Received: 1 February 2019 | Accepted: 31 August 2019

DOI: 10.1111/1365-2664.13516

RESEARCH ARTICLE

Journal of Applied Ecology BRITISH ECOLOGICAL SOCIETY

Seeking compromise across competing goals in conservation translocations: The case of the 'extinct' Floreana Island Galapagos giant tortoise

Elizabeth A. Hunter[1] | James P. Gibbs[2] | Linda J. Cayot[3] | Washington Tapia[3] | Maud C. Quinzin[4] | Joshua M. Miller[4] | Adalgisa Caccone[4] | Kevin T. Shoemaker[5]

[1]Department of Biology, Georgia Southern University, Statesboro, GA, USA

[2]Department of Environmental and Forest Biology, State University of New York College of Environmental Science and Forestry, Syracuse, NY, USA

[3]Galapagos Conservancy, Fairfax, VA, USA

[4]Department of Ecology and Evolutionary Biology, Yale University, New Haven, CT, USA

[5]Department of Natural Resources and Environmental Science, University of Nevada, Reno, NV, USA

Correspondence
Elizabeth A. Hunter
Email: elizabethhunter@georgiasouthern.edu

Funding information
Galapagos Conservancy; Division of Environmental Biology, Grant/Award Number: 1258062; Mohamed bin Zayed Species Conservation Fund; National Geographic Society; Oak Foundation; Belgian American Educational Foundation; Yale Institute for Biospheric Studies

Handling Editor: Jonathan Rhodes

Abstract

1. Conservation translocation projects must carefully balance multiple, potentially competing objectives (e.g. population viability, retention of genetic diversity, delivery of key ecological services) against conflicting stakeholder values and severe time and cost constraints. Advanced decision support tools would facilitate identifying practical solutions.
2. We examined how to achieve compromise across competing objectives in conservation translocations via an examination of giant tortoises in the Galapagos Islands with ancestry from the extinct Floreana Island species (*Chelonoidis niger*). Efforts have begun to populate Floreana Island with tortoises genetically similar to its historical inhabitants while balancing three potentially competing objectives – restoring ecosystem services (sustaining a high tortoise population size), maximizing genome representation of the extinct *C. niger* species and maintaining a genetically diverse population – under realistic cost constraints.
3. We developed a novel approach to this conservation decision problem by coupling an individual-based simulation model with generalized additive models and global optimization. We identified several incompatibilities among programme objectives, with quasi-optimal single-objective solutions (sets of management actions) differing substantially in programme duration, translocation age, incubation temperature (determinant of sex ratio) and the number of individuals directly translocated from the source population.
4. Quasi-optimal single-objective solutions were able to produce outcomes (i.e. population size and measures of genetic diversity and *C. niger* genome representation) to within 75% of their highest simulated outcomes (e.g. highest population size achieved across all simulations) within a cost constraint of *c.* $2m USD, but these solutions resulted in severe declines (up to 74% reduction) in outcomes for non-focal objectives. However, when all programme objectives were equally weighted to produce a multi-objective solution, all objectives were met to within 90% of the highest achievable mean values across all cost constraints.
5. *Synthesis and applications*. Multi-objective conservation translocations are likely to encounter complex trade-offs and conflicts among programme objectives. Here,

we developed a novel combination of modelling approaches to identify optimal management strategies. We found that solutions that simultaneously addressed multiple, competing objectives performed better than single-objective solutions. Our model-based decision support tool demonstrates that timely, cost-effective solutions can be identified in cases where management objectives appear to be incompatible.

KEYWORDS
conservation decision-making, cost constraints, ecosystem restoration, extinct species, Galapagos, giant tortoise, multi-objective optimization, reintroduction

1 | INTRODUCTION

Conservation translocations are motivated by diverse goals, from population restoration (i.e. reinforcement and reintroduction) to climate-change mitigation (e.g. assisted colonization) and ecological replacement (IUCN/SSC, 2013; Seddon, Griffiths, Soorae, & Armstrong, 2014). In general, conservation translocations aim to improve the status of an at-risk species ('species-focused') and/or restore lost or diminished ecosystem functions ('ecosystem-focused'; IUCN/SSC, 2013; Seddon et al., 2014). For example, the reintroduction of California condors (*Gymnogyps californicus*) to former parts of the species' range is a typical example of a species-focused translocation (Walters et al., 2010), with minimal emphasis on restoring ecosystem functions. Conversely, the use of Aldabra giant tortoises (*Aldabrachelys gigantea*) as ecological replacements for extinct tortoises in the Seychelles archipelago is an example of an ecosystem-focused translocation (Hansen, Donlan, Griffiths, & Campbell, 2010). As species extinction rates accelerate (Ceballos et al., 2015) and the loss of ecologically important species continues to degrade ecosystems (Hansen et al., 2010; Seddon et al., 2014), conservation translocation programmes will increasingly be faced with competing goals at both the species and ecosystem levels.

Although programme objectives (measurable targets that indicate progress towards goals, following terminology conventions of IUCN/SSC, 2013) depend in part on specific project goal(s) and focal systems, nearly all conservation translocation programmes have some common objectives: fostering rapid population growth, maximizing genetic diversity and maintaining species integrity. Timely population growth reduces the risk of population collapse (Seddon, 1999) and ensures that the species can perform its characteristic ecological functions (Hansen et al., 2010). Maintenance of high genetic diversity confers long-term resilience to environmental change, and is especially vital for captive breeding programmes with small founder populations that are vulnerable to inbreeding depression and loss of favourable genetic diversity (Armstrong & Seddon, 2008; Milinkovitch et al., 2004; Seddon et al., 2014). Finally, maintenance of species integrity can be compromised by hybridization with closely related species, and conservation translocation programmes often strive to reduce unwanted hybridization. For example, reintroduced red wolves (*Canis rufus*) have hybridized with coyotes (*Canis latrans*) in the Southeastern United States, threatening to undermine this high-profile reintroduction programme (Murray, Bastille-Rousseau, Adams, & Waits, 2015). Similar issues plague recovery efforts for the Scottish wildcat (*Felis silvestris silvestris*), which hybridizes with feral domestic cats (Fredriksen, 2016).

Trade-offs among programme objectives can present additional complications (Converse, Moore, Folk, & Runge, 2013; Martin, Runge, Nichols, Lubow, & Kendall, 2009). With multiple potentially competing programme objectives, fulfilling all objectives can be challenging – especially under existing budgetary constraints. Multi-objective decision support tools could help to identify practical, cost-efficient solutions for these complex conservation problems (Beger et al., 2015; Cohen et al., 2016).

Here, we use a model-based decision support tool (combining individual-based simulation models with generalized additive models and global optimization routines) to identify quasi-optimal translocation strategies that balance multiple competing programme objectives for the restoration of Galapagos giant tortoises to Floreana Island. Over the last two centuries, overexploitation has led to the extinction of three out of 15 species of Galapagos giant tortoises (Marquez et al., 2004; Rhodin et al., 2017), including the Floreana Island giant tortoise (*Chelonoidis niger*, previously referred to as *C. elephantopus*; Rhodin et al., 2017), which was overharvested to extinction by the mid-1800s. Recently, hybrid tortoises with high levels of *C. niger* ancestry were discovered elsewhere in Galapagos (on Wolf Volcano of northern Isabela Island where *C. niger* were likely released by mariners in the 1800s; Miller et al., 2017). *C. niger* and the native *Chelonoidis becki* tortoises have since produced genetically admixed individuals over a period of very few (~4–6) generations (Garrick et al., 2012; Miller et al., 2017; Poulakakis et al., 2008; Quinzin et al., 2019; Figure 1).

This discovery created the opportunity to repopulate Floreana Island with tortoises genetically similar to the historical inhabitants of the island (and possibly possessing adaptations to the local environment) – while simultaneously restoring the ecological role of this extinct ecosystem engineer (Miller et al., 2017). With a captive breeding programme already underway, decisions about how to proceed with subsequent translocations must be made soon, and

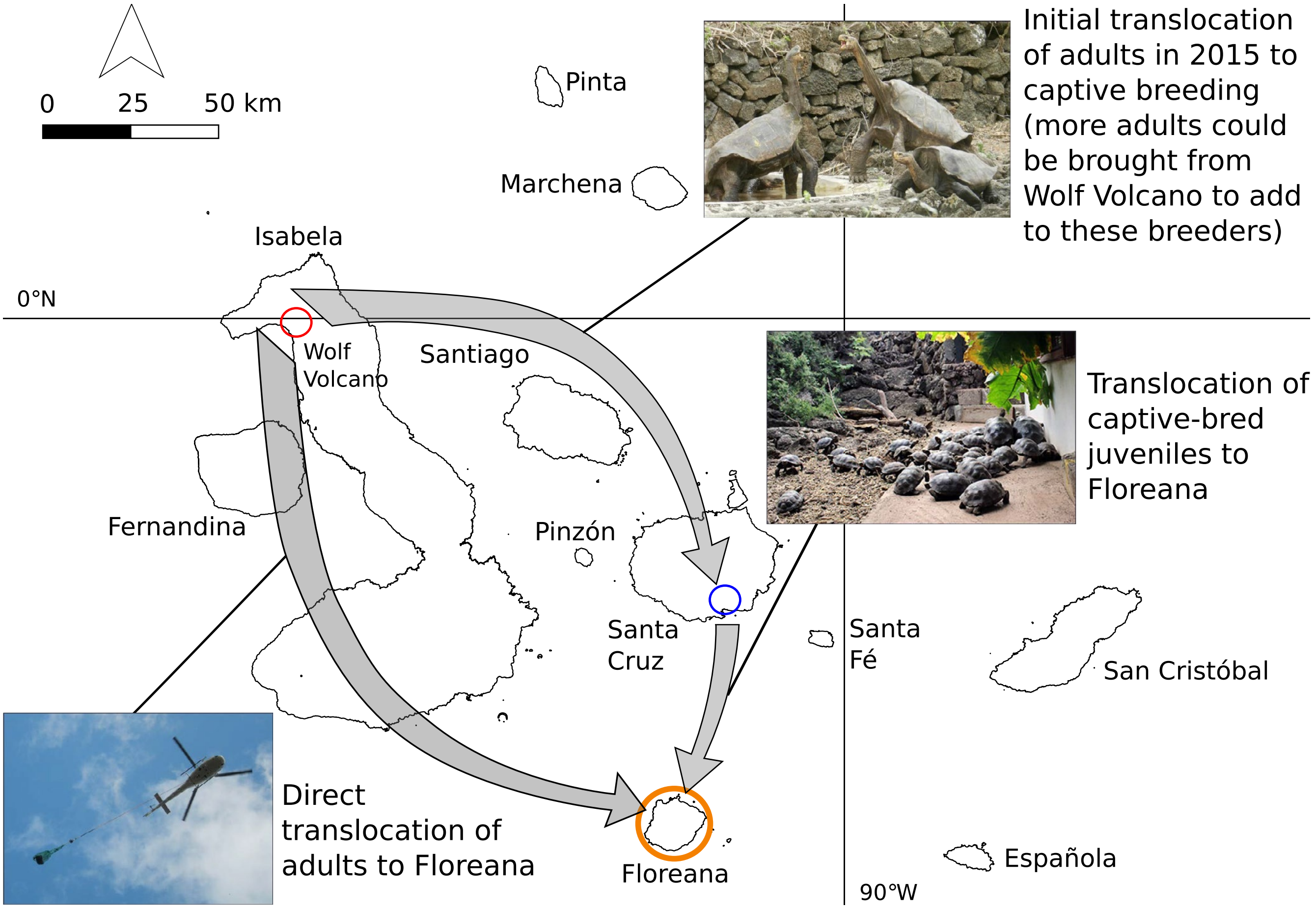


FIGURE 1 Management actions envisioned to restore giant tortoises to Floreana Island in the Galapagos Archipelago. Circles represent tortoise populations: Wolf Volcano, northern Isabela Island (red), where tortoises with *Chelonoidis niger* ancestry serve as the source for the restored population; the Galapagos National Park Directorate Tortoise Center on Santa Cruz Island (blue), where tortoises are bred in captivity to produce juveniles for relocation; Floreana Island (orange), the site of proposed species and ecosystem restoration. Photographs (from top): J. Flanagan, F. Laso, E. Hunter

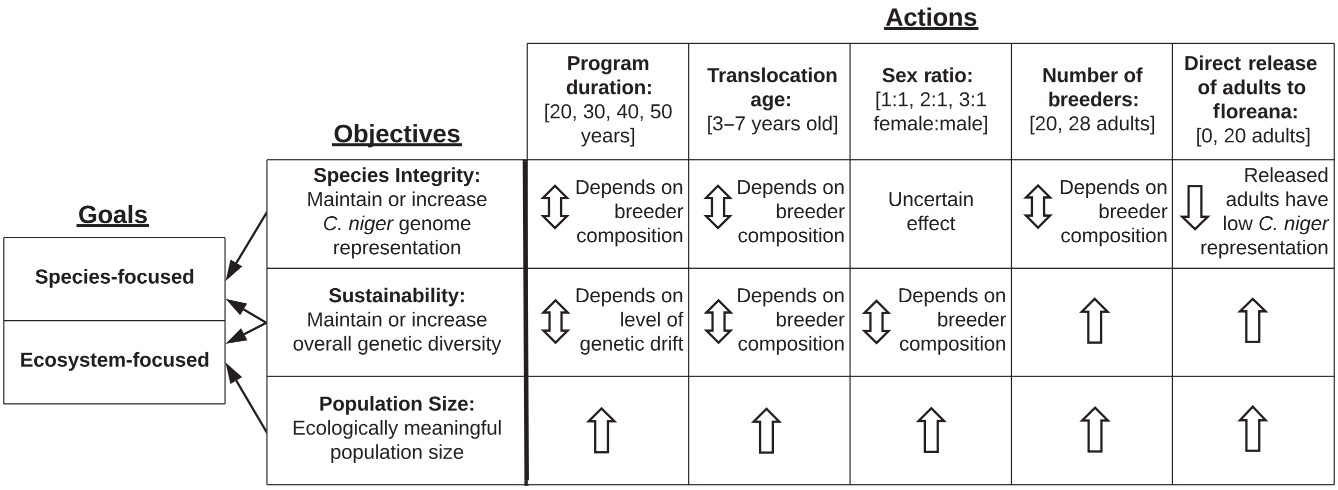
must satisfy both species- and ecosystem-focused goals (Figure 2). However, the primary species-focused objective of maximizing *C. niger* genome representation in a translocated population is in potential conflict with the primary ecosystem-focused objective of quickly restoring a tortoise population that could provide necessary ecosystem functions such as herbivory, suppression of woody vegetation and seed dispersal. Furthermore, it remains unclear whether management strategies designed to satisfy one or both of the main programme objectives would necessarily satisfy the programme objective (common to most captive breeding and conservation translocation programmes) of promoting genetic diversity in the translocated population.

We developed a multi-objective decision support tool to address two main questions germane to the Floreana Island tortoise restoration programme and other conservation translocation projects: (a) to what extent do species-focused and ecosystem-focused programme objectives compete? and (b) can management solutions be identified that fulfil multiple competing objectives simultaneously? Here we test sets of management actions for Floreana tortoises that are broadly applicable to many conservation translocation projects, including programme duration, age of repatriates, captive breeding decisions, incorporation of new individuals into the captive breeding population and direct translocation from a source population (Figure 2).

2 | MATERIALS AND METHODS

2.1 | Study system

A group of mixed ancestry tortoises (n = 23) was translocated in 2015 from Wolf Volcano to the Galapagos National Park Directorate (GNPD) Tortoise Center on Santa Cruz Island with the aim of breeding juveniles with high levels of *C. niger* ancestry for subsequent translocation to Floreana Island (Miller et al., 2017; Figure 1). Additional tortoises with varying levels of *C. niger* ancestry still remain on Wolf Volcano (Miller et al., 2017; Quinzin et al., 2019). All tortoises translocated from Wolf Volcano and currently in the breeding programme have a saddleback morphology similar to the original *C. niger* species (Miller et al., 2017). Galapagos giant tortoises' ecological roles (browsers and grazers) are highly associated with species' dominant



Objectives	Program duration: [20, 30, 40, 50 years]	Translocation age: [3–7 years old]	Sex ratio: [1:1, 2:1, 3:1 female:male]	Number of breeders: [20, 28 adults]	Direct release of adults to floreana: [0, 20 adults]
Species Integrity: Maintain or increase *C. niger* genome representation	⇕ Depends on breeder composition	⇕ Depends on breeder composition	Uncertain effect	⇕ Depends on breeder composition	⇩ Released adults have low *C. niger* representation
Sustainability: Maintain or increase overall genetic diversity	⇕ Depends on level of genetic drift	⇕ Depends on breeder composition	⇕ Depends on breeder composition	⇧	⇧
Population Size: Ecologically meaningful population size	⇧	⇧	⇧	⇧	⇧

FIGURE 2 Goals, objectives and actions (terminology from IUCN/SSC, 2013) used in simulation models of translocations of Galapagos giant tortoises with *Chelonoidis niger* ancestry to Floreana Island. Arrows connecting objectives and goals indicate which objectives address each goal. Arrows in the table indicate the hypothesized effect of the increase of an action (e.g. greater number of years of programme duration) on the measurement unit of the objective (e.g. population size). Management actions could have positive or negative effects on the objectives; double-sided arrows indicate positive or negative effects depending on conditions

morphology (saddleback and dome carapaces), making morphology a strong predictor of ecological niche fulfilment for translocated tortoises (Hunter, Gibbs, Cayot, & Tapia, 2013). Saddleback tortoises would have maintained the predominately arid ecosystems of Floreana Island in an open grassland or savannah state (Gibbs, Hunter, Shoemaker, Tapia, & Cayot, 2014; Hunter & Gibbs, 2014) underlying the importance of restoring saddleback tortoises to the ecosystem.

2.2 | Individual-based model (demography, population genetics and costs)

We simulated population dynamics, genetic processes and the effects of management actions using an individual-based model (Railsback & Grimm, 2012). Simulations were run for 50 years to capture at least two generations of tortoises (~25-year generation time, Table 1) while still being within a management-relevant timeframe. All simulations were run in NetLogo 5.3.1 (Wilensky, 1999).

The demographic component of the simulation model is based largely on Gibbs et al. (2014), who simulated the successful reintroduction of tortoises (*Chelonoidis hoodensis*) to Española Island from 1975 to 2007. Demographic parameters in Gibbs et al. (2014; and the present study) were drawn from existing data on Española tortoises in captivity (clutch size, sex ratios; 1999–2014, GNPD Tortoise Center, W. Tapia, unpublished data) and from mark-recapture data from surveys conducted on Española Island from 1975 to 2007. Population parameters derived from mark-recapture data (age-structured survival and reproductive success) were fitted in a Bayesian framework using Markov-Chain Monte-Carlo (Gelman et al., 2013; Gibbs et al., 2014), and our simulation models were parameterized by drawing directly from the resulting joint posterior distribution (Gibbs et al., 2014; Table 1). As Española Island tortoises (*C. hoodensis*) have a saddleback morphology similar to *C. niger* – and there were no demographic parameters available for *C. niger* tortoises – we assumed that the demographic parameter estimates used by Gibbs et al. (2014) for *C. hoodensis* were also representative of *C. niger*. Española Island has among the harshest conditions (in terms of food and water availability) of all the islands that once harboured saddleback tortoises, and drawing demographic parameters from this population is likely to be conservative (the true population vital rates for Floreana Island are likely to be more favourable for population growth). Unlike Gibbs et al. (2014) we did not include a density dependence process, since the population on Floreana Island is likely to remain well below carrying capacity within the 50-year timeframe of the simulations. In addition, we included both females and males in our model (whereas Gibbs et al., 2014 used a female-only modelling approach) to enable simulation of genetic processes. We modelled individual tortoise genotypes using microsatellite markers for the Floreana tortoises currently in captivity (Miller et al., 2017), using genetic data from 21 loci collected and analysed by Quinzin et al. (2019). Simulated offspring were assigned microsatellite alleles for each locus as a random sample from each parent's alleles (assuming no chromosomal linkages).

We simultaneously modelled two interacting tortoise populations: a captive population at the GNPD Tortoise Center and a wild population on Floreana Island (Figure 1). Of the 23 tortoises with *C. niger* ancestry brought into captivity from Wolf Volcano in 2015 (Miller et al., 2017), only 20 were used in simulations as some individuals did not meet a minimum threshold of *C. niger* ancestry (see Appendix S1 and Quinzin et al., 2019). These 20 tortoises were arranged into four breeding enclosures (corrals), each containing three females and two males (using optimal combinations of breeders and number of corrals from Quinzin et al., 2019).

In each simulation year, events occurred in this order:

1. *Reproduction*. Each adult female (those with an age greater than or equal to age at maturity, Figure 3) mated with a randomly

TABLE 1 Parameters for individual-based model of giant tortoise demography, genetics and management actions

Parameter (units)	Stochastic process	Value	Rationale
Demography			
Adult survival – wild	Estimated posterior distribution	Median: 0.987 Range: 0.898–0.999	Gibbs et al. (2010)
Juvenile survival – wild, ages 5–8	Estimated posterior distribution	Median: 0.972 Range: 0.714–0.999	Gibbs et al. (2010)
Juvenile survival – wild, ages 1–5	Uniform	Range: 0.6–0.9	Gibbs et al. (2010)
Hatchling survival – wild	Estimated posterior distribution	Median: 0.08 Range: 0.03–0.16	Gibbs et al. (2010)
Adult survival – captivity	Constant	0.995	GNPD Tortoise Center, unpublished data
Juvenile survival – captivity, ages 1–8	Constant	0.98	GNPD Tortoise Center, unpublished data
Hatchling survival – captivity	Constant	0.6	GNPD Tortoise Center, unpublished data
Age at maturity (age in years)	Normal	Mean: 25 *SD*: 2	Earliest breeding age for *Chelonoidis hoodensis* is 19 (Marquez, Morillo, & Cayot, 1991); larger size of *Chelonoidis niger* increases maturity age
Clutch size (egg number)	Uniform	Range: 4–10	Marquez, Cayot, and Rea (1999)
Sex ratio – wild (proportion female)	Uniform	Range: 0.35–0.65	Gibbs et al. (2010)
Translocation effect on survival (logit linear effect)	Estimated posterior distribution	Mean: −2.25 *SD*: 0.14	Gibbs et al. (2010)
Costs			
Captive care (US$/tortoise/year)	Constant	190	GNPD Tortoise Center, unpublished data
Translocation: captivity to Floreana (US$/trip)	Constant	10,000	GNPD, unpublished data (boat support)
Translocation: Wolf Volcano to captivity or Floreana (US$/trip)	Constant	100,000	GNPD, unpublished data (boat + helicopter support)
New corral (US$/corral)	Constant	35,000	GNPD Tortoise Center, unpublished data
Genetic testing (US$/sample)	Constant	15	A. Caccone, personal communication

Note: Survival rates are annual probabilities.

selected male (mating is restricted by corral in captivity). We assumed no multiple paternity and an equal chance of paternity for all males in the population – assumptions that should be tested as there is some evidence for reproductive skew in *C. niger* (Miller et al., 2018). Offspring production per female was computed as the product of clutch size and hatchling survival rates (Table 1).

2. *Survival*. Annual stage-specific survival probabilities were drawn from Bayesian joint posterior distributions fitted to data from the Española Island reintroduction programme, following Gibbs et al. (2014; Table 1).
3. *Management*. Management actions (e.g. translocation of juveniles from captivity to Floreana Island, see below) were implemented at the end of the year depending on the action (Figure 3) when management costs (see below) were also computed.

2.3 | Testing alternative management scenarios

To explore the effects of alternative management strategies on programme objectives, we simulated the demography and population genetics of the translocated Floreana Island population under alternative programme durations (20, 30, 40 or 50 years of translocations), ages at translocation (3–7 years old, the age range typically used in GNPD translocations) and captive sex ratios (1:1, 2:1, 3:1 female:male ratio; sex determination in giant tortoises is temperature-dependent and therefore sex ratios can be manipulated in captivity; Sancho et al., 2017; Figure 2). We also ran scenarios in which (a) the captive breeding population was augmented with individuals from the original source population that had high *C. niger* genome representation (Figure 2) and (b) adult individuals with lower *C. niger* genome representation were translocated directly from Wolf Volcano to Floreana Island (figure 1, Quinzin et al., 2019). For the first scenario, we randomly selected (for each simulation) four females and four males from a group of 13 individuals with the highest *C. niger* representation on Wolf Volcano identified in previous work (9.8% higher average *Q*-values [which represent the probability of group membership based on individual allele frequencies] than current breeders; Miller et al., 2017). One female and one male were added to each breeding corral in the first year of simulations (Figure 3), for a total of 28 rather than 20 breeders. For the second scenario, 20 adult tortoises with lower *C. niger* representation

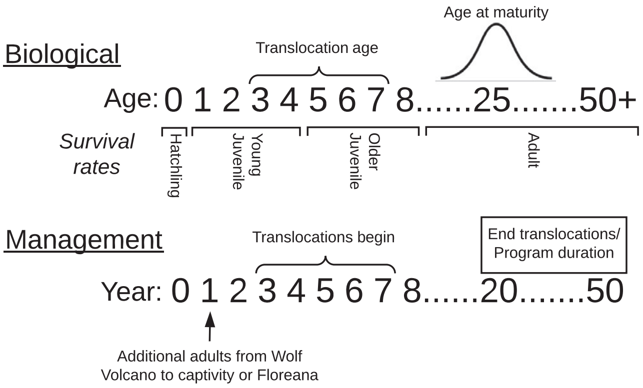


FIGURE 3 Timelines used in giant tortoise population simulations. The biological timeline shows age brackets for survival rates, when tortoises become sexually mature ($\mu = 25$, $\sigma = 2$), and potential ages at which juvenile tortoises would be translocated from captivity to the wild. The management timeline shows simulation years in which different management options could be taken. Boxes indicate management actions that must occur, but with varying timings (e.g. translocation begins at some time between 3 and 7 years after project initiation). Arrow indicates optional management actions that depend on retrieval of more tortoises with *Chelonoidis niger* ancestry

than the breeders currently in captivity (9% lower average *Q*-values) were directly translocated to Floreana in the first simulation year (Figure 3).

We simulated the release of juvenile tortoises produced in captivity every year of the simulation from the first eligible year (based on the translocation age management option) to the number of years of programme duration. Each management action combination (four programme durations, five translocation ages, three sex ratios, two number of breeders and two adult translocation scenarios) was simulated 10 times, for a total of 2,400 simulation runs.

The total cost (USD) of each management scenario was estimated from records acquired from tortoise rearing centre records. Costs included maintaining tortoises in captivity (including all administrative, equipment and maintenance costs), travel to and from Floreana Island and Wolf Volcano, genetic testing for all captive-bred juveniles before translocation and building new corrals (if the simulated captive population exceeded a threshold occupancy limit of 300 juveniles; Table 1). Although we did not account for inflation or cost escalation, doing so would be relatively straightforward.

2.4 | Decision support tool

For each simulation replicate (outcomes for the final year of the 50-year projection) we computed a set of programme 'success' metrics that collectively captured each of the programme objectives, with larger values representing greater programme success: (a) population size, (b) *C. niger* genome representation (relative to founder population) and (c) overall genetic diversity (relative to founder population; see below). *C. niger* genome representation was measured using STRUCTURE 2.3.4 (Pritchard, Stephens, & Donnelly, 2000) to estimate average population *Q*-values (adapted from Miller et al., 2017, see Appendix S1). We used Shannon's index of allelic diversity (SAR), to represent overall genetic diversity in the translocated population. For details on estimation of *Q*-values and genetic diversity measurements, see Appendix S1.

Because management actions could affect each of the programme success metrics in nonlinear, interactive and unknown ways, we used a semi-parametric statistical approach – generalized additive models (GAM; Hastie, 2017) – to describe each programme success metric as a (potentially non-linear) function of a suite of management decisions. To do this, we used the R (R Development Core Team, 2017) package 'mgcv' to identify parsimonious functions with optimal complexity (using generalized cross-validation; Wood, 2011). Prior to running GAMs, we converted each programme success metric to a zero-to-one scale by dividing by the maximum observed value. We used Akaike's information criterion to select the top GAMs from a set of plausible error distributions (Gaussian, Gamma) and combinations of linear, smoothed and interaction terms. Only coefficients with corresponding $p \le .05$ were included in the final GAMs. For visualizing the GAMs and the associated predictive performance and uncertainty, we computed prediction intervals (incorporating both sampling error and prediction error) for specific parameter sets using a Monte-Carlo approach with 1,000 replicates.

For each single-objective programme success metric, we then used constrained global optimization (simulated annealing, implemented in R using 'GenSA'; Xiang, Gubian, Suomela, & Hoeng, 2013) to identify quasi-optimal management solutions (management actions expected to yield the most favourable expected results on the basis of our GAMs) across a range of realistic cost constraints ($0.5m to $5m, in $0.5m increments). Within the optimization routine, management actions were constrained to exclude unreasonable actions (e.g. reduction in the number of breeders from the current level [20 individuals] was not explored). To avoid excessive extrapolation from the GAMs, we allowed the optimization routine to extrapolate the results of management actions up to 50% less than or greater than the range of actions tested in our individual-based simulation models (unless such extrapolation was deemed unreasonable; see above, Table 2).

For each cost constraint, we measured the extent of conflict among management objectives as the degree to which the quasi-optimal management solution for one objective was suboptimal for a different programme objective ('suboptimality statistic' = percent difference (loss in performance) between the optimal value achievable for that metric and the value achieved when optimizing for a different objective). We computed the overall conflict between each pair of objectives by averaging this suboptimality statistic across all cost constraints. We also computed the suboptimality statistic for the minimum cost constraint that satisfied all programme objectives to within 50% of their respective best achievable values.

Multi-objective optimization was used to synthesize trade-offs by optimizing mean success across all three programme objectives (population size, genetic diversity and *C. niger* genome representation).

TABLE 2 Management actions used for model simulations ('Levels simulated'), along with the upper and lower bounds allowed in constrained optimization routines

Action	Levels simulated	Lower bound	Upper bound
Translocation age (years old)	[3, 4, 5, 6, 7]	2	9
Sex ratio (proportion female)	[0.5, 0.67, 0.75]	0.5	0.875
Programme duration (years)	[20, 30, 40, 50]	20	65
Direct release of adults (# individuals)	[0, 20]	0	30
Number of breeders	[20, 28]	20	32

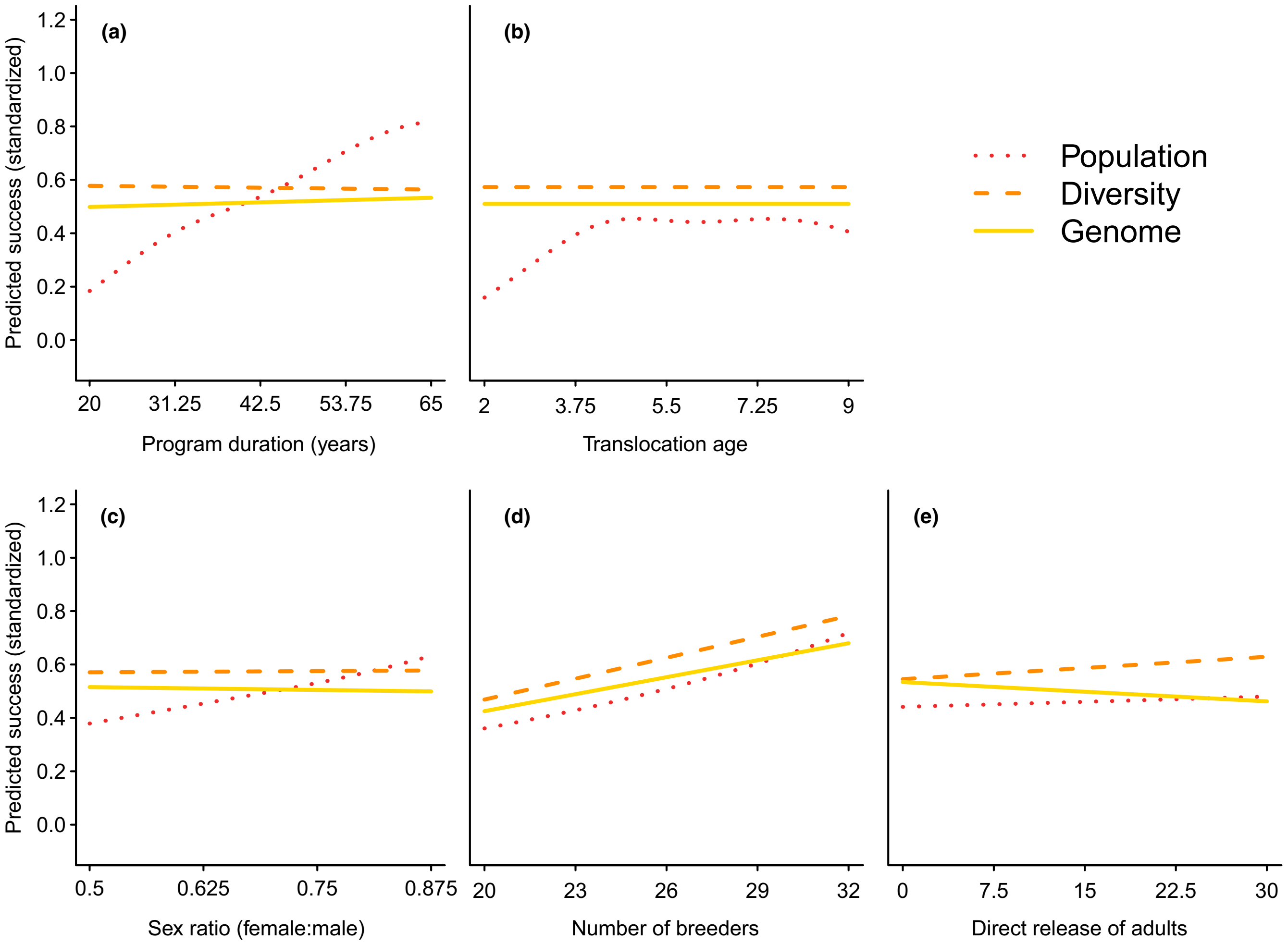


FIGURE 4 Partial dependence plots illustrating the main effects (excluding interaction effects) of five management choices (each panel a–e represents a separate decision axis) on each of the three major programme objectives: population size ('Population', dotted), genetic diversity [Shannon diversity] ('Diversity', dashed) and *Chelonoidis niger* genome representation ('Genome', solid) after 50 years. Success metrics were standardized so that 0 represents the minimum of all simulated values for each objective and 1 represents the maximum. Levels for non-focal management actions were held constant at intermediate values halfway between minimum and maximum values used in simulation scenarios. Because these visualizations do not account for interactions, this figure should be interpreted as a schematic rather than a definitive description of the GAMs linking management actions to expected outcomes (only slopes should be interpreted, not intercepts). More detailed visualizations of the GAMs can be found in the supplementary materials

Although we did not test alternative stakeholder valuations (Converse et al., 2013), such valuations could be incorporated via optimizing a weighted average of the three programme objectives. We then computed, for each cost constraint and for each individual project objective, the percent loss between the quasi-optimal multi-objective solution and the single-objective quasi-optimal solutions (using the 'suboptimality statistic' described above).

3 | RESULTS

Final tortoise population size was best predicted by a smoothed (nonlinear) interaction between sex ratio, translocation age and programme duration, and main and interaction terms involving releasing adult hybrids and increasing the number of breeders (Figure 4; Appendix S2). Genetic diversity and *C. niger* genome representation

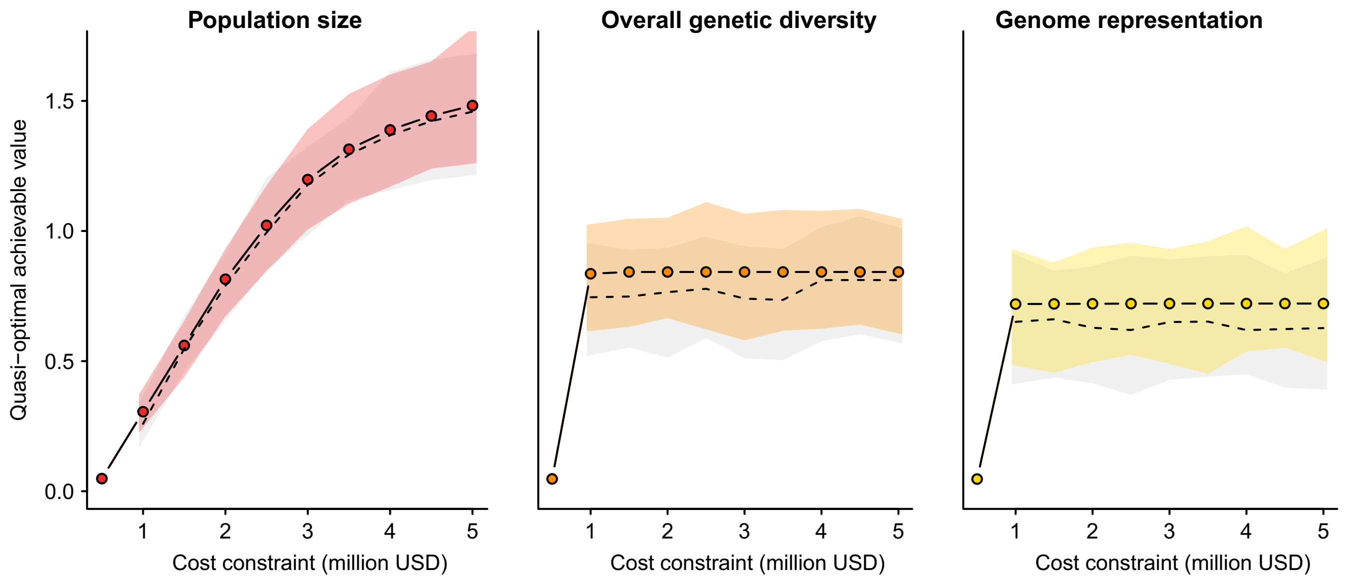
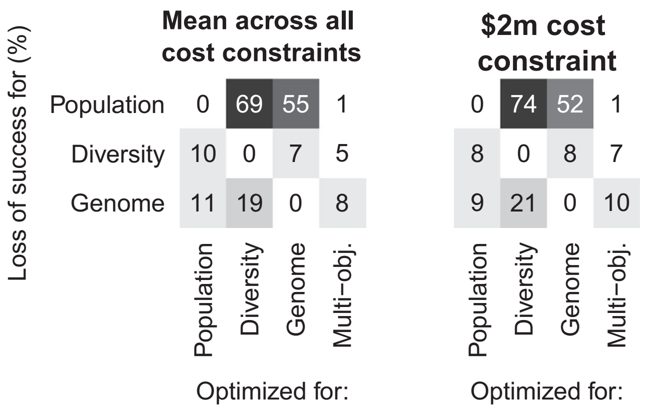


FIGURE 5 Maximum achievable values (standardized) for the three major programme objectives (quasi-optimal expectation for standardized success metrics, where 0 and 1 are the lowest and highest values observed from simulations; *y*-axis) across multiple realistic cost constraints (*x*-axis). Solid lines with points represent cost-constrained quasi-optimal solutions for programme objectives of population size (a), high genetic diversity (Shannon diversity; b) and genome representation of the extinct Floreana Island species (c). Dashed lines represent maximum achievable values for each programme objective under the multi-objective quasi-optimal solution

models exhibited lower predictive performance and excluded translocation age (which had little discernible effect on either programme objective; Figure 4; Appendix S2). Genetic diversity was most influenced by linear main and interactive effects of sex ratio, number of breeders and releasing adult hybrids, and a smoothed term for programme duration. *C. niger* representation was determined by main and interactive effects of programme duration, number of breeders and releasing adult hybrids, and a smoothed term for sex ratio (Figure 4; Appendix S2).

Programme success metrics were affected by the management actions in different and complex ways (Figure 4; Appendix S2). Increasing programme duration strongly and positively influenced final tortoise population size in our simulations and weakly and negatively influenced genetic diversity (Figure 4a). Releasing adult hybrids exerted an opposing effect on genetic diversity (positive) and *C. niger* genome representation (negative; Figure 4e). Increasing translocation age had positive (but diminishing) effects on population size and no detectable effects on overall genetic diversity or *C. niger* genome representation (Figure 4b). Increasing the fraction of female hatchlings in the captive population exerted a strong positive direct effect on final population size, but the influence of sex ratio on the other programme objectives was complex – a higher female:male sex ratio negatively affected genetic diversity, except when paired with the release of adult hybrids, and negatively affected *C. niger* representation only when the number of breeders was increased (Figure 4c; Appendix S2). In contrast to the other management actions, adding breeders from Wolf Volcano to increase the number of breeders from 20 to 28 individuals strongly and positively affected all programme objectives (Figure 4d).

With constrained optimizations, the highest achievable genetic diversity and *C. niger* genome representation was achieved at fairly low cost (≤$1m USD, whereas additional funds would be required to achieve high population sizes (Figure 5). All programme objectives could be met to within 75% of the highest simulated values with a budget of *c.* $2m USD (Figure 5). The highest simulated achievable values for programme objectives were: 2,730 tortoises (population size objective), 1.6% increase in SAR (genetic diversity objective), and 12.9% increase in *Q*-values (*C. niger* genome representation objective; Table S1).



Mean across all cost constraints

	Population	Diversity	Genome	Multi−obj.
Population	0	69	55	1
Diversity	10	0	7	5
Genome	11	19	0	8

$2m cost constraint

	Population	Diversity	Genome	Multi−obj.
Population	0	74	52	1
Diversity	8	0	8	7
Genome	9	21	0	10

FIGURE 6 'Suboptimality matrices' (left panel: average suboptimality across all cost thresholds; right panel; suboptimality at a cost threshold of $2m) representing the percent loss in the expected outcome for a focal programme objectives (row) when using the optimal management strategy for a different programme objective (column). Darker shades indicate greater suboptimality. For example, column 2, row 1 should be interpreted as: 'suboptimality of best-diversity solution (col) for population size (row) at a $2m threshold'

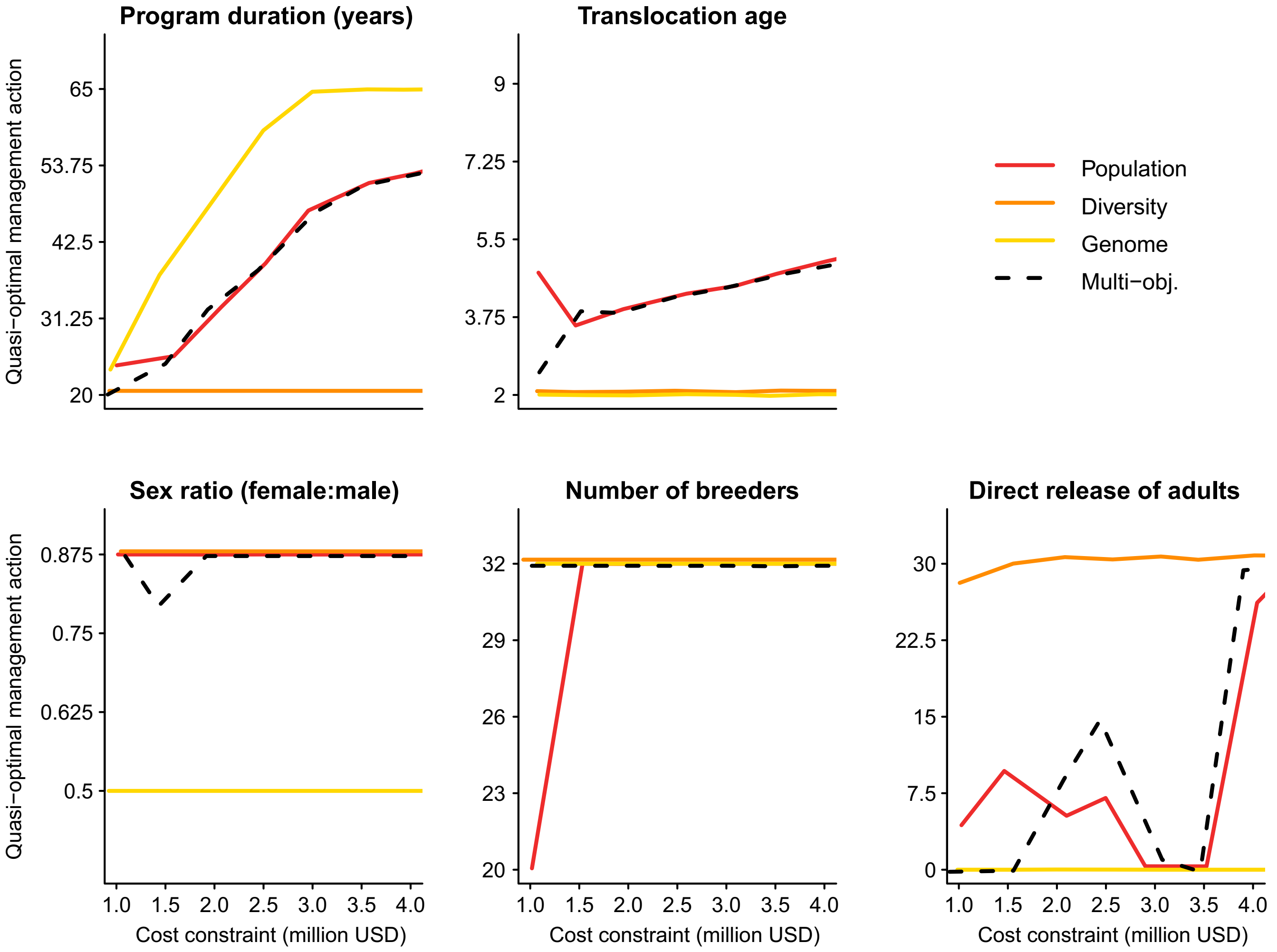


FIGURE 7 Quasi-optimal translocation strategies (each panel represents one of five different management axes explored using simulation models) for achieving the highest possible population size ('Population'), genetic diversity (Shannon diversity; 'Diversity') and genome representation of the extinct former occupant of Floreana island (*Chelonoidis niger*; 'Genome'), respectively, across a range of realistic cost constraints. Black-dashed lines represent a quasi-optimal multi-objective solution designed to maximize programme success across all three programme objectives (unweighted mean of standardized programme success metrics for populations size, genetic diversity and genome representation of *C. niger*)

For genetic diversity and *C. niger* genome representation objectives, these were also the highest values that could be achieved (Figure 5). However, optimizations indicated that population size could greatly exceed highest simulated values if additional funds were spent (Figure 5).

Based on suboptimality analyses, quasi-optimal solutions for genetic diversity and *C. niger* genome representation were highly suboptimal for population size (≥60% loss in expected performance relative to the best-population size solution) – both when averaged across all cost constraints and when computed for a cost constraint of $2m (the lowest cost constraint at which all three objectives could be satisfactorily addressed; Figure 6). In contrast, the quasi-optimal solution for final population size was able to meet genetic diversity and genome representation objectives to within 89%–91% of the optimal solutions (Figure 6). Finally, the multi-objective solution, which closely tracked the best-population size solution, was able to meet all the objectives to within 90% of the highest achievable mean values across all cost constraints (Figures 5 and 6).

Optimal solutions tended to vary substantially across programme objectives (Figure 7); there were clear conflict among programme objectives regarding sex ratio, translocation age and programme duration. However, one management action – augmenting the number of breeders with new tortoises from Wolf Volcano with high levels of *C. niger* ancestry (increasing the number of breeders from 20 to 28) – was consistently included in quasi-optimal solutions (including the multi-objective solution) even under severe cost constraints (Figure 7). Releasing adult hybrids was never part of the optimal solution for maximizing *C. niger* genomic representation but was always optimal for maximizing genetic diversity and entered the best-population size and multi-objective solution under relaxed cost constraints (>$3m budget; Figure 7). Across all cost constraints, optimal solutions for population size and genetic diversity included a highly female-biased sex ratio (a more female-biased sex ratio had a positive effect on genetic diversity when paired with release of adult hybrids); however, even sex ratios (1:1 female:male) were always preferred for optimizing *C. niger* genome representation (Figure 7). With relaxed cost constraints, optimal solutions for population size and *C. niger* genome representation included longer programme durations (Figure 7). As longer programmes had a weakly negative effect on genetic diversity (Figure 4a), programme duration remained short for optimal diversity solutions across all cost constraints (Figure 7). Finally, translocating 5-year-old tortoises to Floreana Island was optimal for population size, whereas using 2-year-old tortoises (least expensive option) was optimal for both *C. niger* genome representation and overall genetic diversity (Figure 7).

4 | DISCUSSION

Conservation planners must carefully balance the goal of maximizing programme success with the realities of resource limitations. The decision-making process becomes even more challenging for programmes with more than one competing goal, which is the case for most conservation translocation and ecosystem restoration programmes (Chadès et al., 2017; Converse et al., 2013). Here, we demonstrate that the use of a model-based decision support tool can discover compromise solutions that produce positive outcomes for competing programme objectives simultaneously across a range of realistic cost constraints (Figures 5 and 6). Our approach discovered these compromise solutions, despite substantial differences among optimal management strategies (sets of management actions) for all three major programme objectives for our case study (Figure 7).

Demographic simulation models are commonly used in conservation science to perform scenario testing – that is ranking scenarios in terms of how well they meet programme objectives (Ellner & Fiebert, 2003; Possingham, Lindenmayer, & Norton, 1993). By examining the cost of all scenarios as well as their benefits for conservation, demographic simulation models are increasingly powering more formal decision support systems that attempt to identify solutions that maximize return-on-investment or meet specified budget constraints (Duca, Yokomizo, Marini, & Possingham, 2009; Torrez-Orozco, Arroyo, Pomarol, & Santangeli, 2016). In our case study, we estimated the cost of each scenario on the basis of records from previous tortoise captive-rearing and translocation efforts. In our simulation models, the cost of tortoise restoration to Floreana Island varied from \$0.62m to \$5.3m (Table S1) over 50 years (with most objectives met with a \$2m cost constraint), which is far lower than the recovery costs (including translocation expenses) reported for high-profile endangered species in the United States (e.g. \$4.5m/year for black-footed ferrets, \$3.9m/year for California condors and \$14.1m/year for Mojave desert tortoises; U.S. Fish & Wildlife Service, 2015). In future iterations of this decision support tool, we hope to integrate more economic realism, including inflation, wage escalation and associated uncertainty.

To our knowledge, our study is the first to incorporate a genetic component into demographic simulation models as part of a decision support tool for conservation planning. Genetics factor heavily in the goals of many conservation programmes, including translocations and ex-situ conservation efforts (O'Brien, 1994). Individual-based models are flexible enough to incorporate nearly any biologically realistic demographic or genetic process; integration of individual-based models with decision support tools theoretically enables model-based decision support tools to account for any demographic-genetic trade-offs that may arise (limited only by data availability); as such, genetically explicit individual-based models could support a wide array of conservation translocation decisions.

Limited conservation resources will often restrict what can be accomplished in conservation translocations (Converse et al., 2013; Joseph, Maloney, & Possingham, 2009), but less frequently acknowledged is the potential that programme success may be restricted by conflict among objectives with demographic versus genetic aims. For example, in this case study, female-biased sex ratios in released cohorts produced larger population sizes but had a negative effect on *C. niger* genome representation, inducing an important conflict between demographic and genetic programme objectives (Figure 4c). Although direct manipulation of sex ratios in captive breeding programmes is most feasible for species (like giant tortoises) for which sex is environmentally determined, sex ratios in release cohorts are commonly manipulated in conservation translocation programmes (i.e. via selective translocations; Lambertucci, Carrete, Speziale, Hiraldo, & Donázar, 2013). Biased sex ratios typically lead to increased genetic drift due to smaller effective population sizes (Frankham, 1995; Milinkovitch et al., 2004), which could partially explain the negative effects of biased sex ratios on *C. niger* genome representation in our case study (assuming a correspondence between female-biased sex ratios in release cohorts and a biased sex ratio in the translocated population). The advantage of female-biased release cohorts for achieving rapid population growth is clear, as population growth is typically limited by the abundance of reproductive females. However, most wild populations (including giant tortoises) have *c.* 1:1 sex ratios for both adults and hatchlings (Carvalho, Sampaio, Varandas, & Klaczko, 1998; Marquez, Gibbs, Carrion, Naranjo, & Llerena, 2013), suggesting that female-skewed populations may have disadvantages from an evolutionary perspective. Furthermore, it is often unclear how a female-skewed population can be without negatively affecting breeding opportunities (Kvarnemo & Ahnesjo, 1996; Milinkovitch et al., 2004).

In our case study, we also observed a conflict between optimizing genome integrity and genetic diversity objectives. Not surprisingly, direct translocation of adult hybrids from the source population with lower *C. niger* representation than the current breeders improved genetic diversity (SAR), but reduced *C. niger* genome representation in the translocated population (Figure 4e). A conflict between species integrity and genetic diversity is well-documented in other conservation translocation projects, especially those that must contend with unwanted hybridization with domestic, invasive or widespread species. For example, introgression of domestic cattle (*Bos taurus*) genes in populations of reintroduced North American bison (*Bison bison*) increases overall genetic diversity but also threatens to undermine the long-term success of bison restoration efforts as hybrid bison may become more vulnerable to prevalent cattle diseases (Hedrick, 2009; Sanderson et al., 2008). Another example includes the hybridization between Scottish wildcats and feral domestic cats, which has contributed to the dramatic decline in pure wildcat populations (Fredriksen, 2016), and urges the question of what the conservation value of existing hybrids is to the restoration of a genetically diverse wild population from few pure founding individuals (Wayne & Shaffer, 2016). In all such cases, scenario testing using coupled demographic/genetic simulation models can help to clarify the extent to which such trade-offs exist, and to suggest which management approaches may simultaneously foster high genetic diversity and species integrity.

In general, achieving ecosystem-focused objectives is likely to be more expensive than achieving population-level objectives in conservation translocation programmes, as ecologically relevant abundances may greatly exceed the minimum viable abundance threshold for many species (Dirzo et al., 2014; Gibbs et al., 2014). The largest simulated population sizes over a 50-year period (~2,700 tortoises) would not achieve the high tortoise densities needed to restore plant communities across all suitable areas on the island (estimated as >0.3 tortoises/ha [Hunter & Gibbs, 2014] or >4,500 tortoises in the ~15,000 ha arid zone of Floreana Island). However, with juvenile tortoises likely to remain near release sites, even after they have matured (Gibbs et al., 2014), longer programme durations could result in effective vegetation restoration across over half of the island after 50 years, if coupled with strategic spatial distribution of tortoise releases. In such cases, decision-makers must decide whether to expend additional resources to achieve ecosystem restoration objectives or whether to be satisfied with successfully establishing a viable population – and decision support tools informed by stakeholder valuations can help to provide much-needed clarity on this issue.

For multi-objective conservation programmes, decision-makers must determine the relative importance of each programme objective (Converse et al., 2013) in order to consider, for example, whether some objectives must be met at all costs, or whether one objective should take precedence over another in cases where conflict occur among programme objectives. In our case study, we simply assigned each programme objective an equal value and examined the resulting pseudo-optimal solutions for relative consistencies or inconsistencies. Although we were able to learn valuable information using our simple approach, there are formal means to quantify the value stakeholders assign to objectives (e.g. Converse et al., 2013; Martin et al., 2009). Involvement of stakeholders in the modelling and decision-making process can help managers and stakeholders agree to recommendations produced by the process (Martin et al., 2009), but in cases where such involvement is not possible, the ‘equal value’ approach we presented here may be useful.

The case of the Floreana Island giant tortoise is remarkable given that the species is extinct and thus the captive breeding population (and the soon-to-be-translocated population) is necessarily composed of mixed ancestry individuals. Unique as this conservation translocation is, it does fall under the definition of ecological replacements, albeit with hybrids with a large component of their genome belonging to the extinct species (IUCN/SSC, 2013; Seddon et al., 2014). Similar examples (actively translocating hybrids or allowing hybrids to persist as ecological replacements) may become increasingly common as species declines and extinctions continue, demanding continued examination of the conservation value of hybrid individuals (Wayne & Shaffer, 2016). For example, the American chestnut (*Castanea dentata*) was at one time a keystone species in Eastern US forests until populations were decimated by introduced chestnut blight (*Cryphonectria parasitica*). Efforts are now underway to establish disease-resistant populations of American chestnut that incorporate resistance genes from an Asian congener (*Castanea mollissima*). Two main strategies have been considered: either perform extensive backcrossing trials from hybrid stock to produce (nearly) pure, disease-resistant American chestnut trees, or use genetic engineering to insert genes for disease resistance (Jacobs, Dalgleish, & Nelson, 2013). However, a third, less-expensive option might be to simply allow hybrid populations to flourish in the wild. Decision support tools, such as those demonstrated here, coupled with rigorous assessment of stakeholder values, will be critical for determining which strategy is best able to meet programme objectives under existing cost constraints for this and other conservation translocation programmes.

ACKNOWLEDGEMENTS

This work was funded by the Galapagos Conservancy's Giant Tortoise Restoration Initiative, with support from the Galapagos National Park Directorate. Additional funding came from the Mohamed bin Zayed Species Conservation Fund, the National Geographic Society, the Oak Foundation, the US National Science Foundation (DEB 1258062), the Belgian American Educational Foundation and the Yale Institute for Biospheric Studies. We thank J. Rhodes, M. Matocq, K. Loope, M. Walden, M. Crowell and three anonymous reviewers for helpful comments.

AUTHORS’ CONTRIBUTIONS

E.A.H., K.T.S., J.P.G., L.J.C. and W.T. conceived the idea; E.A.H. and K.T.S. designed the simulation model with input from M.C.Q., J.M.M. and A.C. on genetic components; E.A.H. and K.T.S. analysed the results and led manuscript writing; all the authors contributed to drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Code and associated data are available via the Zenodo repository https://doi.org/10.5281/zenodo.3403348 (Hunter et al., 2019).

ORCID

Elizabeth A. Hunter https://orcid.org/0000-0003-4710-167X
Joshua M. Miller https://orcid.org/0000-0002-4019-7675

REFERENCES

Armstrong, D. P., & Seddon, P. J. (2008). Directions in reintroduction biology. *Trends in Ecology and Evolution*, *23*, 20–25. https://doi.org/10.1016/j.tree.2007.10.003

Beger, M., McGowan, J., Treml, E. A., Green, A. L., White, A. T., Wolff, N. H., … Possingham, H. P. (2015). Integrating regional conservation priorities for multiple objectives into national policy. *Nature Communications*, *6*, 8208. https://doi.org/10.1038/ncomms9208

Carvalho, A. B., Sampaio, M. C., Varandas, F. R., & Klaczko, L. B. (1998). An experimental demonstration of Fisher's principle: Evolution of sexual proportion by natural selection. *Genetics*, *148*, 719–731.

Ceballos, G., Ehrlich, P. R., Barnosky, A. D., Garcia, A., Pringle, R. M., & Palmer, T. M. (2015). Accelerated modern human-induced species losses: Entering the sixth mass extinction. *Science Advances*, *1*, e1400253. https://doi.org/10.1126/sciadv.1400253

Chadès, I., Nicol, S., Rout, T. M., Péron, M., Dujardin, Y., Pichancourt, J. B., … Hauser, C. E. (2017). Optimization methods to solve adaptive management problems. *Theoretical Ecology*, *10*, 1–20. https://doi.org/10.1007/s12080-016-0313-0

Cohen, J. B., Hecht, A., Robinson, K. F., Osnas, E. E., Tyre, A. J., Davis, C., … Melvin, S. M. (2016). To exclose nests or not: Structured decision making for the conservation of a threatened species. *Ecosphere*, *7*, e01499. https://doi.org/10.1002/ecs2.1499

Converse, S. J., Moore, C. T., Folk, M. J., & Runge, M. C. (2013). A matter of tradeoffs: Reintroduction as a multiple objective decision. *Journal of Wildlife Management*, *77*, 1145–1156. https://doi.org/10.1002/jwmg.472

Dirzo, R., Young, H. S., Galetti, M., Ceballos, G., Isaac, N. J. B., & Collen, B. (2014). Defaunation in the Anthropocene. *Science*, *345*, 401–406. https://doi.org/10.1126/science.1251817

Duca, C., Yokomizo, H., Marini, M. Â., & Possingham, H. P. (2009). Cost-efficient conservation for the white-banded tanager (*Neothraupis fasciata*) in the Cerrado, central Brazil. *Biological Conservation*, *142*, 563–574. https://doi.org/10.1016/j.biocon.2008.11.010

Ellner, S. P., & Fieberg, J. (2003). Using PVA for management despite uncertainty: Effects of habitat, hatcheries, and harvest on salmon. *Ecology*, *84*, 1359–1369. https://doi.org/10.1890/0012-9658(2003)084[1359:UPFMDU]2.0.CO;2

Frankham, R. (1995). Effective population size/adult population size ratios in wildlife: A review. *Genetical Research*, *66*, 95–107. https://doi.org/10.1017/S0016672300034455

Fredriksen, A. (2016). Of wildcats and wild cats: Troubling species-based conservation in the Anthropocene. *Environment and Planning D: Society and Space*, *34*, 689–705. https://doi.org/10.1177/0263775815623539

Garrick, R. C., Benavides, E., Russello, M. A., Gibbs, J. P., Poulakakis, N., Dion, K. B., … Caccone, A. (2012). Genetic rediscovery of an “extinct” Galápagos giant tortoise species. *Current Biology*, *22*, R10–R11. https://doi.org/10.1016/j.cub.2011.12.004

Gelman, A., Stern, H. S., Carlin, J. B., Dunson, D. B., Vehtari, A., & Rubin, D. B. (2013). *Bayesian data analysis*. Boca Raton, FL: Chapman and Hall/CRC.

Gibbs, J. P., Hunter, E. A., Shoemaker, K. T., Tapia, W. H., & Cayot, L. J. (2014). Demographic outcomes and ecosystem implications of giant tortoise reintroduction to Española Island, Galapagos. *PLoS ONE*, *9*, e110742. https://doi.org/10.1371/journal.pone.0110742

Hansen, D. M., Donlan, C. J., Griffiths, C., & Campbell, K. (2010). Ecological history and latent conservation potential: Large and giant tortoises as a model for taxon substitutions. *Ecography*, *33*, 272–284. https://doi.org/10.1111/j.1600-0587.2010.06305.x

Hastie, T. J. (2017). Generalized additive models. In J. M. Chambers & T. J. Hastie (Eds.), *Statistical models in S* (pp. 249–307). New York, NY: Routledge.

Hedrick, P. W. (2009). Conservation genetics and North American bison (*Bison bison*). *Journal of Heredity*, *100*, 411–420. https://doi.org/10.1093/jhered/esp024

Hunter, E. A., & Gibbs, J. P. (2014). Densities of ecological replacement herbivores required to restore plant communities: A case study of giant tortoises on Pinta Island, Galápagos. *Restoration Ecology*, *22*, 248–256. https://doi.org/10.1111/rec.12055

Hunter, E. A., Gibbs, J. P., Cayot, L. J., & Tapia, W. (2013). Equivalency of Galápagos giant tortoises used as ecological replacement species to restore ecosystem functions. *Conservation Biology*, *27*, 701–709. https://doi.org/10.1111/cobi.12038

Hunter, E. A., Gibbs, J. P., Cayot, L. J., Tapia, W., Quinzin, M. C., Miller, J. M., … Shoemaker, K. T. (2019). Data from: Seeking compromise across competing goals in conservation translocations: The case of the “extinct” Floreana Island Galapagos giant tortoise. *Zenodo Digital Repository*, https://doi.org/10.5281/zenodo.3403348

IUCN/SSC. (2013). *Guidelines for reintroductions and other conservation translocations. Version 1.0*. Gland, Switzerland: IUCN Species Survival Commission.

Jacobs, D. F., Dalgleish, H. J., & Nelson, C. D. (2013). A conceptual framework for restoration of threatened plants: The effective model of American chestnut (*Castanea dentata*) reintroduction. *New Phytologist*, *197*, 378–393.

Joseph, L. N., Maloney, R. F., & Possingham, H. P. (2009). Optimal allocation of resources among threatened species: A project prioritization protocol. *Conservation Biology*, *23*, 328–338. https://doi.org/10.1111/j.1523-1739.2008.01124.x

Kvarnemo, C., & Ahnesjo, I. (1996). The dynamics of operational sex ratios and competition for mates. *Trends in Ecology & Evolution*, *11*, 404–408. https://doi.org/10.1016/0169-5347(96)10056-2

Lambertucci, S. A., Carrete, M., Speziale, K. L., Hiraldo, F., & Donázar, J. A. (2013). Population sex ratios: Another consideration in the reintroduction – Reinforcement debate? *PLoS ONE*, *8*, e75821. https://doi.org/10.1371/journal.pone.0075821

Marquez, C., Cayot, L. J., & Rea, S. (1999). *La crianza de tortugas gigantes en cautiverio: Un manual operativo*. Quito, Ecuador: A & B Editores.

Marquez, C., Gibbs, J. P., Carrion, V., Naranjo, S., & Llerena, A. (2013). Population response of giant Galápagos tortoises to feral goat removal. *Restoration Ecology*, *21*, 181–185. https://doi.org/10.1111/j.1526-100X.2012.00891.x

Marquez, C., Morillo, G., & Cayot, L. J. (1991). A 25-year management program pays off: Repatriated tortoises on Espanola reproduce. *Noticias De Galapagos*, *50*, 17–18.

Marquez, C., Wiedenfeld, D., Snell, H., Fritts, T., MacFarland, C., Tapia, W., & Naranjo, S. (2004). Estado actual de las poblaciones de tortugas terrestres gigantes (*Geochelone* spp., Chelonia: Testudinae) en las Islas Galápagos. *Ecologia Aplicada*, *3*, 98–111. https://doi.org/10.21704/rea.v3i1-2.277

Martin, J., Runge, M. C., Nichols, J. D., Lubow, B. C., & Kendall, W. L. (2009). Structured decision making as a conceptual framework to identify thresholds for conservation and management. *Ecological Applications*, *19*, 1079–1090. https://doi.org/10.1890/08-0255.1

Milinkovitch, M. C., Monteyne, D., Gibbs, J. P., Fritts, T. H., Tapia, W., Snell, H. L., … Powell, J. R. (2004). Genetic analysis of a successful repatriation programme: Giant Galápagos tortoises. *Proceedings of the Royal Society of London*, *271*, 341–345. https://doi.org/10.1098/rspb.2003.2607

Miller, J. M., Quinzin, M. C., Poulakakis, N., Gibbs, J. P., Beheregaray, L. B., Garrick, R. C., … Caccone, A. (2017). Identification of genetically important individuals of the rediscovered Floreana Galápagos giant tortoise (*Chelonoidis elephantopus*) provide founders for species restoration program. *Scientific Reports*, *7*, 11471.

Miller, J. M., Quinzin, M. C., Scheibe, E. H., Ciofi, C., Villalba, F., Tapia, W., & Caccone, A. (2018). Genetic pedigree analysis of the pilot breeding program for the rediscovered Galapagos giant tortoise from Floreana

Island. *Journal of Heredity*, *109*(6), 620–630. https://doi.org/10.1093/jhered/esy010

Murray, D. L., Bastille-Rousseau, G., Adams, J. R., & Waits, L. P. (2015). The challenges of red wolf conservation and the fate of an endangered species recovery program. *Conservation Letters*, *8*, 338–344. https://doi.org/10.1111/conl.12157

O'Brien, S. J. (1994). A role for molecular genetics in biological conservation. *Proceedings of the National Academy of Sciences of the United States of America*, *91*, 5748–5755. https://doi.org/10.1073/pnas.91.13.5748

Possingham, H. P., Lindenmayer, D. B., & Norton, T. W. (1993). A framework for the improved management of threatened species based on population viability analysis (PVA). *Pacific Conservation Biology*, *1*, 39–45. https://doi.org/10.1071/PC930039

Poulakakis, N., Glaberman, S., Russello, M. A., Beheregaray, L. B., Ciofi, C., Powell, J. R., & Caccone, A. (2008). Historical DNA analysis reveals living descendants of an extinct species of Galapagos tortoise. *Proceedings of the National Academy of Sciences of the United States of America*, *105*, 15464–15469. https://doi.org/10.1073/pnas.0805340105

Pritchard, J. K., Stephens, M., & Donnelly, P. (2000). Inference of population structure using multi-locus genotype data. *Genetics*, *155*, 945–959.

Quinzin, M. C., Sandoval-Castillo, J., Miller, J. M., Beheregaray, L. B., Russello, M. A., Hunter, E. A., … Caccone, A. (2019). Genetically informed captive breeding of hybrids of an extinct species of Galapagos giant tortoise. *Conservation Biology*, https://doi.org/10.1111/cobi.13319

R Development Core Team. (2017). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.

Railsback, S. F., & Grimm, V. (2012). *Agent-based and individual-based modeling*. Princeton, NJ: Princeton University Press.

Rhodin, A. G. J., Iverson, J. B., Bour, R., Fritz, U., Georges, A., Shaffer, H. B., & van Dijk, P. P. (2017). Turtles of the world: Annotated checklist and atlas of taxonomy, synonymy, distribution, and conservation status. In A. G. J. Rhodin, J. B. Iverson, P. P. van Dijk, R. A. Saumure, K. A. Buhlmann, P. C. H. Pritchard, & R. A. Mittermeier (Eds.), *Conservation biology of freshwater turtles and tortoises: A compilation project of the IUCN/SSC Tortoise and Freshwater Turtle Specialist Group* (8th edn., Vol. *7*, pp. 1–292). Chelonian Research Monographs. https://doi.org/10.3854/crm.7.checklist.atlas.v8.2017

Sancho, A., Gutzke, W. H. N., Snell, H. L., Rea, S., Wilson, M., & Burke, R. L. (2017). Temperature sex determination, incubation duration, and hatchling sexual dimorphism in the Española Giant Tortoise (*Chelonoidis hoodensis*) of the Galápagos Islands. *Amphibian & Reptile Conservation*, *11*, 44–50.

Sanderson, E. W., Redford, K. H., Weber, B., Aune, K., Baldes, D., Berger, J., … Stephenson, B. (2008). The ecological future of the North American bison: Conceiving long-term, large-scale conservation of wildlife. *Conservation Biology*, *22*, 252–266. https://doi.org/10.1111/j.1523-1739.2008.00899.x

Seddon, P. J. (1999). Persistence without intervention: Assessing success in wildlife reintroductions. *Trends in Ecology and Evolution*, *14*, 503. https://doi.org/10.1016/S0169-5347(99)01720-6

Seddon, P. J., Griffiths, C. J., Soorae, P. S., & Armstrong, D. P. (2014). Reversing defaunation: Restoring species in a changing world. *Science*, *345*, 406–412. https://doi.org/10.1126/science.1251818

Torres-Orozco, D., Arroyo, B., Pomarol, M., & Santangeli, A. (2016). From a conservation trap to a conservation solution: Lessons from an intensively managed Montagu's harrier population. *Animal Conservation*, *19*, 436–443. https://doi.org/10.1111/acv.12260

U.S. Fish and Wildlife Service. (2015). Federal and state endangered and threatened species expenditures: Fiscal year 2015.

Walters, J. R., Derrickson, S. R., Michael Fry, D., Haig, S. M., Marzluff, J. M., & Wunderle, J. M. (2010). Status of the California Condor (*Gymnogyps californianus*) and efforts to achieve its recovery. *The Auk*, *127*, 969–1001.

Wayne, R. K., & Shaffer, H. B. (2016). Hybridization and endangered species protection in the molecular era. *Molecular Ecology*, *25*, 2680–2689.

Wilensky, U. (1999). *NetLogo*. Evanston, IL: Center for Connected Learning and Computer-Based Modeling.

Wood, S. N. (2011). Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *Journal of the Royal Statistical Society (B)*, *73*, 3–36. https://doi.org/10.1111/j.1467-9868.2010.00749.x

Xiang, Y., Gubian, S., Suomela, B., & Hoeng, J. (2013). Generalized simulated annealing for efficient global optimization: The GenSA package for R. *The R Journal*, *5*, 13–28.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

How to cite this article: Hunter EA, Gibbs JP, Cayot LJ, et al. Seeking compromise across competing goals in conservation translocations: The case of the 'extinct' Floreana Island Galapagos giant tortoise. *J Appl Ecol*. 2019;00:1–13. https://doi.org/10.1111/1365-2664.13516