Optimal release strategies for cost-effective reintroductions

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Running title:

Optimal releases for reintroductions
Summary

1. Ex-situ programmes for endangered species generally focus on two objectives: insurance against extinction and reintroduction. Releases influence the size of captive and wild populations and may present managers with a trade-off between the two objectives. This can be further complicated when considering the costs of the captive population and the possible release of different life stages.

2. We approached this decision problem by combining population models and decision-analytic methods. We assessed the reintroduction program for the southern Corroboree frog *Pseudophryne corroboree* in Australia. We identified the optimal release rates of eggs and sub-adults that would achieve management objectives for two scenarios: a long-term program for a stable-age-distributed captive population and a short-term program with non-stable age distribution and realistic resource constraints. We accounted for parametric uncertainty and demographic stochasticity, testing the sensitivity of our results to post-release changes in the vital rates of individuals.

3. Assuming a stable age distribution, large proportions of individuals could be released without depleting the captive population. The optimal strategy was sensitive to the post-release survival of both life stages, but sub-adult releases were generally most effective, producing a large wild population and requiring a cheaper captive one. Egg releases were optimal for high expected juvenile survival, whereas mixed releases of both life stages were never optimal.

4. In the short-term realistic scenario, sub-adult releases also produced the largest wild population, but they required a large increase in the size and cost of the captive population that exceeded the available budget. Egg releases were cheaper but less effective, whereas joint releases of both life stages provided better returns, meeting budget constraints without depleting the captive population.
57.  **Synthesis and application.** Optimal release strategies reflect the trade-offs between
insurance and reintroduction objectives, and depend on the vital rates of the released
individuals. Although focusing on a single life stage may have practical advantages, in
real programs mixed strategies can allow managers to find the optimal combination
between the relative advantages of releasing early and late life stages.

62.  **Keywords**

63.  Age structure; amphibian; captive breeding; cost-effective; growth rate; Leslie matrix;

64.  optimisation; population viability analysis; uncertainty; zoo.
Introduction

Reintroductions from captive-bred individuals remain a controversial conservation tool, with generally low success rates against high required costs and effort (Snyder et al. 1996; Fischer & Lindenmayer 2000). However, they may represent the last resort for species at imminent risk of extinction, particularly when threats cannot be abated by in-situ conservation alone (Balmford, Mace & Leader-Williams 1996; Bowkett 2009). Captive programs generally focus on two fundamental objectives: establishing insurance populations to minimize the short-term risk of extinction, and reintroducing individuals in the wild (Armstrong & Seddon 2008). In the short term, large captive populations will have a greater insurance value; in the long term, they will allow an increase in the number of individuals released, which can improve the success rate of reintroduction attempts (Griffith et al. 1989; Fischer & Lindenmayer 2000). However, releases can deplete the captive population, potentially generating a trade-off between the “insurance” and “reintroduction” objectives. Decisions may also be complicated by resource constraints: for example, large captive populations can increase management costs (often already high for ex-situ conservation programmes: Lindburg 1992; Snyder et al. 1996; Bowkett 2009).

The cost of the captive population can also vary depending on the length of time that individuals spend in captivity, for example if individuals must reach adulthood before release. Releasing early life stages may represent a cheaper option, as they need to be retained in captivity for less time: however, they generally have lower survival (Sarrazin & Legendre 2000). Conversely, individuals released as adults may have higher survival: however, they will spend more time in captivity, resulting in higher costs. Therefore, the vital rates of the respective life stages will influence the trade-offs associated with the choice of actions (which life stage to release) and the importance of fundamental objectives (insurance and reintroduction).
In the context of captive breeding programmes, the time spent in captivity can further influence the trade-offs between release strategies. Several studies have shown an immediate post-release reduction in vital rates, especially mortality, across different taxa (reviews by Fischer & Lindenmayer 2000; Jule, Leaver & Lea 2008; McCarthy, Armstrong & Runge 2012). Retaining juveniles in captivity may bypass natural selection and favour traits that are advantageous for captivity but detrimental after release. This process of adaptation to captivity has been shown to occur within a few generations in several taxa, including amphibians (Kraaijeveld-Smit et al. 2006). Later life stages may thus incur greater post-release effects in species in which the incidence of selection affects mainly early stages, such as amphibians (Wells 2007).

In this study, we show how population models can be incorporated in a decision-analytic framework to assess the consequences of release strategies in the face of uncertainty and multiple objectives, when dealing with species with complex life histories. We applied our approach to an on-going program for a critically endangered amphibian. We identified the optimal release rates for eggs or sub-adults of the species, in regard to both insurance and reintroduction objectives, accounting for management costs and parametric uncertainty.

Under a long-term program, assuming a captive population with constant size and stable age distribution, large releases of sub-adults were the optimal choice. Conversely, for a short-term release plan mixed releases of variable proportions of both eggs and sub-adults provided larger and cheaper wild and captive populations.

**Methods**

*Matrix population model*
In a stage-structured population model, the vector $N_{(t+1)}$ of stage-specific abundances at a time $t+1$ can be described as the product of the vector $N_{(t)}$ of abundances in the previous time step and the transition matrix $L$:

$$N_{(t+1)} = N_{(t)} L = N_{(t)} \begin{pmatrix} f_1 & f_2 & \cdots & f_j \\ s_{11} & s_{21} & \cdots & s_{1j} \\ s_{12} & s_{22} & \cdots & s_{1j} \\ \vdots & \vdots & \ddots & \vdots \\ s_{1j} & s_{2j} & \cdots & s_{jj} \end{pmatrix}$$

Eq. 1

where $f_j$ is the reproductive output of individuals in age class $j$, and $s_{ij}$ is the probability of transitioning (survival) from stage $i$ to stage $j$ (Crouse, Crowder & Caswell 1987; Caswell 1989). For a matrix $L_c$ associated with a captive population, $N_{(t+1)}$ depends on $N_{(t)}$ and the survival of individuals that have not been released. Therefore, it is possible to interpret release rates as another matrix $R$ of the same dimensions, whose elements act as multipliers for the parameters in $L_c$:

$$N_{(t+1)} = N_{(t)} L_c R_{(t)} = N_{(t)} L_c \begin{pmatrix} r_{1(t)} & r_{2(t)} & \cdots & r_{n(t)} \\ r_{1(t)} & r_{2(t)} & \cdots & r_{n(t)} \\ \vdots & \vdots & \ddots & \vdots \\ r_{1(t)} & r_{2(t)} & \cdots & r_{n(t)} \end{pmatrix}$$

Eq. 2

where $r_{i(t)}$ is the proportion of individuals in age class $i$ that are retained (not released) in the captive population in year $t$. Note that here we assume releases are carried out after reproduction: therefore, in captivity multipliers for fecundities are equal to 1, and the release rate of the first captive life stage changes the probability of transitioning to the second stage.

The left eigenvector of $L$ provides the stable age distribution, the proportion of individuals within each age class in the population when this is growing at the rate $\lambda$ (the dominant eigenvalue of $L$: Caswell 1989). For a stable captive population, an “insurance” objective could be represented as maintaining a non-negative growth rate for the captive population.
(λ≥1) whilst releasing individuals. A “reintroduction” objective might be measured by the number of individuals in a recipient population, either in total or in a specific age class. The vector $W$ of age-structured abundances of this recipient population at any time $t+1$ can also be represented as the product of a vector of abundances at time $t$ and a matrix of vital rates specific to that population ($L_w$):

$$W_{(t+1)} = W_{(t)}L_w$$  \hspace{1cm} \text{Eq. 3}

At any given time, this population can be augmented by releases from the captive population:

$$W_{(t+1)} = W_{(t)}L_{w(t)} + N_{(t)}(1 - R)_{(t)}L_r$$  \hspace{1cm} \text{Eq. 4}

where $(1-R)_{(t)}$ is the matrix of release rates (the proportion of individuals that are not retained at year $t$), and $L_r$ is the matrix that describes the vital rates of individuals post-release. These can correspond to the rates of the wild population if no post-release effects are assumed ($L_r = L_w$), or can be represented as another matrix of estimated vital rates that describe any post-release effects such as increased mortalities or decreased fecundities. Eq. 4 can be expanded to accommodate scenarios in which these effects go beyond the immediate post-release period, by adding specific matrices and vectors for individuals in the $n$th year after release. The optimal release strategy corresponds to the values of $R$ that maximise the criteria of success for the chosen objectives.

Given a sufficiently long time frame (as measured by the damping ratio of $L$: Caswell 1989) with constant vital rates, all populations will reach an asymptotic phase of stable age distribution. However, in actual reintroduction programs initial numbers may deviate from the stable age distribution, and this may not be achieved within short time frames. In this case, the discrete growth rate might be an unsuitable metric for the chosen objectives. However, if a different objective function is chosen, the matrix framework (Eq. 1-4) can still
be used to identify the optimal matrix of release rates for every time step, for example to
maximise the size of the wild population while meeting all required constraints, such as
maintaining the size of the captive population above a certain abundance, or keep its cost
under an allocated budget. Simulations can help incorporate parametric uncertainty and
evaluate the effects of demographic and environmental stochasticity on the choice of optimal
release rates and on the expected outcomes.

**Study species**

To demonstrate the application of our approach, we evaluated the ongoing release program
for the Southern Corroboree frog *Pseudophryne corroboree* Moore (Anura: Myobatrachidae).
This species, endemic of south-eastern Australia, has undergone a continuous decline since
the late 1980s (Osborne 1989) and is listed as critically endangered in the IUCN Red List
with a high risk of extinction in the wild (IUCN 2011). The need for a captive breeding
program has been recognized since the first proposed recovery plan for the species (Hunter et
al. 1999; NSW National Parks and Wildlife Service 2001), and has become particularly
significant with the discovery of the fungal disease chytridiomycosis in wild populations
(Hunter et al. 2010). *P. corroboree* is now being bred in captivity at several Australian
institutions (IUCN 2011). Currently, the aim of the project is to maintain a presence of
individuals in the wild to improve knowledge and maintain the possibility of development of
tolerance to the pathogen. At the same time, it is necessary not to deplete the captive
population to allow for future full-scale reintroductions.

We represented the reintroduction program for *P. corroboree* as a combination of two
populations (one wild and one captive). We modelled only females, assuming equal sex ratio
(REF) and defined six age classes, counted after breeding: eggs (*N₀*), one-, two- and three-
year-old juveniles (*N₁*, *N₂*, *N₃*), four-year-old sub-adults (*N₄*) and sexually mature adults (*N₅*)
According to Eq 1-4, we parameterised the transition matrices $L_c$ and $L_w$, for the captive and wild population respectively, using values elicited from experts, relying on their knowledge and on published information (Hunter et al. 1999; Hunter 2000). We defined a most-likely, a worst-case and a best-case estimate for every parameter (Table 1). To fully characterize uncertainty, for each parameter we then used the estimates to fit a beta-PERT distribution, a modified beta distribution specifically developed for the treatment of expert-elicited information (Vose 1996). All the following analyses were carried out using R (R Development Core Team 2011) and the Solver and MCSimSolver add-ins in MS Excel.

**Stable age distribution**

Initially, we assumed a stable age distribution and sought to identify the maximum release rate of individuals (either eggs or sub-adults) that could be sustained indefinitely ($\lambda_c \geq 1$). We used Markov Chain Monte Carlo simulation to account for parametric uncertainty in the parameters of $L_c$ and $L_w$. For each of 10,000 iterations, we constructed a version of $L_c$ in which the value of each parameter was drawn randomly from its distribution and found the maximum release rate ($1-r_i$) of the chosen life stage, constraining for $\lambda_c \geq 1$. We then calculated the average value of this maximum release rate across all iterations, together with 95% confidence intervals. We repeated the analysis three times, calculating the maximum release rate for either eggs or sub-adults whilst retaining all the other life stages, and the maximum rate of each stage when both eggs and sub-adults were released simultaneously.

To illustrate the consequences of applying these release rates for a reintroduction objective, we then simulated the trajectories of a hypothetical system of two populations when the maximum rates were used to populate $R$ (Eq. 2, 4). For the captive population, we assumed a stable age distribution from $t=0$, as inferred from the dominant eigenvector of the matrix.
We also calculated the trajectory of a wild population, with initial size set to zero, which were to receive the corresponding number of released individuals at every time step. Again, we accounted for parametric uncertainty in the wild population by simulating $L_w$ 10,000 times, with values drawn from the distribution of each parameter, and calculating means and 95% confidence intervals. We expressed the result in terms of the ratio of individuals in the wild per individual in the captive population: assuming the captive population remains stable, its size could be easily translated into resource requirements for any given time step. We then repeated the analysis for a different objective function, in which we assessed the ratio between the wild population size and the yearly cost of maintaining the captive population. We estimated costs based on expert opinion, with yearly figures of 58A$ for an egg, and to 50 A$ for a post-metamorphic individual (EXPLANATION). We did not include the cost of releases, assuming they would be equal for different life stages. All costs were borne after breeding and before any reintroduction.

Initially, we ran all analyses assuming the released individuals had equal survival to the corresponding wild age classes. We then assessed the sensitivity of each release strategy to three key parameters: the post-release survival of released individuals in both life stages and the fecundity of released sub-adults (we assumed that the fecundity of individuals released as eggs, after being exposed to four years of natural selection, would equal that of the wild-born adults). We calculated the expected outcome of each strategy as the ratio of wild and captive individuals after 30 years across all parameter values over the [0, 1] interval for survival rates and the estimated range [6, 15] for fecundity. For clarity, we ignored parametric uncertainty by setting all parameters equal to the mean values of their distributions, and applied the average optimal release rates identified for those values. We repeated the calculation for each release strategy and identified the optimal choice for each parameter combination by comparing the expected outcomes.
Variable initial values and demographic stochasticity

We then simulated the application of our approach to a more realistic scenario in which the stable age assumption was violated and the time frame shortened, so that stability could not be reached. We set the initial values for the captive population as \( N_0(0) = 300 \), \( N_1(0) = 150 \), \( N_2(0) = 250 \), \( N_3(0) = 900 \), \( N_4(0) = 300 \) and \( N_5(0) = 340 \), based on actual numbers held in captivity at the beginning of this study. We identified the release rates that maximised the average number of adult individuals in the wild \((W_5)\) over a 10-year period. We compared the optimal release rates for eggs only, sub-adults only and a mixture of the two age classes. Again, we used 10,000 simulations drawing from parameter distributions to represent parametric uncertainty, and calculated means and 95% confidence intervals of the optimal release rates for each strategy.

We set two constraints to the optimisation: the number of captive breeding adults at any given time should not be smaller than that at the beginning of the program \((N_5(t) \geq N_5(0))\), and the total cost of the captive population at any time step should not exceed 250,000 A$. We chose the yearly budget to reflect actual funding figures in the years 2008-2012 (REF).

We then compared the outcomes of each strategy, accounting for demographic stochasticity in the fate of individuals. Using the average values for \( L_e \) and \( L_w \), we re-fitted the models in RAMAS Metapop (Akçakaya & Root 2002) assuming that fecundity and individual survival followed Poisson and binomial distributions respectively (Akçakaya 1991). We ran 10,000 simulations for each strategy over ten years, using the optimal release rates. We assumed no density-dependence, allowing the populations to grow exponentially. We then compared the average number of adults in the wild and the cost of the resulting captive population.

Results
Assuming a stable age distribution, the average discrete growth rate of the captive population was $\lambda_c = 1.636$ (95% CI: 1.698, 1.574) across 10,000 stochastic iterations under parametric uncertainty. The maximum release rate that could be sustained by releasing either eggs or sub-adults was on average $r = 0.983$ (95% CI: 0.973, 0.994; Table 2). If releasing equal proportions of both eggs and sub-adults at every time step, the maximum release rate that could be sustained for each life stage averaged $r = 0.86$ (95% CI: 0.851, 0.906; Table 2). The stable age distribution in the captive population was also influenced by the release strategy. For egg and joint releases, adults represented more than half the population, whereas for sub-adult releases they were only 2% of all individuals (Table 2). On the other hand, sub-adult releases produced a more diverse stable age distribution, with similar proportions of the first four stages.

The discrete growth rate for the wild population was $\lambda_w = 0.754$ (95% CI: 0.709, 0.801), suggesting that without continuous releases the population would not persist. When releasing 98% of eggs, the wild population became stable at a constant size equal to 41% of the stable captive population (31%, 54%; Table 2). When releasing sub-adults, the ratio increased to 249% (191%, 325%; Table 2). Finally, when releasing both eggs and sub-adults at $r = 86\%$, the stable wild population was 102% the size of the captive one (80%, 131%; Table 2).

Population trajectories are described in Figure 1. The cost of the captive population was slightly higher for sub-adult releases (57 A$ compared to 51 A$ for egg and joint releases), since they implied retaining eggs. However, this difference was marginal and the cost of the captive population at stability was similar under all scenarios: therefore, the optimal choice did not change when including costs in the objective function.
For any combination of tadpole and sub-adult survival, the joint release strategy was always sub-optimal to one of the single-stage ones (Figure 2). Egg releases were only optimal for low sub-adult survival rates and unrealistically high tadpole survival ($s_3 > 0.75; s_4 < 0.2$). Outcomes were largely insensitive to the fecundity of individuals in the year post-release: even assuming that released sub-adults would not breed in the first year ($f = 0$), the wild/captive population ratio at stability varied by less than 0.01, and the optimal strategy did not change.

Variable initial values and demographic stochasticity

Under a more realistic scenario with different initial abundances in captivity, budget constraints and short-term objectives, the optimal release rates differed for every year. Over a 10-year period, a strategy focusing on egg releases required large releases (>98% in years 1-9 and 65% in year 10). This strategy was generally cheaper than the available budget, but it never produced more than 150 breeding adults in the wild (Figure 3). A strategy focusing on sub-adult releases also required high release rates (>90% every year), and was expected to provide the highest number of wild individuals (Figure 3). However, this strategy required a very large captive population, and it was not possible to satisfy both constraints: when aiming not to deplete the captive population, the yearly budget was exceeded (Figure 3). The optimal strategy using joint releases of both stages required partial retention of eggs (averaging 20 to 70%) in the first two years, to reach capacity and maximise production in the following years, partial retention of sub-adults in years three and four (39% and 40%) to ensure that the desired number of adults was maintained, and finally large releases of both stages in years 5-9 (>80%). This strategy provided better outcomes than egg releases alone, and although in the last five years it produced fewer individuals than a sub-adult-only strategy, its total cost was 68% lower, without exceeding the yearly budget (Figure 3).
The first objective of ex-situ programs for critically endangered species is often the establishment of a viable captive population as insurance in the event of extinction in the wild (Conway 2011). The growth rate of the captive population will determine whether this objective can be met, and how it can be balanced with future reintroduction efforts. Populations with high predicted growth are more likely to be able to sustain large release rates without declining. For *P. corroboree*, long-term persistence of the captive population could be ensured even when releasing a large proportion (0.98 on average) of either eggs or sub-adults, due to high survivorship and productivity in captivity. Releasing different life stages will also change the stable age distribution, and this should be considered if managers have specific objectives regarding the structure of the captive population. If all life stages have the same maintenance requirements, the cost of a stable and constant captive population will be the same for every release strategy. In the stable age distribution scenario for *P. corroboree*, the difference between maintenance costs for eggs and other life stages was not sufficient to change the optimal strategy. However, if differences are significant (for example, when breeding adults need large individual enclosures), different release strategies may entail different costs, influencing the optimal decision when cost is an objective. In the stable age distribution scenario, the insurance objective for the captive *P. corroboree* population was to maintain $\lambda_c=1$. Managers may initially seek a higher growth rate, to increase the size of the captive population and release greater absolute numbers in the future: however, resource constraints are likely to impose an upper limit to the captive population size. Once this carrying capacity is reached, then the “insurance” objective may again shift to $\lambda_c=1$. In a theoretical study, Tenhumberg et al. (2004) suggested that it is generally optimal to
increase the size of the captive population as rapidly as possible, and to start releases once
this approaches its carrying capacity. In real programs, the practical challenge for managers
lies in estimating the exact duration of this “build-up” phase and the subsequent proportion of
individuals to release. Framing population models in a clear decision-analytic framework can
help in assessing the optimal decision.

In regard to the reintroduction objective, the trajectory of the wild population depends on its
intrinsic growth rate. If $\lambda_{w} > 1$, then the population will grow accordingly after the initial
releases, and assuming exponential growth, constant releases from a stable and constant
captive population will become progressively less important in the long term. On the other
hand, if $\lambda_{w} < 1$, as it was for *P. corroboree* in this study, continuous releases are needed to
prevent the wild population from declining to extinction. Whether such an approach is
justified depends entirely on the objectives of the specific program. In the case of *P.
corroboree*, where the wild population depended on continuous releases, egg releases were
less effective, yielding a smaller number of individuals in the wild for every individual
maintained in captivity. If cost is an objective, it is necessary to consider that when releasing
eggs a greater population will need to be maintained to provide the same absolute numbers of
individuals in the wild.

The effectiveness of releases of different life stages will reflect the differences in their
respective reproductive value (the expected number of offspring an individual will produce
over its lifetime: REF). For amphibian species with non-breeding early stages and no
senescence, juveniles will always have a lower reproductive value than individuals released
at later stages. Assuming survival in captivity is higher than in the wild, individuals that are
released later in life will have greater reproductive values than those released early, and thus
produce a greater wild-to-captive ratio. However, the magnitude of this difference depends on
the expected vital rates of the relevant life stages, and can be significantly modified by post-
release effects (Sarrazin & Legendre 2000).

Post-release effects can also include high rates of dispersal of individuals: this behavioural
aspect has been observed in several taxa (Le Gouar, Mihoub & Sarrazin 2012). The use of
environmental cues for dispersal has been demonstrated for amphibians, particularly for
juveniles learning dispersal routes post-metamorphosis (Ferguson 1971; Popescu et al. 2012).

In this case, the effects of post-release dispersal on the establishment of a reintroduced
population may be higher for late-age-class release strategies, in which individuals have had
no opportunity to learn dispersal routes. Although no information is available in this sense for
*P. corroboree*, we assumed post-release dispersal could be considered as additional mortality,
to which results were indeed sensitive.

However, for many species, including most amphibians, mortality in early life stages can
naturally be an order of magnitude higher than for adults. Therefore, it may still be
advantageous to release later stages where their better survival compensates the greater
incidence of post-release effects on reproductive values. For example, Sarrazin and Legendre
(2000) modelled releases of Griffon vultures (*Gyps fulvus*) in Europe, suggesting that where
post-release effects remain small, releases of adults should indeed prove more effective for
long-lived species due to the high expected reproductive value. In our example, even
assuming high post-release mortality, sub-adult releases were always more effective than egg
releases, unless tadpole survival was unrealistically high (>0.5).

Environmental stochasticity can also have life stage-specific effects that will influence the
relative effectiveness of release strategies (Sarrazin & Legendre 2000). In *P. corroboree*, egg
survival can be affected by environmental stochasticity: since eggs are laid in nests on the
ground, they need sufficient precipitation to be flushed to a water body that must retain water
throughout the period of tadpole development (Hunter et al. 2009). High mortality of eggs and low recruitment have been observed in drought years (Osborne 1989). On the other hand, wet years can facilitate the spread and virulence of chytrid fungus, again with potential age-specific effects (Kriger 2009). In light of this complexity, not entirely understood for *P. corroboree*, we chose not to explicitly model environmental stochasticity in our study: however, it may affect the efficiency of egg releases in particular, and monitoring is being carried out to evaluate this possibility.

Results were not sensitive to the short-term fecundity of released sub-adults. This was a result of the longevity of adults and our assumption of no long-term variation in fecundity (from the second year after release all individuals would have the same reproductive output). Greater sensitivity might be expected in the case of long-term variations in fecundity that differed between life stages (for example, if early-age releases achieved full reproductive potential, and late-age releases never did). In this sense, our results are consistent with those of Sarrazin and Legendre (2000), who found greater sensitivity of reintroduction success to post-release survival than to fecundity for *Gyps fulvus* in France (for reductions both in the short and long term).

When the size of the captive population is not constant, retaining individuals in captivity for a longer period will increase the overall financial cost of a program and may generate conflicts where limited resources are available (such as space or human resources at zoo institutions). In this case, strategies that envisage releases of single life stages releases inevitably bear the consequences of this trade-off. Focusing only on releases of early life stages might be appealing to risk-seeking managers with strict budget constraints. This was clearly reflected in our realistic, short-term example for *P. corroboree* with multiple objectives (insurance, reintroduction and costs). Across the full range of parametric uncertainty, mixed strategies including joint releases of eggs and sub-adults provided the most cost-effective solution.
Although egg releases allowed the lowest costs, they were also less effective towards the reintroduction objective. The reduction of age-class diversity in the captive population might be another concern. Conversely, releasing sub-adults was predicted to produce a greater presence in the wild. This potential risk-averse solution, however, led to high and increasing costs, making it impossible to meet both cost and insurance objectives. In this sense, mixed strategies allow managers to combine the advantages of releasing different life stages, for example releasing sub-adults to improve viability and managing egg releases to control the size and cost of the captive population.

Ultimately, the evaluation of the trade-off between additional costs and the predicted improvements in viability associated with releasing later life stages must be solved on the basis of the importance given to each objective. For example, Martínez-Abraín et al. (2011) used population viability analysis to assess translocation options for crested coots (*Fulica atra*) in Spain: they found that releasing adults improved viability, but this remained generally poor. They concluded that a 160% increase in costs “outweighed” the marginal conservation benefits of releasing adults rather than juveniles. However, the definition of the threshold above which benefits are outweighed by costs will differ among programs: the adoption of an explicit decision-analytic approach may help define priorities and consequently the optimal decision.

A mixed strategy can also prove useful when uncertainty, for example about post-release effects, must be reduced. In this sense, the value of accumulating knowledge about the outcomes of alternative actions can be explicitly incorporated within an adaptive management framework (Walters & Hilborn 1978; McCarthy & Possingham 2007). In the case of *P. corroboree*, monitoring the outcome of releasing both eggs and sub-adults could help in assessing post-release effects. It may also be advantageous to solve uncertainty
surrounding the suitability of release sites for breeding (Rout, Hauser & Possingham 2009) or the requirements of reintroduced populations (Armstrong, Castro & Griffiths 2007).

The definition of clear objectives is the key to a rigorous approach to decision making (Possingham et al. 2001). In the more realistic scenario, we chose a short time frame to reflect the current requirement of the release program for *P. corroboree* and used the number of breeding adults as a metric of success, whereas a longer program may focus on growth rates or probability of extinction. Our choices are influenced by the current difficulty in mitigating threats for this species, reflected by the expected negative growth rate of the wild population and its reliance on releases of captive-bred individuals. Reintroduction programmes aimed at establishing self-sustaining populations, or involving species with longer generation times, may need to consider longer time-frames, which can be easily accommodated in our approach.

Additional aspects would also need to be considered in a more realistic analysis. For example, our models did not include non-linearities such as density dependence, allowing exponential growth. However, this assumption may be violated, for example when small populations are affected by social dysfunctions such as Allee effects (Deredec & Courchamp 2007). The time required to learn optimal husbandry techniques for the species may also influence the ability to achieve the vital rates assumed in our model, and more time in captivity may be necessary before releases can take place. Release rates can be modified to reflect these needs.

The ex-situ conservation program for *P. corroboree* shows characteristics common to most similar efforts worldwide; the rapid and seemingly irreversible decline of the target species, the unknown feasibility and time frame of threat abatement, the need to minimise time in captivity and maximise production of release candidates, while containing costs. Population
models can provide useful information for managing a captive insurance population, while
life stage-specific release plans can help in addressing trade-offs between numbers of
releases, the probability of establishing a wild population and management costs. Framing
models in an explicit decision-analytic framework can assist in evaluating key objectives,
uncertainty and trade-offs.

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Table 1. Parameter estimates for the three considered scenarios (best-, worst- and most likely case). Parameters: $u$ indicates the survival of eggs to one-year old froglets, $s_1$ to $s_5$ indicate survival for the corresponding age class post-metamorphosis, $s_r$ indicates the survival in the wild of sub-adults released from captivity and $f$ indicates the fecundity of adult frogs.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Captive population</th>
<th>Wild population</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Best</td>
<td>Likely</td>
</tr>
<tr>
<td>$u$</td>
<td>0.82</td>
<td>0.7</td>
</tr>
<tr>
<td>$s_1$</td>
<td>0.85</td>
<td>0.85</td>
</tr>
<tr>
<td>$s_2$</td>
<td>0.9</td>
<td>0.85</td>
</tr>
<tr>
<td>$s_3$</td>
<td>0.95</td>
<td>0.9</td>
</tr>
<tr>
<td>$s_4$</td>
<td>0.95</td>
<td>0.9</td>
</tr>
<tr>
<td>$s_5$</td>
<td>0.95</td>
<td>0.9</td>
</tr>
<tr>
<td>$s_r$</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$f$</td>
<td>15</td>
<td>12</td>
</tr>
</tbody>
</table>
Table 2. Outcomes of applying the maximum release rates to a captive population with stable-age distribution.

<table>
<thead>
<tr>
<th>Release strategy</th>
<th>Eggs only</th>
<th>Sub-adults only</th>
<th>Joint and equal releases</th>
</tr>
</thead>
<tbody>
<tr>
<td>Maximum release rate(^1)</td>
<td>0.98</td>
<td>0.98</td>
<td>0.86</td>
</tr>
<tr>
<td>Stable age distribution of captive population</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Eggs</td>
<td>0.14</td>
<td>0.30</td>
<td>0.13</td>
</tr>
<tr>
<td>1-yr</td>
<td>0.10</td>
<td>0.21</td>
<td>0.10</td>
</tr>
<tr>
<td>2-yr</td>
<td>0.08</td>
<td>0.18</td>
<td>0.09</td>
</tr>
<tr>
<td>3-yr</td>
<td>0.07</td>
<td>0.15</td>
<td>0.09</td>
</tr>
<tr>
<td>Sub-adults</td>
<td>0.06</td>
<td>0.14</td>
<td>0.08</td>
</tr>
<tr>
<td>Adults</td>
<td>0.56</td>
<td>0.02</td>
<td>0.50</td>
</tr>
<tr>
<td>Yearly cost of captive population(^2)</td>
<td>51.1</td>
<td>57.1</td>
<td>51.1</td>
</tr>
<tr>
<td>Wild/captive ratio(^3)</td>
<td>0.41</td>
<td>2.41</td>
<td>1.80</td>
</tr>
</tbody>
</table>

\(^1\) Maximum release rate for \(\lambda_c \geq 1\)

\(^2\) Calculated by multiplying the stable-age proportion for each class by its respective cost (58 A$ for eggs, 51 A$ for post-metamorphic individuals)

\(^3\) Number of wild individuals for every individual maintained in captivity
**Figure 1.** Outcomes of optimal release strategies under the stable age distribution assumption. Y-axis values correspond to the number of wild individuals for every individual existing in captivity at a given time. Maximum release rates calculated for a captive population with $\lambda=1$, for each scenario (eggs or adults only: 98%; joint releases: 86% each). The shaded areas correspond to 95% confidence intervals over 10,000 simulations across the parametric uncertainty of vital rates.
**Figure 2.** Sensitivity of optimal release strategies to post-release effects, assuming maximum release rates under a stable age distribution with average vital rates. The colour reflects the difference in the ratio of wild/captive individuals between the optimal and the second-best choice for every combination of post-release survival of tadpoles and sub-adults. For example, a value of 0.2 indicates that the optimal release is 20% more productive than the second-best choice. Labels indicate the optimal choice for different regions of the parameter space.
Figure 3. Outcomes of the optimal strategies for a 10-year programme with non-stable initial age distribution in the captive population. Plots represent the annual costs of maintaining the captive population (top) and numbers of adults in the wild population (bottom). The shaded areas represent demographic stochasticity (95% confidence intervals).