



# Cost-Effectiveness of Translocation Options for a Threatened Waterbird

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**Abstract:** *Reintroduction of captive-reared animals has become increasingly popular in recent decades as a conservation technique, but little is known of how demographic factors affect the success of reintroductions. We believe whether the increase in population persistence associated with reintroduction is sufficient to warrant the cost of rearing and relocating individuals should be considered as well. We examined the trade-off between population persistence and financial cost of a reintroduction program for Crested Coots (*Fulica cristata*). This species was nearly extirpated from southern Europe due to unsustainable levels of hunting and reduction in amount and quality of habitat. We used a stochastic, stage-based, single-sex, metapopulation model with site-specific parameters to examine the demographic effects of releasing juveniles or adults in each population for a range of durations. We parameterized the model with data from an unsuccessful reintroduction program in which juvenile captive-bred Crested Coots were released between 2000 and 2009. Using economic data from the captive-breeding program, we also determined whether the strategy that maximized abundance coincided with the least expensive strategy. Releasing adults resulted in slightly larger final abundance than the release of nonreproductive juveniles. Both strategies were equally poor in achieving a viable metapopulation, but releasing adults was 2–4 times more expensive than releasing juveniles. To obtain a metapopulation that would be viable for 30 years, fecundity in the wild would need to increase to the values observed in captivity and juvenile survival would need to increase to almost unity. We suggest that the most likely way to increase these vital rates is by increasing habitat quality at release sites.*

**Keywords:** captive breeding, *Fulica cristata*, habitat quality, metapopulation model, reintroduction success, stochasticity

Rentabilidad de las Opciones de Translocación de una Especie de Ave Acuática Amenazada

**Resumen:** *En décadas recientes, la reintroducción de animales criados en cautiverio se ha vuelto cada vez más popular como una técnica de conservación, pero se conoce poco sobre el efecto de factores demográficos sobre el éxito de las reintroducciones. Creemos que también se debe considerar si el incremento en la persistencia de la población asociada con la reintroducción es suficiente para garantizar el costo de criar y reubicar individuos. Examinamos la compensación entre la persistencia de la población y el costo financiero de un programa de reintroducción de *Fulica cristata*. Esta especie fue casi extirpada del sur de Europa debido a niveles de cacería no sustentable y la reducción en la cantidad y calidad de hábitat. Utilizamos un modelo metapoblacional estocástico, unisex, basado en etapas con parámetros de sitios específicos para examinar los efectos demográficos de la liberación de juveniles o adultos en cada población en un rango de duraciones. Alimentamos el modelo con datos de un programa de reintroducción no exitoso en el que se liberaron *F. cristata* juveniles criados en cautiverio entre 2000 y 2009. Mediante datos económicos del programa de reproducción en cautiverio, también determinamos si la estrategia que maximizaba la abundancia coincidía con*

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la estrategia menos costosa. La liberación de adultos resultó en una abundancia final ligeramente mayor que la liberación de juveniles no reproductivos. Ambas estrategias fueron igualmente pobres para lograr una metapoblación viable, pero la liberación de adultos fue 2-4 veces más costosa que la liberación de juveniles. Para alcanzar una metapoblación que fuera viable por 30 años, la fecundidad en el medio natural tendría que incrementar hasta valores observados en cautiverio y la supervivencia de juveniles tendría que incrementar casi hasta la unidad. Sugerimos que la forma más probable de incrementar estas tasas vitales es mediante el incremento de la calidad del hábitat en los sitios de liberación.

**Palabras Clave:** calidad del hábitat, estocasticidad, *Fulica cristata*, modelo metapoblacional, reintroducción exitosa, reproducción en cautiverio

## Introduction

Conservation relies on in situ and ex situ strategies to reduce high rates of species extinction resulting from loss of species' habitats. Although in situ activities, such as habitat restoration, can effectively reverse declines in abundance at the population level, ex situ activities are often carried out by environmental agencies worldwide because they are more visible to the donating public (Pullin 2002). One of the most commonly used conservation methods is the reintroduction of captive-bred threatened animals and plants to sites from which they were recently extirpated (Griffith et al. 1989; Ebenhard 1995; Wolf et al. 1996). Reintroductions have increased over the last 30 years, but lack a strong theoretical basis (Armstrong & Seddon 2007; Seddon et al. 2007). Simulation models are helpful for understanding the potential effects of reintroduction strategies on populations because they allow for many manipulations and comparisons that cannot be easily implemented in practice (e.g., Bustamante 1998; Bar-David et al. 2005).

Many factors influence the success of reintroductions: habitat quality of the release site, timing of introduction, duration and geographical extent of the program, health of individuals in wild and captive populations, ongoing disturbances at the release site, whether released animals receive supplementary food, previous exposure of introduced individuals to local predators or to food sources in the wild, and willingness of people to coexist with the species (Wolf et al. 1998; Blackburn & Cassey 2004). Demographic factors such as the number and age of reintroduced individuals and the sex ratio of individuals in recipient populations affect success of introductions (Blackburn & Duncan 2001; Cassey et al. 2004). Nevertheless, little is known of how demographic factors affect the success of reintroductions (Fischer & Lindenmayer 2000), although Blackburn and Cassey (2004) contend that the characteristics of introductions and reintroductions are sufficiently similar that conclusions from studies of the former inform studies of the latter. Results of previous studies on long-lived species suggest adults should be released, whereas studies on shorter-lived species suggest juveniles should be released (Stearns 1992; Sarrazin

& Legendre 2000). However, the success of such strategies depends on the environment into which individuals are released and the economic costs associated with each strategy (Sarrazin & Barbault 1996). Hence, it is important to assess whether the increase in abundance or probability of population persistence associated with different reintroduction approaches is sufficient to warrant the cost of rearing and relocating individuals.

We examined the trade-off between population persistence and financial cost of a reintroduction program for Crested Coots (*Fulica cristata*), a species extirpated from southern Europe at the end of the 19th century by unsustainable levels of hunting and loss and alteration of its habitat. Because this species occurs in spatially separated habitat patches, we used a metapopulation model with site-specific parameters to examine the demographic effects of releasing juveniles and adults in each population or patch. The habitat into which birds were released was of poor quality because food was scarce (Martínez-Abraín et al. 2007; Varo & Amat 2008). This reintroduction program has not been considered successful for 2 reasons. First, juveniles have high mortality for 1 year following release, especially during the first month after release (Tavecchia et al. 2009). Other vertebrate reintroduction projects also report an initial period of high mortality of released individuals (Wear et al. 2005; Brown et al. 2006; Bertolero et al. 2007). Second, a number of reintroduced Crested Coots that survive the initial cost of release join flocks of common coots (*F. atra*), which are hunted in winter (Martínez-Abraín et al. 2007).

We compared the final abundance of Crested Coots in the metapopulation in the study area (i.e., the number of individuals in the set of populations in the wild) when releasing adults and juveniles. We used available economic data on the captive breeding and reintroduction program to examine the trade-off between financial cost and increase in abundance and persistence to evaluate whether the demographic strategy most likely to increase abundance and persistence was the cheapest strategy. We also calculated the improvement in vital rates necessary to sustain a stable metapopulation.

**Table 1.** Number of juvenile Crested Coots (*Fulica cristata*) released in patches of habitat in the study metapopulation yearly from 2000 to 2009 as part of an ongoing reintroduction program.

Year	Albufera	Moro	Hondo	Galvany	Almenara	Xeraco	Llobregat	Mallorca	Total
2000		13							13
2001	19	45							64
2002	12	39	21						72
2003	29	51	24	6					110
2004	22	74			10		20		126
2005	22	33	15			20		20	110
2006	23	22				19		12	76
2007	10	23			3	21		8	65
2008		11			8	8		12	39
2009		18			11			8	37
Total	137	329	60	6	21	68	20	60	701

## Methods

### Study Species

Crested Coots live approximately 6–7 years (Tavecchia et al. 2009) and are monogamous. The species' center of distribution is in eastern and southern Africa; the Mediterranean, the area of focus in our study, is the northern geographical limit of the species. Because the African and Mediterranean populations are separated by the Sahara desert, movements >500–1000 km are extremely rare (Skead 1980). Time of nesting is variable and clutch size varies between 5 and 8 eggs. Second and third broods are possible, depending on food availability. Hatching occurs between February and September and peaks between May and June. Both sexes incubate the eggs, and incubation takes 24–28 days. Pairing and breeding occurs when birds are at least 1 year old (Raya & Amat 2003). The species is categorized regionally (Generalitat Valenciana, local government in the study region) and nationally (government of Spain) as critically endangered (highest level of threat), although the International Union for Conservation of Nature (IUCN) categorizes the bird globally as least concern (IUCN 2010).

### Existing Reintroduction Program

From 1999 to 2008, Crested Coots were bred in captivity at a rehabilitation center in eastern Spain from a stock of eggs collected from a wild population in Morocco. Juveniles (nonbreeding birds <1 year) were released annually in eight different wetlands and were not fed supplementally. These wetlands are relicts of a former belt that extended along the coast for hundreds of kilometers. The remaining wetland patches are protected by the laws of Comunidad Valenciana, but the water is polluted, and waterfowl hunting is allowed. A total of 701 juvenile Crested Coots were released between 2000 and 2009, and each bird was individually marked by a neck collar with an alphanumeric code. Sixty-seven percent of birds were released in 2 patches: Marjal dels Moros and Albufera (Table 1). Released individuals were monitored

weekly in all wetlands by resighting marked individuals with spotting scopes. Hence data consisted of annual resighting of individually marked birds and information on coot reproduction for the captive-bred and the wild populations from 2000 to 2008. For further details on the reintroduction see Tavecchia et al. (2009).

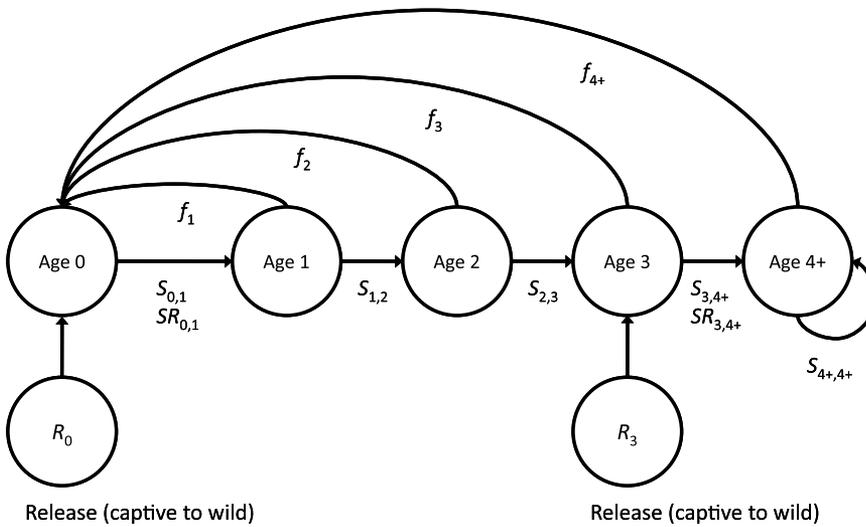
### Metapopulation Model

We developed a single-sex, age-structured metapopulation model in RAMAS Metapop (Akçakaya & Root 2005). The model was spatially explicit to account for movements of birds among populations. Each population occupied one habitat patch. Initial abundance of birds in each of the 11 patches in which coots were released or known to occur was measured as the maximum number of breeding females observed in that patch in 2007 and 2008 (Table 2).

We modeled the dynamics of each population with a female-only age-structured matrix metapopulation model. We included demographic stochasticity in the model because most populations had a few individuals. Demographic stochasticity was simulated with a binomial

**Table 2.** Abundance of coots in, carrying capacity of, and immigration to each patch (i.e., subpopulation) in the metapopulation (proportion of marked coots resighted in each patch) used to initialize the population model.

Patch	Carrying capacity (K)	Initial abundance	Max. final population size	Immigration index
Albufera	40	3	42.3	0.38
Moro	20	1	15.1	0.13
Hondo	40	0	34.1	0.02
Almenara	20	2	30.8	0.19
Xeraco	20	3	23.0	0.03
Mallorca	20	5	20.7	0
Ebro delta	40	5	33.7	0.17
Pego-oliva	30	1	19.8	0.01
Cauce nuevo	5	1	7.0	0.02
Llobregat	10	0	7.8	0.01
Galvany	5	0	7.3	0.04



Parameter and age class	Captive population (SD)	Wild population (SD)
<b>Fecundity</b>		
1	0.66 (0.62)	0.18 (0.62)
2	0.94 (0.60)	0.28 (0.60)
3	2.00 (0.52)	0.51 (0.52)
4+	1.43 (1.65)	0.58 (1.65)
<b>Survival (<math>i, j</math>)</b>		
0, 1	0.96 (0.07)	0.20 (0.001)
1, 2	1.00 (0.0001)	0.66 (0.22)
2, 3	0.99 (0.02)	0.66 (0.22)
3, 4	0.98 (0.06)	0.66 (0.22)
4+, 4+	0.86 (0.21)	0.66 (0.22)
Released		0.14 (0.03)

Figure 1. Life cycle and vital rates of the Crested Coot population ( $R_0$ , juveniles released from captivity;  $R_3$ , 3-year-old adults released from captivity;  $f_i$ , fecundity of individuals in age class  $i$  [1, 2, 3, 4+];  $S_{i,j}$ , survival of individuals from age class  $i$  to age class  $j$  [in the wild or captivity];  $SR_{i,j}$ , survival from age class  $i$  to age class  $j$  of individuals released from captivity to the wild).

distribution for survival rates and a Poisson distribution for fecundities. We also included environmental stochasticity in the model because water levels and thus food availability in the Mediterranean region are highly variable (Blondel & Aronson 1999). We represented each demographic parameter (survival rates and fecundities) in the matrix models as a lognormal distribution and calculated a mean and standard deviation from the available data (Fig. 1) (Akçakaya 1991). In each year of the simulation, each parameter in the matrix model was randomly sampled from its associated lognormal distribution via Monte Carlo simulation. This procedure was replicated to incorporate the full range of variability in parameters in population-level abundance. Stochastic variation in fecundities and survival rates was positively correlated (e.g., when survival was low in a given year, so was fecundity).

We ran a simulation with 1000 replications for each of 2 sets of release scenarios for 30 years. Females were translocated from the captive-bred population to each of the 11 patches where Crested Coots were known to have been released or to have bred after being released elsewhere. The first set of scenarios was 5 juvenile females released in each of the 11 patches annually for 5, 15, and

25 years beginning in 2008. The second set of scenarios was 5, 3-year-old females released annually in each patch within the same time frame as the first scenario.

We used final abundance of individuals in the metapopulation to compare between the 2 sets of release scenarios. The probability of metapopulation extinction over 30 years was also calculated.

### Survival Rates

Two-stage matrices were constructed for the system: one for the wild populations and another for the captive-bred population. We considered 5 age classes: juveniles (< 1 year old) (age 0); birds  $\geq 1$  but < 2 years old (age 1); birds  $\geq 2$  but < 3 years old (age 2); birds  $\geq 3$  but < 4 years old (age 3); and birds  $\geq 4$  years old (age 4+) for the wild and captive populations. For the wild populations, we also included released birds as a stage (Fig. 1) to account for the low survival rates of newly released juveniles or adults (in this case age-3 birds). We assumed survival of birds hatched in the wild was higher than the survival of birds just released (0.20 vs. 0.14) (Tavecchia et al. 2009). We assumed annual survival rates of newly released juveniles and 3-year-old adults were

equal (mean [SE] = 0.14 [0.03]), although an empirical estimate was available only for newly released juveniles (Tavecchia et al. 2009). We used the captive-bred population stage matrix to simulate the captive-bred population from which birds were translocated to populations in the wild. This stage matrix was parameterized with data collected from the wildlife rehabilitation center (Fig. 1). We assumed the probability of survival assigned by Tavecchia et al. (2009) to birds surviving in the wild more than 1 year after release (age-1 coots) (mean [SE] = 0.66 [0.22]) was the same for the older age classes (Fig. 1).

### Fecundities

We calculated the mean number of fledglings produced in captivity per pair annually (i.e., breeding success) over 12 years (1997–2008) in each of the 5 age classes (age 1,  $n = 25$  pairs; age 2,  $n = 24$  pairs; age 3,  $n = 23$  pairs; age 4+,  $n = 95$  pairs). The sex ratio in captivity was approximately 1:1 (48% males, 52% females at hatching for  $n = 698$ ). We multiplied mean number of female fledglings per adult female by the age-0 probability of survival ( $S_{01} = 0.20$ ) (i.e., probability of surviving from age 0 to age 1) (prebreeding census) and then by the percentage of breeding individuals in each age class. We used the variances in  $S_{01}$  and breeding success to estimate the effects of environmental stochasticity. We added the 2 variances and calculated the square root of the sum. To estimate breeding success in the wild, we mapped coot territories in Marjal dels Moros and assigned chicks that were a few weeks old to individual females in each territory from 1999 to 2008. This method underestimates the actual breeding success because not all territories can be detected and some of the pre fledging chicks observed may not fledge successfully. Hence, our estimates of breeding success in the wild are conservative. We assumed that variability in fecundity for the wild population was equal to that of the captive population because our sample size of captive individuals was greater than for wild individuals. Variability in fecundity was similar for all age classes except for age 4+ because age 4+ contained individuals 4 years and older (Fig. 1).

### Density Dependence and Carrying Capacity

We assumed ceiling-type density dependence (i.e., exponential population growth until the population reaches a maximum, at which point the population size becomes level) and constant carrying capacities over time. The carrying capacity for each patch was estimated on the basis of patch size and quality (Table 2). Dispersal rates varied across patches. The number of breeding pairs of common coots in each patch was used as a proxy for patch quality because common coots occur with, and are ecologically similar to, Crested Coots. The breeding success (i.e., number of fledglings per pair) of Crested Coots was not used as a measure of patch quality because informa-

**Table 3. Models explaining final metapopulation abundance in each Crested Coot metapopulation as a function of its carrying capacity ( $K$ ), initial number of breeding pairs (Init), and immigration rate (Disp).<sup>a</sup>**

Model code and model <sup>b</sup>	Deviance	$N_p$	$AIC_C$	$\Delta AIC_C$	$w_i$
(1) $K$	650.59	2	85.52	0	0.55
(2) $K$ +Disp	423.87	3	89.79	4.27	0.42
(3) $K$ +Init	610.98	3	90.07	4.55	0.00
(4) Disp	1136.2	2	90.73	5.21	0.00
(5) Init	1440.5	2	94.27	8.74	0.01
(6) $K$ +Init +Disp	390.39	4	96	10.48	0.02

<sup>a</sup> $AIC_C$ , Akaike information criterion corrected for small sample size;  $N_p$ , number of estimable parameters;  $w_i$ , Akaike weight.

<sup>b</sup>Models 1 and 2 are the best models.

tion on the relation between breeding success and habitat quality was only available for a single patch. Carrying capacity for each patch of the metapopulation was calculated as one-third of the mean number of common coots breeding in each patch from 1984 to 2007 (Table 2). We assigned a high value (400 individuals) to the carrying capacity for the captive-bred population so that translocations from the captive population to each patch would not be compromised by a lack of birds. We were not interested in the absolute number of individuals in the final metapopulation; rather, we were interested in relative abundance when adults and juveniles were released. Hence, our conclusions did not depend on the fact that carrying capacities were somewhat arbitrary.

### Dispersal

We estimated there were 22 dispersal connections between patches (17% of the 132 possible connections between pairs of patches) on the basis of field resightings of marked individuals from 2000 to 2006 and the assumption of a constant resighting probability among sites. We calculated immigration (Table 2) for each patch as the percentage of resightings of immigrants in that patch. An ad hoc sensitivity analysis indicated that results were not affected by correlations in environmental stochasticity among patches. To assess the effect of dispersal on final metapopulation-level abundance, we compared several general linear models in which maximum final abundance in each patch was the dependent variable and carrying capacity, initial population size, and dispersal rate were the independent variables. We compared and selected models with Akaike information criterion corrected for small sample size:  $AIC_C = AIC + (2K[K + 1]) / (n - K - 1)$ , where  $AIC = \text{model deviance} + 2K$ ,  $K$  is the number of identifiable parameters in the model, and  $n$  is the sample size. Akaike weights indicated the relative likelihood of the models we considered (Burnham & Anderson 1998) (Table 3). The  $\Delta AIC$  was the difference between the AIC of each individual model and the model with the lowest AIC (i.e., the most parsimonious

model). We followed Anderson (2008) and did not consider a model with a  $\Delta\text{AIC} > 2$  a poor model. Instead, we considered models with  $\Delta\text{AIC} < 5$  equivalent and based our final selection of the best models on Akaike weights.

### Costs of Reintroduction

We calculated costs of captive breeding as Euros required annually to maintain either a juvenile or an adult coot in captivity. To evaluate the return on investment of releasing juveniles compared with adults, we examined the costs of captive breeding relative to the probability of metapopulation extinction between the years 2008 and 2038. Costs included the initial fixed cost of construction of breeding cages (different for raising juveniles and adults), salary for a person (keeper) to maintain the facilities (equal cost for juveniles and adults), and the variable cost of providing food to the birds. We calculated the arithmetic mean and standard deviation of the number of days coots spent in captivity from 1999 to 2008 ( $n = 706$  individuals) to obtain an interval of days spent in captivity. Because adults have not been captive bred in the program, we applied the coefficient of variation (CV) of the cost of rearing juveniles to 3-year-old adults (i.e., mean age of 1095 days [SD 1095]  $\times$  CV obtained for juveniles) and assumed that an equal number of juveniles and adults were raised. Given that the survival of age-3 coots maintained in captivity as breeders is 0.98 (SD 0.06), we did not consider any possible additional costs of mortality of adults during the period of captivity. We calculated the annual cost of providing 5 juveniles or adults per year to be released into each of the 11 patches.

### Sensitivity Analyses

We explored the effect that increase in habitat quality could have on population growth in the wild because evidence from the reintroduction project suggests that habitat quality is the main determinant of local survival and reproduction rates (Martínez-Abraín et al. 2007; Tavecchia et al. 2009). To determine the combination of parameter increases that could influence metapopulation viability after releases ceased, we progressively increased age-0 survival rates ( $S_{01}$ ) in the wild from 0.20 to a theoretical maximum of 1.0 while keeping fecundities at their current rates and assuming fecundities in the wild are the same as those in captivity. Because the existing reintroduction program focuses on juvenile releases, in all scenarios 5 juveniles were released for the first 15 years of the simulation, after which reintroduction ceased. For simplicity, we assumed released juveniles have the same survival rate as juveniles bred in the wild.

## Results

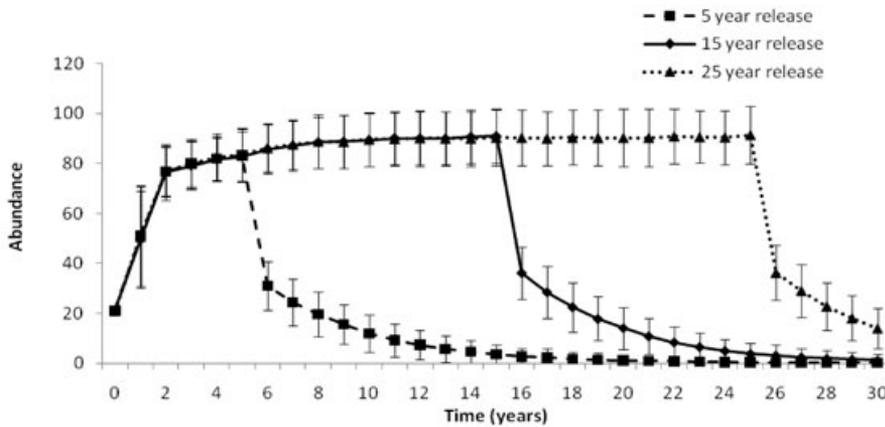
Metapopulation-level abundance was slightly higher when adults were released than when juveniles were released for all release periods except 5 years. A maximum average abundance of 115 was achieved for adult release versus 91 for juvenile release over 25 years, 113 versus 91 for adult and juvenile release (respectively) over 15 years, and 68 versus 83 for adult and juvenile release (respectively) over 5 years. However, the metapopulation was not viable over 30 years without continued release of either juveniles or adults (Fig. 2). A steep drop in population size across all patches consistently occurred 1 year after the release of birds was discontinued. The probability of extinction at the end of 30 years for juvenile-release and adult-release populations was 0.97 and 0.98 (respectively) for releases over 5 years, 0.64 and 0.54 (respectively) for releases over 15 years, and 0.001 and 0.002 (respectively) for releases over 25 years.

The influence of dispersal among patches on the final size of the population in each patch was a relevant variable because it was included in one of the best models (models 1, 2, and 3 were equivalent under our cut-off criterion, but models 1 and 2 had the largest Akaike weights) that explained variance in final population size (Tables 2 & 3).

The estimated cost of releasing adults was 1.62–1.67 times higher than that of releasing juveniles. Releasing 55 juveniles annually (5 individuals per patch) would cost between €166,274 and €167,690 (depending on how many months the birds are in captivity as juveniles before release), whereas releasing 55 adults annually would cost between €271,470 and €277,153. These figures are heavily influenced by the start-up costs in the initial year of the captive-breeding program because cage construction was the main expense (€137,848 for a juvenile release program and €238,848 for an adult release program). The costs of a keeper (€27,032) and daily food provisioning per individual (€0.14) are similar in both cases. In subsequent years, the cost of releasing one adult equaled the cost of releasing 4 juveniles. Hence, for all release scenarios, the difference in probability of extinction between adult and juvenile release scenarios far outweighed the difference in cost. Releasing juveniles into patches with poor habitat quality was nearly 2 times cheaper than releasing adults, whereas the best relative scenarios for adult releases resulted in a 26% improvement (for average abundances over the 25-year release period) and an 18% improvement (for extinction probability over the 15-year release period) over juvenile releases.

Achieving population viability over 30 years required a substantial increase in fecundities of all reproductive age classes and a substantial increase in age-0 survival rates in the wild (Fig. 3). Fecundities currently range between 0.18 and 0.58 female chicks per adult female in

## (a) Releasing juveniles



## (b) Releasing adults

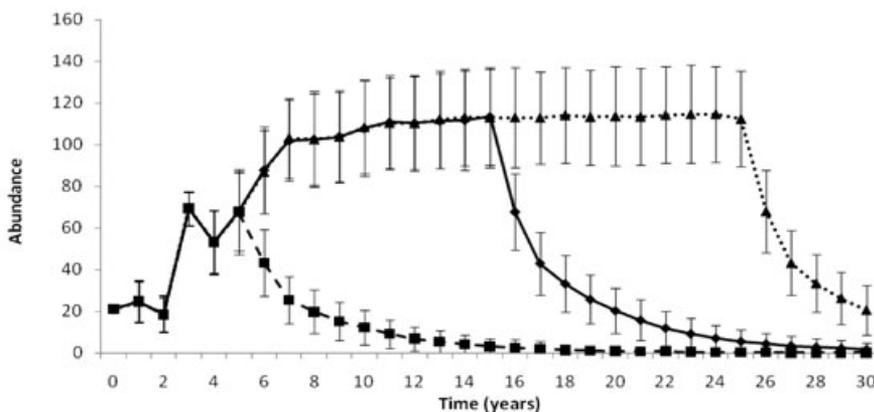


Figure 2. Model results for average (SD) metapopulation-level abundance for (a) juvenile and (b) adult releases of 5 female Crested Coots released annually into each wild population for 5, 15, and 25 years.

the wild. These values would need to be increased to the fecundity values observed in captivity (Fig. 1) in addition to increasing age-0 survival to almost unity (Fig. 3) to achieve population viability over 30 years.

## Discussion

Only a few authors have used population viability analysis to assess or predict the success of vertebrate reintroduction programs (Leaper et al. 1999; Slotta-Bachmayr et al. 2004; Armstrong & Davidson 2006). Our model showed that releasing juveniles or adults had a positive effect on metapopulation-level abundance during the period of release because the low survival rate for released birds (assumed to be equal for released adults and juveniles) was countered by the annual release of new birds. Adult releases yielded slightly higher abundances than juvenile releases as the reintroduction period increased because, in our model, released adults could reproduce and contribute to future generations in the population, whereas juveniles could not. However, even offspring of released adults had a high probability of mortality (80%), so the benefit was small and short lived. Once releases ceased, abundance decreased and probabilities of metapopulation extinction increased to almost 1.0 as the time since

last release increased for both juvenile and adult release scenarios. Again, this was due to low fecundities and survival rates in the wild; few offspring are produced in the wild and 80% of them die in their first year.

Dispersal explained considerable variance in final population size. However, the magnitude of the effect of dispersal on population size in our models may not be applicable to other systems. Results of these types of statistical model-selection analyses depend on the range of dispersal rates and dispersal functions used in the model. We considered exponentially decreasing dispersal as a function of distance between patches. If the model had also included various types of density-dependent dispersal or different dispersal kernels, the results may have been different. The conclusions that can be drawn from a statistical analysis of simulation results are limited by the assumptions and the structure of the underlying model. In any case, comparison of our general linear models showed that an explicit dispersal function should be included in the metapopulation model. The dispersal rates we used were also supported by independent observations, albeit the functional form is uncertain. Nevertheless, it is highly unlikely that dispersal determines whether a reintroduction program is successful.

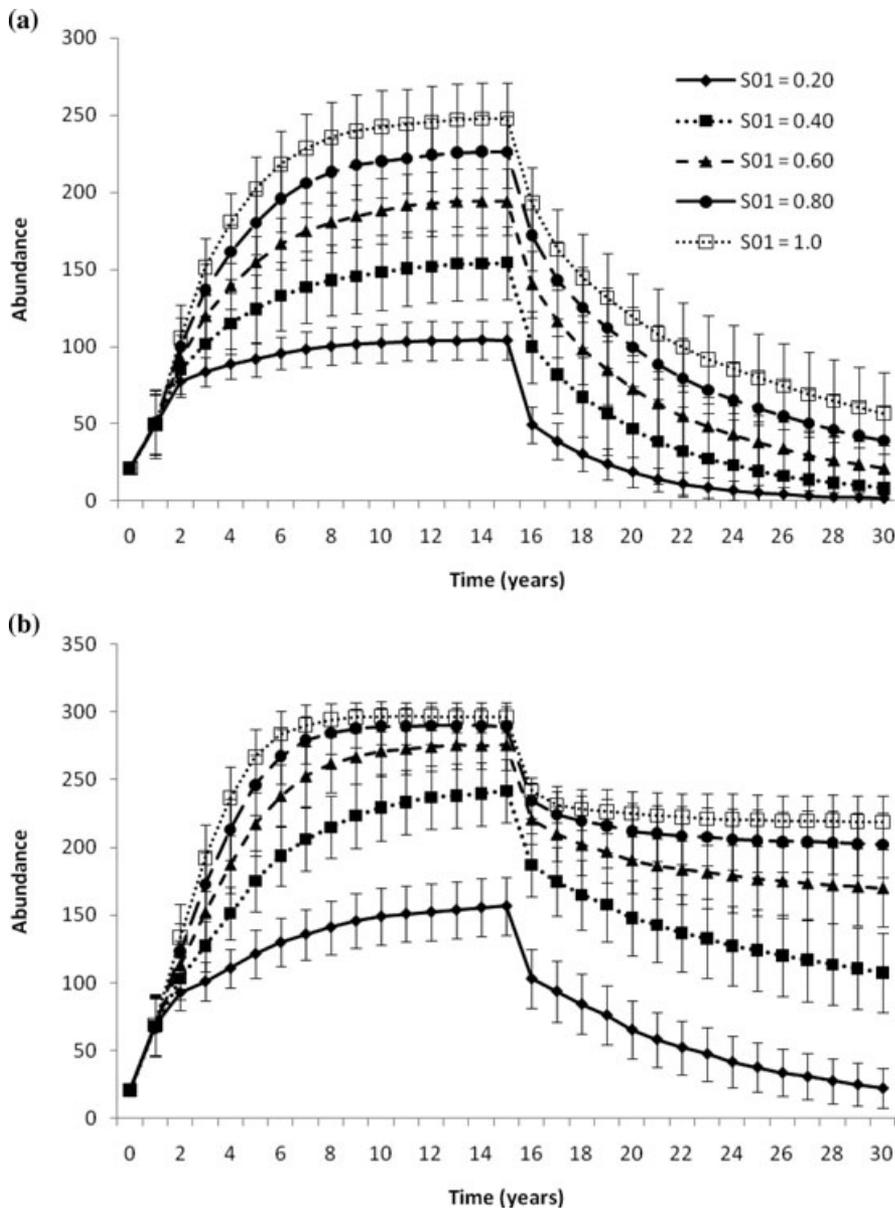


Figure 3. Results of sensitivity analyses showing the response of the study metapopulation after juvenile releases are stopped when age-0 survival in the wild ( $S_{01}$ ) is incrementally increased from 0.20 to 1.0 for (a) fecundities currently observed in the wild and (b) when fecundities in the wild are increased to those observed in captivity. In both cases, 5 juveniles are released annually for 15 years (vertical line, SD).

In a review of 180 case studies on animal relocations, Fischer and Lindenmayer (2000) found that 3% reported the cost of the relocation attempt. To the best of our knowledge, only Larson et al. (2003), Tisdell et al. (2005), and Duca et al. (2009) have taken into account realistic economic costs when conducting population viability analyses. We found that the return on investment from releasing juveniles was greater than that for adult releases, albeit temporary. The probability of metapopulation persistence was similar whether juveniles or adults were released, but the cost of releasing juvenile coots was almost half (if start-up costs were included) to a quarter (after start-up costs) of the cost of releasing adults. Managers overseeing the project had released juveniles because the behavior of other threatened waterbirds after long periods in captivity was different than that of wild birds (Green et al. 2005), possibly leading to decreased survival

and fecundity on release into the wild. Our results show that not only is it more prudent to release juveniles than adults for behavioral reasons, it is also cheaper. However, none of the strategies we considered resulted in sustained increases in abundance, and costs would need to be borne in perpetuity in the absence of permanent improvement in habitat quality.

Although releases temporarily elevate population-level abundance, substantial increases in survival rates and fecundities in the wild are necessary to maintain high abundances at the population level. An increase in survival of age-0 birds, including those immediately released, led to higher abundance at the metapopulation level. The low survival probability of newly released juveniles has been attributed to limited availability of high-quality food (Varo & Amat 2008; Tavecchia et al. 2009), and food availability is also likely affecting coots hatched in the

wild. Most wetlands in the region have low densities of submerged macrophytes, which are the main food source for Crested Coots, mostly because water quality is low and densities of introduced non-native aquatic herbivores such as carp (*Cyprinus carpio*) are high. Realistically, the survival rate of juveniles, released from captivity or hatched in the wild, will increase as habitat quality increases. Reduction in accidental hunting of the species when they occur in mixed flocks with common coots during the winter may also be necessary to increase metapopulation persistence. However, our results show that improving juvenile survival rates through increasing habitat quality is insufficient on its own to achieve stable abundances. Fecundities also must increase to levels observed in captivity to achieve population stability.

In the absence of continued release of Crested Coots, metapopulation viability will depend on a substantial financial investment to purchase land with habitat or to increase habitat quality for the species in wetlands across the study region. Management to increase habitat quality might benefit wetland-associated species other than the Crested Coot. However, our analyses did not include costs of habitat acquisition or increasing habitat quality.

It is currently unknown what the costs of increasing habitat quality would be and how this would relate to increases in survival and fecundity. However, it is clear that this type of information is relevant to maximizing the success of reintroduction programs. The value of combining population modeling with economic analyses in evaluating reintroduction programs lies in identifying the most important factors for improving program success in both economic and demographic terms.

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