RESEARCH ARTICLE

Journal of Applied Ecology | BRITISH ECOLOGICAL SOCIETY

Designing an optimal large-scale reintroduction plan for a critically endangered species

Stefano Canessa[1] | José Salgado-Rojas[2] | Dani Villero[3] | Lluís Brotons[3,4,5] | Fèlix Amat[6] | Daniel Guinart[7] | Sonia Solórzano[7] | Lluís López[7] | Xavier Comas[7] | Virgilio Hermoso[3]

[1]Division of Conservation Biology, Institute of Ecology and Evolution, University of Bern, Bern, Switzerland; [2]Department of Statistics and Operations Research, Polytechnic University of Catalonia, Barcelona, Spain; [3]Centre de Ciència i Tecnología Forestal de Catalunya (CTFC), Lleida, Spain; [4]CREAF, Cerdanyola del Vallés, Barcelona, Spain; [5]CSIC, Cerdanyola del Vallés, Barcelona, Spain; [6]Area d'Herpetologia, BiBIO, Museu de Granollers—Ciencies Naturals, Catalonia, Spain and [7]Servei de Gestió de Parcs Naturals, Diputació de Barcelona, Barcelona, Spain

Correspondence

Stefano Canessa, Division of Conservation Biology, Institute of Ecology and Evolution, University of Bern, Baltzerstrasse 6, 3012 Bern, Switzerland.
Email: stefano.canessa@unibe.ch

Abstract

1. Optimization methods are routinely used for landscape-level conservation planning, but still underused in supporting species recovery programs. A possible barrier is the difficulty in representing and optimizing complex multidimensional problems: for example, many species recovery programs require management at the population level, but also allocation of effort and resources across populations and over time. Optimization methods can help, but they must strike a balance: too much realism can be computationally unfeasible, but too much simplification can limit relevance for complex programs, exactly where decision support might be most needed.

2. We show how integer linear programming can be used to solve such a complex problem, combining multiple site-level demographic models with realistic management constraints under different sources of stochasticity and uncertainty. We apply this protocol to reintroduction planning for the critically endangered Montseny brook newt *Calotriton arnoldi*, optimizing site restoration efforts, captive releases from limited and variable stocks, and short- and long-term monitoring, all across 17 sites over 10 years.

3. For *C. arnoldi*, the optimal solution was generally to open as many sites as possible, as soon as allowed by budget, and to reinforce sites with additional releases. The number of new populations that could be established was limited not only by the high initial costs of restoring and preparing sites for releases, but also because opening new sites would require subsequent monitoring, eventually adding up to unsustainable costs.

4. *Synthesis and applications.* Our results suggest releases of *Calotriton arnoldi* should be dictated first by habitat restoration capacity, then by long-term sustainability. More generally, our study shows how quantitative decision-support

methods can improve the value of science for conservation, and help managers find solutions to complex problems. However, deploying those methods requires close collaboration between managers and scientists, to ensure models are realistic, results are relevant, and the whole process is informative.

KEYWORDS
captive breeding, decision-making, integer linear programming, monitoring, survival, translocation

1 | INTRODUCTION

Uncertainty and constraints are well-known hurdles on the road to conservation success (Milner-Gulland & Shea, 2017). Faced with species declines, imminent threats, incomplete knowledge and limited resources, managers implement whatever actions they think best, and hope they work (Hermoso et al., 2012; Scheele et al., 2018). In the face of such challenges, most managers proceed by intuition and, where possible, by relying on existing evidence for similar problems (Pullin et al., 2004; Walsh et al., 2015). However, many conservation problems are so complex that finding the best solution is challenging (Game et al., 2014). Quantitative decision-support methods, including optimization algorithms, are increasingly used in such situations (Schwartz et al., 2018).

Quantitative decision-support methods are essentially a way of using models not only for describing biological reality, but also to interpret those descriptions and rationally select the best decision. In reintroduction biology, the use of quantitative models for planning is relatively well established (Armstrong & Reynolds, 2012). Planners routinely use population viability analyses to predict the outcome of a chosen reintroduction strategy (Bozzuto et al., 2017). A more advanced use is to compare the predicted outcomes of different strategies, by varying parameters such as the number of individuals released, then pick the strategy with the best prediction (Schaub et al., 2009; Taylor et al., 2017). This is an improvement over pure expertise-based intuition, but remains limited to the set of candidate strategies modelled, especially when there are many or infinite possibilities. Consider, for example, a situation where managers of a conservation translocation must choose which animals to release (sex and age), how many, where to source them, where to put them and how to move them (Canessa, Guillera-Arroita, et al., 2016). All these parameters combine into thousands of possible permutations: even if they could all be modelled, it would be nearly impossible for a manager to simultaneously compare their results by looking at thousands of plots and tables, and to intuitively choose the best one.

In such complex problems, optimization algorithms can be used to support human cognition. Formal optimization has long been applied to large-scale problems such as reserve design, leading to the development of systematic conservation planning (Margules & Pressey, 2000). However, such applications remain less common for small-scale, single-species problems like conservation translocations (Converse et al., 2013; Taylor et al., 2017). Applications are mostly limited to theoretical simplified examples or small single-population programs (e.g. Canessa et al., 2014; Helmstedt & Possingham, 2017; Rout et al., 2009; Tenhumberg et al., 2004), often forced to ignore parts of the problem, uncertainty and spatial aspects.

In this study, we show how optimization can be applied to a complex recovery plan across multiple years and sites, with different constraints and uncertainty sources. Focusing on the reintroduction of a critically endangered amphibian, we optimized the allocation of variable captive stocks to multiple candidate sites over several years, given limited budgets and complex management costs, and including parametric uncertainty and stochasticity both in biological dynamics and management effectiveness.

2 | MATERIALS AND METHODS

2.1 | Study species and decision context

The Montseny brook newt *Calotriton arnoldi* is an endemic amphibian which only occurs within a single watershed (Tordera river) in the Montseny massif in Catalonia, NE Spain. *C. arnoldi* is a stream-dwelling newt living along a total of less than 5 linear km of mountain streams, separated in two isolated subpopulations within the range (eastern and western). Given its small range and population size (estimated <2000 individuals across seven extant populations; Carranza & Martínez-Solano, 2009), and a range of threats including habitat loss and fragmentation, water extraction, invasive species and stochastic events, it is listed as Critically Endangered in the IUCN Red List (Carranza & Martínez-Solano, 2009) and included in Annex II of the EU Habitats Directive (92/43/EEC). To improve the species conservation status, the project LIFE Tritó Montseny (LIFE15 NAT/ES/000757) was implemented in the period 2016–2022, promoting a series of actions including in-situ habitat management (Guinart et al., 2022), legal protection and a large captive breeding and release program (www.lifetritomontseny.eu). Our study was conceived within this management context, with the aim of helping managers decide where, when and how many individuals to release over the next 10 years.

The objective was to design an optimal release strategy to maximize the overall population size of *C. arnoldi* in year 10 (2030), meeting the annual constraints of budget and number of captive-bred individuals available for release. The management team selected a total of 17 candidate sites (stream reaches) to establish new populations, all within the existing species' range in the Montseny massif, 10

in the western part of the species range and seven in the eastern part (Table S1). Because of genetic differences (Carranza & Amat, 2005; Valbuena-Ureña et al., 2013), these two subpopulations are managed independently and were treated separately throughout the study.

First, we built and parameterized population models for each candidate site, and defined the costs associated with establishing, reinforcing and monitoring new populations. Second, we developed an optimization algorithm and applied it to the demographic and cost models to identify the optimal release strategy.

2.2 | Demographic models and management costs

We represented each population using a simple logistic growth model

$$N_{t+1} = N_t + N_t\, r_{max} \frac{K - N_t}{K}, \tag{1}$$

reflecting density dependence as hypothesized for this species (Colomer et al., 2014) and observed in other stream-dwelling newts (Gill, 1979; Petranka & Sih, 1986; Vignoli et al., 2018). We parameterized the model using available evidence for *C. arnoldi* or for its sister species *C. asper* (ecologically broadly similar), and formally elicited expert judgement (Table 1).

We calculated r_{max} in Equation (1) as the natural logarithm of the finite annual population growth rate λ, in turn calculated by solving the two-stage Lotka–Euler equation

$$f = \frac{\lambda^\alpha \left(1 - \frac{s}{\lambda}\right)}{1 - \left(\frac{s}{\lambda}\right)^{\omega - \alpha + 1}} \tag{2}$$

(Lande, 1988), where s is adult survival, α and ω are age at first and last breeding respectively and f is recruitment (in our case the product of clutch size, sex ratio and larval and juvenile survival). For the parameter values in Table 1, the approximated solution was $\lambda \approx 1.155$ (range 1.085–1.201) and therefore $r_{max} \approx 0.144$ (range 0.082–0.183).

To simulate annual variability, we added further stochasticity around the realized growth rate in a given year, using a gamma distribution to simulate 1000 r values (these could include negative values to simulate stochastic population declines).

To calculate site-specific carrying capacities K in Equation (1), we first elicited site-specific potential densities per unit of habitat (linear m of stream) from 14 experts in the LIFE project team, a large group that ensured diversity in expertise, gender and age, as recommended by best practice for expert consultation (Sutherland & Burgman, 2015). We elicited estimates using the IDEA protocol (Hemming et al., 2018). For each parameter, we elicited minimum, most likely and maximum values (Table 1). We used these parameters to define a PERT distribution, a modified beta distribution widely used in risk analysis to fit expert-elicited subjective estimates, and defined by most likely, minimum and maximum values (Vose, 1996). We then drew 1000 values of density from that distribution, and multiplied them by the length of each site's stream reach (mean across sites 705 m, min–max 218–1591 m). This created a distribution of 1000 possible values of K for each site.

The number of individuals available for release each year (always subadults) was uncertain, reflecting fluctuations in captive productivity. Following discussion with captive breeding staff, we modelled this by sampling uniformly in the range 100–300, in increments of 50 (to reduce the number of options for the optimization, while ensuring a minimum release size), to create 1000 scenarios of annual release availability over the duration of the program. All candidate sites were assumed to be unoccupied by *C. arnoldi* at the beginning of the simulation. We assumed the minimum release at a new site would be 50 subadult individuals (2- or 3-year-old), as agreed by the management team for logistic and monitoring purposes. We considered that newly released individuals might incur additional mortality, a commonly observed phenomenon in conservation translocations (Armstrong & Reynolds, 2012; Bertolero et al., 2018; Cayuela et al., 2019), so we formally elicited this parameter (survival in the first year after release) as above. Elicitation showed the expert group was divided over two very different values, reflecting different expectations about the fitness of captive-bred individuals, for which

TABLE 1 Parameters used in the demographic model for each population. Mean and range values were obtained from literature or averaged across the expert group, then used to fit PERT distributions to reflect uncertainty. All estimates reflect 'ideal' conditions for *Calotriton arnoldi*, assuming sites would be restored adequately prior to any release

Parameter	Mean (range)	Source
Age at first breeding (years)	3.5 (3–4)	Montori (1988)
Age at last breeding (years)	13.5 (12–15)	Expert elicitation
Larval survival	0.023 (0.02–0.026)	Montori and Herrero (2004)
Clutch size	35 (30–40)	Montori et al. (2002)
Sex ratio	0.5	Montori (1988)
Juvenile survival	0.8	Colomer et al. (2014)
Adult survival	0.95 (0.92–0.98)	Montori (1990); expert elicitation
Adult survival (first year post-release)	0.179 or 0.678[a]	Expert elicitation
Density (N/m of stream)	0.87 (0.29–2.85)	Expert elicitation

aThe expert group was approximately split over these two possible mean values, so we ran simulations separately with both, instead of fitting a PERT distribution.

we have no empirical evidence in our system. We judged that imposing a 'consensus' value here, either by discussing a compromise or by taking the overall average value, could hide an important source of uncertainty (Martin et al., 2012). Therefore, we preferred to recognize this divergence of opinions and applied a sensitivity analysis approach by re-running the simulations using both mean values (Table 1). Finally, to represent uncertainty from all sources (carrying capacities, numbers available for release and realized growth rates), we combined the respective distributions described above to create 1000 scenarios. Each scenario was then solved in the optimization step of the analysis.

In addition to the demographic model, we worked with the management team to estimate the cost of reintroduction-related actions. To be suitable for releases, each site would require a specific set of habitat improvements (Guinart et al., 2022), ranging from 0 to 264,900 €, plus the corresponding one-off cost of 5,082 € for the first release. After a new site has received animals once, every additional release in subsequent years would cost 3,300 €. On top of these costs, each new population would need to be monitored intensively during the first year (4,400 €) and less intensively every following year (2,400 €). The team set two possible annual budgets: 15,000 and 20,000 €. Whenever this annual budget was not fully invested, we allowed surpluses to be used in subsequent years.

2.3 | Optimization

We used mixed integer linear programming to identify an optimal release strategy across the candidate sites for 10 years that maximizes the total population size at the end of year 10, subject to cost constraints, number of individuals available each year and carrying capacity of each site. We ran independent models for each subpopulation. Therefore, our optimization problem was:

$$Max \sum_{i \in I} v_{it_f}^{\pi}, \tag{3}$$

s.t.

$$\sum_{i \in I} x_{it}^{\pi} + q_t^{\pi} = b_t^{\pi} \, \forall t \in T; \, \forall \pi \in \Pi,$$

$$\sum_{i \in I} \left(y_{it}^{\pi} c_i + z_{it}^{\pi} cm_i + \left(w_{it}^{\pi} - z_{it}^{\pi} \right) cm_i' \right) \leq Bd \forall t \in T,$$

where $v_{it_f}^{\pi}$ is the population size of site i at the last optimization period ($t_f \in T$) for each of the 1000 simulated scenarios ($\pi \in \Pi$); c_i is the cost of opening site i (i.e. the cost of preparing the site and of the first release); cm_i is the cost of monitoring site i during the first period of time after release, cm_i' is the cost of monitoring site i after the first period of time; Bd is the budget available for period t; y_{it}^{π}, z_{it}^{π} and w_{it}^{π} are binary auxiliary variables that determine whether the different costs apply or not to a given unit and time period depending on the release of individuals. The opening cost only applies the first time that site i receives individuals, while monitoring costs apply recursively after that release,

being higher during the first period after release given the more intense monitoring needed during this period. See Supplementary material for more detail on these and other restrictions applied to make the model functional. We built the mathematical model using PySP (Watson et al., 2012), an extension of Pyomo that uses Python-based open-source optimization modelling language specifically designed for formulating stochastic programming optimization problems, and solved it using CPLEX (IBM, v12.6). All code is available at https://doi.org/10.5281/zenodo.7402277 (Salgado-Rojas, 2022), together with simulated data. Original data about populations and site locations are confidential, given the high risk of poaching and accidental introduction of pathogen by unauthorized visitors (Martel et al., 2020). This study did not require ethical approval or field permits.

We repeated the optimization for the two levels of postrelease survival (0.179 and 0.678; Table 1) and for the two levels of annual budget (15,000 and 20,000 €). Additionally, in the western subpopulation release sites for the first 2 years had already been determined by the management team at the time of our study, with releases due to begin in 2020. Therefore, we repeated the simulation for this subpopulation with and without 'fixing' these sites (i.e. the simulation was or was not forced to select them for releases in years 1–2).

3 | RESULTS

The optimal solution generally involved establishing populations at all suitable sites for which the opening costs were within the annual budget. Sites were mostly opened in consecutive years, that is, the algorithm preferred to start new populations as soon as possible, before reinforcing previously created ones. For example, in the western subpopulation, with a 15,000-€ budget, all new sites had already been opened by year 5 in 95% of simulations (Figure 1, Figure S1); with a 20,000-€ budget and the corresponding greater number of sites, new sites were mostly opened in the first 6 years (Figure 2, Figure S1). Because of budget constraints, it was also generally optimal to concentrate annual releases (new openings or reinforcements) at one or few sites: for example, for a 20,000-€ budget in the western subpopulation, less than 31% of scenarios involved releases at two or more sites in the same year. Finally, for both subpopulations optimal solutions were highly robust to variation among experts, even for the two different values of postrelease survival: site selections and release strategies were identical, and there were only very small quantitative differences in the numbers released and final outcomes (Figures S5–S7; all other figures and results refer to aggregate simulation outcomes for both values).

3.1 | Western subpopulation

For the western subpopulation, the optimal strategy under a 15,000-€ budget involved releases at sites 5–6 (fixed in the simulation) and predominantly site 8 (Figure 3a), for a maximum of three sites in 99% of scenarios and a mean total population in year 10 of
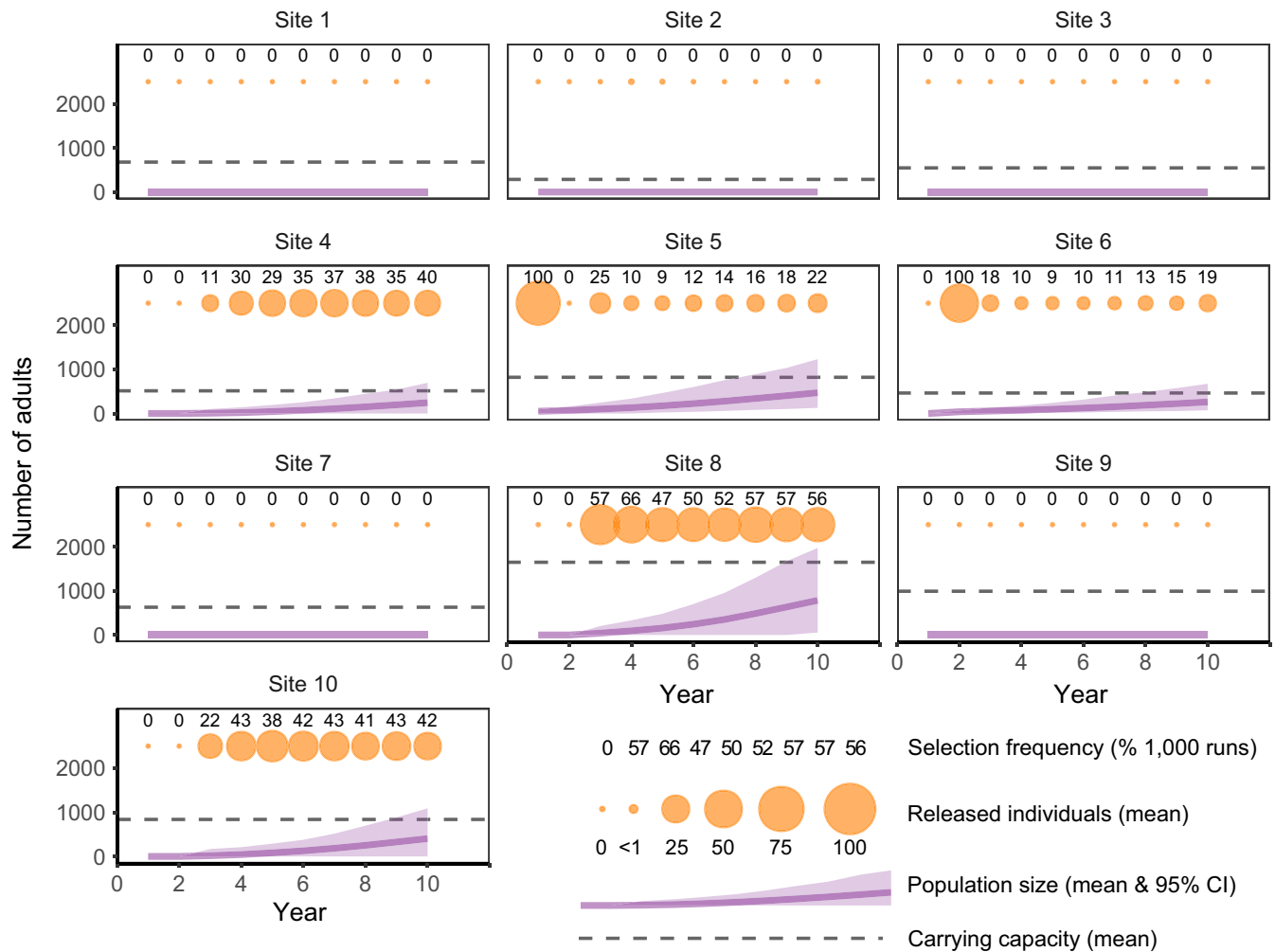
FIGURE 1 Site- and year-level demographics for the western subpopulation of *Calotriton arnoldi*, under the optimal strategy for a 20,000-€ budget. Plots indicate selection frequency (labels), mean number of released animals (circles), mean and 95% confidence intervals of the population size (solid line and shaded bands) and mean carrying capacity (dashed line). Sites 5–6 were fixed for release in years 1–2 to match predetermined real-world plans; for the unconstrained results, see Figure 2. For the eastern subpopulation, see Figure S3.

1760 newts (95% CI 473–4663). Increasing to a 20,000-€ annual budget expanded releases to sites 4 and/or 10 (Figure 3b), to a maximum of five new populations in 94% of scenarios and a mean total population in year 10 of 2165 newts (95% CI 573–5638; Figure 1). When facing the smaller budget, the algorithm discarded sites for which opening costs were no longer within the budget, and favoured more frequent and numerous releases at sites with high carrying capacity (Figure 1).

When we relaxed the fixed releases at sites 5–6 for years 1–2 and let the algorithm find the unconstrained optimal strategy, results changed only partly (Figure 2; note these differences only concern the western subpopulation). There was no change in the optimal total number of sites (3 and 5 for low and high budgets respectively) or in the quick opening strategy (Figure 3c,d). On the other hand, the sites of choice and their opening sequence changed: for example, site 6 was never selected, and site 5 was rarely chosen in the first year of releases (Figure 3c,d). Moreover, when not constrained for the first 2 years, in 9% of runs the algorithm was able to open

two sites simultaneously in year 1 (Figure 3d). Most importantly, the "free" strategy provided a greater final population size (Figure 2): for the low and high budgets respectively, mean N = 2113 (95% CI 545–5526) and N = 2410 (95% CI 647–6171).

3.2 | Eastern subpopulation

In the eastern subpopulation optimal strategies only involved two sites (1 and 5; Figures S2 and S3), which were selected in the same order in all scenarios (Figure S2) and rapidly opened (in 90% of scenarios both populations had already been established by year 6). This solution did not change with budget (Figures S2 and S3), because sites were mostly selected based on the initial cost—which for the discarded sites remained beyond either budget level—rather than of the subsequent monitoring. For this subpopulation, the mean total population in year 10 was 1162 newts (95% CI 259–3019) under either budget level.
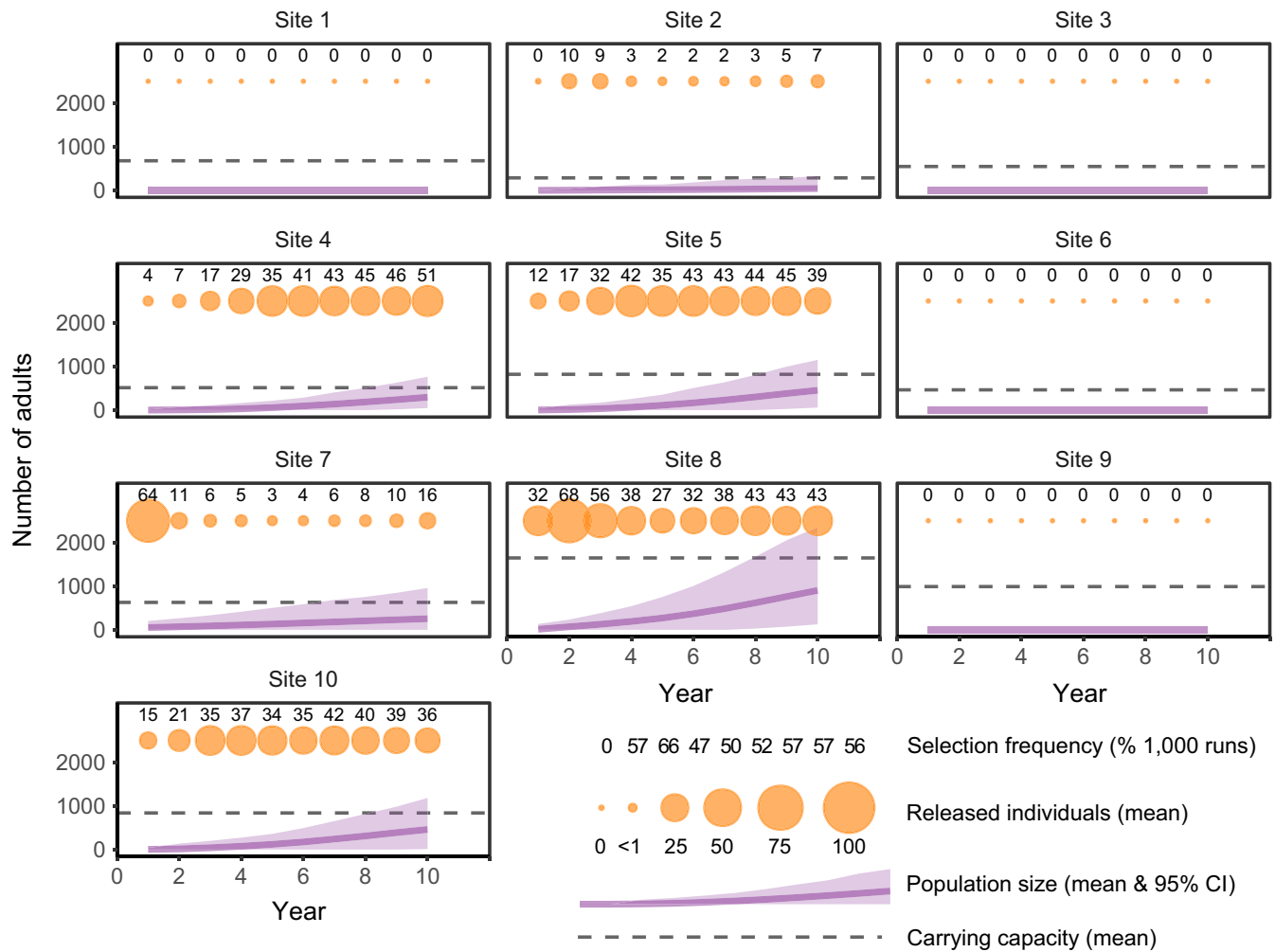
FIGURE 2 Site- and year-level demographics for the western subpopulation of *Calotriton arnoldi*, under the optimal strategy for a 20,000-€ budget and unconstrained site selection (cf. Figure 1). Plots indicate selection frequency (labels), mean number of released animals (circles), mean and 95% confidence intervals of the population size (solid line and shaded bands) and mean carrying capacity (dashed line). For the eastern subpopulation, see Figure S3.
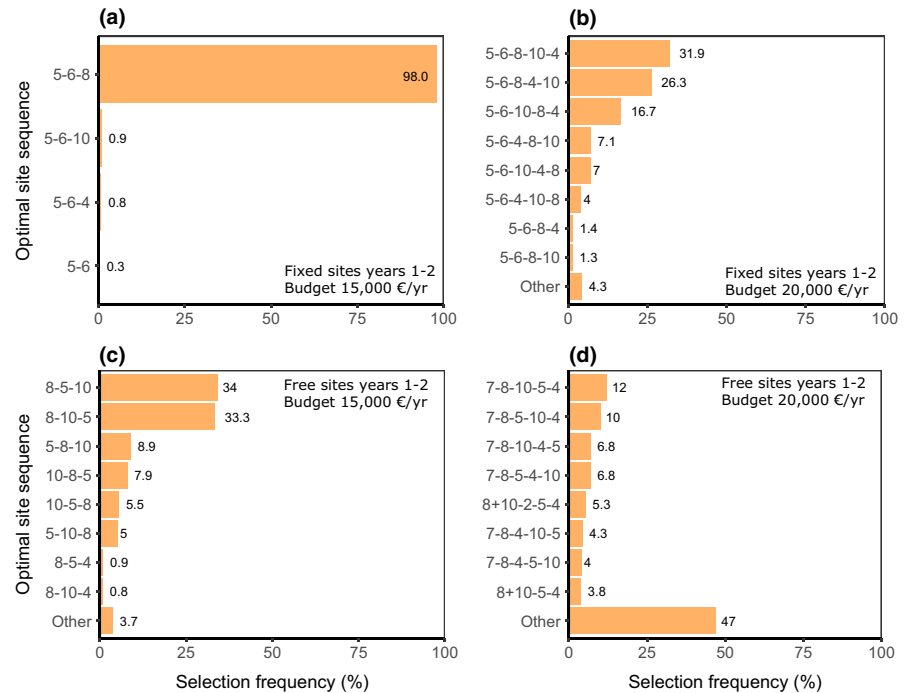
4 | DISCUSSION

The results of our study illustrate the need and potential for optimal planning in species recovery programs. For recovery plans that require the release of animals, optimization can especially help to account for both pre- and postrelease management efforts and costs. To achieve this aim, models need to be complex enough to be believable, but not so much as to be unwieldy (Converse et al., 2013; McGowan et al., 2020). Finding this balance requires participation and information sharing between stakeholders, managers and scientists (Lees et al., 2021). These multiple aspects are important because results and decisions are likely to be highly context dependent. In our case, for the western *C. arnoldi* subpopulation, the optimal sequence of sites for release varied depending on the exact available budget and predetermined constraints. Conversely, for the eastern subpopulation the optimal solution was straightforward and robust to current uncertainty and budget estimates. In the following sections, we discuss both those local results and general implications.

4.1 | Optimizing conservation translocations

The optimal release strategy for *C. arnoldi* was influenced by constraints in multiple ways. First, the available budget heavily influenced results for the western *C. arnoldi* subpopulation. Opening costs had the greatest effect, determining which sites were ruled out from the beginning, and forcing new sites to be opened one at a time. As long as sites were within the annual budget, the optimization prioritized the sites with the greatest carrying capacity, to allow the greatest population growth before the end of the 10 years. In this sense, having a smaller budget simplified the decision problem by putting some sites beyond reach; indeed, the optimal solution was much more variable for the higher budget levels (Figure 1).

We also allowed the algorithm to spend the full budget every year, which encouraged opening new sites that might contribute at least in part to the final outcome. Results might have changed if we had framed this constraint differently, for example as minimizing total cost rather than meeting a set budget (Chauvenet et al., 2016). The relationship between

FIGURE 3 Frequency of selection of the optimal sequence of releases, over 1000 scenarios, for the western *Calotriton arnoldi* subpopulation, for annual budgets of (a–c) 15,000 and (b–d) 20,000 €. In plots (a) and (b), sites 5–6 were fixed for release in years 1–2 to match predetermined real-world plans; in plots (b)–(d), this constraint was removed. In plot (d), 8 + 10 indicates both sites received animals in the same year. For the eastern subpopulation, strategy 1–5 was selected in 100% of scenarios under either budget (Figures S2 and S3).

(a) Fixed sites years 1-2, Budget 15,000 €/yr

Optimal site sequence	Selection frequency (%)
5-6-8	98.0
5-6-10	0.9
5-6-4	0.8
5-6	0.3

(b) Fixed sites years 1-2, Budget 20,000 €/yr

Optimal site sequence	Selection frequency (%)
5-6-8-10-4	31.9
5-6-8-4-10	26.3
5-6-10-8-4	16.7
5-6-4-8-10	7.1
5-6-10-4-8	7
5-6-4-10-8	4
5-6-8-4	1.4
5-6-8-10	1.3
Other	4.3

(c) Free sites years 1-2, Budget 15,000 €/yr

Optimal site sequence	Selection frequency (%)
8-5-10	34
8-10-5	33.3
5-8-10	8.9
10-8-5	7.9
10-5-8	5.5
5-10-8	5
8-5-4	0.9
8-10-4	0.8
Other	3.7

(d) Free sites years 1-2, Budget 20,000 €/yr

Optimal site sequence	Selection frequency (%)
7-8-10-5-4	12
7-8-5-10-4	10
7-8-10-4-5	6.8
7-8-5-4-10	6.8
8+10-2-5-4	5.3
7-8-4-10-5	4.3
7-8-4-5-10	4
8+10-5-4	3.8
Other	47

the number and size of populations, and how much money is available and how freely it can be allocated, highlights an additional consideration. Under an annual budget threshold, when money was reduced the model was forced to concentrate on fewer sites, as others could no longer be opened. However, having fewer populations increases stochastic risks, for example by extreme climatic events or disease incursions, particularly relevant threats for *C. arnoldi* (Colomer et al., 2014; Martel et al., 2020).

Although opening new sites would increase monitoring costs in the following years, this was not a major constraint in our case. Initial monitoring was expensive, which further limited our ability to open multiple sites simultaneously. However, because the total number of sites was constrained by opening costs anyway, after all those sites had been opened total monitoring costs for the following years usually remained within budget. On the other hand, this also meant all new sites should be opened as soon as possible, before the budget already had to include ongoing monitoring. The clearest example was the consistent selection of one of the sites (site 7) in the first year of the unconstrained optimization for the western population, for the higher budget level (Figure 3d, Figure S3). This site did not have the highest carrying capacity, but the algorithm consistently selected it first because its opening cost alone was close to the budget limit, meaning that it could not be combined with any ongoing monitoring. Fixing releases for the first 2 years effectively removed this desirable site from the feasible options (Figure 3b).

The allocation of budget to acting or learning is a realistic problem for translocations, where monitoring is both highly necessary and difficult to maintain long term (Canessa, Genta, et al., 2016; Sutherland et al., 2010). An optimization approach helped us find a clear solution to this trade-off. It should also encourage managers to carefully cost all actions (Iacona et al., 2018) and to consider the purpose of monitoring, for subsequent decisions and appraisal of success (Lyons et al., 2008; Nichols & Armstrong, 2012).

As a further constraint, when we started the study, release sites in the western subpopulation for the first 2 years had already been decided, and we implemented this constraint in the optimization. When we relaxed the constraint, optimal strategies followed the same pattern of early openings and ultimately resulted in the same number of populations. However, the choice of sites and sequence of releases differed: even removing this partial constraint (i.e. allowing free choice of sites in years 1–10, rather than just 3–10), we estimated that the optimal strategy could have improved the final population size by 15%–20%, with proportionally greater benefits in the case of a smaller budget.

These differences between ideal strategies and actual constraints highlight the need to strike a balance between realism and utility. Teams might not be able to freely decide every detail of a release strategy; in our case, the main constraint to selection of sites for the initial years was access to some sites located on private property, which was still being negotiated and dictated the 'locked-in' strategy we implemented in our models, even if it meant a 20% loss in effectiveness as shown by our results. In other situations, funding might be locked in for specific actions and impossible to reallocate at will (Wu et al., 2021), while some release strategies might be impractical or perceived as too risky to even contemplate (Ferrière et al., 2020). On one hand, constraining the optimization to predetermined strategies and decision criteria can increase its realism and facilitate its uptake by managers. On the other hand, restrictions can reduce the potential of desk-based optimization to safely explore extreme scenarios, which can provide useful and even unexpected insights for the whole decision-making process (Garrard et al., 2017). Finding this balance requires close work between managers and scientists to best combine expert judgements and algorithms, and flexibility and trust to be able to modify both analyses and management in a participatory approach (Lees et al., 2021).

Our optimization approach could also be further refined, particularly as regards uncertainty. The ideal extension of our model would

be to implement a fully stochastic model to better represent uncertainty in this dynamic system (Shoo et al., 2021). We represented uncertainty as 1000 scenarios, and the algorithm found the optimal strategy for each scenario independently, assuming perfect knowledge of the system: in other words, what we would do if we knew which scenario we were in. We repeated this 1000 times to find 1000 optimal strategies, and averaged *across strategies*. However, realistically managers are likely to face uncertainty at every step, because the system is both poorly known (e.g. uncertain survival estimates), and fluctuates randomly (e.g. annual demographic stochasticity). In this case, it might be more informative to find one optimal strategy *across scenarios*, in other words, a solution that already accounts for the uncertainty we face in each year, and for the possible effects of learning (Rout et al., 2009; Runge, 2013). This adaptive approach could also highlight key uncertainties, that is, those parameters for which further research would be most beneficial (Canessa et al., 2015). However, we could not implement such a process in our analyses because it would far exceed the available computing power, a well-known barrier in realistic implementation of adaptive management using optimization techniques (Péron et al., 2020).

4.2 | Lessons for implementation

As recovery plans require more numerous, urgent and complex decisions, but resources remain limited, optimization will become increasingly necessary. This need is explicitly recognized, for example, in the IUCN Guidelines for Conservation Planning (IUCN, 2017) and for Conservation Translocations (IUCN, 2013). However, the development of a conservation plan can be a time-consuming process that requires willingness to engage, patience and good communication on all sides (Wright et al., 2020). Cutting this process short may end up producing a tool that is not quantitatively adequate and might not address a real management need.

Collaboration is especially important where an optimization approach requires programming skills that at first might seem daunting to many recovery groups, especially since increasing complexity and realism will require at least some customized code. This barrier is well known but is already receding, as conservation broadens its skillset and interacts more deeply with computer science and technology (Toomey et al., 2017; Valle & Berdanier, 2012). In our case, multiple meetings between programmers, technicians, managers and other team members took place to understand the decision context, develop a reasonably realistic model, elicit parameters and interpret results, producing additional quantitative and visual aids like tables and maps. Teams should also be open to constant revision of model assumptions and parameters. For example, recent analysis of monitoring data for *C. arnoldi* appears to confirm the survival estimates used in the model (A. Montori, pers. comm.). Regular revisions, not only of estimates but also of the general planning and decision context, will be especially important in the long term for *C. arnoldi*, considering the potential negative effects of changes in land use and climate (Colomer et al., 2014) and the extreme range restriction of the species.

This type of collaboration cannot rely on goodwill alone, but should be facilitated as much as possible by management and funding frameworks (Addison et al., 2013). In our case, the longer timeframe of the EU LIFE program for *C. arnoldi* gave us time to develop the model. However, the LIFE framework itself does not always facilitate optimal planning: for example, the funding application requires a priori specification of release cohorts, which, when the time of implementation comes, might differ from the optimal state-dependent solutions. If managers are asked to justify in detail such deviations, they might opt for a more conservative strategy of sticking to the initial plan, leading to suboptimal decisions (Canessa et al., 2020; Ritov & Baron, 1992). An option for improvement might be to grant selected programs a preliminary period to develop an optimal plan which, if funded, can then be implemented in subsequent years. Providing such frameworks could be a key step in reducing the implementation gap between optimal planning and common practice (Wright et al., 2020).

By applying an optimization algorithm to translocation planning for *C. arnoldi*, we were able to provide general recommendations for a complex problem with multiple objectives, constraints and uncertainty across locations and years. Optimizing real-world conservation programs means finding the ideal balance between realism and generality, to ensure that solutions match real needs and constraints, but also that the whole optimization process truly helps managers explore the decision space. Close collaboration between managers and scientists is key to realizing these benefits.

CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

All data, including code and simulated data, are available at Zenodo via https://doi.org/10.5281/zenodo.7402277 (Salgado-Rojas, 2022). Original data about populations and site locations are confidential, given the high risk of poaching and accidental introduction of pathogens by unauthorized visitors.

ORCID

Stefano Canessa https://orcid.org/0000-0002-0932-826X
Dani Villero https://orcid.org/0000-0002-5562-3809
Lluís Brotons https://orcid.org/0000-0002-4826-4457
Virgilio Hermoso https://orcid.org/0000-0003-3205-5033

REFERENCES

Addison, P. F., Rumpff, L., Bau, S. S., Carey, J. M., Chee, Y. E., Jarrad, F. C., McBride, M. F., & Burgman, M. A. (2013). Practical solutions for making models indispensable in conservation decision-making. *Diversity and Distributions*, 19, 490–502.

Armstrong, D. P., & Reynolds, M. H. (2012). Modelling reintroduced populations: The state of the art and future directions. In J. G. Ewen, D. P. Armstrong, K. A. Parker, & P. J. Seddon (Eds.), *Reintroduction biology: Integrating science and management* (pp. 165–222). John Wiley & Sons, Ltd.

Bertolero, A., Pretus, J. L., & Oro, D. (2018). The importance of including survival release costs when assessing viability in reptile translocations. *Biological Conservation*, 217, 311–320.

Bozzuto, C., Hoeck, P., Bagheri, H., & Keller, L. (2017). Modelling different reintroduction strategies for the critically endangered Floreana mockingbird. *Animal Conservation*, 20, 144–154.

Canessa, S., Genta, P., Jesu, R., Lamagni, L., Oneto, F., Salvidio, S., & Ottonello, D. (2016). Challenges of monitoring reintroduction outcomes: Insights from the conservation breeding program of an endangered turtle in Italy. *Biological Conservation*, 204, 128–133.

Canessa, S., Guillera-Arroita, G., Lahoz-Monfort, J. J., Southwell, D. M., Armstrong, D. P., Chadès, I., Lacy, R. C., & Converse, S. J. (2015). When do we need more data? A primer on calculating the value of information for applied ecologists. *Methods in Ecology and Evolution*, 6, 1219–1228.

Canessa, S., Guillera-Arroita, G., Lahoz-Monfort, J. J., Southwell, D. M., Armstrong, D. P., Chadès, I., Lacy, R. C., & Converse, S. J. (2016). Adaptive management for improving species conservation across the captive-wild spectrum. *Biological Conservation*, 199, 123–131.

Canessa, S., Hunter, D., McFadden, M., Marantelli, G., & McCarthy, M. A. (2014). Optimal release strategies for cost-effective reintroductions. *Journal of Applied Ecology*, 51, 1107–1115.

Canessa, S., Taylor, G., Clarke, R. H., Ingwersen, D., Vandersteen, J., & Ewen, J. G. (2020). Risk aversion and uncertainty create a conundrum for planning recovery of a critically endangered species. *Conservation Science and Practice*, 2, e138.

Carranza, S., & Amat, F. (2005). Taxonomy, biogeography and evolution of *Euproctus* (Amphibia: Salamandridae), with the resurrection of the genus *Calotriton* and the description of a new endemic species from the Iberian Peninsula. *Zoological Journal of the Linnean Society*, 145, 555–582.

Carranza, S., & Martínez-Solano, I. (2009). *Calotriton arnoldi*. The IUCN red list of threatened species. https://www.iucnredlist.org/species/136131/4246722

Cayuela, H., Gillet, L., Laudelout, A., Besnard, A., Bonnaire, E., Levionnois, P., Muths, E., Dufrêne, M., & Kinet, T. (2019). Survival cost to relocation does not reduce population self-sustainability in an amphibian. *Ecological Applications*, 29, e01909.

Chauvenet, A. L., Canessa, S., & Ewen, J. G. (2016). Setting objectives and defining the success of reintroductions. In D. S. Jachowski, P. Angermeier, R. Slotow, & J. Millspaugh (Eds.), *Reintroduction of fish and wildlife population*. California Press.

Colomer, M. À., Montori, A., García, E., & Fondevila, C. (2014). Using a bioinspired model to determine the extinction risk of *Calotriton asper* populations as a result of an increase in extreme rainfall in a scenario of climatic change. *Ecological Modelling*, 281, 1–14.

Converse, S. J., Moore, C. T., & Armstrong, D. P. (2013). Demographics of reintroduced populations: Estimation, modeling, and decision analysis. *The Journal of Wildlife Management*, 77, 1081–1093.

Ferrière, C., Zuël, N., Ewen, J. G., Jones, C. G., Tatayah, V., & Canessa, S. (2020). Assessing the risks of changing ongoing management of endangered species. *Animal Conservation*, 24, 153–160.

Game, E. T., Meijaard, E., Sheil, D., & McDonald-Madden, E. (2014). Conservation in a wicked complex world; challenges and solutions. *Conservation Letters*, 7, 271–277.

Garrard, G. E., Rumpff, L., Runge, M. C., & Converse, S. J. (2017). Rapid prototyping for decision structuring: An efficient approach to conservation decision analysis. In N. Bunnefeld, E. Nicholson, & E. Milner-Gulland (Eds.), *Decision-making in conservation and natural resource management: Models for interdisciplinary approaches* (p. 46). Cambridge University Press.

Gill, D. E. (1979). Density dependence and homing behavior in adult red-spotted newts *Notophthalmus viridescens* (Rafinesque). *Ecology*, 60, 800–813.

Guinart, D., Solórzano, S., Amat, F., Grau, J., Fernández-Guiberteau, D., & Montori, A. (2022). Habitat management of the endemic and critical endangered Montseny brook newt (*Calotriton arnoldi*). *Land*, 11, 449.

Helmstedt, K. J., & Possingham, H. (2017). Costs are key when reintroducing threatened species to multiple release sites. *Animal Conservation*, 20, 331–340.

Hemming, V., Burgman, M. A., Hanea, A. M., McBride, M. F., & Wintle, B. C. (2018). A practical guide to structured expert elicitation using the IDEA protocol. *Methods in Ecology and Evolution*, 9, 169–180.

Hermoso, V., Pantus, F., Olley, J., Linke, S., Mugodo, J., & Lea, P. (2012). Systematic planning for river rehabilitation: Integrating multiple ecological and economic objectives in complex decisions. *Freshwater Biology*, 57, 1–9.

Iacona, G. D., Sutherland, W. J., Mappin, B., Adams, V., Armsworth, P. R., Coleshaw, T., Cook, C., Craigie, I., Dicks, L., & Fitzsimons, J. A. (2018). Standardized reporting of the costs of management interventions for biodiversity conservation. *Conservation Biology*, 32, 979–988.

IUCN. (2013). *Guidelines for reintroductions and other conservation translocations*. IUCN Species Survival Commission.

IUCN. (2017). *Guidelines for species conservation planning*. IUCN Species Survival Commission.

Lande, R. (1988). Demographic models of the northern spotted owl (*Strix occidentalis caurina*). *Oecologia*, 75, 601–607.

Lees, C., Rutschmann, A., Santure, A., & Beggs, J. (2021). Science-based, stakeholder-inclusive and participatory conservation planning helps reverse the decline of threatened species. *Biological Conservation*, 260, 109194.

Lyons, J. E., Runge, M. C., Laskowski, H. P., & Kendall, W. L. (2008). Monitoring in the context of structured decision-making and adaptive management. *The Journal of Wildlife Management, 72*, 1683–1692.

Margules, C. R., & Pressey, R. L. (2000). Systematic conservation planning. *Nature, 405*, 243–253.

Martel, A., Vila-Escalé, M., Fernández-Guiberteau, D., Martinez-Silvestre, A., Canessa, S., Van Praet, S., Pannon, P., Chiers, K., Ferran, A., Kelly, M., Picart, M., Piulats, D., Li, Z., Pagone, V., Pérez-Sorribes, L., Molina, C., Tarragó-Guarro, A., Velarde-Nieto, R., Carbonell, R., … Pasmans, F. (2020). Integral chain management of wildlife diseases. *Conservation Letters, 13*, e12707.

Martin, T. G., Burgman, M. A., Fidler, F., Kuhnert, P. M., Low-Choy, S., McBride, M., & Mengersen, K. (2012). Eliciting expert knowledge in conservation science. *Conservation Biology, 26*, 29–38.

McGowan, C., Lyons, J., & Smith, D. (2020). Decision implementation and the double-loop process in adaptive management of horseshoe crab harvest in Delaware Bay. In M. C. Runge, S. J. Converse, J. E. Lyons, & D. R. Smith (Eds.), *Structured decision making: Case studies in natural resource management* (pp. 258–268). John Hopkins University Press.

Milner-Gulland, E., & Shea, K. (2017). Embracing uncertainty in applied ecology. *Journal of Applied Ecology, 54*, 2063–2068.

Montori, A. (1988). *Estudio sobre la biología y ecología del tritón pirenaico Euproctus asper (Duges, 1852) en la Cerdanya.* (PhD thesis). Universitat de Barcelona.

Montori, A. (1990). Skeletochronological results in the pyrenean newt *Euproctus asper* (Dugès, 1852) from one prepyrenean population. *Annales des Sciences Naturelles—Zoologie et Biologie Animale, 11*, 209–211.

Montori, A., & Herrero, P. (2004). Caudata. In M. A. Ramos (Ed.), *Amphibia, Lissamphibia* (pp. 43–275). Museo Nacional de Ciencias Naturales, CSIC.

Montori, A., Llorente, G., Santos, X., & Carretero, M. (2002). *Euproctus asper* (Dugs, 1852). Tritón pirenaico. *Atlas y Libro Rojo de los Anfibios y Reptiles de España.*

Nichols, J. D., & Armstrong, D. P. (2012). Monitoring for reintroductions. In J. G. Ewen, D. P. Armstrong, K. A. Parker, & P. J. Seddon (Eds.), *Reintroduction biology: Integrating science and management* (pp. 223–255). John Wiley & Sons, Ltd.

Péron, M., Baker, C. M., Hughes, B. D., & Chadès, I. (2020). A continuous time formulation of stochastic dual control to avoid the curse of dimensionality. *arXiv preprint arXiv:2004.13295.*

Petranka, J. W., & Sih, A. (1986). Environmental instability, competition, and density-dependent growth and survivorship of a stream-dwelling salamander. *Ecology, 67*, 729–736.

Pullin, A. S., Knight, T. M., Stone, D. A., & Charman, K. (2004). Do conservation managers use scientific evidence to support their decision-making? *Biological Conservation, 119*, 245–252.

Ritov, I., & Baron, J. (1992). Status-quo and omission biases. *Journal of Risk and Uncertainty, 5*, 49–61.

Rout, T. M., Hauser, C. E., & Possingham, H. P. (2009). Optimal adaptive management for the translocation of a threatened species. *Ecological Applications, 19*, 515–526.

Runge, M. C. (2013). Active adaptive management for reintroduction of an animal population. *The Journal of Wildlife Management, 77*, 1135–1144.

Salgado-Rojas, J. (2022). Data from: Designing an optimal large-scale reintroduction plan for a critically endangered species. *Zenodo,* https://doi.org/10.5281/zenodo.7402277

Schaub, M., Zink, R., Beissmann, H., Sarrazin, F., & Arlettaz, R. (2009). When to end releases in reintroduction programmes: Demographic rates and population viability analysis of bearded vultures in the Alps. *Journal of Applied Ecology, 46*, 92–100.

Scheele, B. C., Legge, S., Armstrong, D., Copley, P., Robinson, N., Southwell, D., Westgate, M. J., & Lindenmayer, D. B. (2018). How to improve threatened species management: An Australian perspective. *Journal of Environmental Management, 223*, 668–675.

Schwartz, M. W., Cook, C. N., Pressey, R. L., Pullin, A. S., Runge, M. C., Salafsky, N., Sutherland, W. J., & Williamson, M. A. (2018). Decision support frameworks and tools for conservation. *Conservation Letters, 11*, e12385.

Shoo, L. P., Catterall, C. P., Beyer, H. L., Cockbain, P., Duncan, M., Robson, T., Roche, D., Taylor, H., White, Z., & Wilson, K. (2021). Smart allocation of restoration funds over space and time. *Ecological Applications, 31*, e02448.

Sutherland, W. J., Armstrong, D. P., Butchart, S. H., Earnhardt, J. M., Ewen, J. G., Jamieson, I. G., Jones, C. G., Lee, R., Newbery, P., & Nichols, J. D. (2010). Standards for documenting and monitoring bird reintroduction projects. *Conservation Letters, 3*, 229–235.

Sutherland, W. J., & Burgman, M. A. (2015). Policy advice: Use experts wisely. *Nature, 526*, 317–318.

Taylor, G., Canessa, S., Clarke, R. H., Ingwersen, D., Armstrong, D. P., Seddon, P. J., & Ewen, J. G. (2017). Is reintroduction biology an effective applied science? *Trends in Ecology & Evolution, 32*, 873–880.

Tenhumberg, B., Tyre, A. J., Shea, K., & Possingham, H. P. (2004). Linking wild and captive populations to maximize species persistence: Optimal translocation strategies. *Conservation Biology, 18*, 1304–1314.

Toomey, A. H., Knight, A. T., & Barlow, J. (2017). Navigating the space between research and implementation in conservation. *Conservation Letters, 10*, 619–625.

Valbuena-Ureña, E., Amat, F., & Carranza, S. (2013). Integrative phylogeography of *Calotriton* newts (Amphibia, Salamandridae), with special remarks on the conservation of the endangered Montseny brook newt (*Calotriton arnoldi*). *PLoS ONE, 8*, e62542.

Valle, D., & Berdanier, A. (2012). Computer programming skills for environmental sciences. *The Bulletin of the Ecological Society of America, 93*, 373–389.

Vignoli, L., Velletrani, F., Venditti, C., Luiselli, L., Yadid, Y., & Macale, D. (2018). Short, medium and long-term effects of density on the demographic traits of a threatened newt. *Ecological Research, 33*, 1039–1048.

Vose, D. (1996). *Quantitative risk analysis: A guide to Monte Carlo simulation modelling.* John Wiley & Sons Ltd.

Walsh, J. C., Dicks, L. V., & Sutherland, W. J. (2015). The effect of scientific evidence on conservation practitioners' management decisions. *Conservation Biology, 29*, 88–98.

Watson, J.-P., Woodruff, D. L., & Hart, W. E. (2012). PySP: Modeling and solving stochastic programs in python. *Mathematical Programming Computation, 4*, 109–149.

Wright, A. D., Bernard, R. F., Mosher, B. A., O'Donnell, K. M., Braunagel, T., DiRenzo, G. V., Fleming, J., Shafer, C., Brand, A. B., & Zipkin, E. F. (2020). Moving from decision to action in conservation science. *Biological Conservation, 249*, 108698.

Wu, C. H., Dodd, A. J., Hauser, C. E., & McCarthy, M. A. (2021). Reallocating budgets among ongoing and emerging conservation projects. *Conservation Biology, 35*, 955–966.

SUPPORTING INFORMATION

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