**RESEARCH ARTICLE**

# Evaluating the efficacy of independent versus simultaneous management strategies to address ecological and genetic threats to population viability

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## Abstract

1. Small, declining populations can face simultaneous, interacting, ecological and genetic threats to viability. Conservation management strategies designed to tackle such threats independently may then prove ineffective. Population viability analyses that evaluate the efficacy of management strategies implemented independently versus simultaneously are then essential to the design of effective management plans, yet such quantitative evaluations are typically lacking.

2. We used stochastic individual-based models, parameterised with high-quality multi-year demographic and genetic data, to evaluate the efficacy of independent or simultaneous ecological (supplementary feeding) and genetic (translocations to alleviate inbreeding) management strategies for a red-billed chough (*Pyrrhocorax pyrrhocorax*) population of major conservation concern. This population is experiencing ecological threats from food limitation and genetic threats from escalating inbreeding. Conservation managers therefore face a dilemma: supplementary feeding may be ineffective if inbreeding is limiting stochastic population growth rate ($\lambda_s$), while translocations may be ineffective if food is limiting.

3. Model simulations suggested that the focal population will decline to extinction relatively rapidly with no conservation management (mean $\lambda_s \approx 0.86$) and with genetic management alone ($\lambda_s \approx 0.90$). Ecological management alone reduced, but did not halt the population decline ($\lambda_s \approx 0.93$). However, simultaneous genetic and ecological management yielded population stability ($\lambda_s \approx 1$), with genetic rescue lasting ~25 years.

4. These outcomes arose because the capacity for translocations to alleviate inbreeding depression is limited by food availability, while supplementary feeding cannot achieve population viability in the presence of accumulating inbreeding. However, supplementary feeding improved environmental quality enough to allow expression of variance in fitness and thus inbreeding depression, meaning that reductions in inbreeding following translocations can increase $\lambda_s$.

5. *Synthesis and applications.* Our analyses suggest that simultaneous management of ecological and genetic threats will be critical to ensuring viability of Scotland's

chough population; neither strategy independently is likely to achieve population persistence and may consequently waste conservation resources. Managers of other resource-limited, inbred populations should consider that the efficacy of strategies designed to alleviate ecological and genetic threats may be interdependent, such that holistic management is essential to ensure population viability.

# 1 | INTRODUCTION

Small, declining populations can face multiple ecological, genetic and demographic threats that act simultaneously to decrease viability (Fagan & Holmes, 2006; Soulé & Mills, 1998). Conservation managers often focus on tackling such threats independently, yet the efficacy of individual strategies may be interdependent (Ewen, Armstrong, Parker, & Seddon, 2012). Independent management of threats may then fail to ensure population viability, meaning that managers must tackle threats holistically or risk further population decline and wasted conservation resources (Brook, Sodhi, & Bradshaw, 2008). Evaluating the efficacy of multiple management strategies implemented independently versus simultaneously is therefore key to designing management plans that effectively and efficiently achieve long-term population viability.

Ecological threats causing population declines can include predation (Wiles, Bart, Beck, & Aguon, 2003), disease (Preece et al., 2017) and decreased resources (e.g. food limitation, Ford, Ellis, Olesiuk, & Balcomb, 2010). Managers can therefore focus on alleviating these threats, for example, through predator or disease–vector control (Liao, Atkinson, LaPointe, & Samuel, 2017; Russell et al., 2015), habitat management (Eglington et al., 2010) or supplementary feeding (González, Margalida, Sánchez, & Oria, 2006). However once a population becomes small and isolated, demographic stochasticity, and genetic threats from inbreeding and genetic drift can further decrease population viability (Keller & Waller, 2002). In particular, inbreeding can threaten short-term viability by decreasing individual fitness (i.e. inbreeding depression, Charlesworth & Willis, 2009; Keller & Waller, 2002), and is therefore of immediate concern. One potential management response is population reinforcement through translocations of suitable conspecifics (Seddon, 2010). Such translocations can have demographic benefits because increased population size reduces demographic stochasticity and Allee effects (Brown & Kodric-Brown, 1977; Hufbauer et al., 2015), and genetic benefits through reduced inbreeding and increased genetic diversity (Frankham, 2015; Whiteley, Fitzpatrick, Funk, & Tallmon, 2015).

However, translocations may fail to increase population viability if ecological threats are an overriding constraint on stochastic population growth rate ($\lambda_s$) compared to inbreeding depression. This may occur if inbreeding depression is weak or depends on environmental conditions (inbreeding-by-environment interactions, Cheptou & Donohue, 2011). Inbreeding depression is often expected to be greater in harsh environments (Figure 1, Fox & Reed, 2011), although such effects are not always evident in wild populations (Kruuk, Sheldon, & Merilä, 2002; Laws, Townsend, Nakagawa, & Jamieson, 2010; Walling et al., 2011). However, in very harsh environments, the magnitude of inbreeding depression may be constrained by low phenotypic variation in fitness (low "opportunity for inbreeding depression", Crow, 1958; Waller, Dole, & Bersch, 2008). Specifically, inbreeding depression would be negligible in very harsh environments where all individuals perform poorly, and actually increase as environmental quality, and hence the opportunity for variation in fitness, increases (Figure 1). Such weak inbreeding depression in very harsh experimental environments was observed in *Brassica rapa* (Waller et al., 2008) and *Rhinanthus alectorolophus* (Sandner & Matthies, 2017), and may explain inconsistent environmental effects on inbreeding depression in Soay sheep (*Ovis aries*, Pemberton, Ellis,
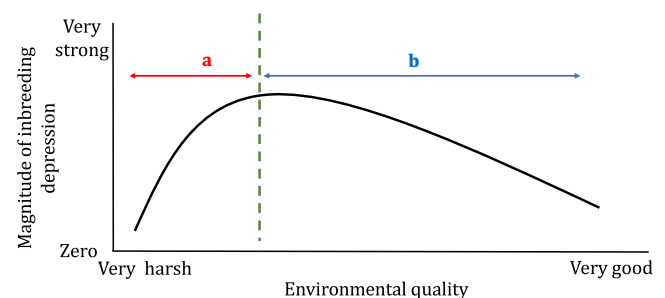


**FIGURE 1** Conceptualised magnitude of inbreeding depression (zero to very strong) expressed in relation to environmental quality (very harsh to very good). (a) For a population experiencing a very harsh environment, the magnitude of inbreeding depression expressed is constrained by low variance in fitness, and will increase as environmental quality increases. (b) Above some environmental quality (dashed green line), the standard expectation that magnitude of inbreeding depression expressed decreases as environmental quality increases applies. The exact shape of the relationship will vary among traits, environments, populations and species

Pilkington, & Bérénos, 2017). Translocations to reduce inbreeding may then provide little improvement in population viability and instead waste conservation resources. Indeed, translocations negligibly increased persistence probability in American martens *(Martes Americana)* experiencing ecological threats (Manlick, Woodford, Gilbert, Eklund, & Pauli, 2017). Similarly, long-term population viability of greater prairie-chickens *(Tympanuchus cupido pinnatus)* may be limited by ecological threats despite apparent short-term efficacy of translocations (Bouzat et al., 2009). For such populations, translocations may only be worthwhile when environmental conditions are good enough that resulting outbred offspring can express relatively higher fitness (Figure 1).

Conversely, management strategies that focus on alleviating ecological threats but disregard genetic threats may also fail to ensure population viability (Ralls et al., 2018). Inbreeding has been associated with increased extinction risk in wild populations (e.g. Glanville fritillary butterfly *Melitaea cinxia*, Saccheri et al., 1998; Shore campion *Silene littorea*, Vilas, San Miguel, Amaro, & Garcia, 2010; and *Clarkia Pulchella*, Newman & Pilson, 1997), and may significantly decrease predicted time to extinction (O'Grady et al., 2006). Furthermore, inbreeding will inevitably increase if populations remain small and isolated (Crow & Kimura, 1970), and thereby increasingly threaten population viability across generations. Rigorous evaluations of the efficacy of ecological and genetic management strategies to ensure population viability should therefore consider the interdependence of these strategies over appropriate time frames. Yet, while the general need to consider joint ecological and genetic management approaches has been noted (e.g. Bouzat et al., 2009; Kenney, Allendorf, McDougal, & Smith, 2014), population viability analyses (PVAs) that quantitatively evaluate the efficacy of independent and simultaneous ecological and genetic management strategies are lacking, particularly in the context of environment-dependent inbreeding depression.

One such population that is facing genetic and ecological threats and is of major conservation concern is the Scottish red-billed chough *(Pyrrhocorax pyrrhocorax*, hereafter "choughs") population. Choughs are Annex 1 listed (EU Birds Directive) placing a legal duty of conservation on national agencies (i.e. Scottish Natural Heritage). Scotland's chough population decreased from ~105 breeding pairs in 1986 (Monaghan, Bignal, Bignal, Easterbee, & McKay, 1989) to ~49 pairs in 2018, with most pairs inhabiting the island of Islay (~87% in 2017). This population has been the subject of individual-based demographic monitoring, comprising colour-ringing, resightings and nest-monitoring, since 1983 (Appendices 1 and 2, Reid et al., 2008; Reid, Bignal, Bignal, McCracken, & Monaghan, 2003b, 2004). The main demographic rate causing population decline is low first-year survival, reflecting low food availability (Reid et al., 2008; Reid, Bignal, Bignal, McCracken, & Monaghan, 2004). Critically low first-year survival during 2007–2009 caused a rapid projected population decline (deterministic growth rate $\lambda \approx 0.87$, Reid et al., 2011), sparking emergency intervention through targeted supplementary feeding during 2010–2018 (Bignal & Bignal, 2011). However, Islay's chough population is isolated from other UK populations (Appendix

1) and has a critically small effective size ($N_e \sim 30$, Trask, Bignal, McCracken, Piertney, & Reid, 2017). Inbreeding is therefore inevitable and will increase relatively rapidly across generations. While the full magnitude of inbreeding depression is unknown, it is likely to be non-trivial, evidenced by phenotypic expression of a lethal recessive allele causing blindness (Trask et al., 2016). Conservation managers therefore face a dilemma of whether to continue investing in managing ecological threats, begin alternative or additional management of genetic threats, or consider ceasing management if all strategies are likely to be ineffective. Quantitative evaluation of these potential strategies to achieve population viability is therefore urgently required.

PVAs for threatened populations are often impeded by lack of data on baseline demography and/or management impacts, greatly increasing uncertainty regarding population outcomes. We use detailed demographic data, including estimated effects of supplementary feeding, and available genetic data, to parameterise PVAs designed to evaluate $\lambda_s$ and population viability given four potential management scenarios for the focal chough population. The four scenarios, formulated in consultation with key stakeholders and conservation managers, are (i) no management (i.e. cease supplementary feeding); (ii) genetic management only (i.e. translocations to reduce inbreeding, with associated short-term increase in population size, but cease supplementary feeding); (iii) ecological management only (i.e. continued supplementary feeding); (iv) simultaneous genetic and ecological management (i.e. translocations and supplementary feeding). We thereby evaluate the efficacy of independent and simultaneous strategies to mitigate ecological and genetic threats, and provide management recommendations.

## 2 | MATERIALS AND METHODS

### 2.1 | Model structure and demography

We used an individual-based population model to evaluate the four proposed management scenarios. Our approach incorporates among-individual variation in inbreeding coefficient alongside demographic and environmental stochasticity and dynamic age-structure, and incorporates uncertainty in the magnitude of inbreeding depression and effects of supplementary feeding.

The model considered an annual pre-breeding census, with first-year, second-year and adult (i.e. third year and older) stage classes. This structure adequately captures observed chough population dynamics (Reid et al., 2004). To capture known spatial variation in habitat and demography across Islay (Reid, Bignal, Bignal, McCracken, & Monaghan, 2006), the model was structured into five subpopulations (A–E, Appendix 1). Subpopulation carrying capacities were set to the maximum number of historically occupied territories in each area, plus the number of associated sub-adults (i.e. fledging to age three) at peak population size in the 1980s (Monaghan et al., 1989, Appendix 4). Additional mortality was applied if subpopulation size exceeded the defined local carrying capacity (Appendix 1). Other forms of density-dependent

restrictions, such as from food-resource limitation, were implicitly captured in model scenarios. This formulation allowed simulations to explore effects of management scenarios, with hard density-dependence only restricting $\lambda_s$ under the best simulated conditions (Appendix 1).

Sub-adult choughs form non-breeding flocks before pairing and acquiring a breeding territory (Reid, Bignal, Bignal, McCracken, & Monaghan, 2003a; Reid et al., 2006). All modelled individuals were assumed to breed annually from age three. Dispersal between subpopulations was therefore modelled to occur at age three, with the subadult flock implicit. Dispersal was modelled from the probability of individual movement from natal subpopulation to another subpopulation within Islay, as estimated from observations of colour-ringed individuals' natal and breeding locations.

We first built and parameterised a baseline model representing scenario (i) no management. To capture an appropriate baseline, this model was parameterised with demographic rates estimated across the pre-supplementary feeding period of 2003–2009 (Appendix 2). Individual annual reproductive success was modelled in two steps: whether a female successfully produced a brood, and realised brood size conditional on success (Lacy, Miller, & Traylor-Holzer, 2017). Reproductive success was estimated for each subpopulation in each year as the proportion of females that produced a brood, and the mean and standard deviation of the number of fledglings in successful broods. Since observed brood sex ratios are equal on average (Trask et al., 2017), simulated offspring were assigned as female or male with equal probability. Stage-specific survival probabilities ($\phi_s$) for first-years ($\phi_1$, fledging to age one year), second-years ($\phi_2$, age one to age two) and adults ($\phi_{Ad}$), and hence mortality rates, for each subpopulation were estimated from colour-ring resighting data (Appendices 1 and 2). $\phi_s$ values were estimated for both sexes together because sexes of sub-adult individuals that died before breeding were typically unknown, and previous analyses indicate no sex-specific differences in $\phi_{Ad}$ (Reid, Bignal, Bignal, McCracken, & Monaghan, 2003b; Reid et al., 2004). Among-year environmental variation in $\phi_s$ was estimated excluding sampling variance (Appendix 2). Since $\phi_1$ is tightly correlated with cyclic population dynamics of the chough's tipulid prey (Reid et al., 2008), simulated environmental variation in $\phi_1$ was partitioned so that half followed cyclic variation and half was stochastic, and was correlated across subpopulations (Appendix 2). As environmental variation in reproductive success is relatively small (Reid et al., 2004), it was sufficiently captured through the high simulated variance in $\phi_1$. Mortality of simulated individuals was realised at each annual time-step based on $\phi_s$ for each age class in each subpopulation.

## 2.2 | Inbreeding and inbreeding depression

To ensure the initial simulated population's mean inbreeding coefficient ($F_p$) and coefficient of kinship ($K$) reflected the Islay chough population's, we estimated $F_p$ and pairwise relatedness ($r$, where $r = 2K$) between individuals from microsatellite genotype data from adult choughs sampled across Islay in 2013–2014, using the Dyadic likelihood estimator (Milligan, 2003) in program Coancestry v1.0.1.8 (Wang, 2011, Appendix 3). These analyses yielded estimates of $F_p = 0.08 \pm .02SE$ and $r = 0.15 \pm .01SE$. To account for likely underestimation of $F_p$ and $r$ due to microsatellite ascertainment bias, as well as expected increases between sampling and implementation of any translocations given the small $N_e$ (Trask et al., 2017), we set founder individuals' coefficients of inbreeding ($F_i$) to 0.1 and founder $K$ to 0.1 (Appendix 3). In practice, simulations were relatively insensitive, and key conclusions remained unchanged, given starting $F_i$ and $K$ between 0.05 and 0.15 (Appendix 3). $F_i$ values in subsequent generations were calculated from the simulated pedigree using standard algorithms (Lacy et al., 2017).

Inbreeding depression expressed given $F_i$ was modelled as the number of diploid lethal equivalents ($2B$, where $B$ is the slope of a regression of log(fitness) on $F_i$, Charlesworth & Willis, 2009; Keller & Waller, 2002). $B$ can be estimated from breeding experiments (Darwin, 1876), genomic analyses (Remington & O'Malley, 2000) or pedigree analyses (Keller & Waller, 2002). However, as complete pedigree and genomic data are unavailable for the focal population and breeding experiments are not feasible, we modelled a range comprising $2B = 3$–$15$. The lower and upper limits reflect the mean estimated across captive populations and the sum of published mean estimates of inbreeding load across life-history stages, respectively (Appendix 3). Model replicates drew values from this range using Latin Hypercube Sampling to optimally sample parameter space (Lacy et al., 2017). Inbreeding depression was modelled entirely through a reduction in $\phi_1$ (Appendix 4); $\phi_1$ is the main demographic constraint on $\lambda_s$ in choughs (Reid et al., 2011, 2004) and the reduction in overall lifetime reproductive success is likely to be reasonably well captured whether total inbreeding load is applied entirely to $\phi_1$ or split over life-history stages (Lacy et al., 2017). Overall, this formulation ensured that initial simulated individuals could immediately experience inbreeding depression, and that genetic rescue could potentially restore the putative outbred $\phi_1$ as opposed to only the currently observed $\phi_1$ (Appendix 4).

## 2.3 | Modelled genetic and ecological management scenarios

Genetic management (scenario ii) was modelled as translocations of unrelated (i.e. $K = 0$) and outbred (i.e. $F_i = 0$) age one individuals into the focal population. Translocated individuals were therefore envisaged to originate from a suitable external source population (Appendix 5). Scenarios were designed to evaluate the potential for successful genetic rescue to achieve population viability. We initially considered one translocation of 24 individuals (12 females, 12 males) in year 3 introduced across subpopulations A–C, or two such translocations in years 3 and 6 (i.e. a total of 48 individuals, Appendix 5). These moderate-sized translocations comprised enough individuals to ensure that some would survive to breed, while avoiding "genetic swamping" of the existing population

(Appendix 5). We also considered an additional scenario of two large translocations of 48 individuals (24 females, 24 males in each translocation) in years 3 and 6, designed to ensure that more translocated individuals would survive to breed (Appendix 5). Translocated individuals took the same baseline demographic rates as existing natives and mated randomly, generating outbreeding and potentially relatively high survival in offspring of immigrant-native pairs.

Ecological management (scenario iii) was modelled by adding estimated effects of supplementary feeding on $\phi_1$, $\phi_2$ and $\phi_{Ad}$ and the probability of producing a brood onto the baseline probabilities for individuals inhabiting subpopulations A–C (Appendices 1 and 4). As supplementary feeding on Islay was implemented as an emergency conservation intervention, there is no formal randomised, replicated case–control experiment to rigorously quantify effects on key demographic rates. However, comparisons between colour-ringed individuals that were and were not observed to attend supplementary feeding (hereafter "fed" and "unfed") can provide broad estimates. Effects on $\phi_{Ad}$ and reproductive success were estimated using before-after control-impact (BACI) analyses that compared individuals inhabiting areas with and without supplementary feeding with individuals inhabiting these areas before supplementary feeding commenced (Fenn et al. unpublished data, Appendix 6). Effects on $\phi_1$ were directly estimated from the proportions of fed and unfed colour-ringed fledglings that survived to age one year (Appendix 6). Since almost all unfed fledglings died before age one and individual utilisation of supplementary food was highly consistent across ages, this approach could not be used to evaluate effects on $\phi_2$. Effects were therefore estimated by comparing mean population-wide values of $\phi_2$ between feeding and pre-feeding periods (Appendix 6). For current purposes, we assumed no effect of supplementary feeding on age at first breeding or dispersal.

To incorporate uncertainty in modelled effects of supplementary feeding, each model iteration drew values from the range of 10%–100% of estimated effect sizes using Latin Hypercube Sampling (Lacy et al., 2017). This conservative range was chosen because supplementary feeding was not carried out as a controlled experiment, meaning that differences between fed and unfed individuals might partly reflect differences in local habitat quality.

We modelled simultaneous ecological and genetic management (scenario iv) by parameterising the model with the same estimated effects of supplementary feeding plus each of the same three translocation scenarios as for the independent ecological and genetic management scenarios above.

## 2.4 | Model implementation and analysis

The model was built in program VORTEX v10.2.17.0 (Lacy & Pollak, 2017). Initial subpopulation sizes were estimated from the number of breeding pairs in each area, plus the number of individuals fledged from each area that survived to age one or two in 2017 (i.e. subadults), with an initial stable age distribution calculated given the specified baseline demographic rates (Appendix 4).

For species like choughs with moderately long mean generation times (~6.7 years, Trask et al., 2017), the most appropriate time-frame for PVAs represents a trade-off between including sufficient generations to incorporate demographic and genetic processes affecting viability (Armbruster, Fernando, & Lande, 1999), and avoiding error and unreliable predictions due to unknown future environmental conditions (Beissinger & Westphal, 1998; Crone et al., 2013). Since we were interested in effects of inbreeding that may impact population viability over relatively short time-frames (Keller & Waller, 2002) we defined a 50 year time-frame, thereby encompassing ~7.5 chough generations, and allowing examination of how long genetic rescue effects last before inbreeding re-accumulates.

Each model was replicated 5,000 times. To compare the focal management scenarios, for each replicate we extracted population size in year 50, time to functional extinction (defined as a single sex remaining) and $\lambda_s$ calculated as the mean of the growth rate across extant years. Means and 95% confidence intervals (95%CIs) for these metrics were calculated across replicates, using R v3.2.2 (R Development Core Team, 2017). The extinction probability ($P_E$) was calculated as the proportion of replicate populations that went extinct within 50 years.

# 3 | RESULTS

## 3.1 | No management

The baseline model, representing the "no management" scenario, suggests that Islay's chough population would decline to extinction relatively rapidly following cessation of supplementary feeding; all replicates went extinct within the projected 50 years (Figure 3a). This outcome was effectively independent of the magnitude of inbreeding depression; the rank correlation between $\lambda_s$ and 2B across replicates was very small (−0.03).

## 3.2 | Genetic management

Models that considered proposed genetic management scenarios (i.e. translocations), but no ecological management, suggest that Islay's chough population would still decline to extinction within the projected 50-year time-frame under proposed genetic management scenarios (Figure 3b). With up to two translocations of 24 individuals, and even with 48 individuals, $\bar{\lambda}_s \leq 0.92$, $P_E \geq 0.94$, and mean time to extinction was 27–35 years. Genetic management alone is therefore unlikely to achieve population viability.

## 3.3 | Ecological management

Supplementary feeding was estimated to have positive effects on $\phi_1$, $\phi_2$, $\phi_{Ad}$ and breeding success (Figure 2, Appendix 6). Models that included these effects, representing current ecological management without genetic management, showed slower population decline (Figure 3c): ~37% of replicate populations
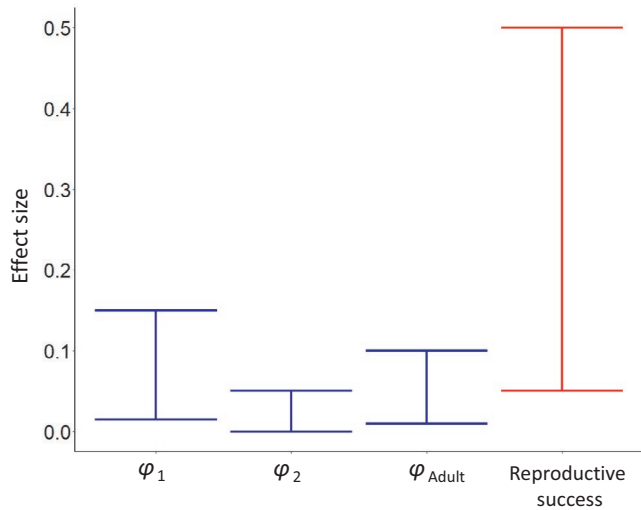
**FIGURE 2** Range of effects of supplementary feeding added on to first-year ($\phi_1$), second-year ($\phi_2$) and adult ($\phi_{Adult}$) survival probabilities (blue bars) and probability of producing a brood (red bar) considered in models of ecological management

were still extant in year 50, when mean population size was 18 (95%CI: 0–175). The large 95%CI demonstrates considerable uncertainty around the quantitative outcome (Figure 3c). However,

the overall qualitative difference from the "no management" and "genetic management" scenarios is reasonably clear; current ecological management has a positive effect in slowing the likely rate of population decline, but may not result in $\lambda_s \geq 1$ or hence population viability (Figure 3).

To provide some validation of this assessment, the observed change in the Islay chough population size through the supplementary feeding period (2010–2017) falls within the 95%CI of the projected population sizes (Figure 3c, Appendix S8), implying that projections are reasonable.

## 3.4 | Simultaneous genetic and ecological management scenario

Models that included simultaneous ecological and genetic management with one translocation of 24 individuals predicted higher $\overline{\lambda}_s$ than for current ecological management alone, but still predicted population decline (Figure 3d, Appendix 7). With two translocations each of 24 individuals, population size was initially stable on average ($\overline{\lambda}_s$=1.00, 95%CI: 0.89–1.08 across years 8–25, Figure 3d). However, there was a tendency for renewed decrease from year 25, reflecting reaccumulation of inbreeding ($\overline{\lambda}_s$ = 0.97, 95%CI: .82–1.06 across years 26–50, Figure 3d, Appendix 3). With two larger
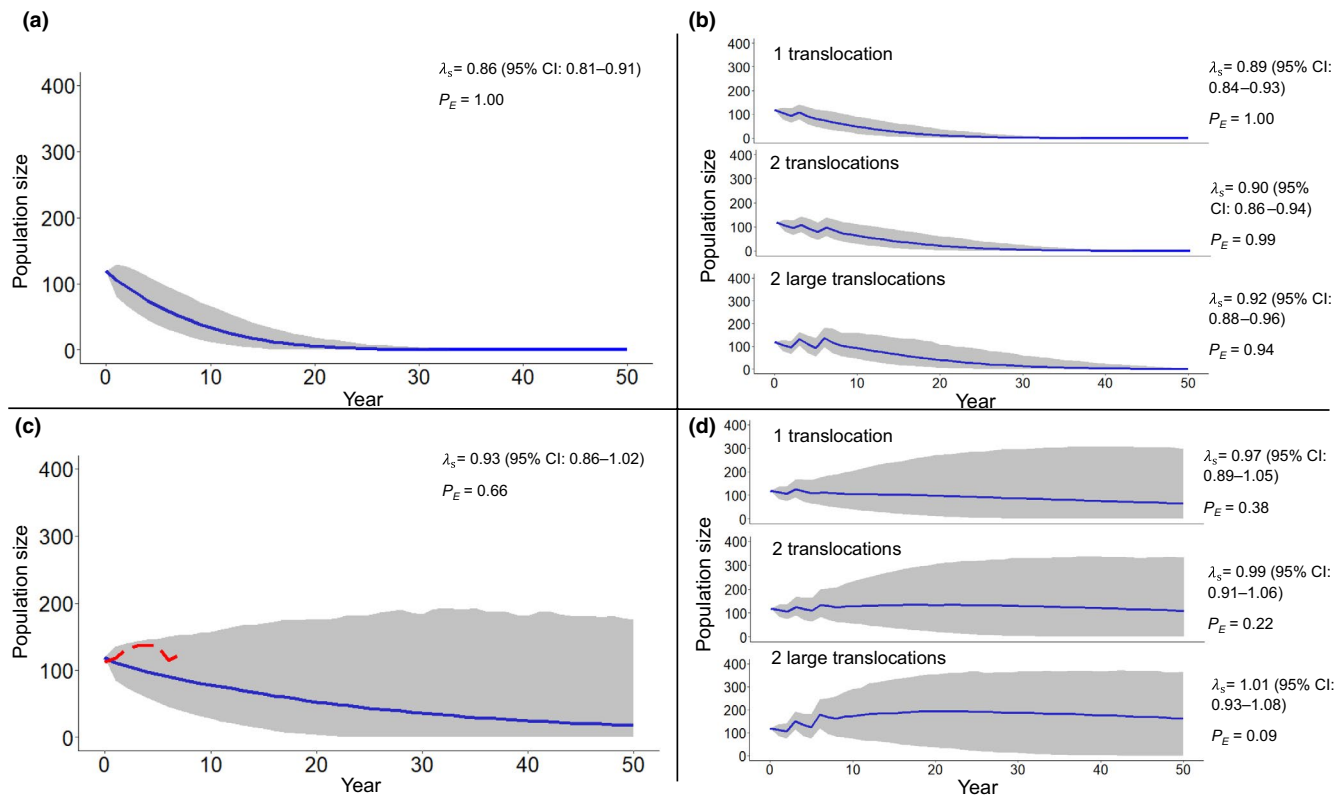


**FIGURE 3** Size of Islay's chough population projected 50 years into the future (2017–2067) with (a) no management, (b) genetic management only consisting of one or two translocations of 24 individuals each, or two large translocations of 48 individuals each, (c) ecological management only, and (d) simultaneous ecological and genetic management comprising the same three translocation scenarios. Mean population size (solid blue lines) with 95% CI (grey shaded area), mean stochastic population growth rate ($\overline{\lambda}_s$) with 95% CI and extinction probability within 50 years ($P_E$) are shown. For (c), the estimated size of the real chough population after the start of supplementary feeding (red dashed line) is also shown

translocations each of 48 individuals, population size was stable on average over the full 50-year time-frame (Figure 3d). Again, there was substantial uncertainty in quantitative outcomes. However, the overall qualitative pattern compared to other modelled scenarios was again reasonably clear: simultaneous ecological and genetic management was the only scenario that yielded likely population viability.

# 4 | DISCUSSION

Effective conservation of populations experiencing interacting ecological and genetic threats requires explicit evaluation of the efficacy of different potential management strategies. We used unusually detailed demographic data from the Scottish chough population, which is of major conservation concern, to evaluate the efficacy of independent and simultaneous management strategies designed to alleviate the known ecological threat of food limitation, and the emerging genetic threat of accumulating inbreeding due to small $N_e$. We show that capacity to alleviate inbreeding depression through translocations is limited by ecological constraints attributable to food availability, while current supplementary feeding designed to alleviate these constraints may on its own be insufficient to ensure population viability in the presence of accumulating inbreeding. The only strategy that appears capable of achieving population viability is to ameliorate both inbreeding and food limitation through translocations alongside supplementary feeding. Our results therefore suggest that managers aiming to maintain the focal population must tackle ecological and genetic threats holistically, or risk failing to achieve management objectives and wasting conservation resources.

Our PVA suggests that, with no management, the Scottish chough population is likely to go extinct relatively rapidly regardless of the magnitude of inbreeding depression (Figure 3a). Rapid population decline was also projected with genetic management alone (Figure 3b). This concurs with the concept that inbreeding depression, and hence the potential for genetic rescue, will be minimal in very harsh environments where all individuals have low fitness (Figure 1, Waller et al., 2008). Here, outbred offspring of matings between translocated and native individuals still experience high mortality because resources are simply insufficient to survive. Indeed, an immigrant into the Isle Royale wolf (*Canis lupus*) population had negligible impact on $\lambda$ despite increased heterozygosity, attributed to poor environmental conditions (Adams, Vucetich, Hedrick, Peterson, & Vucetich, 2011). Alternatively, genetic rescue may be negligible because most translocated individuals die before reproducing due to high environmentally-induced mortality, and hence generate negligible outbreeding. For example, Eurasian otter (*Lutra lutra*) translocations in Sweden resulted in little evidence of genetic rescue, probably due to low survival of translocated individuals (Arrendal, Walker, Sundqvist, Hellborg, & Vilà, 2004). However, even our simulated large translocations, that ensured some translocated individuals survived

to reproduce, resulted in little increase in $\lambda_s$ (Figure 3b). This implies that genetic rescue may be negligible in choughs because of high offspring mortality regardless of $F_i$, rather than because high mortality of translocated individuals would impede outbreeding. Thus, our simulations highlight the critical need to ensure adequate habitat quality, or alleviate other ecological constraints, before attempting translocations to alleviate inbreeding depression.

While available data suggest that current supplementary feeding of Scottish choughs is having valuable positive demographic effects (Figure 2, Appendix 6), our PVA suggests that this intervention alone may be insufficient to ensure population viability (Figure 3c). Continuing current supplementary feeding without mitigating genetic threats may ultimately fail to achieve conservation objectives. The only simulated management scenario that achieved population viability was simultaneous supplementary feeding and translocations. Here, supplementary feeding improved environmental quality enough to allow expression of inbreeding depression, meaning that the reduction in inbreeding resulting from translocations could increase $\lambda_s$ (Figures 1 and 3). Ideally, improvements in environmental quality would be achieved through agri-environment schemes that increase the abundance and availability of the chough's invertebrate prey, for example through maintaining spatio-temporal diversity in vegetation height and managing anti-helminthic treatment of livestock to increase dung invertebrates (Trask et al., 2019a). Resultant increases in chough prey would need to be sufficient to achieve increases in key demographic rates comparable to current supplementary feeding. Indeed, our simulations assume that baseline environmental quality, and hence key demographic rates, do not deteriorate further. Translocated individuals were also assumed to experience the same demographic rates as existing natives. However, translocated individuals may have lower demographic rates than natives, as observed in captive-bred individuals (e.g. VanderWerf, Crampton, Diegmann, Atkinson, & Leonard, 2014), and thus may have less impact on $\lambda_s$. Ensuring viability of the Scottish chough population will therefore require ecological management that is sufficient to maintain or improve environmental quality and thus achieve high demographic rates of both native and translocated individuals, alongside translocations from a suitable source population. While concurrent ecological and genetic management strategies have been suggested for other threatened populations, including greater prairie chickens (Bouzat et al., 2009) and tigers (*Panthera tigris*, Kenney et al., 2014), our analyses quantitatively demonstrate the need for such holistic approaches.

The scenario of two moderate-sized translocations and supplementary feeding resulted in stable $\overline{\lambda}_s$ for ~25 years (~3 chough generations), due to the joint genetic and demographic benefits of translocations alongside supplementary feeding (Appendix 7). However, $\overline{\lambda}_s$ subsequently decreased due to re-accumulating inbreeding (Figure 3d, Appendix 3). Additional simulations showed that this can be resolved with a third translocation at year 25 or larger initial translocations, thereby ensuring population stability over the full 50-year period (Figure 3d, Appendix 7). A similar

pattern of decrease in inbreeding and increase in $\lambda$, followed by re-accumulation of inbreeding, was observed after immigration into a Scandinavian wolf population (Liberg et al., 2005); subsequent immigration then caused another decrease in inbreeding and increased $\lambda$ (Akesson et al., 2016). This implies that longer-term viability of the Scottish chough population would require periodic future translocations, or re-establishment of population connectivity and dispersal that facilitates natural gene-flow.

Quantitative evaluations of proposed management approaches may be impeded by the inherent stochasticity of small, declining populations (Beissinger & Westphal, 1998). Additionally, key demographic and genetic parameters are commonly unknown; effects cannot be directly estimated for strategies that have not yet been implemented, and current strategies are often implemented as emergency interventions rather than controlled experiments (e.g. Oro, Margalida, Carrete, Heredia, & Donázar, 2008; Powlesland & Lloyd, 1994, Appendix 6). Our study is valuable because the high-quality demographic data available allows such quantitative evaluations of ecological and genetic management strategies, including consideration of their interdependence. Despite inevitable uncertainty in our model outcomes, the overall qualitative conclusions from scenario comparisons seem reasonably clear; conditional on model assumptions, simultaneous ecological and genetic management is the only scenario that is likely to result in a viable Scottish chough population. Management actions should therefore focus on implementing appropriate grassland management, complemented with translocations, with continued supplementary feeding until grassland management has sufficiently improved environmental quality. Decision makers must now urgently consider this biological conclusion within a wider socio-economic framework to assess the feasibility of these management strategies (Trask et al., 2019a).

## AUTHORS' CONTRIBUTIONS

All authors contributed to conceptual development, with A.E.T. and J.M.R. devising the models. A.E.T. and S.R.F. undertook demographic analyses. A.E.T. undertook the PVA and molecular genetic analyses. All authors contributed to data collection. A.E.T. wrote the manuscript, assisted by J.M.R. and with input and final approval for publication from all authors.

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