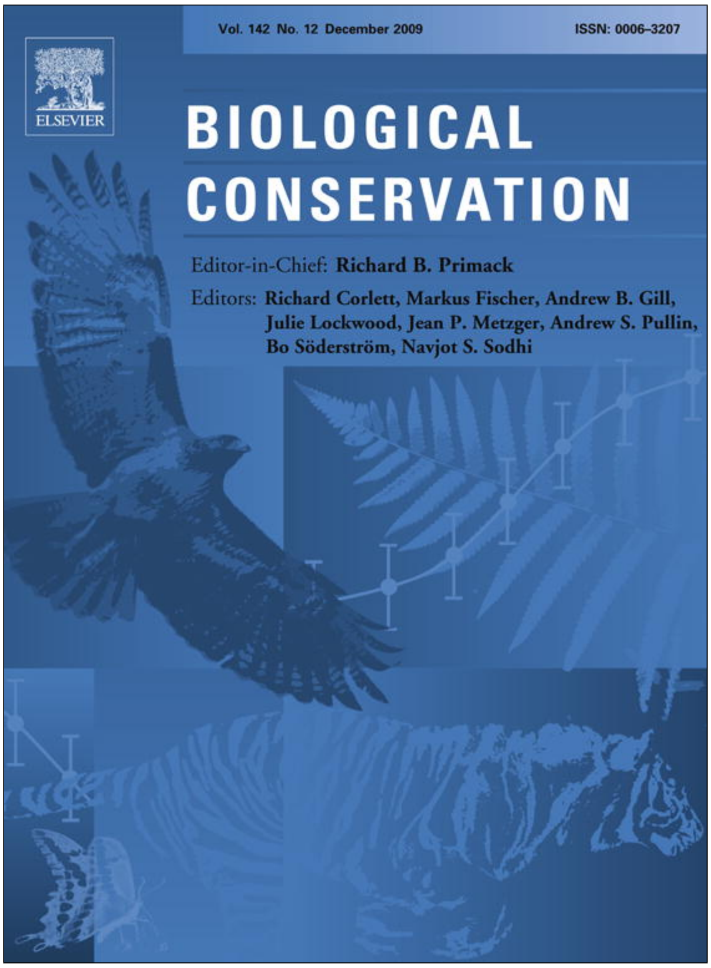
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Maximizing re-introduction success: Assessing the immediate cost of release in a threatened waterfowl

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ABSTRACT

Translocations have become one of the most commonly used tools for biodiversity restoration worldwide, however one out of three re-introduction plans fails to create a viable population or to successfully reinforce the existing one. We used results from the analysis of individual-based information on the re-introduction of a threatened waterfowl species, the crested coots *Fulica cristata*, to provide guidelines to maximise re-introduction success. We found that about a third of the post-release mortality took place within the first month after release. This immediate 'cost of release' in terms of local survival or 'release risk factor' seems to be a common feature of re-introduction projects, and it is likely due to the inexperience of captive-born individuals to face the new environment. This hypothesis was supported by the positive association between survival and time spent in the wild Results suggested that coots released between February and May have a slightly higher survival. A joint measure of survival and breeding probabilities indicated that birds released in late winter (February-March) had a higher chance to survive and reproduce compared to birds released later in the year. From an applied perspective our results can be used within an adaptive management framework to determine the optimum period of release, providing substantial support for future decision-making in the management of waterfowl, and other long-term projects of re-introduction of threatened vertebrate species.

1. Introduction

Translocation projects have been frequently used as a conservation tool on many taxa, including mammals, birds, fish and reptiles, with the goal of enhancing or sustaining local biodiversity (Seddon et al., 2007, 2005). *A posteriori* evaluations of these projects delivered contrasting results on their efficiency (Fisher and Lindenmayer, 2000; Griffith et al., 1989; Sarrazin and Barbault, 1996). In a survey of 421 avian and mammalian translocations, including game species, Wolf et al. (1996) reported that 33% failed to meet the target (Dodd and Siegel, 1991; Griffith et al., 1989). Despite a general scepticism on their efficacy (Sarrazin and Barbault, 1996), animal translocations represent sometimes the only management action available to try to reverse the trend of local biodiversity loss (Bright and Morris, 1994; Cade and Temple, 1995). To enhance the chances of success, translocation plans are often assessed by an interactive monitoring of their efficiency (Dodd and Siegel, 1991; Holling, 1978; Sarrazin and Barbault, 1996; Seddon et al., 2007; Sutherland, 2000). If the interactive monitoring is generally associated with difficult concepts and institutional resistance at a large-scale (Johnson, 1999; Johnson and Williams, 1999; Walters, 1986), it can be applied successfully at a local scale to tweak protocols or future management actions according to the targets established (Johnson, 1999; Sarrazin and Barbault, 1996). Animal re-introduction or restoration projects, in particular, have the long-term goal of establishing self-sustainable (viable) populations. While persistence largely depends on good habitat conditions, establishment of a new group of individuals depends on the short-term local survival of released individuals (Armstrong and Seddon, 2007). Short-term post-release survival is thus a crucial parameter for the success of projects, and depends on many factors, such as the age of individuals (Sarrazin and Legendre, 2000), the release method (Eastridge and Clark, 2001; Green et al., 2005), and the rearing conditions (Bright and Morris, 1994). Furthermore, post-release survival can be negatively affected by the inexperience of released animals to face the new environment (Brown et al., 2006). In fact, a common feature of translocations seems to be a high loss of animals immediately after release (Griffith et al., 1989). The consequence is that a larger numbers of individuals has to be released

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to reach management targets. We show here a procedure to assess the immediate cost of release based on the longitudinal analysis of presence–absence data using observations of released crested coots, *Fulica cristata* that permits the refinement of release protocol through an evidence-based management (Sinclair et al., 2007).

The crested coot is a middle-size fowl distributed mainly in the wetlands of the Ethiopic region (del Hoyo et al., 1996). The few western Palearctic populations are in the southern part of Spain and northern Morocco where the species is considered critically endangered (Amat and Raya, 2004). The species was historically distributed along the coastal areas of south and eastern Spain, but the natural populations are now confined to the south part of the country (Doñana National Park) where their numbers are currently supplemented by individuals bred in captivity. The decline of Spanish populations is thought to have occurred as a consequence of a change in the agricultural practices and the corresponding decrease in food availability and quality (Varo and Amat, 2008). In year 2000 it began a project for the re-introduction of the crested coot in the wetlands of Comunidad Valenciana (eastern Spain), together with a plan of habitat restoration. Conditions before release were optimal to maximise the survival probability of released birds, but an high survival probability alone it is not a guarantee of a viable population and the probability that released individuals would breed in the wild is an equally important target for the re-introduction project. A minority of released coots have been seen breeding successfully within, or nearby, the releasing areas. We used the observations on marked birds made throughout the year: (i) to obtain a first estimate of the annual survival probability of released birds, (ii) to quantify the immediate cost of release, (ii) to identify any inter-annual variation in survival in response to stochastic environmental conditions and (iv) to identify the optimal period of release combining the estimates of survival and breeding probabilities.

2. Methods

2.1. Data collection and releasing protocol

We analysed observations of crested coots collected between April 2000 and March 2006. Birds were born in captivity and reared by captive parents in open-air cages at the rehabilitation centre near the city of Valencia (eastern Spain), and subsequently soft-released in six wetlands along the coastal areas of the province after a period spent in captivity ranging from 2 to 12 months after hatching. Conditions before release were optimal, i.e. birds had unlimited amount of food available and were kept in large cages near the release area. Birds were released continuously throughout the year with the exception of the hunting season (from mid October to the end of January). The crested coot is protected under Spanish hunting regulations, but the species flocks with the common coot by heterospecific attraction and is sometimes accidentally shot (Martínez-Abraín et al., 2007). To minimise mortality due to hunting, releases occurred in hunting-free areas. Before release, coots were marked using a collar-band with a unique alphanumeric code that allowed resighting from the distance. Resighting was done systematically by visiting each wetland area along the coast in which coots were released or might have moved to.

2.2. Survival probability and the immediate cost of release

We used capture–resightings models (Burnham et al., 1987; Lebreton et al., 1993) to estimate local survival from resightings of marked coots accounting for detection probability. We did two analyses using partially independent data. In a first analysis, we estimated survival over an interval of one year. For this analysis we used the capture and resightings of birds released in February and March from 2000 to 2006. We denote φ_i, the probability that an animal seen at year i is alive at year $i + 1$, and P_i, the probability of seeing an animal at occasion i. In this analysis, coots were sorted into three groups according with their age (in months) at the time of release. The first group included birds less than 3 months old, the second group birds between 3 and 6 months old and the last group birds older than 6 months. In this first analysis we were interested in the effect of year (denoted 'y') and the age at release (denoted 'a') on the survival probability. We were also interested in measuring the difference between the survival during the first year of release, denoted φ'_i, and the subsequent one, φ_i. A positive association between survival and the time spent after release, regardless the age of the bird, would indicate a positive effect of the experience. In model notation the levels of 'y' are '0', '1', '2', '3', '4', '5' and '6' for years 2000–2006, respectively. Similarly, those of 'a' are denoted '1', '2', '3' for the three age classes considered. The full interaction between main effects is denoted with '$*$', while ' + ' denotes an additive relationship. To shorten notation we used the symbol '!' when all levels were considered, so that the notation '$y(0, 1, 2, 3, 4, 5, 6) * a(1, 2, 3,)$' refers to a model assuming year and age-dependent parameters and can be noted in short '$y(!) * a(!)$'.

To further investigate the association between survival and the time spent in the wild and to identify the best period of release in terms of survival probability, we did a second analysis. This time, we focussed on the estimate of survival during interval shorter than a year and again on the difference between the survival of newly marked birds, denoted S'_i to avoid confusion with the annual value noted φ'_i, and the one of already marked ones, noted S_i. The cost of release in term of survival probability, denoted CoR hereafter, during the interval i can be expressed as the relative difference between S'_i, and S_i, (Tavecchia et al., 2005), so that:

$$\mathrm{CoR}_i = 1 - S'_i/S_i. \tag{1}$$

The continuous nature of the release protocol complicated the estimation of mortality within the year because the probabilistic framework is based on discrete rather than continuous time intervals. Hence we first categorized the releasing-resighting data to match the requirements of the model as follows: we divided the year into six within-year intervals of different length over which we estimated monthly local survival (Fig. 2). The first four intervals were approximately 30 days long and included releases and resightings made in February, March, April and May, respectively. The interval of 30 days was chosen to maximise the number of releases and recaptures that will be included in the data set and to be able to compare survival with other studies (e.g. Tavecchia et al., 2003). The other two intervals included the period from June to September and October to January, hereafter 'summer' and 'winter' periods, respectively. Each of these period is 4 months long so that summer and winter estimates can be compared directly. For each interval, we retained only those releases and observations made during the first 15 days because pooling data over a period more than half the length of the interval can generate biased estimators (see Hargrove and Borland, 1994). In summary, data were sorted into 36 occasions from April 2000 to March 2006, which corresponds to 35 time intervals (22 of *c.* 30 days and 12 of *c.*120 days, Table 1). Note that although intervals were of different length, survival probabilities were always estimated on a monthly basis. The annual survival in relation to a specific release month can be calculated by multiplying the appropriate survival estimates. The annual survival of coots released in March, for example, is the product of the March survival of newly released birds by the February, April and May survivals of experienced birds, by the probability to survive the summer and winter intervals.

Table 1
Number of coots released according to year and within-year intervals retained for the analysis of the cost of release.

Within-year interval	Interval length (days)	Year							N
		2000	2001	2002	2003	2004	2005	2006	
February	28	0	28	56	41	0	63	0	188
March	31	0	12	20	15	58	0	25	130
April	30	11	0	0	0	1	0	0	12
May	31	0	0	18	26	0	0	0	44
Summer (June–September)	123	12	0	0	0	0	0	0	12
Winter (October–January)	122	0	0	0	0	0	0	0	0
Total	365	23	40	94	82	59	63	25	386

Our design is similar to that used by Tavecchia et al. (2002, 2003) for the analysis of recovery data, with the difference that monthly survival is allowed to vary between consecutive within-year intervals. The within-year survival estimates provide an indication of the cost of release and of when birds should be released to maximise their survival, but it cannot inform the annual survival value. Annual estimates from this analysis will be obtained by combining estimates over short time intervals and compared with those obtained in the first analysis. The parameters S', S, and P are modelled simultaneously using the year (denoted 'y'), and the within-interval (denoted 's') as linear predictors of survival and recapture parameters (Burnham et al., 1987). In this analysis the 'y' and 's' effects have 7 and 6 levels, respectively, specified in brackets. The levels of 'y' are denoted as above, while those of 's' are denoted '*fe*', '*mr*', '*ap*', '*ma*', '*sm*' and '*wt*' for February, March, April, May, Summer and Winter intervals, respectively. As before, we used the symbol '!' to indicate that all levels were considered to shorten notation. For example, a full-time effect is denoted '$y(0,1,2,3,4,5,6) * s(fe, mr, ap, ma, sm, wt)$' or in short '$y(!) * s(!)$'.

2.3. Model selection procedure

Model selection procedure classically begins by verifying the goodness-of-fit of a general model (Pollock et al., 1990). A lack of fit reveals that substantial extra-binomial deviance remains unexplained. This would suggest that individuals differ in capture and/or survival probability (Pradel et al., 2005). In the first case, additional parameters can be added to the model. In the second case, model deviance should be scaled to account for the effect of the unexplained variability (Lebreton et al., 1993). In both analyses we began model selection by verifying the goodness-of-fit of a general model, assuming survival and detection probabilities fully time dependent. The goodness-of-fit of this model was calculated using program U_CARE (Choquet et al., 2003). Model selection then proceeded by progressively removing effects on survival and recapture parameters separately (Grosbois and Tavecchia, 2003). Model selection was based on Akaike's Information Criterion (Burnham and Anderson, 1998). The model with the lowest AIC value is considered the best compromise between model fit and model complexity. However, the difference in AIC is an arbitrary measure of the discrepancy between two models (Burnham and Anderson, 2002). Here we shall arbitrarily assume a cut-off value of 2 points and when models are within two points we retain the one with the lowest AIC value. Although model set is not specified a priori, this analysis provides a hypothesis for the pattern of release costs, and further testing of this hypothesis and model can occur by collecting independent data over time through on-going adaptive management. We used the program M_SURGE (Choquet et al., 2003) to fit capture–recapture models. This program was preferred over others as it calculated with reliability the number of estimable parameters using the formal procedure in Catchpole and Morgan (1997). We calculated the proportion of the temporal variance explained by the retained model as [(Deviance(0)-Deviance(retained.model))/(Deviance(0)-Deviance(general.model)], where Deviance(0) is the deviance of the model with constant parameters and Deviance(general.model) is the one of the model including all parameters time dependent (see also Harris et al., 2005). Finally, when survival is estimated over a short period (i.e. in the second analysis) estimates near 1.00 should be expected. Standard errors of near-boundary estimates are generally underestimated. In this case, the 95% confidence interval was estimated by profile likelihood, that is to say by fixing the parameter to progressively lower values until model deviance changed significantly. (As the change in deviance of nested models follows a chi-square distribution, a statistically significant difference of 3.84 corresponds to chi-square with 1 degree of freedom, and 5% upper tail probability).

2.4. Breeding proportion and optimum period of release

A small number of marked individuals were seen successfully breeding, i.e. feeding the young, within, or nearby, the releasing areas during early summer. The number of birds seen breeding was too small to apply capture–recapture models. Nevertheless these data can be used to obtain an estimate, conditional on detection, of the proportion of observed breeders, B_s, according to month of release, 's'. Specifically, if 'b_s' is the number of marked birds seen feeding their chicks and, 'n_s', the total number of birds released during the s-month, the probability of breeding, B_s, is simply b_s/n_s. This proportion can be viewed as the probability of breeding for a bird release during the month s. In contrast with the probability of survival, the probability of breeding is conditional on detection, i.e. on only those birds that have been observed, and it is assumed to be constant due to the small number of birds in the sample. Comparisons among groups however, are informative as detection probability does not depend on the month of release and all birds have the same detection probability during breeding (see Section 3). The variance of B can be estimated as $B(1-B)/n$ (Sokal and Rohlf, 1981). Finally, we multiplied survival probability and breeding probability to detect the best period of release. Assuming that the number of chicks produced by a breeding coot does not depend on the month of release, the measure is equivalent to the relative difference between the fitness of individuals released in different months. In all tests, the probability threshold for a statistically significant effect was set at 0.05 and the 95% confidence interval of estimates, derived by the combination of multiple values, was calculated by using the δ-method to account for the covariance between the estimates (Morgan, 2000).

3. Results

3.1. Survival probability and the cost of release

We first obtained an estimate of annual survival by analysing the resighting history of birds released and re-observed between February and March of each year ($N = 445$). The goodness-of-fit test of a model in which all parameters varied over time (Model A, Table 2) suggested a survival difference between newly and already marked birds ($Z = 3.31$; $P = 0.001$). It also suggested the

Table 2
Modelling recapture and annual survival probability of crested coots released in the Valencia province. φ' = survival of newly released coots, φ = survival of already released coots, P = detection probability. Effects: 'y' = year (six levels), 'a' = age at release (three levels), '$*$' = interaction between effects, ' + ' = additive relation between effects, '·' = no effects considered, '–' = parameter not included in the model. Levels: ! = all levels considered, AIC = Aikaike's information criterion, ΔAIC = difference with the lowest AIC value, DEV = model deviance, K = number of identifiable parameters. Retained model in bold (effective sample size = 434).

Model	Parameter			K	DEV	ΔAIC	AIC
	φ'	φ	P				
A	–	y(!)	y(!)	11	290.67	12.28	317.79
B	y(!)	y(!)	y(!)+m	17	266.77	1.23	306.74
C	y(!)	y(!)	m	14	283.40	11.39	316.90
D	**y(!)**	·	**y(!)+m**	**12**	**276.27**	**0**	**305.51**
E	·	y(!)	y(!)+m	13	282.77	8.62	314.13
F	·	·	y(!)+m	8	286.05	1.38	306.89
G	y(!)*a(!)	y(!)	y(!)+m	23	261.22	8.91	314.42
H	a(!)	y(!)	y(!)+m	15	281.58	11.71	317.22
I	a(!)	·	y(!)+m	11	283.77	5.39	310.90

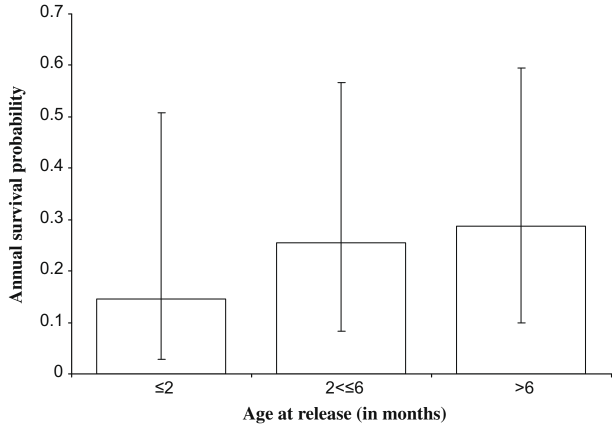

Fig. 1. Annual survival from the histories of 445 coots according to the age of the bird at release (in months). Bars indicate 95% confidence intervals.

presence of resighting heterogeneity ($Z = -2.69$; $P = 0.001$). We corrected for this lack of fit by introducing specific parameters, φ', to account for the survival of the first-year after release and a trap-dependent effect, designated 'm' (Pradel, 1993). Time dependent models accounting for survival and detection heterogeneity simultaneously have redundant parameters (Gimenez et al., 2004). This complicates model selection as the AIC values are calculated on estimable parameter only. For this reason, we assumed that the heterogeneity in detection probability was constant over time, i.e. that there was an additive relationship between 'y' and 'm'. A model including φ' and a trap-dependent effect described the data adequately ($\chi^2_1 = 1.91, P = 0.05$) and was used as a new stating point for model selection (Model B, Table 2). Model selection led to a model assuming a time variation in recapture probability and two sets of survival parameters one for newly released birds which was variable over time, and another for already marked birds (Model D, Table 2). This model captured 69.7% of the variance due to the variation over time of parameters. According to a model assuming constant survival probabilities, yearly survival of newly released birds was 0.14 (SE = 0.03) and survival during the second year after release was high (0.66, SE = 0.20). This last estimate, however, is not precise due to the small number of birds that survived more than 12 months ($N = 33$). Age at release had a slightly positive effect on survival during the first year (Fig. 1), however the effect was weak and was not retained (Models G–I Table 2). Note that due to the small number of birds that survived the first-year after release, we avoided models assuming an additive relationship between φ' and φ because results would reflect largely the variation in φ' only.

The first analysis allowed us to obtain estimates of survival over an interval of a year, however, because of the high mortality most of the information was within the first-year after release. As a consequence in the second analysis we considered intervals shorter than a year (Table 1). We used 386 encounter histories of coots released from April 2000 to March 2006 (Table 1). Those birds marked during the first 15 days of February and March appeared in both datasets. Also, for simplicity, we did not consider the age at release as this effect was not retained previously (Table 2). As before, the model assuming a full-time effect, Model_0, did not capture data variance adequately ($\chi^2_{71} = 169.46; P = 0.001$). This lack of fit was due to the presence of an immediate cost of release, i.e. a lower survival of newly released birds ($Z = 6.07$; $P = 0.001$), an equivalent of the transient effect, and to a heterogeneity in recapture probability, i.e. some animals were systematically seen more than others, an effect called the 'trap-happiness' effect ($Z = -7.22$; $P = 0.001$). As before, we introduced specific parameters, S'_i, to account for the immediate cost of release, CoR, and a trap-dependent effect. The model including φ' and the effect 'm', named Model_2, had a lower AIC value (ΔAIC = 89.56; Table 3) and a better fit to the data ($\chi^2_{33} = 33.28; P = 0.45$). We continue model selection from Model_2 by modelling S' and S separately. As before, models with an additive relationship between these two parameters were not considered: (i) because we were interested in a fine modelling of the immediate survival and (ii) because of the great difference in sample size between already and newly marked birds. A model with only 'y' for newly marked bird survival had a lower AIC value than the one that also assumed a variable monthly survival (Model_5; Table 2). An opposite result was obtained for previously released birds whose survival was constant between years but variable within the year (Model_9 vs. Model_10; Table 2). A further reduction in AIC value was reached when monthly survival was categorized into two groups, one with survival of February, March, April and May, and the second one including the Summer and Winter survivals (Model_18; Table 2). According to this model, the monthly survival of experienced birds was 0.999 (SE = 0.001) from February to the end of May and 0.826 (SE = 0.014) from June to the end of January. The first value, i.e. the survival of experienced birds from February to May, was near the upper boundary value of the survival interval (0.00–1.00). The 95% confidence interval calculated in this way for the 0.999 estimate ranged from 0.947 to 1.00. The division of the year into two shorter intervals with specific survival parameters was retained also in newly released birds, in addition to the year-to-year variation (Table 3). These results suggest a time-variant cost of release (Table 4). The probability of detection varied over the year and according to the previous resighting history (average values. 0.55 for trap-happy animals and 0.28 for trap-shy animals). Model_18 captured 91.7% of the variation over time of the parameters. Estimates from the retained model (Model_18) suggested that survival was higher for coots released during the period February–May in 2001 and 2004 (Table 4). Average expected annual survival of birds released between February and May was 0.137 (SE = 0.017), a value in agreement with the one found in the previous analysis based on annual intervals (0.14). The expected survival for birds released outside this period was virtually 0. Indeed, out of the eleven birds released in June 2000 (Table 1), none has been seen again afterwards. These average values led to an estimate of CoR of 0.314 (SE = 0.011; Eq. (1) Table 3). All models indicate that coots released in March had a small survival advantage (about 15%; Table 4). Estimates of the expected annual survival of experienced birds, i.e. after the first month spent in the

Table 3
Modelling recapture and monthly survival probabilities. φ' = survival of newly released coots, φ = survival of already released coots, P = detection probability. Effects: 'y' = year, 's' = within-year interval, '$*$' = interaction between effects considered, ' + ' = additive relation between effects. Levels: ! = all levels considered, AIC = Aikaike's information criterion, DEV = model deviance-1500, K = number of identifiable parameters. Retained model in bold (effective sample size = 946).

Model	Parameter			K	DEV	ΔAIC	AIC
	φ′	φ	P				
0	–	y(!) ∗ s(!)	y(!) ∗ s(!)	64	309.91	119.84	437.91
1	–	y(!) ∗ s(!)	y(!) ∗ s(!)+m	65	247.29	59.22	377.29
2	y(!) ∗ s(!)	y(!) ∗ s(!)	y(!) ∗ s(!)+m	75	198.36	30.29	348.36
4	y(!) ∗ s(!)	y(!) ∗ s(!)	y(!)+s(!)+m	56	269.53	63.46	381.53
5	y(!)	y(!) ∗ s(!)	y(!) ∗ s(!)+m	71	206.66	30.59	348.66
6	s(!)	y(!) ∗ s(!)	y(!) ∗ ∗ s(!)+m	70	223.97	45.9	363.97
7	y(!)+s(!)	y(!) ∗ ∗ s(!)	y(!) ∗ s(!)+m	74	201.78	31.71	349.78
8	y(!) ∗ s(!)	y(!)+s(!)	y(!) ∗ s(!)+m	58	216.47	14.4	332.47
9	y(!) ∗ s(!)	y(!)	y(!) ∗ s(!)+m	53	238.77	26.7	344.77
10	y(!) ∗ s(!)	s(!)	y(!) ∗ s(!)+m	54	221.70	11.63	329.70
11	y(!)	s(!)	y(!) ∗ s(!)+m	48	233.81	11.74	329.81
12	y(!)+s(!)	s(!)	y(!) ∗ s(!)+m	51	224.99	8.92	326.99
13	s(!)	s(!)	y(!) ∗ s(!)+m	47	246.77	22.7	340.77
14	y(!)+s(!)	s(fe,mr,ap,ma,sm_wt)	y(!) ∗ s(!)+m	50	225.25	7.18	325.25
15	y(!)+s(!)	s(fe,mr,ap,ma_sm_wt)	y(!) ∗ s(!)+m	49	273.96	53.89	371.96
16	y(!)+s(!)	s(fe,mr_ap_ma,sm_wt)	y(!) ∗ s(!)+m	48	225.76	3.69	321.76
17	y(!)+s(!)	s(fe_mr_ap_ma,sm_wt)	y(!) ∗ s(!)+m	47	225.77	1.7	319.77
18	**y(!)+s(fe_mr_ap_ma, sm_wt)**	**s(fe_mr_ap_ma,sm_wt)**	**y(!) ∗ s(!)+m**	**44**	230.07	0	318.07

Table 4
Cost of release, CoR, estimated from Model_18 assuming a year-dependent survival in new released birds and a two-type characterisation of the monthly survival for new- and already- released animals. The cost is expressed as the relative difference between newly and already released animals. Expected annual survival of the first-year after released is calculated combining the appropriate monthly survival estimates (see text). Standard errors via the δ-method are in brackets.

Year	Release cost ($1-\varphi'/\varphi$)		Expected annual survival	
	February–May	Summer–winter	February–May	Summer–winter
2000	0.385 (0.183)	0.997 (0.000)	0.133 (0.094)	0.001 (0.000)
2001	0.158 (0.022)	–	0.182 (0.059)	–
2002	0.502 (0.010)	–	0.108 (0.036)	–
2003	0.486 (0.011)	–	0.111 (0.037)	–
2004	0.153 (0.025)	–	0.183 (0.059)	–
2005	0.425 (0.014)	–	0.124 (0.043)	–
Mean[a]	0.314 (0.011)	0.997 (0.000)	0.137 (0.017)	0.001 (0.000)

[a] Geometric mean.

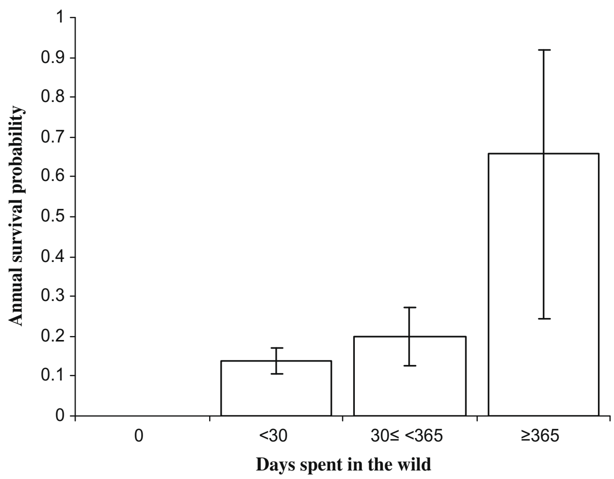

Fig. 2. Annual survival in relation to the number of days spent in the wild.

wild, were consistent across models, varying from 0.21 to 0.22 (Table 4). This survival is not strictly comparable with the one of experienced birds in the previous analysis as the time spent in the wild is not equivalent. In the first analysis already marked birds had spent at least 1 year in the wild, while in the second analysis they have spent at least a month. These values can be used to illustrate how annual survival changes with the time spent in the wild. Indeed, newly released birds have a survival of 0.14. This value increase to about 0.20 if they survive the immediate cost of release during the first month and further increases to 0.66 once they survive the first-year after release (Fig. 2). As this association was not due to the age of birds at release (Fig. 1), it is likely to be due to an increase in experience (see Table 5 and Fig. 2).

Table 5
Annual survival estimates according to the month of release from models assuming different monthly survival. Values from several competing models are consistent and suggested that coots released in March had a small advantage in survival.

	Model_10	Model_12	Model_13	Model_18	Mean[a]
February	0.1227	0.129	0.123	0.128	0.126
March	0.142	0.143	0.160	0.141	0.146
April	0.134	0.094	0.097	0.133	0.113
May	0.138	0.110	0.140	0.109	0.123
Summer	0.0002	0.111	0.0003	0.0006	0.001
Experienced birds[b]	0.214	0.217	0.214	0.216	0.215

[a] Geometric mean.
[b] More than one month in the wild.

3.2. Breeding proportion and the optimum period of release

Among the 386 birds considered above, 53 have been seen as breeders at the beginning of the summer. The highest breeding proportion was found for coots released in March (0.20, n = 26), followed by those released in February (0.14, n = 26), followed by May (0.02, n = 1), while no birds have been seen as breeders among those released in April and in between June and September. The proportion of birds seen breeding among those released after March was lower than those released before (released before March vs. released after March: $\chi^2_1 = 6.87; P = 0.01$) but there was not a significant difference between those release in February and birds released in March ($\chi^2_1 = 1.52; P = 0.22$). Despite being based on a relatively small sample size, the monthly differences are informative because recapture probability did not change according to the month of release. To test this, we sorted birds

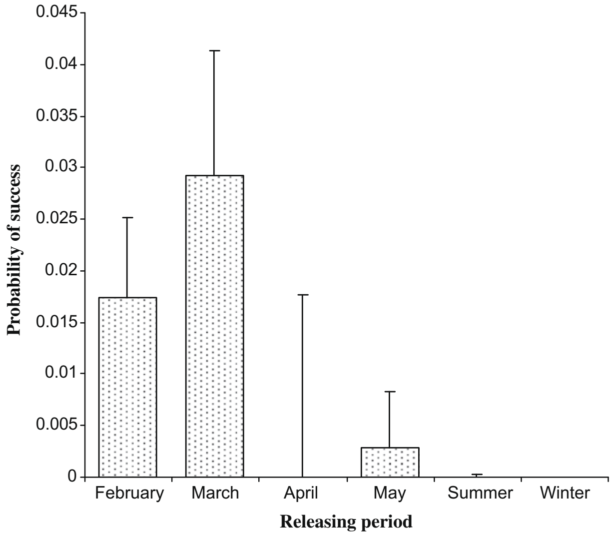

Fig. 3. Probability of success depending on the month of release. The probability of success is calculated as the product of the average expected annual survival and the probability of breeding and it is equivalent to the probability that a bird will survive *and* breed during the first-year after release. Bars indicate 95% confidence intervals. Note that the value for winter cannot be calculated as there were no newly released birds in this period.

according to month of release and included a group effect in the probability of resighting in Model 1. Note that Model 1 has a general structure on survival and the retained structure of recapture parameters. The new model had a similar AIC value to Model 1 (ΔAIC = −0.94) indicating that the additional parameter did not improve the explanatory power of the model and we did not consider this effect any further.

A measure of release success according to the month of release can be obtained by multiplying the breeding proportion and the respective survival probabilities. As breeding proportion had no sampling variance we calculated the variance of each proportion, B, as $B(1 - B)/n$. For numerical reasons, we assumed $b_s = 1$ when no birds were seen breeding, i.e. for birds released in April and during the Summer period. The combined measure of survival and breeding proportion had a large variance (Fig. 3) mainly due to the small sample size of breeding birds, however coots released before March have a greater short-term fitness compared with those released in other periods ($Z = -4.57$, $P < 0.001$).

4. Discussion

Griffith et al., (1989) reported that about one out of three translocations failed to create a self-sustaining population. They provided a formula to predict the probability of success of a translocation project based on individual- and species-specific characteristics (see also Wolf et al., 1996). While this can be useful in planning a translocation, it does not provide information on which mechanisms caused the different outcomes (Nichols and Williams, 2006). Armstrong and Seddon (2007) separated the potential factors influencing the persistence of a new population from those influencing the establishment of translocated animals. While persistence largely depends on good habitat conditions, establishment of a new group of individuals depends on the short-term local survival of released individuals (Armstrong and Seddon, 2007). By closely monitoring the survival and breeding probability of reintroduced crested coots, we found that about a third of the losses occurred during the first month. This high short-term mortality was different between years and within the year, and cannot be associated with captive conditions (captive-born chicks were reared by parents in open-air cages and released in hunting-free areas). We detected an optimal period in which animals should be released to maximise their chances to establish in the releasing areas.

4.1. Cost of release in re-introduction plans

Importantly, the immediate loss of reintroduced individuals identified in our study and referred to here as 'cost of release', seems to be a general feature of translocation plans (see for example Bright and Morris, 1994; Brown et al., 2006; Calvete and Estrada, 2004; Hellstedt and Kallio, 2005) resulting from immediate dispersal or from the difficulty to cope with the new habitat (Armstrong et al., 2007; but see Nicoll et al., 2004). This is particularly evident in the comparison between the fates of wild versus captive-reared animals. For example, the first-year survival of aplomado falcons *Falco femoralis* reared in captivity was about 50% lower than wild-born falcons (Brown et al., 2006). The short-term mortality of translocated European wild rabbits, *Oryctolagus cuniculus*, was concentrated in the first nine days after release and was mainly due to predation (Calvete and Estrada, 2004). In our case, we cannot estimate which part of this immediate cost (i.e. local mortality) was due to emigration and which was due to true mortality. It might well be due to a combination of both factors. The dispersal hypothesis is supported by occasional resightings ($n = 6$) of marked coots in areas up to 500 km from the release sites (authors, unpubl.). On the other hand, we found that survival increases with the time elapsed since release. This is probably a result of natural selection (supporting the selection hypothesis) or of an increased experience acquired with the time spent in the wild. Alternatively, birds may progressively be less prone to disperse or survival may increase with age *per se*. We cannot strictly tease apart these hypotheses. A progressive increase in survival of released individual has also been reported in other birds and mammals (Brown et al., 2006; Wear et al., 2005). Whether an immediate cost of release is due to movements or progressive selection, it results in a real local cost for the re-introduction program that should be taken into account. Griffith et al. (1989) reported that translocations of captive-reared animals have twice the chance of failure compared to those of wild-reared individuals. We suggest that this difference is generated shortly after release and that the success of these projects largely depends on reducing this immediate cost.

4.2. Survival of crested coot

The survival probabilities found here are the first for the species and cannot be directly compared with other estimates. Nevertheless, with the exception of survival probability of birds in the wild for more than 1 year, annual values seem too low to sustain a viable population. Using a ring-recovery analysis, Clobert et al. (1985) estimated the annual survival of adults of the closely related but legally hunted common coot *Fulica atra* between 0.30 and 0.57. These estimates are low compared to those of other game species, i.e., Mallards *Anas platyrhynchos* (Tavecchia et al., 2003), but still about 50% higher than the average estimates found for adult crested coots, which more closely resemble those of first-year common coots (Brinkhof et al., 1997). Our estimates do not include permanent emigration or cases of collar loss. Six (1%) out of the 445 coots released have been seen in other areas and about 4% are known to have lost their collar during the first-year after release. Although these proportions are only an approximation of the true dispersal and collar loss probabilities, accounting for these cases the annual survival probability appears too low for a medium-size fowl.

4.3. Tweaking the release protocol to minimise the immediate cost

As a first measure, we investigated refinements of the releasing time that might increase re-introduction success. Time and frequency of release is known to affect post-release survival and ultimately population viability (Green et al., 2005; Robert et al., 2004). In our case, the few animals released after May have never been seen again. This is most likely because summer droughts promote dispersal, and hunting activity during autumn increases mortality of those birds that stay in the region. Indeed, out of 26 coots recovered dead whose cause of mortality was known, 8 (30%) were shot during the hunting season of the closely related common coot (C.V. unpubl. data). Other mortality causes included raptor and carnivore predation, intoxication, infection and road casualties, in minor proportions. A contribution of our study is the combined use of the estimates of survival and breeding probabilities, a measure that can be considered a proxy for short-term individual fitness and an indication of reintroduction success. Absolute values of the probability of breeding have to be taken with caution because are based on few observations and they are conditional on detection probability. Nevertheless, the comparison of month-specific estimates is valid as the probability of detection did not vary with the month of release. In addition all birds were seeing breeding at the same time period, i.e. early summer, and shared the same probability of detection. Results from the survival analysis only suggested a positive influence of the month of release when made between February and June. However, when the probability of breeding was considered, birds released before March had a clear fitness advantage. It might also be that the onset of the hormonal cycle linked to reproduction or better environmental conditions during the period of February–March (i.e., optimal water level, food availability and the absence of hunting) make birds less prone to leave the area and more likely to breed. The life-span of coots is relatively short. As a consequence, in natural conditions short- and long-term fitness are expected to be similar. Information available on coot reproduction (both from captive-breeding and observations in the wild) indicate that coots have a great potential to breed during their first year of life and as a consequence coots released earlier in the season need to survive fewer months to reproduce. With a high immediate cost of release on survival, enhanced breeding chances give an immediate fitness advantage. We can calculate a relative probability of success according to the month of release by multiplying the estimates in Fig. 3 by the respective numbers of birds released in each month (Table 1). If the 386 birds were released all in March, the re-introduction project would increase its chances of success by approximately 30% and it would ultimately reduce the average immediate cost of release.

Our study focussed on the short-term factors influencing establishment of new individuals and it does not consider the long-term probability of success of the re-introduction projects. In agreement with other authors (Armstrong and Seddon, 2007; Griffith et al., 1989) we believe that the growth rate of the established population depends on habitat conditions. Varo and Amat (2008) suggested that the Spanish populations of crested coots are limited by the availability and the quality of the food. Ultimately the long-term probability of success of the re-introduction of the crested coots in eastern Spain will depend on the efficacy of the measures to improve habitat quality.

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