a, c & e) males and (b, d**

722　**& f) females. Triangles and circles denote period-before and period-during**

723　**supplementary feeding respectively, in "area-fed" and "area-unfed". Dotted lines aid**

724　**visualisation of between-period changes within each area.**

725

726

Figure 4: Estimated asymptotic chough population growth rate (with 95% confidence intervals) by area and time-period, with reproductive success estimated from colour-ringed males (open symbols) or females (filled grey symbols). Triangles and circles denote period-before and period-during supplementary feeding respectively, in "area-fed" and "area-unfed". Dotted lines aid visualisation of between-period changes within each area.

733

1 **Supporting information**
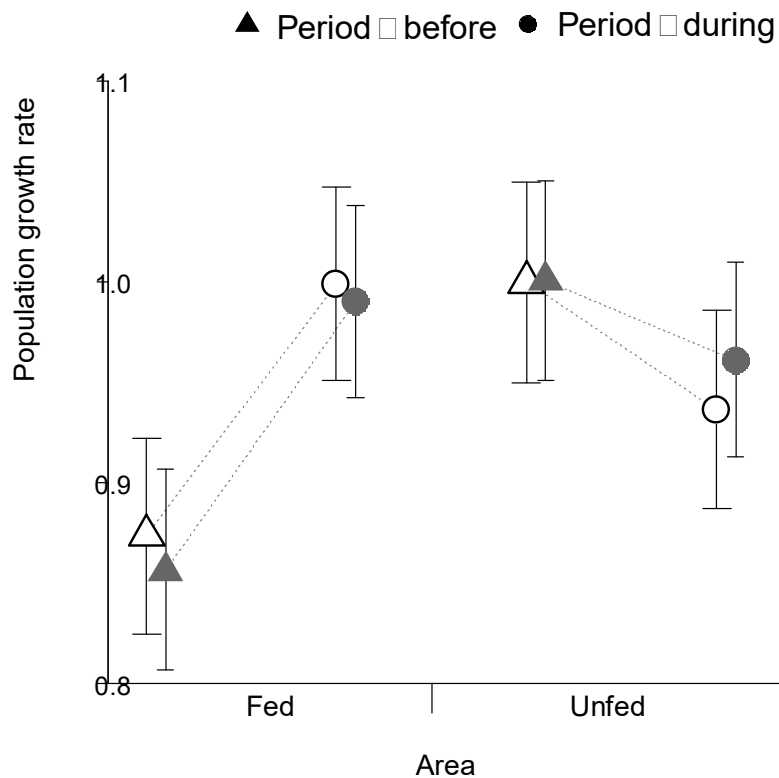
2

3 **Collateral benefits of targeted supplementary feeding on demography and growth rate**

4 **of a threatened population.**

5

6 **Sarah R. Fenn, Eric M. Bignal, Amanda E. Trask, Davy I. McCracken, Pat Monaghan**

7 **and Jane M. Reid**

8

9 **Contents:**

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15 **Appendix 2. Survival and reproductive success model coefficients**

16 **Appendix 3. Pair-level reproductive success**

17 **Appendix 4. Influence of uncertain feeding and area assignment**

18 **Appendix 5. Further details of matrix projection models**

Appendix 1. Details of supplementary feeding

20 *1.1 Supplementary feeding programme*

21   The supplementary feeding programme, funded primarily by Scottish Natural

22 Heritage (SNH), was introduced as an emergency conservation intervention in response to

23 critically low first-year annual survival rates observed during 2007-2009 (Bignal & Bignal,

24 2011). This low first-year survival, attributed to low food availability in late summer (Reid et

25 al., 2008; Reid et al., 2011), threatened short-term population viability (deterministic

26 population growth rate $\lambda \approx 0.87$, Reid et al., 2011). Consequently, the feeding programme

27 purposefully targeted sub-adult choughs in late summer, and throughout the rest of the non-

28 breeding season. On Islay, juvenile choughs fledge approximately six weeks post-hatch, and

29 leave their natal territories within a few weeks post-fledging to join sub-adult foraging and

30 roosting flocks that generally occupy two traditional areas (primarily associating with two

31 sand dune systems, Bignal, Bignal, & McCracken, 1997). They typically remain in these

32 flocks until they disperse to acquire a territory and breed aged three years, with little

33 subsequent breeding dispersal (Reid, Bignal, Bignal, McCracken, & Monaghan, 2003). To

34 minimise influencing natural chough behaviour, supplementary feeding was consequently

35 targeted at these two areas, where sub-adults were already present. While it was anticipated

36 that some adults (i.e. individuals aged $\geq$3 years) that joined sub-adult flocks may also

37 consume supplementary food, improving adult survival or reproductive success was not the

38 primary motivation for providing supplementary food. In that case, the protocols would likely

39 have been very different. Indeed, there was no expectation that adult survival or reproductive

40 success was food-limited, and therefore no expectation that food supplementation would

41 significantly influence these rates. Consequently, any effects observed on adult demographic

42 rates were unplanned.

43   During the winter of 2009-2010, a trial supplementary feeding programme was

44   implemented at one site to test feasibility and develop methods (Bignal & Bignal, 2011).

45   Based on the success of this trial, choughs were provided with supplementary food during the

46   non-breeding seasons between 2010-2011 and 2017-2018 (i.e. eight years) at two main sites

47   on Islay (hereafter food-station-1 and food-station-2; Fig. S1, Fig. S2), typically between late-

48   June (i.e. post breeding) and mid-April the following spring. Since there was no evident

49   decrease in reproductive success in previous years, or evidence that reproductive success was

50   particularly food-limited, supplementary feeding during the breeding season was not

51   considered necessary. Therefore, supplementary food was only provided during the non-

52   breeding season. Supplementary feeding commenced at food-station-1 in 2010-2011, and at

53   food-station-2 in 2011-2012. These two sites (Fig. S2) were chosen because they were

54   naturally and commonly used by the sub-adult flocks during pre- or post-roosting, and so

55   were good locations to target sub-adults without changing their natural behaviour. Food-

56   station-1 was near a known roost site, where sub-adult flocks foraged in the evenings prior to

57   roosting (Bignal & Bignal, 2011). Food was provided here once a day in the evening before

58   birds went to roost. Food was provided at food-station-2 once a day during late morning to

59   early afternoon in an open farm field where sub-adult choughs were regularly seen foraging

60   post-roosting. An additional supplementary feeding site, hereafter food-station-3, was also

61   temporarily used when sub-adult choughs used the local area.

62
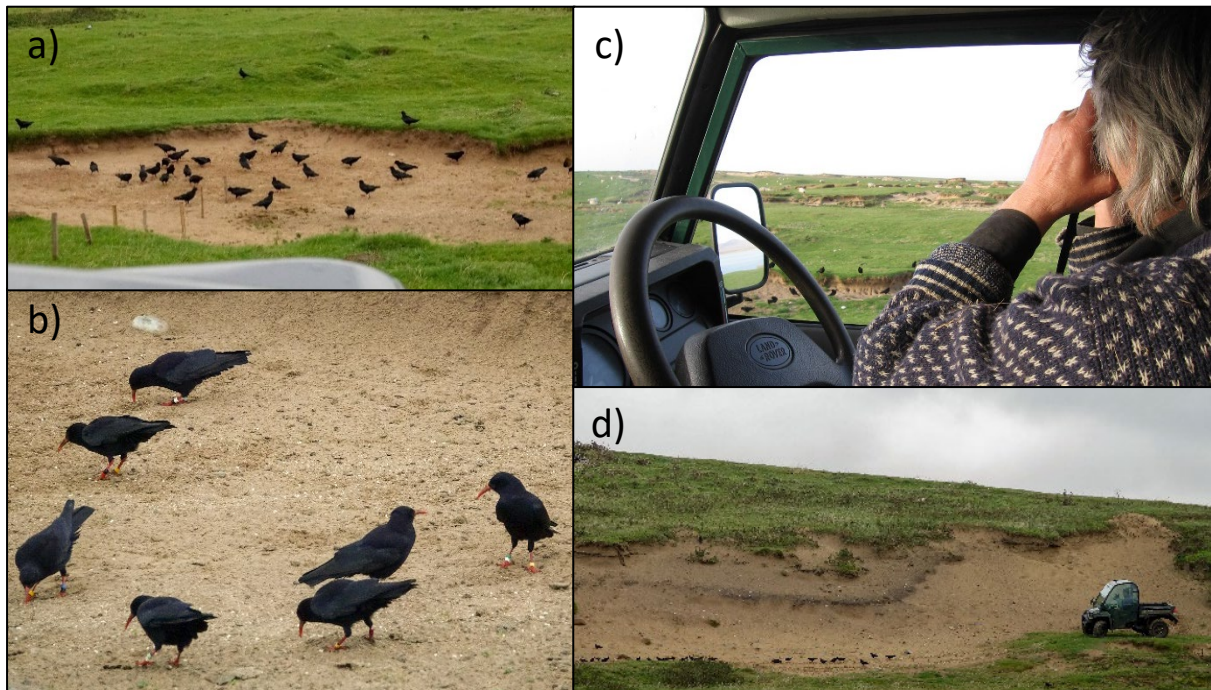
Figure S1: Chough supplementary feeding sites and feeding observations. a) & b) Flock feeding at food-station-1. Observations of choughs feeding on supplementary food at c) food-station-1 and d) food-station-2 made from a vehicle.

The supplementary food consisted of a mixture of live mealworms (*Tenebrio molitor* larvae) and suet pellets with pinhead oatmeal (Bignal & Bignal, 2011), and was provided almost daily at food-station-1 and food-station-2 over the non-breeding season. A restricted quantity of supplementary food was provided, estimated to give approximately 15% of an individual's daily energy requirement (Bignal & Bignal, 2011). Therefore, individuals must still forage effectively for themselves to survive, reducing the risk that they would become entirely reliant on the artificial food source. This protocol also aimed to limit change in the natural behaviour of the sub-adult flock, and reduce the risk of disease transmission through attracting non-target species, such as rooks and jackdaws. The feeding sites were managed to

77 reduce the potential risk of disease and parasite transmission between birds, with the

78 underlying sand regularly replaced.

79   To allow quantitative assessment of the efficacy of supplementary feeding as a

80 conservation intervention, territory and nest monitoring data and detailed colour-ring

81 resightings (from feeding sites and elsewhere) were collected throughout the supplementary

82 feeding programme, continuing a long-running programme of demographic monitoring

83 (Reid, Bignal, Bignal, McCracken, & Monaghan, 2004; Reid et al., 2008). A sample of

84 territories were monitored for reproductive success between 2003-2018 (Fig. S2; precise

85 territory location not shown since choughs are a protected species). As choughs are a

86 Schedule 1 protected species in Scotland and the UK (Wildlife & Countryside Act, 1981), to

87 keep disturbance to a minimum, nest visits were restricted to a single visit for colour-ringing

88 offspring. Consequently, detailed information such as egg laying dates, clutch size and

89 hatching success were typically unknown or uncertain.

90   Supplementary feeding observations were made from a vehicle (Fig. S1c), starting

91 directly after supplementary food was provided, and ending generally after all individuals

92 attending were confidently recorded. Near-daily records of supplementary feeding colour-

93 ringed choughs were made at food-station-1 and food-station-3, resulting in exceptionally

94 high quality, high frequency data of individual attendance at supplementary feeding sites.

95 Food at food-station-2 was provided approximately as regularly as at food-station-1, but

96 observations of colour-ringed choughs were made less frequently. Nevertheless, these

97 observations still generally spanned the whole of each non-breeding season, and so provided

98 enough information to assign individual seasonal supplementary food use. To summarise

99 resighting effort at each feeding site, the total number of days on which any resightings were

100 recorded and the total number of resightings recorded at each site over each non-breeding

101 season, were extracted (Table S1).

102

Table S1. Total number of days that supplementary feeding and recording of attending colour-ringed choughs were carried out at the three supplementary feeding sites, and total number of resightings of attending colour-ringed choughs during each non-breeding season. Supplementary food was not provided at all sites in all years (i.e. number of days of supplementary feeding = NA). *At food-station-2, colour-ring resightings were not carried out every day that supplementary food was provided. The total number of days on which food was provided was similar to that at food-station-1.

Non-breeding season	Number of days of supplementary feeding and colour-ring resighting at each food-station (FS)			Total no. of colour-ring resightings
	FS-1	*FS-2**	*FS-3*	
2010-2011	228	NA	NA	5603
2011-2012	244	29	39	8979
2012-2013	295	30	233	13017
2013-2014	246	32	200	12313
2014-2015	296	25	NA	16852
2015-2016	215	23	274	11304
2016-2017	252	44	NA	9878
2017-2018	259	44	65	9507

110

111   Data from the trial supplementary feeding programme during winter 2009-2010

112 (Bignal & Bignal, 2011) were excluded from current survival and reproductive success

113 analyses; only two adults were observed attending a supplementary feeding site during this

114 period, and since supplementary feeding only began in late December, the feeding of these

115 two individuals was not comparable to subsequent non-breeding seasons.

116

117   *1.2 Assessing adult use of supplementary food*

118   Previous studies on other systems demonstrated that supplementary food may not be

119   used equally by all individuals in a population, and this heterogeneity may have substantial

120   consequences for inferring effects of supplementary feeding. Tendency to use supplementary

121   food can vary across years, locations, species, ages, sexes and breeding states (Crates et al.,

122   2016; López-Bao, Rodríguez, & Palomares, 2009; Maggs et al., 2019; Robb et al., 2011).

123   Furthermore, individuals that primarily inhabit unfed "control" areas may take food from fed

124   areas (Schoech et al. 2008; Sim, Wilkinson, Scridel, Anderson, & Roos, 2015).

125   Consequently, simple comparisons between individuals in areas that were or were not

126   exposed to supplementary food may not fully capture the heterogeneity in individual food

127   usage, and hence individual and demographic consequences of supplementary feeding (Robb,

128   McDonald, Chamberlain, & Bearhop, 2008). Since single or few observations of individuals

129   using supplementary food may give little indication of overall frequency of food consumption

130   (Weidman & Litvaitis, 2011), repeated records of individual food use are necessary, but

131   rarely achieved. Therefore, for each colour-ringed adult chough (aged ≥3 years), the degree

132   of supplementary food use over the course of each non-breeding season was assessed by

133   comparing the frequency of colour-ring resightings at supplementary feeding stations to

134   specific site and monthly resighting effort. Specifically, as resighting effort varied by site

135   (Table S1), and also monthly at food-station-2 and food-station-3, frequency of individual

136   attendance at supplementary feeding sites was compared to the number of days feeding

137   observations were made in each month at each site. Differences in ring-resighting frequency

138   between sites prohibited examination of demographic rates in relation to individual-level

139   variation in daily supplementary food use rates.

140   Feeding observations showed that food usage was highly bimodal, with individual

141   adults observed at supplementary food-stations either frequently and regularly throughout the

142   non-breeding season, or never or very infrequently (Appendix 4). Accordingly, each colour-

143   ringed adult was assigned as "fed" or "unfed" for each non-breeding season. Because of the

144   exceptionally high resighting effort at food-station-1, individual attendance and therefore

145   feeding assignment as fed or unfed was generally very clear for individuals feeding here.

146   Detailed examination showed that key results and conclusions were highly robust to

147   alternative assignments for a small number of less clear-cut individuals (Appendix 4).

148   When an individual was strongly suspected or known to have died during a given

149   non-breeding season, to avoid misassignment of feeding status as "unfed" from the low

150   annual frequency of resightings at supplementary feeding sites, care was taken to assign

151   feeding state based on resighting frequency and behaviour from prior to the suspected date of

152   mortality. Individuals that died part way through a non-breeding season were classified based

153   on their resightings during that winter up until their death, and where the timing of death was

154   uncertain or suspected to occur early in the non-breeding season, classification was based on

155   the individual's attendance at supplementary feeding stations in previous seasons. Although

156   previous feeding activity may not necessarily accurately predict the current behaviour (e.g. an

157   individual that died in their first year of adulthood, and thereby potentially holding a territory

158   in a different area to the sub-adult home range), there were very few cases of this (n = 10),

159   and are unlikely to bias results.

160   As individual food use was reassessed for each non-breeding season, individuals

161   could change feeding state between years. While some (n=16, i.e. 15.2%) adults changed

162   feeding state ≥1 times between years, 89 individuals were consistent between years, with 59

163   assigned as fed each year, and 30 as unfed. Of the 16 individuals that changed feeding state

164   between years, seven were primarily fed, five were primarily unfed, and four split between

165   fed and unfed.

166

1.3 Defining area and time-period groups for BACI analyses

1.3.1 Area

169   The data showed that adult choughs assigned as unfed and fed generally used specific

170 areas and occupied territories in particular regions of Islay, predominantly but not exclusively

171 close to and further away from feeding sites respectively, thereby generating a strong and

172 consistent spatial structuring of occupied territories in relation to food use over time (Fig.

173 S2). Consequently, supplementary food use, and any associated demographic effects, were

174 geographically non-random. Therefore, a proxy area parameter ("area-unfed" and "area-fed")

175 was defined to specify the control and impact groups for the BACI analyses.

176   Individuals were assigned to an area based on the locations of their breeding

177 territories (Fig. S2). Some pairs remained on or near their breeding territory through most of

178 the year, while other pairs moved to communal feeding and roosting areas during the non-

179 breading season. This difference in behaviour was broadly spatially structured; pairs from

180 territories around flocking areas and in the east of Islay, generally used the flocking areas in

181 the non-breeding season, and were consequently "fed". Pairs with territories elsewhere

182 commonly remained there, and were consequently "unfed". Hence, while individuals were

183 assigned to "area-fed" or "area-unfed" based on their breeding territory location, it was not

184 assumed that all individuals were tied to their territories during the non-breeding season.

185 Rather, the key BACI assumption is that the behaviour of choughs did not changed

186 substantially within each area group across time-periods (i.e. individuals from each area

187 generally used similar areas over winter, including flocking and roosting areas, both before

188 and during the supplementary feeding programme). Indeed, there has been no indication that

189   there has been a substantial change in this behaviour from prior, to during, the supplementary

190   feeding programme.
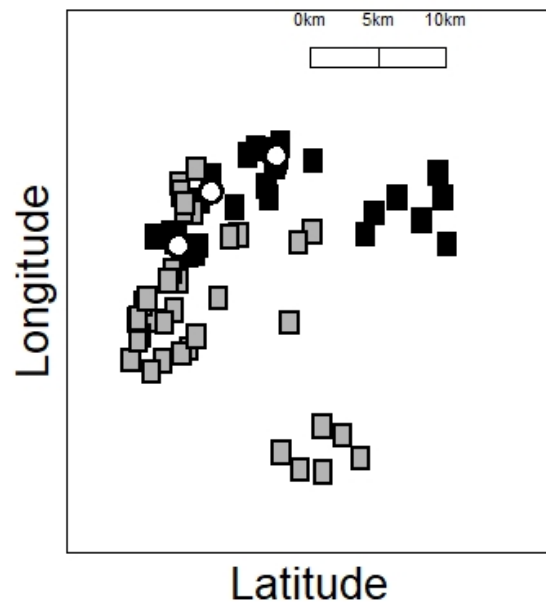
191

192   **Figure S2: Approximate representation of chough territories in "area-unfed" (grey**

193   **squares) or "area-fed" (black squares). Choughs are a protected species, and therefore**

194   **exact nest locations cannot be shown. The approximate location of the three**

195   **supplementary feeding sites are shown by the open points.**

196

197   While attendance at supplementary feeding is partly related to distance between

198   territory and food-stations, some pairs from territories further from the food-stations fed at

199   supplementary feeding sites, while some pairs from close territories did not. This might be

200   because choughs from poorer quality habitats and territories, which are therefore more food-

201   limited, are more likely to come to the food-stations. This would also help explain why adult

202   annual survival was lower in "area-fed" than in "area-unfed" during period-before (see main

203   Results). However, there was no *a priori* assumption that territories in "area-fed" would

204   differ from those in "area-unfed" on average, although territory quality likely varies

205   substantially both between and within defined areas. However, while individual territory

206   quality may influence response to supplementary feeding, the current objective was to assess

207   population-level effects of supplementary feeding. Territory-level effects were neither

208   investigated nor captured in current analyses, since the BACI analysis is designed to average

209   over such effects.

210

211   **1.3.2 Time-period**

212   Period-before and period-during reflect the "before" and "during" intervention time-

213   periods, respectively; generally, 7 years for period-before (2003-2004 to 2009-2010), and 8

214   years for period-during (2010-2011 to 2017-2018). However, since supplementary feeding

215   was introduced gradually across multiple feeding sites, the defined time-period boundaries

216   differ slightly between food-stations. Because supplementary feeding at food-station-2

217   commenced during the 2011-2012 non-breeding season, the distinction between period-

218   before and period-during was set to reflect this for choughs living in this area. While ring

219   resighting and reproductive success data were additionally collected during 1983-2003, for

220   current analyses "period-before" was defined as starting in 2003 to try to ensure that

221   environmental conditions (such as habitat) remained relatively stable within this time-period.

222

223   *1.4 Proportion of adults that used supplementary food*

224   To estimate the total collateral effect of the current supplementary feeding programme

225   on overall population growth rate (λ) and hence likely population viability, we estimated the

226   proportion of adults that were fed, and used this to calculate a weighted value of λ from the

227   values estimated for "area-fed" and "area-unfed". However, if the proportion of individuals

228   attending supplementary feeding changed across period-during, an average proportion taken

229   across all years in period-during may not be the most appropriate value to weight λ. A basic

230   analysis showed that a large proportion of adult choughs regularly attended supplementary

231   feeding, and that the proportion increased significantly during the feeding programme from

232   21.4% in 2010-2011 to a peak of 70.5% in 2015-2016 (binomial generalized linear mixed

233   model with logit link function, latent scale $\beta=0.26\pm0.05SE$; $Z=5.6$, $p<0.001$, Fig. S3). The

234   proportion of adults regularly using supplementary food appears to have stabilised between

235   2015-2018, at an average of 69% of individuals in each year. Consequently, to capture recent

236   effects, we weighted the estimated value of λ in "area-unfed" and "area-fed" in period-during

237   by this estimated proportion of unfed to fed individuals (i.e. 31% unfed and 69% fed).

238

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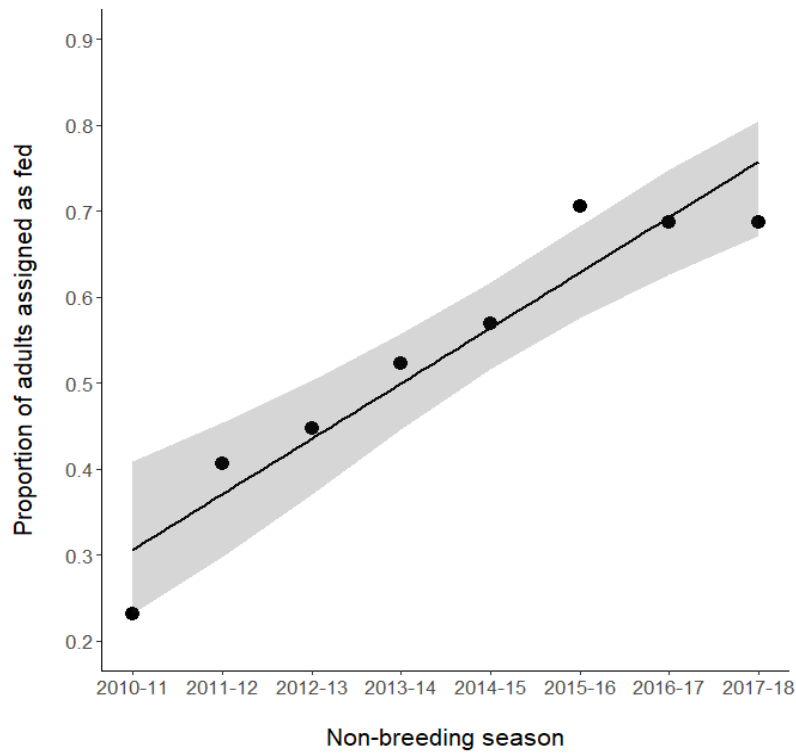
Figure S3: Increasing use of supplementary feeding by adult choughs during the supplementary feeding programme. Points show the observed proportion of adults assigned as fed (i.e. regularly using supplementary food) during each non-breeding season. The solid line shows modelled linear regression, and the grey ribbon shows the 95% confidence interval.

246   <u>Appendix 2. Survival and reproductive success model coefficients</u>

247   Table S3 shows full details of the generalised linear mixed models (GLMMs) fitted to

248   assess the effects of supplementary feeding on annual adult survival probability, nest success,

249   conditional brood size and overall breeding success. Model estimates presented in the main

250   manuscript text were back-transformed onto the observed scale using the "effect" function

251   from the effects package (Fox, 2003).

252   Age was best or most parsimoniously described as a linear term, but estimated effects

253   of area and time-period remained qualitatively similar regardless of whether age was

254   modelled as linear, quadratic, or factorial younger (ages 3-12 years) versus old (ages ≥13

255   years) ages. Exploratory analyses indicated that there was low power to detect a three-way

256   area by time-period by year effect, and hence test for variation in potential supplementary

257   feeding effects among years.

258   There was no detectible variance in random identity or year effects in the survival, or

259   male and female conditional brood size models (Table S2), suggesting that there is little

260   among individual or year variation for either survival or conditional brood size.

261

Table S2: Estimated coefficients from generalised linear mixed models of the effect of

area and time period on annual survival probability and reproductive success of adult

choughs. Estimated effect sizes (Estimate) and associated standard errors (SE), and test

Z-value and probabilities (p-value) are presented. Model intercepts are set as area-

unfed, period-before. Models controlled for age effects (fixed effect, linear mean–

centred), with random individual identity and year effects. Area and period were

modelled as fixed effects, with the two-way interaction.

Fixed effects	Estimate	SE	Z-value	P-value
Annual survival				
Variance of random effects: Individual identity = 0.00; Year = 0.00				
Intercept	1.87	0.27	6.91	<0.001
Area-fed	-0.86	0.33	-2.64	0.008
Period-during	-0.23	0.35	-0.66	0.511
Centred-age	-0.06	0.03	-1.96	0.051
Area-fed: Period-during	1.10	0.45	2.46	0.014

Comparison of model without interaction term (a) to model with interaction term (b):

(a) model deviance = 568.85; (b) model deviance = 562.73; ANOVA χ^2_1 = 6.12, p = 0.013

Nest success for known-age males				
Variance of random effects: Individual identity = 1.26; Year = <0.001				
Intercept	2.55	0.77	3.32	0.001
Area-fed	-1.07	0.87	-1.23	0.220
Period-during	-1.88	0.92	-2.04	0.042
Islay-centred-age	-0.03	0.07	-0.37	0.710
Area-fed: Period-during	1.90	1.09	1.74	0.082

Comparison of model without interaction term (a) to model with interaction term (b):

(a) model deviance = 188.36; (b) model deviance = 184.96; ANOVA χ^2_1 = 3.40, p = 0.065

(Table S2 continued below)

	Estimate	SE	Z-value	P-value

Nest success for known-age females

Variance of random effects: Individual identity = 0.44; Year = 0.02

	Estimate	SE	Z-value	P-value
Intercept	2.23	0.60	3.70	<0.001
Area-fed	-1.62	0.71	-2.28	0.023
Period-during	-1.04	0.69	-1.51	0.130
Islay-centred-age	0.10	0.07	1.50	0.133
Area-fed: Period-during	1.82	0.84	2.16	0.031

Comparison of model without interaction term (a) to model with interaction term (b):

(a) model deviance = 239.28; (b) model deviance = 234.40; ANOVA χ^2_1 = 4.89, p = 0.027

Conditional brood size for known-age males

Variance of random effects: Individual identity = 0.00; Year = 0.00

	Estimate	SE	Z-value	P-value
Intercept	0.99	0.12	8.60	<0.001
Area-fed	0.12	0.15	0.76	0.448
Period-during	-0.15	0.18	-0.80	0.425
Islay-centred-age	0.00	0.02	-0.19	0.847
Area-fed: Period-during	0.17	0.22	0.77	0.441

Comparison of model without interaction term (a) to model with interaction term (b):

(a) model deviance = 490.72; (b) model deviance = 490.12; ANOVA χ^2_1 = 0.60, p = 0.440

Conditional brood size for known-age females

Variance of random effects: Individual identity = 0.00; Year = 0.00

	Estimate	SE	Z-value	P-value
Intercept	1.01	0.11	9.49	<0.001
Area-fed	0.09	0.16	0.57	0.570
Period-during	0.06	0.14	0.41	0.680
Islay-centred-age	0.00	0.02	-0.23	0.822
Area-fed: Period-during	-0.09	0.19	-0.48	0.632

Comparison of model without interaction term (a) to model with interaction term (b):

(a) model deviance = 577.92; (b) model deviance = 577.69; ANOVA χ^2_1 = 0.23, p =0.633

(Table S2 continued below)

270

	Estimate	SE	Z-value	P-value
Overall annual breeding success for known-age males				
Variance of random effects: Individual identity = 0.05; Year = 0.01				
Intercept	0.85	0.14	5.99	<0.001
Area-fed	-0.04	0.18	-0.22	0.824
Period-during	-0.45	0.21	-2.13	0.033
Islay-centred-age	-0.004	0.02	-0.24	0.809
Area-fed: Period-during	0.48	0.24	1.95	0.051

Comparison of model without interaction term (a) to model with interaction term (b):

(a) model deviance = 692.23; (b) model deviance = 688.36; ANOVA χ^2_1 = 3.87, p = 0.049

	Estimate	SE	Z-value	P-value
Overall annual breeding success for known-age females				
Variance of random effects: Individual identity = 0.08; Year = 0.003				
Intercept	0.86	0.14	6.07	<0.001
Area-fed	-0.25	0.19	-1.26	0.207
Period-during	-0.15	0.17	-0.87	0.386
Islay-centred-age	0.02	0.02	0.81	0.418
Area-fed: Period-during	0.27	0.23	1.18	0.237

Comparison of model without interaction term (a) to model with interaction term (b):

(a) model deviance = 831.22; (b) model deviance = 829.83; ANOVA χ^2_1 = 1.39, p = 0.238

271

272   <u>Appendix 3. Pair-level reproductive success</u>

273   Previous analyses demonstrated age effects on reproductive success in choughs (Reid,

274   Bignal, Bignal, McCracken, & Monaghan, 2003). It is therefore desirable to fit models that

275   control for age. Reproductive success was therefore necessarily analysed at the level of

276   colour-ringed (i.e. known age) individuals. Since measures of reproductive success are

277   identical for both individuals within a breeding pair, both individuals were not separately

278   included within the same analyses (such replication of observations cannot be accounted for

279   by including random "nest" effects, since there is zero within-level variance). Analyses were

280   consequently split by sex. However, this unavoidably reduced the sample size of breeding

281   events included within each analysis, because models of female reproductive success

282   excluded breeding events where only the male was colour-ringed, and vice versa.

283   However, since chough pairs remain with their mate year-round (i.e. forage and roost

284   together, Bignal, Bignal, & McCracken, 1997), paired females and males had very similar

285   attendance at supplementary feeding. When both paired individuals were colour-ringed they

286   were almost always (97% of occasions; 63 out of 65 pairs) both assigned the same feeding

287   state (i.e. fed or unfed). Consequently, a reasonable assumption is that when only one paired

288   adult was colour-ringed, its unringed mate could typically be assigned to the same state, and

289   hence that pairs could be assigned as "fed" or "unfed" and hence to "area-fed" or "area-

290   unfed". Therefore, to maximise use of data from all occupied territories where at least one

291   adult was colour-ringed, thereby increasing sample size and power compared to sex-specific

292   analyses (Table S3), we fitted further GLMMs to test for area by time-period interactions on

293   measures of reproductive success at the pair-level. Pairs with colour-ringed individuals of

294   unknown sex (n = 13 datapoints of 7 individuals) that were previously excluded from sex-

295   specific analyses could then be included. However, individual age effects could no longer be

296   included in these analyses. Yet, since age effects estimated in the single sex analyses were

297 weak, results of the pair-level analyses are unlikely to be substantially biased by any

298 unmodelled age effects.

299

300 **Table S3: Sample sizes for each measure of reproductive success, for each reproductive**

301 **success dataset (male, female or pair). Reproductive success measure: (1) nest success or**

302 **overall breeding success, (2) conditional brood size. Sample size (n): number of**

303 **datapoints (number of individual adults); mean observations per individual: $\bar{x}$±SD.**

Reproductive success measure	Model	Area-period							
		Fed-before		Fed-during		Unfed-before		Unfed-during	
		n	$\bar{x}$±SD	n	$\bar{x}$±SD	n	$\bar{x}$±SD	n	$\bar{x}$±SD
1	Male	43(18)	2.4±1.3	82(23)	3.6±1.7	33(11)	3.0±1.9	30(13)	2.3±1.9
	Female	41(19)	2.2±2.0	94(23)	4.1±2.3	36(11)	3.3±1.9	55(15)	3.7±1.9
	Pair	73(34)	2.1±1.6	132(42)	3.1±2.0	52(19)	2.7±1.7	78(31)	2.5±1.7
2	Male	30(16)	1.9±1.2	55(18)	3.1±2.0	15(8)	1.9±1.0	16(7)	2.3±2.2
	Female	18(12)	1.5±1.2	44(16)	2.8±2.3	30(9)	3.3±1.8	36(14)	2.6±1.6
	Pair	49(29)	1.7±1.2	101(35)	2.9±2.1	45(17)	2.4±1.6	55(24)	2.3±1.7

304

305 Pair-level models for the three measures of reproductive success showed broadly

306 similar results as the sex-specific models (Table S4). Variation in pair-level nest success was

307 significantly explained by the area by time-period interaction; nest success increased in "area-

308 fed" between time-periods by approximately 0.08, but decreased in "area-unfed" by

309 approximately 0.18 (Fig. S4a; Z=2.8, *p*=0.023), constituting an overall change of 0.26

310 between areas over time-periods. These overall changes are comparable to those found with

311 the reduced datasets using only male (0.27) or female (0.29) data.

312 Variation in pair-level conditional brood size was not significantly explained by the

313 area by time-period interaction (Z=-0.48, *p*=0.63, Table S4). Pair-level conditional brood size

314 remained approximately constant in "area-fed" and "area-unfed" between time-periods (Fig.

315 S4b).

316   Consequently, for pair-level overall breeding success, the area by time-period

317 interaction was not significant ($Z=1.26$, $p=0.21$), as found for the separate female ($Z=1.2$,

318 $p=0.24$), but not male ($Z=2.0$, $p=0.05$) models. Pair-level overall breeding success followed a

319 similar pattern to that found using male or female only data: overall breeding success

320 approximately remained stable over time-periods in "area-fed", but decreased in "area-

321 unfed", resulting in an overall change of approximately 0.45 fledglings (Fig. S4c). This effect

322 size was, however, smaller than that estimated from male (0.91 fledglings) and female (0.57

323 fledglings) models. This difference may partially reflect that pair-level overall breeding

324 success models do not control for age effects.

325
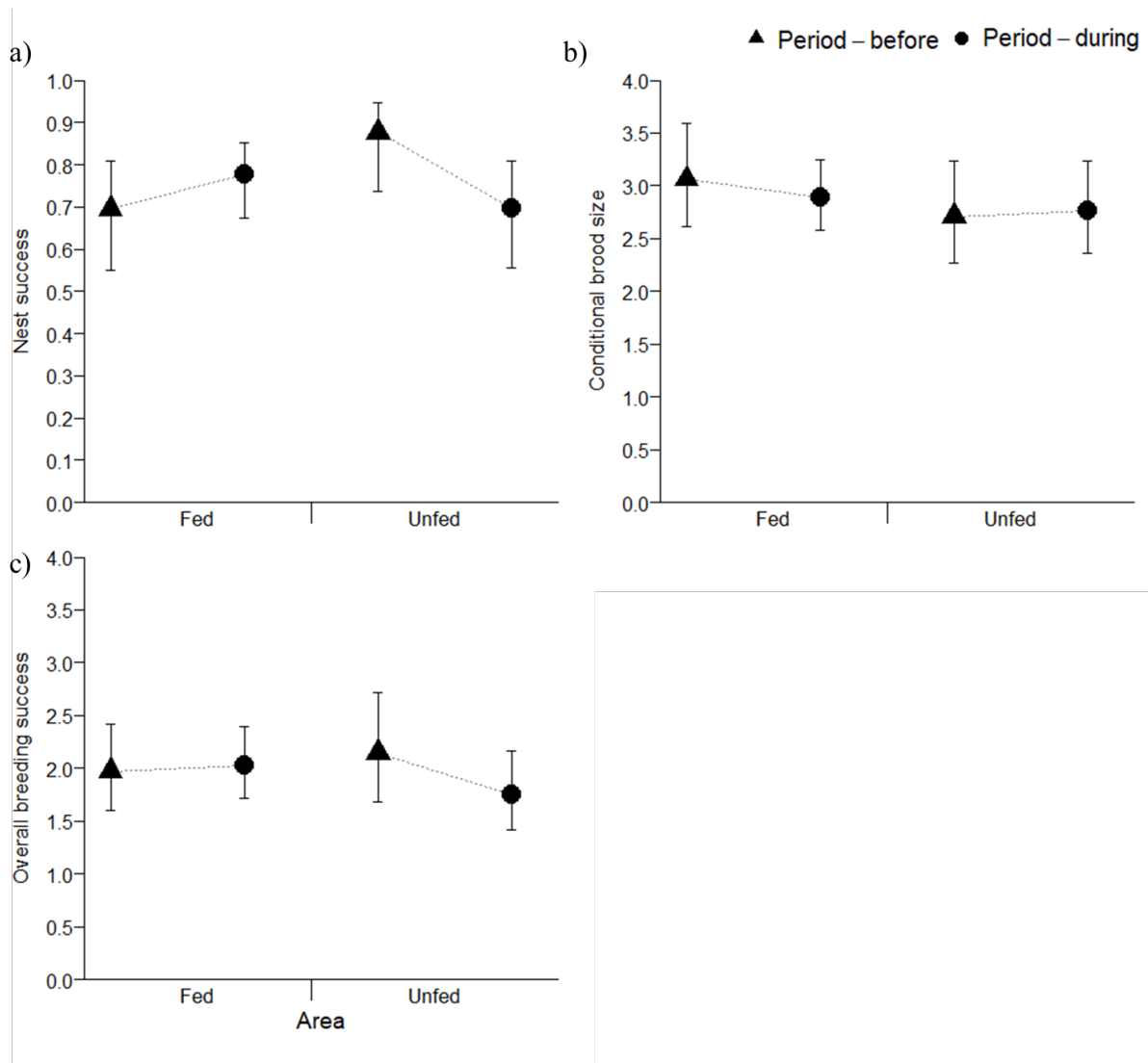
Figure S4: Estimated measures of pair-level reproductive success (with 95% confidence intervals) of adult choughs: (a) nest success, (b) brood size conditional on nest success and (c) overall breeding success. Triangles and circles denote period-before and period-during supplementary feeding respectively, in "area-fed" and "area-unfed". Dotted lines aid visualisation of between-period changes within each area.

Table S4: Estimated coefficients from generalised linear mixed models of the effect of

area and time period on pair-level reproductive success of adult choughs. Estimated

effect sizes (Estimate) and associated standard errors (SE), and test Z-value and

probabilities (p-value) are presented. Model intercepts are set as area-unfed, period-

before. Models controlled for random pair identity and year effects. Area and period

were modelled as fixed effect, categorical variables.

Fixed effects	Estimate	SE	Z-value	P-value
Nest success				
Variance of random effects: Pair identity = 0.67; Year = <0.001				
Intercept	1.96	0.48	4.10	<0.001
Area-fed	-1.14	0.57	-2.00	0.045
Period-during	-1.13	0.55	-2.04	0.041
Area-fed: Period-during	1.55	0.68	2.28	0.023

Comparison of model without interaction term (a) to model with interaction term (b):

(a) model deviance = 371.91; (b) model deviance = 366.47; ANOVA χ^2_1 = 5.44, p = 0.020

Fixed effects	Estimate	SE	Z-value	P-value
Conditional brood size				
Variance of random effects: Pair identity = <0.001; Year = <0.001				
Intercept	1.00	0.09	11.0	<0.001
Area-fed	0.12	0.12	1.00	0.319
Period-during	0.02	0.12	0.16	0.875
Area-fed: Period-during	-0.08	0.16	-0.48	0.628

Comparison of model without interaction term (a) to model with interaction term (b):

(a) model deviance = 830.54; (b) model deviance = 830.31; ANOVA χ^2_1 = 0.23, p = 0.628

Fixed effects	Estimate	SE	Z-value	P-value
Overall annual breeding success				
Variance of random effects: Pair identity = 0.09; Year = 0.01				
Intercept	0.76	0.12	6.25	<0.001
Area-fed	-0.08	0.15	-0.55	0.583
Period-during	-0.20	0.14	-1.40	0.161
Area-fed: Period-during	0.23	0.18	1.26	0.208

Comparison of model without interaction term (a) to model with interaction term (b):

(a) model deviance = 1232.0; (b) model deviance = 1230.5; ANOVA $\chi^2_1 = 1.57$, p = 0.210

Appendix 4. Influence of uncertain feeding and area assignment

341   In general, individuals that were classed as "fed" were observed to attend

342 supplementary feeding on ≥75% of days on which food was provided, and individuals classed

343 as "unfed" attended on ≤25% of days. However, given the lower resighting effort at food-

344 station-2 (Table S1), individuals were generally considered fed if they were seen on over ~

345 half of resighting occasions. In most cases, attendance was substantially higher or lower than

346 these nominal thresholds, meaning that individual assignments were generally clear and

347 unambiguous. However, for a small number of individuals, assignment was not always clear.

348 These points of uncertain feeding and area assignment may have consequences for model

349 results and conclusions. We consequently thoroughly assessed such effects.

350   Some individuals consistently attended the supplementary feeding, but only in a few

351 months, rather than spanning the whole non-breeding season. Meanwhile, some individuals

352 attended throughout the non-breeding season, but more sporadically. These individuals could

353 be best defined as 'partially-fed'. However, there were insufficient cases to define a separate

354 "partially fed" group (total of 48 annual datapoints from 23 individuals; 20 datapoints from

355 11 individuals in "area-unfed", and 28 datapoints from 12 individuals in "area-fed").

356 Consequently, the partially-fed individuals were grouped with fed individuals for the main

357 analyses. However, these different groups of individuals could potentially have different

358 background demographic rates, or respond to supplementary feeding differently.

359   Additionally, for some individuals it was unclear whether they would best be defined

360 as unfed versus partially-fed, or partially-fed versus fed, largely because of lower ring-

361 resighting effort at food-station-2 making definitive classification more difficult. Incorrect

362 assignment of food use may bias results, and so in such cases, a judgement of the most

363 plausible classification of feeding status was made, alongside a "conservative" and "liberal"

364 estimate. In other words, when an individual was assigned as "fed", but there was uncertainty

365 as to whether it should actually have been assigned as "unfed", it was reclassed as "unfed"

366 for "conservative" models, and when an individual was assigned as "unfed", but there was

367 uncertainty as to whether it should actually have been assigned as "fed", it was reclassed as

368 "fed" for "liberal" models.

369   Furthermore, area did not always perfectly align with individual food use and territory

370 area; for 18.8% of datapoints (76 of 405), the food use of an individual did not match the area

371 they were assigned to, based on the location of their breeding territory. Consequently, some

372 individuals that were grouped into "area-unfed" were in fact fed (n = 20 individuals, 40 of

373 405 datapoints), and some individuals that were grouped into "area-fed" were unfed (n = 16

374 individuals, 36 of 405 datapoints). Such individuals are termed here as "area-status-

375 mismatch" individuals. Conclusions drawn based on testing an area by time-period

376 interaction may be misleading if overlap between these groups masks true differences

377 between them. For example, if supplementary feeding does increase adult survival and/or

378 reproductive success, inclusion of unfed individuals in "area-fed" may downwardly bias

379 "area-fed" demographic estimates, and vice versa, inclusion of fed individuals in "area-

380 unfed" may upwardly bias "area-unfed" demographic estimates.

381   Therefore, to ensure that, 1) grouping of fed and partially-fed individuals, 2) uncertain

382 food use grouping and 3) "area-status-mismatch" individuals did not substantially bias

383 results, additional models with the same structure as the models presented in the main text

384 (hereafter referred to as a "standard model") were fitted using a reduced dataset, where a)

385 partially-fed individuals and b) "area-status-mismatch" individuals were excluded from both

386 standard (most plausible), conservative and liberal classifications of individual feeding status.

387 Effect sizes of the area by time-period interaction using reduced and modified datasets were

388 quantitatively very similar to models presented in the main text for both survival (Table S5)

389 and reproductive success (Tables S6, S7 & S8) models. Therefore, these points of uncertainty

390 do not alter the inferences made about the effects of supplementary feeding. If anything, the

391 models presented in the main text in some cases estimated slightly smaller effect sizes and

392 higher p-values.

393

394 **<u>Reduced datasets:</u>**

395 **Partially fed removed:** using standard (i.e. the most plausible) estimates of individual

396 supplementary food use; data from individuals who were neither clearly unfed or fed, and so

397 could be best called partially fed, were excluded.

398 **Partially fed removed, conservative status:** using conservative estimates of individual

399 supplementary food use; data from individuals who were neither clearly unfed or fed, and so

400 could be best called partially fed, were excluded.

401 **Partially fed removed, liberal status:** using liberal estimates of individual supplementary

402 food use; data from individuals who were neither clearly unfed or fed, and so could be best

403 called partially fed, were excluded.

404 **Mismatch removed:** using standard (i.e. the most plausible) estimates of individual

405 supplementary food use; data from fed individuals who held territories in "area-unfed", and

406 unfed individuals who held territories in "area-fed" (i.e. area-status-mismatch), were

407 excluded.

408 **Mismatch removed, conservative status:** using conservative estimates of individual

409 supplementary food use; data from fed individuals who held territories in "area-unfed", and

410 unfed individuals who held territories in "area-fed" (i.e. area-status-mismatch), were

411 excluded.

412 **Mismatch removed, liberal status:** using liberal estimates of individual supplementary food

413 use; data from fed individuals who held territories in "area-unfed", and unfed individuals who

414 held territories in "area-fed" (i.e. area-status-mismatch), were excluded.

415

416 **Table S5: Estimated annual survival probabilities (and 95% confidence intervals) for**

417 **each area-period group, and effect sizes and significance of the area-period interaction,**

418 **from generalised linear mixed models fitted to assess model sensitivity to datapoints of**

419 **uncertainty. The 'standard model' refers to models presented in the main text.**

Model	Area-Period combination (area-period)				Effect size	P-value
	Fed-before	Fed-during	Unfed-before	Unfed-during		
Standard model	0.73 (0.65 -0.80)	0.87 (0.81-0.91)	0.87 (0.79-0.92)	0.84 (0.77-0.89)	0.16	0.014
Partially fed removed	0.73 (0.65-0.80)	0.86 (0.80-0.90)	0.87 (0.79-0.92)	0.83 (0.75-0.89)	0.16	0.018
Partially fed removed; Conservative status	0.73 (0.65-0.80)	0.86 (0.80-0.90)	0.87 (0.79-0.92)	0.85 (0.77-0.91)	0.14	0.049
Partially fed removed; Liberal status	0.73 (0.65-0.80)	0.86 (0.80-0.90)	0.87 (0.79-0.92)	0.82 (0.74-0.88)	0.17	0.012
Mismatch removed	0.73 (0.65-0.80)	0.87 (0.82-0.91)	0.86 (0.79-0.92)	0.85 (0.77-0.91)	0.16	0.034
Mismatch removed; Conservative status	0.73 (0.65-0.80)	0.87 (0.81-0.91)	0.86 (0.79-0.92)	0.85 (0.77-0.91)	0.16	0.032
Mismatch removed; Liberal status	0.73 (0.65-0.80)	0.87 (0.82-0.91)	0.86 (0.79-0.92)	0.85 (0.76-0.91)	0.16	0.028

420

Table S6: Estimated nest success values (and 95% confidence intervals) for each area-period group, and effect sizes and significance of the area-period interaction, from generalised linear mixed models fitted to assess model sensitivity to datapoints of uncertainty. * The female nest success model with area-status-mismatch points removed failed to converge with random year effect included, and so the random year effect was removed.

Model	Area-Period combination (area-period)				Effect size	P-value
	Fed-before	Fed-during	Unfed-before	Unfed-during		
Nest success for known-age males						
Standard model	0.81 (0.61-0.92)	0.82 (0.66-0.90)	0.93 (0.74-0.98)	0.66 (0.39-0.85)	0.27	0.082
Partially fed removed	0.80 (0.61-0.91)	0.80 (0.66-0.89)	0.91 (0.72-0.97)	0.64 (0.38-0.84)	0.27	0.083
Partially fed removed; Conservative status	0.80 (0.61-0.91)	0.86 (0.72-0.94)	0.91 (0.72-0.98)	0.61 (0.34-0.83)	0.36	0.033
Partially fed removed; Liberal status	0.80 (0.61-0.91)	0.80 (0.64-0.90)	0.92 (0.73-0.98)	0.63 (0.35-0.84)	0.29	0.084
Mismatch removed	0.82 (0.61-0.93)	0.84 (0.66-0.93)	0.93 (0.73-0.98)	0.61 (0.29-0.85)	0.35	0.058
Mismatch removed; Conservative status	0.81 (0.61-0.93)	0.81 (0.62-0.92)	0.93 (0.73-0.98)	0.59 (0.29-0.83)	0.34	0.069
Mismatch removed; Liberal status	0.83 (0.61-0.94)	0.83 (0.64-0.92)	0.94 (0.74-0.99)	0.57 (0.24-0.84)	0.36	0.058

(Table S6 continued below)

428

Model	Area-Period combination (area-period)				Effect size	P-value
	Fed-before	Fed-during	Unfed-before	Unfed-during		
Nest success for known-age females						
Standard model	0.65 (0.46-0.80)	0.80 (0.68-0.88)	0.90 (0.74-0.97)	0.77 (0.60-0.88)	0.29	0.031
Partially fed removed	0.65 (0.46-0.80)	0.78 (0.65-0.87)	0.90 (0.74-0.97)	0.75 (0.58-0.86)	0.29	0.034
Partially fed removed; Conservative status	0.65 (0.46-0.81)	0.80 (0.66-0.89)	0.90 (0.74-0.97)	0.74 (0.56-0.87)	0.31	0.029
Partially fed removed; Liberal status	0.65 (0.46-0.81)	0.78 (0.65-0.87)	0.90 (0.74-0.97)	0.74 (0.56-0.86)	0.29	0.035
Mismatch removed	0.66 (0.46-0.81)	0.80 (0.67-0.88)	0.90 (0.74-0.97)	0.72 (0.53-0.86)	0.32	0.024
Mismatch removed; Conservative status	0.66 (0.46-0.82)	0.77 (0.62-0.87)	0.91 (0.74-0.97)	0.74 (0.54-0.87)	0.28	0.046
Mismatch removed; Liberal status	0.66 (0.45-0.82)	0.80 (0.66-0.89)	0.91 (0.74-0.97)	0.71 (0.48-0.87)	0.33	0.024

429

430

431   Table S7: Estimated conditional brood size values (and 95% confidence intervals) for

432   each area-period group, and effect sizes and significance of the area-period interaction,

433   from generalised linear mixed models fitted to assess model sensitivity to datapoints of

434   uncertainty.

Model	Area-Period combination (area-period)				Effect size	P-value
	Fed-before	Fed-during	Unfed-before	Unfed-during		
Conditional brood size for known-age males						
Standard model	3.03 (2.49-3.69)	3.10 (2.70-3.57)	2.70 (2.16-3.38)	2.33 (1.76-3.09)	0.44	0.441
Partially fed removed	3.03 (2.49-3.69)	3.11 (2.67-3.62)	2.71 (2.16-3.39)	2.41 (1.73-3.34)	0.38	0.543
Partially fed removed; Conservative status	3.03 (2.49-3.68)	3.04 (2.61-3.54)	2.71 (2.16-3.39)	2.34 (1.68-3.26)	0.38	0.530
Partially fed removed; Liberal status	3.03 (2.49-3.69)	3.07 (2.64-3.58)	2.71 (2.16-3.40)	2.41 (1.73-3.34)	0.35	0.576
Mismatch removed	3.03 (2.49-3.68)	3.09 (2.65-3.61)	2.71 (2.16-3.39)	2.32 (1.62-3.32)	0.46	0.478
Mismatch removed; Conservative status	3.03 (2.49-3.69)	3.15 (2.68-3.72)	2.71 (2.16-3.39)	2.34 (1.68-3.26)	0.49	0.441
Mismatch removed; Liberal status	3.03 (2.49-3.68)	3.13 (2.69-3.63)	2.71 (2.16-3.39)	2.35 (1.62-3.40)	0.46	0.490

(Table S7 continued below)

435

Model	Area-Period combination (area-period)				Effect size	P-value
	Fed-before	Fed-during	Unfed-before	Unfed-during		
Conditional brood size for known-age females						
Standard model	3.00 (2.40-3.75)	2.90 (2.53-3.32)	2.75 (2.23-3.39)	2.91 (2.44-3.48)	-0.27	0.632
Partially fed removed	3.00 (2.40-3.75)	2.99 (2.58-3.46)	2.74 (2.23-3.38)	2.97 (2.47-3.57)	-0.24	0.677
Partially fed removed; Conservative status	3.00 (2.40-3.75)	2.93 (2.53-3.39)	2.75 (2.23-3.39)	2.96 (2.44-3.59)	-0.28	0.623
Partially fed removed; Liberal status	3.00 (2.40-3.75)	3.00 (2.59-3.48)	2.74 (2.22-3.38)	3.00 (2.47-3.63)	-0.26	0.656
Mismatch removed	3.00 (2.40-3.75)	2.96 (2.56-3.43)	2.75 (2.23-3.38)	2.98 (2.43-3.37)	-0.28	0.637
Mismatch removed; Conservative status	3.00 (2.40-3.74)	3.09 (2.65-3.59)	2.74 (2.23-3.38)	2.95 (2.41-3.62)	-0.12	0.825
Mismatch removed; Liberal status	3.00 (2.40-3.74)	2.95 (2.56-3.40)	2.75 (2.23-3.39)	3.02 (2.43-3.75)	-0.32	0.588

436

437

438

Table S8: Estimated overall breeding success values (and 95% confidence intervals) for

each area-period group, and effect sizes and significance of the area-period interaction,

from generalised linear mixed models fitted to assess model sensitivity to datapoints of

uncertainty.

Model	Area-Period combination (area-period)				Effect size	P-value
	Fed-before	Fed-during	Unfed-before	Unfed-during		
Overall breeding success for known-age males						
Standard model	2.24 (1.76-2.85)	2.31 (1.90-2.80)	2.33 (1.77-3.07)	1.49 (1.07-2.09)	0.91	0.051
Partially fed removed	2.26 (1.79-2.85)	2.33 (1.92-2.83)	2.34 (1.80-3.06)	1.48 (1.03-2.14)	0.93	0.057
Partially fed removed; Conservative status	2.28 (1.82-2.86)	2.49 (2.06-3.02)	2.35 (1.82-3.03)	1.46 (1.01-2.11)	1.10	0.025
Partially fed removed; Liberal status	2.22 (1.74-2.83)	2.22 (1.80-2.74)	2.33 (1.77-3.08)	1.45 (1.00-2.11)	0.88	0.074
Mismatch removed	2.26 (1.79-2.85)	2.33 (1.90-2.84)	2.32 (1.77-3.04)	1.38 (0.92-2.07)	1.01	0.046
Mismatch removed; Conservative status	2.24 (1.73-2.84)	2.28 (1.83-2.83)	2.29 (1.74-3.03)	1.36 (0.92-2.01)	0.97	0.048
Mismatch removed; Liberal status	2.25 (1.77-2.86)	2.29 (1.86-2.81)	2.30 (1.74-3.05)	1.33 (0.87-2.04)	1.01	0.045

(Table S8 continued below)

443

Model	Area-Period combination (area-period)				Effect size	P-value
	Fed-before	Fed-during	Unfed-before	Unfed-during		
Overall breeding success for known-age females						
Standard model	1.84 (1.40-2.42)	2.09 (1.72-2.55)	2.35 (1.78-3.10)	2.03 (1.60-2.59)	0.57	0.237
Partially fed removed	1.84 (1.40-2.42)	2.11 (1.72-2.60)	2.34 (1.78-3.08)	2.01 (1.58-2.57)	0.59	0.223
Partially fed removed; Conservative status	1.84 (1.39-2.43)	2.09 (1.70-2.58)	2.32 (1.76-3.08)	1.97 (1.51-2.57)	0.61	0.216
Partially fed removed; Liberal status	1.84 (1.40-2.42)	2.11 (1.71-2.60)	2.35 (1.79-3.10)	2.01 (1.55-2.60)	0.62	0.214
Mismatch removed	1.86 (1.41-2.44)	2.13 (1.74-2.62)	2.35 (1.78-3.10)	1.95 (1.48-2.58)	0.67	0.178
Mismatch removed; Conservative status	1.85 (1.41-2.44)	2.13 (1.72-2.64)	2.34 (1.77-3.10)	1.96 (1.49-2.58)	0.67	0.186
Mismatch removed; Liberal status	1.85 (1.39-2.45)	2.10 (1.70-2.58)	2.35 (1.77-3.12)	1.92 (1.42-2.60)	0.68	0.182

444

445

446   Appendix 5. Further details of population projection models

447   Matrix projection models, which represent a basic form of population viability

448 analysis, were built to assess how the collateral effects of supplementary feeding on adult

449 survival and reproductive success are likely to impact chough population growth rate and

450 hence viability. Matrix models assumed a pre-breeding census and birth-pulse dynamics, and

451 comprised four stage classes: age one, age two, age three and adult (ages $\geq$ four years),

452 following Reid, Bignal, Bignal, McCracken, & Monaghan, 2004, and Reid et al., 2011 (Fig.

453 S5). The asymptotic population growth rate (λ) was calculated as the dominant eigenvalue of

454 the corresponding projection matrix, using the "lambda" function from the popbio R package

455 (Stubben & Milligan, 2007). One-year-old choughs have never been observed to breed on

456 Islay, and so the probability of breeding aged one was set to zero. Equal sex ratio was

457 assumed, and so fecundity terms were multiplied by 0.5.

458

459 **Figure S5. Four stage-class matrix projection model. Terms are defined in Table S9.**

0	$\frac{1}{2}(c_2 m_2 \phi_1)$	$\frac{1}{2}(c_3 m_3 \phi_1)$	$\frac{1}{2}(c_{ad} m_{ad} \phi_1)$
ϕ_2	0	0	0
0	ϕ_{ad}	0	0
0	0	ϕ_{ad}	ϕ_{ad}

460

461

462 **Table S9. Definitions of matrix projection model terms and specified parameter values.**

Parameter	Definition	Value
Fixed value parameters		
ϕ_1	First-year survival probability (ringing to age one)	0.22
ϕ_2	Second-year survival probability (age one to age two)	0.63
c_2	Probability that a two year-old will breed	0.28
c_3	Probability that a three year-old will breed	0.81
c_{ad}	Probability that an adult will breed	1.00
m_2	Overall breeding success of a two year-old	1.20
m_3	Overall breeding success of a three year-old	1.50
Variable value parameters		
ϕ_{ad}	Adult survival probability	See Table S10
m_{ad}	Overall breeding success of an adult	See Table S10

463

464   For each reproductive success dataset (male, female, or pair-level), one matrix model

465 was built for each of the four BACI groups, using estimated adult survival and overall

466 breeding success values from the respective analyses (Table S10). All other demographic

467 rates (relating to sub-adult survival, probability of breeding and breeding success) were set as

468 constants across all models, using values estimated by Reid et al. (2011) (Table S9). For all

469 matrix models, first-year survival was set as the average first-year survival across period-

470 before, estimated based on a fully time-dependent, three stage (first-year, second-year, adult)

471 Cormack–Jolly–Seber model (as in Reid, Bignal, Bignal, McCracken, & Monaghan, 2003).

472 These matrix models thereby estimate effects of variable adult demography on population

473 growth rate. Mean values of λ and 95% confidence intervals were estimated by resampling

474 (10,000 times) from Gaussian distributions of values corresponding approximately to the

475 mean and 95% confidence intervals estimated from BACI analyses (Table S10), with the

476 mean set as the point estimate for survival or breeding success.

477

478 **Table S10: Mean and variance values used for sampling demographic rate values for**

479 **matrix projection models.**

| Demographic rate	Area	Period	Mean	Variance
Survival	Fed	Before	0.73	0.025
		During	0.87	0.025
	Unfed	Before	0.87	0.025
		During	0.84	0.025
Overall breeding success: male	Fed	Before	2.24	0.24
		During	2.31	0.20
	Unfed	Before	2.33	0.27
		During	1.49	0.20
Overall breeding success: female	Fed	Before	1.84	0.25
		During	2.09	0.20
	Unfed	Before	2.35	0.25
		During	2.03	0.21
Overall breeding success: pair-level	Fed	Before	2.00	0.2
		During	2.02	0.20
	Unfed	Before	2.14	0.22
		During	1.75	0.18

480

481

482 **Table S11. Estimated asymptotic population growth rates (λ) from matrix projection**

483 **models parameterised using estimated adult survival probability and reproductive**

484 **success for each BACI group. Estimated λ are presented for estimates of male, female**

485 **and pair-level breeding success, with 95% confidence intervals shown in brackets.**

Reproductive success dataset	Model (area-period)			
	Fed-Before	**Fed-During**	**Unfed- Before**	**Unfed-During**
Male	**0.87**	**0.99**	**1.00**	**0.94**
	(0.82 - 0.92)	(0.95 - 1.05)	(0.95 - 1.05)	(0.89 – 0.98)
Female	**0.86**	**0.99**	**1.00**	**0.96**
	(0.81 - 0.91)	(0.94 - 1.03)	(0.95 - 1.05)	(0.91 - 1.00)
Pair	**0.86**	**0.99**	**0.99**	**0.95**
	(0.81 - 0.91)	(0.94 - 1.04)	(0.94 - 1.04)	(0.90 - 1.00)

486

487   Matrix projection models using male, female or pair-level reproductive success

488 estimates all gave quantitatively similar results (Table S11, Fig. S6). There was a substantial

489 increase in λ between period-before and period-during in "area-fed" (male 0.13; female 0.13;

490 pair-level 0.13), and but a decrease in "area-unfed" (male 0.07; female 0.04; pair-level 0.04).

491 Consequently, the inferred positive effects of supplementary feeding on adult chough survival

492 and nest success translate into substantial increases in λ, almost stabilising population size

493 irrespective of any positive impact on the target demographic of sub-adult survival. This

494 conclusion remains the same regardless of which dataset is used to estimate effects on

495 reproductive success.

496
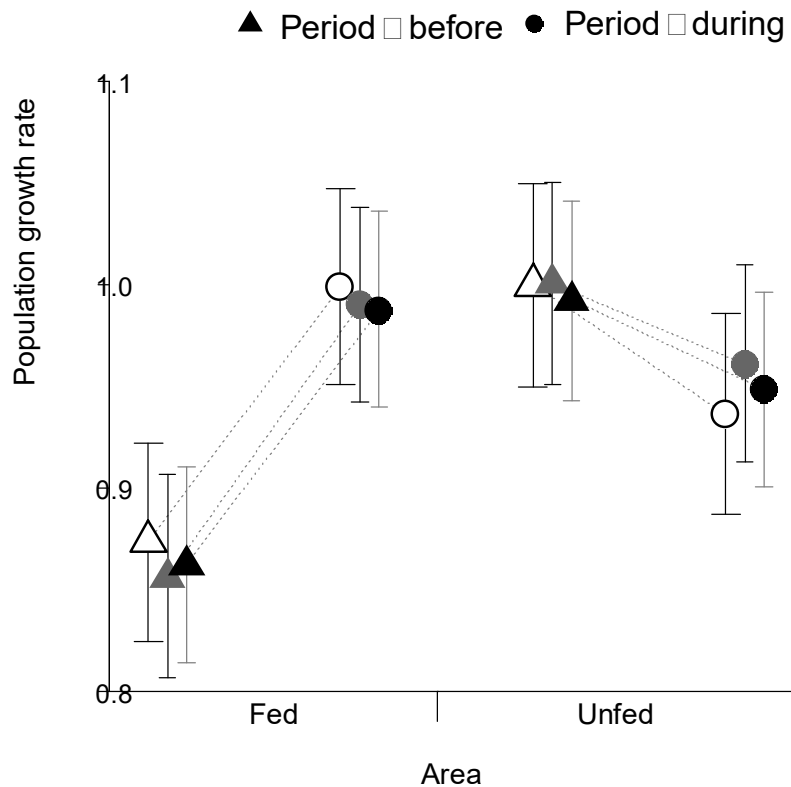
Figure S6: Estimated asymptotic population growth rate (with 95 % confidence intervals) of adult choughs by area and time-period, with reproductive success estimated from colour-ringed males (open symbols), females (filled grey symbols) or pairs (filled black symbols). Triangles and circles denote period-before and period-during supplementary feeding respectively, in "area-fed" and "area-unfed". Dotted lines aid visualisation of between-period changes within each area.

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