

How do different releasing techniques affect the survival of reintroduced grey partridges *Perdix perdix*?

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The quality of released individuals can have a significant impact on the success of reintroduction projects. We tested which of the following release techniques resulted in the highest survival of released grey partridges *Perdix perdix* in Switzerland: 1) translocation of wild adult birds, 2) release of captive parent-reared adults as family groups, and 3) fostering of captive parent-reared chicks to wild barren pairs. Wild hatched offspring (F1 birds) from our re-established breeding pairs served as the control group. We used a multi-state capture-recapture model to estimate monthly survival rates from the data based on monitoring of radio-tagged individuals and reobservation and recovery of ringed individuals. Survival tended to be highest in wild-hatched partridges of the founder population (mean \pm SE; 0.90 ± 0.03), followed by that of fostered chicks (0.86 ± 0.03) and translocated adult wild birds (0.82 ± 0.06). While survival of these groups was not statistically different from each other, survival of captive-reared adults was significantly lower (0.70 ± 0.06). We discuss the implication of our results for further partridge reintroduction projects.

Key words: multi-state model, parent fostering, parent rearing, Perdix perdix, translocation

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Releases of individuals into areas where they have occurred previously (reintroductions), have become an important conservation method to restore locally extinct species (Fischer & Lindenmayer 2000, IUCN Re-introduction Specialist Group 2004).

However, many reintroduction attempts have failed because released animals are often highly susceptible to predation or unable to breed successfully (Beck et al. 1994, Fischer & Lindenmayer 2000, Wallace 2000). Detailed knowledge about the be-

haviour and life history of a target species is required to determine the suitable age class, timing and number and source (i.e. captive or wild) of stock for the planned release (Kleiman et al. 1986, Miller et al. 1994, Sarrazin & Legendre 2000, Green et al. 2005).

Different kinds of individuals can be released in reintroduction projects. One commonly used technique is the release of captive-bred individuals, with the advantage that large numbers can be released. However, predator avoidance behaviour is often not well developed in captive-bred individuals, as the ability to cope with predators is not only genetically determined but is learned during parental attention (Menzdorf 1976, 1977, Dowell 1990, Beck et al. 1994, Beani & Dessi-Fulgheri 1998). The survival of released individuals may be improved if they are reared under semi-natural conditions, e.g. parent- or cross-fostering (Sherrod et al. 1982, Lewis 1990, Cade & Temple 1995) or if anti-predator behaviour is trained before release (Ellis et al. 1978, Hölzer 1999). Another technique is the translocation of wild individuals with the advantage that they have already established anti-predator behaviour. Yet survival of these individuals may still be inferior compared to local conspecifics, perhaps because they have no knowledge of local conditions (Church 1993, Sarrazin & Barbault 1996, Stanley Price & Fairclough 1997, Reed 1999). A third release technique is fostering of chicks to wild parents. Captive hatched young are fostered at an early age to wild pairs that failed to successfully produce their own chicks. The advantage of this technique is that young become imprinted and socialised by experienced parents (e.g. predator avoidance), which may enhance their survival (Thomas 1987, Putaala & Hissa 1998). Estimates of survival of individuals released by these techniques are lacking. Such knowledge is important to increase the efficiency of release programs (Brittas et al. 1992, Kleiman et al. 2000, Meretsky et al. 2001).

The threatened grey partridge *Perdix perdix* has been the subject of many re-introduction projects throughout its range, either for harvesting purposes or for conservation. These projects have mainly depended on the release of large numbers of pen-reared individuals. The majority of these releases have failed to establish self-sustaining populations, mainly because of severe losses of released individuals due to predation (e.g. Rands & Hayward 1987, Putaala et al. 2001, Meriggi et al. 2002) and low breeding success (e.g. Rands & Hayward 1987,

Church 1993, Putaala & Hissa 1998). We tested whether survival rates of grey partridges differed among three different release techniques (translocated wild adults, pen-reared adults, fostered chicks) and compared their merits for establishing a self-sustaining population.

Material and methods

Study area

We conducted the study in the intensively cultivated Klettgau region (ca 30,000 ha) near Schaffhausen, Switzerland (430 m a.s.l.). Once a common breeding bird in the Klettgau, grey partridge populations declined dramatically after 1970 due to a severe loss of unimproved meadows, hedges and embankments, and fallow ground; as well as to an increase of chemical crop protection products and artificial fertilisers (Jenny et al. 2002). By 1996 the species was extirpated from the entire Klettgau region (Jenny et al. 1998).

Since 1991, the Klettgau has been the target of habitat enhancements by the Swiss Ornithological Institute, which has promoted the sowing of wild-flower strips to recreate an arable landscape suitable for grey partridge. In the most enhanced area of the Klettgau (530 ha), the amount of wild-flower strips had increased from 0 to 13 ha by 2001 and the area of hedgerows from 2 ha to 2.7 ha. This area was chosen as the site for all the birds released in our study. The study area was comprised primarily of cereal grains (49%), oil-seed rape and sunflowers (14%) and root crops (12%). Grassland covered 11% and another 11% was bare of vegetation (e.g. buildings and roads). The field size ranged within 0.1–5.5 ha (for further details see Buner et al. 2005).

Several partridge experts judged the habitat quality to be suitable for partridges prior to this release project (see also Buner et al. 2005). Between December and February of 1997/98, 1998/99 and 1999/2000, an intensive fox reduction program (shooting foxes with the help of spot lights) was carried out on the study area as well as on an additional buffer zone of approximately 2 km in radius to lower predator pressure. No further predator control was applied.

Releases of grey partridges

During 1998–2000, we released three different treatment groups totalling 130 partridges in the study area (Table 1), all genetically originating from the

Table 1. Number of grey partridges released per treatment group in the Klettgau, Switzerland, 1998-2000. Individuals from treatment group 4 were not released but hatched by re-established pairs in the study area and served as control group. The figures in brackets refer to the number of individuals that were radio-tagged.

Treatment group	Total number of birds								Total	
	1998		1999		2000		2001		N	Tagged
1) Translocated wild adults	10	(10)	11	(11)	0	-	0	-	21	100%
2) Pen-reared adults	0	-	0	-	77	(59)	0	-	77	77%
3) Fostered chicks	0	-	8	(7)	24	(7)	0	-	32	44%
4) Wild-hatched chicks	15	(8)	0	-	26	(11)	26	(0)	67	28%
Total number/Tagged	25	(72%)	19	(95%)	127	(61%)	26	(0%)	197	(57%)

western clade of the subspecies *Perdix perdix* (see Liukkonen-Attila et al. 2002). The first treatment group was adults caught from different coveys in Germany and the Czech Republic in February (hereafter: translocated wild adults, eight males and 13 females). These birds were kept in pens until they were released in April. Upon release they immediately paired with each other or with individuals released at an earlier stage of the project. By releasing them in spring, we hoped to minimise predation losses during winter. The second treatment group was captive parent-reared adults that were released as family groups (i.e. coveys) in December or January (hereafter: pen-reared adults, 44 males and 33 females in seven coveys). We released them in winter, rather than in spring, because we believe that the adaptation to predators is easier when the birds are still in a covey rather than in pairs. The third treatment group was captive parent-reared chicks that were all successfully fostered at the age of 5-8 weeks in August (hereafter: fostered chicks, N = 32, gender not determined on all birds) to three wild pairs, which failed to produce their own chicks. Our control group was comprised of the offspring of successful broods of re-established partridges (hereafter: wild-hatched chicks, N = 67, gender not determined on all birds, five broods).

All released birds were kept in quarantine for at least one month prior to release. Each covey was kept in a separate 4 × 10 m outdoor pen near the study area, containing short grass, sandy areas and bare soil for foraging with tussocky grass and branch heaps for cover. The food provided was a mixture of seeds and pellets with a low dose of Phlubenol added to prevent endogen parasite infections. The day before release, all birds were ringed and moved into release-pens in the study area where they were kept overnight. The pens were opened the following morning. For pen dimensions and the selection of release sites we followed the instructions provided by Game Conservancy Limited (1996).

All birds used in this study were released in a healthy status, confirmed prior to release by the local veterinarian who analysed blood samples, faeces and measured body weight.

Data collection

During 1998-2001, 113 full-grown individuals were equipped with 10-g radio transmitters (< 3% of body mass) with an expected battery life of eight months and a transmission range of about 3.5 km (Titley Electronics Ltd, Ballina, Australia, Model GPI). The transmitters were mounted using a Rappole harness (Rappole & Tipton 1990) made of 3 mm PTFE (COOK Medical Products, Switzerland, Flat Wound Drain). The transmitters were painted brown to make them less visible. Only adult birds (treatment groups 1 and 2) could be radio-tagged before release. Fostered chicks (treatment group 3) were only ringed, but caught for tagging after they were full grown (60 days after hatching). Wild-hatched chicks (control group) were, by definition, individuals without rings, and were eventually caught and ringed when either subadult or adult (see Table 1).

To catch birds we used mist-nets (18.0 × 2.4 m, mesh size 30 mm) set as a large 'funnel' trap (Bub 1991). We approached the birds with two cars to prompt them to walk into the trap. We were able to radio-tag at least one bird in each existing covey or pair on the study area. All radio-tagged birds were located and sighted at least once every week and the total number of birds in each covey or pair was counted. After the mating season, all pairs and singles in the study area were caught, their identity verified and at least one individual per pair was radio-tagged. If an individual was found dead, we noted the cause of death, as assessed by inspection of the carcass.

Under the assumption that individuals which were only ringed did not change their covey or pair (never observed in radio-tagged birds) and given the

large effort to count all individuals of each group at least once a week, we constructed encounter histories on a monthly basis for all birds. The information included encounter histories for each individual and month whether it was observed alive with or without a radio transmitter, not observed or found dead.

Estimation of survival

Because of a mixture of radio-tagged (hereafter: tagged) and ringed birds (hereafter: untagged), and because previously untagged birds possibly became tagged or previously tagged birds possibly became untagged (battery dead on radio transmitter), classical methods for the estimation of survival of radio-tagged animals (White & Garrot 1990) were not applicable. Therefore we used a multi-state capture-recapture model (Hestbeck et al. 1991, Williams et al. 2002) which allowed a separate estimation of survival for tagged and untagged individuals as well as the estimation of probabilities that birds were tagged and that active tags stopped functioning. We defined a model with five different states at time i : 1) untagged living individuals, 2) untagged dead individuals, 3) tagged living individuals, 4) tagged dead individuals, and 5) living individuals with non-functioning radio transmitters. State transition probabilities are equivalent to the joint probability of survival and changes with tag status. Specifically, the parameters in the model are S_i , the probability that an untagged individual survives from the beginning of month i to the beginning of month $i + 1$, S_i^R the probability that an individual with a tag (active or non-functioning) survives from the beginning of month i to the beginning of month $i + 1$, p_i the probability that an individual without a non-functioning tag and that is alive at the beginning of month i is relocated in that month, p_i^R the probability that an individual with an active tag and that is alive at the beginning of month i is relocated in that month, r_i the probability that an individual with an active tag that died in the interval $i-1$ to i is found at i , Ψ_i^R the probability that an individual without a functioning tag is caught at the beginning of month i and gets a functioning tag, and Ψ_i^P the probability that a tag that was active at time $i-1$ became non-functioning at time i . The model is written as a matrix of state transition probabilities and a vector of state-specific encounter probabilities. The states of departure (time $i-1$) are in columns, the states of arrival (time i) are in rows, the order of states 1 to 5 is from top to

bottom and from left to right:

$$\begin{bmatrix} (1-\psi^R)S & 0 & 0 & 0 & 0 \\ (1-\psi^R)(1-S) & 0 & \psi^P(1-S^R) & 0 & (1-\psi^R)(1-S^R) \\ \psi^R S & 0 & (1-\psi^P)S^R & 0 & \psi^R S^R \\ \psi^R(1-S) & 0 & (1-\psi^P)(1-S^R) & 0 & \psi^R(1-S^R) \\ 0 & 0 & \psi^P S^R & 0 & (1-\psi^R)S^R \end{bmatrix} \begin{bmatrix} p \\ 0 \\ p^R \\ r \\ p \end{bmatrix} \quad (1).$$

The parameters in the model may vary according to the age of the bird, the month and the treatment group an individual belongs to.

States 2 and 4 ('dead') are absorbing (i.e. individuals that enter one of these states stay there, and can only be reencountered on the occasion when they enter these states). Because of the low probability of finding dead untagged individuals we decided to define state 2 as unobservable to reduce model complexity. Powell et al. (2000) used a similar approach to estimate survival and movement rates from combined mark-recapture and radio-tagging data.

We used program MARK (White & Burnham 1999) to estimate the parameters. However, MARK uses a parameterisation that does not allow us to fit this model directly. With MARK it is possible to estimate only one transition probability for each step of time, hence the product of the parameters we intend to estimate (e.g. for the transition from state 1 (time $i-1$) to state 3 (time i) in Equation 1). Yet, we can write the state transition matrix in (1) with two succeeding transition matrices, in which the entries are only single parameters:

$$\begin{bmatrix} 1-\psi^R & 0 & 0 & 0 & 0 \\ \psi^R & 0 & 0 & 0 & 0 \\ 0 & 0 & 1-\psi^P & 0 & \psi^R \\ 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & \psi^P & 0 & 1-\psi^R \end{bmatrix} \begin{bmatrix} S & 0 & 0 & 0 & 0 \\ 1-S & 0 & 0 & 0 & 1-S^R \\ 0 & S & S^R & 0 & 0 \\ 0 & 1-S & 1-S^R & 0 & 0 \\ 0 & 0 & 0 & 0 & S^R \end{bmatrix} \quad (2).$$

The first transition matrix now models the probabilities associated with changes in tag status, the second transition matrix models survival and mortality. Because one step of time is now prolonged into two time steps, the data file was adjusted accordingly: a dummy occasion (a column of zeros) after each real occasion was inserted. Grosbois & Tavecchia (2003) and Schaub & Pradel (2004) provide detailed descriptions and further examples of this modelling technique.

We estimated the 12 monthly survival rates from June (year x) to June (year $x + 1$), because partridge chicks usually hatch in June. Individuals that were known to be alive for > 1 year were treated as if they would have been removed from the population at

the last observation in year x , and released as a new individual at first encounter in year $x + 1$. This was done to eliminate year-specific parameters in the model, although we lost some information about survival and re-encounter probabilities during the time interval without observations. However, as encountering rates were high, this loss of information was regarded as a minor problem.

We assumed that survival rates of partridges that were >3 months old did not change anymore with increasing age. Only fostered chicks and wild-hatched chicks were monitored during the juvenile phase (≤ 3 months old), all other birds were only monitored during the adult phase (i.e. they were >3 months old). We did not consider a relative age effect, i.e. the change of survival as a function of time after release. Thus, a time effect in the model denotes variation in survival between specific times of the year.

A critical assumption for our data was that all individuals were independent from each other (Lebreton et al. 1992). Due to the fact that grey partridges live in either coveys or pairs throughout the year, this assumption was unlikely to be met. Non-independence of individuals (overdispersion) does not lead to biased parameter estimates, but the standard errors of the estimates are underestimated which affects model selection and inferences from the data (Anderson et al. 1994). Standard errors could be adjusted for overdispersion if the overdispersion coefficient, \hat{c} , could be estimated, but this was not possible for our specific model. In order to get a rough estimate of overdispersion, we removed the recoveries of all dead birds in our data set (i.e. as if they had never been found), and assumed that resighting rates of the birds were similar regardless of whether they had a functioning tag, a non-functioning tag, or were untagged. This was justified *a posteriori* by the high and similar resighting rates of tagged and untagged birds (see Results). Further, we assumed that the tag had no effect on survival. The original data set became a single-state capture-recapture data set for which a goodness-of-fit (GOF) test is available and an estimate of \hat{c} can be obtained (Lebreton et al. 1992). We tested the goodness-of-fit for a model with time and treatment group specific survival and recapture rates with program U-CARE (Choquet et al. 2005). The GOF did not indicate significant lack of fit ($\chi^2 = 18.90$, $df = 14$, $P = 0.17$). The variance inflation factor is estimated to be $\hat{c} = 1.35$ ($\hat{c} = \chi^2/df$; Lebreton et al. 1992). This estimate of \hat{c} is an approximation only.

To evaluate whether our inferences from model selection are robust with respect to different estimates of \hat{c} , we also considered more conservative values for \hat{c} (2.0, 3.0, 4.0).

We followed the model selection strategy recommended by Burnham & Anderson (1998). We defined *a priori* a set of possible candidate models and used the quasi-likelihood adjusted Akaike Information Criterion corrected for small sample sizes (QAIC_c) to rank the models according to their support by the data.

Because we localised the tagged individuals and tried to see all other individuals at least once every week throughout the year, and because we pooled the data to monthly periods, we could confidently assume that the probabilities of relocalising, resighting and recovering (p , p^R , r) the birds did not vary over the year. By contrast, the probability that a bird without a functioning tag would receive a functioning tag (Ψ^R) varied, because we only made an effort to catch birds during specific periods. Also, the probability that a functioning tag would become non-functioning due to battery failure (Ψ^P) was always kept time-dependent.

The most complex model for monthly survival considered a separate estimate for each of the four treatment groups in each month, separate survival rates for juvenile (≤ 3 months) and older birds, and an additive tag effect (Putala et al. 1997, Bro et al. 1999). This model is denoted by $S_{[R+g^*a^*t]}$, where R refers to tag effect, g to treatment group effect, a to age effect, and t to time effect. We considered several simpler models which either assumed additive time effects on all treatment group and age combinations (referring to the hypothesis that all treatment groups are affected in the same way by environmental variation), no time-effect at all (referring to the hypothesis that variation between monthly survival rates was marginal), additive effect of treatment group on age (referring to the hypothesis that the treatment effect was the same in both age classes), without treatment effects (referring to the hypothesis that survival does not differ among treatment groups), and combinations thereof. We also considered all these models with and without an additive tag effect. In total, we fitted 14 models.

Results

Survival

Model selection clearly showed that survival differed among treatment groups. Models without

Table 2. Modelling survival rates (S) of released grey partridges (Klettgau, Switzerland, 1998-2000), based on the most complicated model ($S_{[R+g^*a^*t]}$, Ψ_t^R , Ψ_t^P , p , p^R , r) and simplifications thereof. For each model the number of estimated parameters, the quasi-likelihood adjusted relative deviance, the difference of the small sample size and quasi-likelihood adjusted Akaike Information Criterion ($\Delta QAIC_{ci} = QAIC_{ci} - QAIC_{cmin}$), and the Akaike weight ($QAIC_c \text{ weight}_i = \exp(-0.5\Delta QAIC_{ci}) / \sum \exp(-0.5\Delta QAIC_{ci})$) are shown. Subscript R refers to the radio-tag effect, subscript g to the treatment group effect, subscript a to an age effect, and subscript t to a time effect. Model selection was based on a variance inflation factor of $\hat{c} = 1.35$. Since only the model structure of the survival parameters differ among the candidate models, we only show this part of the model notation.

Model	Number of parameters	QDeviance	$\Delta QAIC_c$	$QAIC_c$ weight
$S_{[R+g^*a]}$	28	6586.9	0.00	0.50
$S_{[R+g+a]}$	27	6590.9	1.94	0.19
$S_{[g^*a]}$	27	6591.2	2.16	0.17
$S_{[g+a]}$	26	6595.0	3.85	0.07
$S_{[g^*a+t]}$	38	6571.1	5.96	0.03
$S_{[g+a+t]}$	37	6574.9	7.57	0.01
$S_{[R+g^*a+t]}$	39	6570.6	7.65	0.01
$S_{[R+g+a+t]}$	38	6574.5	9.36	0.00
$S_{[R+a]}$	24	6608.3	12.95	0.00
$S_{[R+a+t]}$	35	6586.9	15.17	0.00
$S_{[a+t]}$	34	6589.3	15.35	0.00
$S_{[g^*a^*t]}$	73	6509.4	24.59	0.00
$S_{[a]}$	23	6622.9	25.36	0.00
$S_{[R+g^*a^*t]}$	74	6509.0	26.61	0.00

treatment effect were consistently lower ranked than models with treatment effects (Table 2). It also appeared that there was low support for a significant temporal variation in survival, and some evidence for an effect of tag on survival. If larger values of \hat{c} are considered, the ranking of the models changes slightly, but the main conclusions remain. In particular, the best ranked model was always one with a treatment group effect, and the sum of the Akaike weights of all models containing a group effect on survival was always > 0.7 , irrespective of the chosen \hat{c} (Table 3). This suggests that our conclusions regarding the effect of treatment group on survival are robust. More uncertainty existed with respect to the effect of tag on survival. For large values of \hat{c} , the best ranking models did not contain a tag effect (see Table 3). Because the main inferences were not strongly dependent on \hat{c} , subsequent inferences are based on $\hat{c} = 1.35$.

Based on the most parsimonious model ($S_{[R+g^*a]}$), estimates of encountering grey partridges were high ($p = 0.96$ (95% confidence interval: 0.93-0.98), $p^R = 0.99$ (0.95-1.00), $r = 0.80$ (0.68-0.88)), reflecting our intense monitoring efforts. The probability that an

Table 3. Comparison of model selection with different values of the variance inflation factor \hat{c} . Shown are the Akaike weights of the corresponding models and the sum of the Akaike weights of all 10 models containing a treatment group effect, and of all seven models containing a radio-tag effect. For model notation see Table 2.

Model	$\hat{c} = 1.35$	$\hat{c} = 2.0$	$\hat{c} = 3.0$	$\hat{c} = 4.0$
$S_{[R+g^*a]}$	0.50	0.33	0.19	0.12
$S_{[R+g+a]}$	0.19	0.24	0.22	0.17
$S_{[g^*a]}$	0.17	0.23	0.21	0.17
$S_{[g+a]}$	0.07	0.18	0.26	0.26
$S_{[g^*a+t]}$	0.03	0.00	0.00	0.00
$S_{[g+a+t]}$	0.01	0.00	0.00	0.00
$S_{[R+g^*a+t]}$	0.01	0.00	0.00	0.00
$S_{[R+g+a+t]}$	0.00	0.00	0.00	0.00
$S_{[R+a]}$	0.00	0.02	0.11	0.23
$S_{[R+a+t]}$	0.00	0.00	0.00	0.00
$S_{[a+t]}$	0.00	0.00	0.00	0.00
$S_{[g^*a^*t]}$	0.00	0.00	0.00	0.00
$S_{[a]}$	0.00	0.00	0.01	0.06
$S_{[R+g^*a^*t]}$	0.00	0.00	0.00	0.00
$\Sigma(\text{models with g})$	0.98	0.98	0.88	0.72
$\Sigma(\text{models with R})$	0.70	0.59	0.52	0.52

untagged individual became tagged varied among months from 0.04 (95% confidence interval: 0.01-0.20) to 0.41 (95% confidence interval: 0.27-0.58), and the monthly tag failure rate varied from 0.00 to 0.29 (95% confidence interval: 0.07-0.67).

Mean monthly survival rates were highest for adult grey partridges that hatched in the study area (control group) and lowest for captive-reared adult grey partridges (Fig. 1). To test *a posteriori* which group of adult grey partridges had different monthly survival rates, we fitted two more models. In the first we considered adult survival of wild-hatched and fostered adult individuals to be the same. This model (number of parameters = 27; QDeviance = 6587.18) was better than the best model so far ($\Delta QAIC_c = -1.826$). Next, we fitted a model in which survival rates of wild-hatched, fostered and translocated wild adults were the same. This model (number of parameters = 26; QDeviance = 6589.07) was even more parsimonious ($\Delta QAIC_c = -2.066$). Given that the models without survival differences among groups were clearly worse (see Table 2), the main difference between these four treatment and control groups was survival of pen-reared adults, which was clearly lower than survival of birds in other groups. Within the primary treatment groups, fostered chicks tended to have the highest survival rate. This conclusion also held for other values of \hat{c} .

The monthly juvenile survival of wild-hatched partridges appeared to be lower than that of their

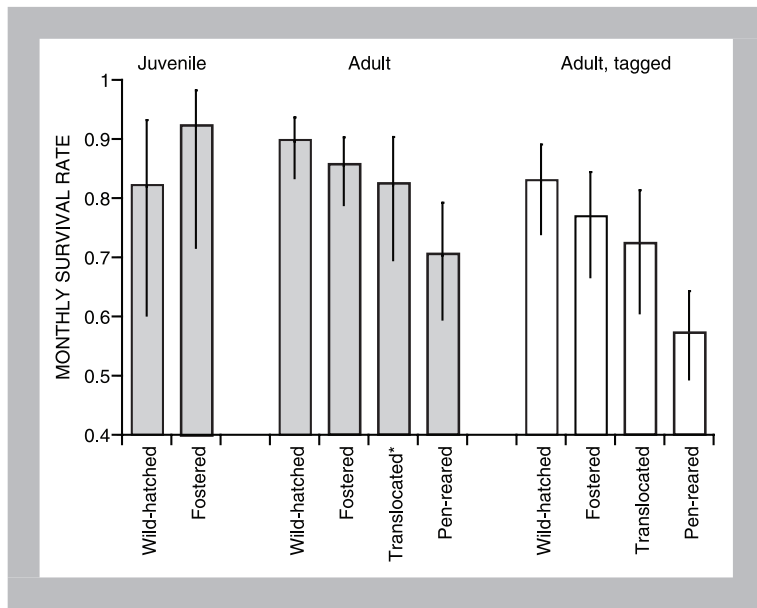


Figure 1. Probabilities of monthly survival of different groups of released grey partridges (Klettgau, Switzerland, 1998-2000) estimated with the most parsimonious model ($S_{[R+g^*a]}$, Ψ_t^R , Ψ_t^R , p , p^R , r). Light grey bars refer to birds without radio-tags, white bars to birds with radio-tags. The vertical lines show the limits of the upper and lower 95% confidence interval of the estimates ($\hat{c} = 1.35$). * The survival estimate of untagged translocated birds was predicted by the model, since there were no data within this group. Juvenile survival refers to the period between the age of two and three months.

fostered conspecifics. However, this was because estimated juvenile survival of wild hatched birds was calculated as an average rate over the first three months of life (from hatching to the age of three months), whereas juvenile survival of fostered birds refers to individuals from the age of two months. To obtain comparable estimates, we reran the *a priori* best model, but considered time(age)-dependent survival rates for wild-hatched juveniles. Monthly survival of wild-hatched juveniles from hatching to the age of one month was 0.58 (SE = 0.08), from the age of one month to the age of two months 0.88 (SE = 0.06), and from the age of two months to the age of three months 0.82 (SE = 0.08). This last estimate corresponds to birds at the same age as that of the fostered juveniles (0.92; SE = 0.06), and is not significantly lower ($z = -1.01$; $P = 0.16$). The survival rates of tagged individuals was slightly lower than survival rates of individuals without tags (difference on the logit scale: -0.58 ; SE = 0.28).

Causes of death

We found the carcasses of 85 partridges; 82 had apparently been killed by predators, one died from disease, one died in a traffic accident and one died as

a result of a territorial fight. Predation by mammals appeared more frequent (46 in total; 36 by red fox *Vulpes vulpes*, and 10 by domestic cat *Felis domesticus*) than predation by avian predators (24 in total; 20 by common buzzard *Buteo buteo*, three by sparrowhawk *Accipiter nisus*, and one by a wintering hen harrier *Circus cyaneus*). For 12 partridges the predator could not be identified. All four treatment and control groups of partridges suffered from mammalian and avian predators in similar proportions ($\chi^2 = 2.92$, $df = 3$, $P = 0.40$).

Discussion

Our study provides evidence that survival probability of released partridges depends on release strategy. While the survival rate of fostered chicks and translocated wild adults was not different from survival

of wild-hatched chicks (control, offspring of established pairs), survival of pen-reared adults was significantly lower.

The difference in monthly survival rates between pen-reared adults ($S = 0.718$, SE = 0.055) and the mean of the other groups ($S = 0.870$, SE = 0.025) may appear marginal. However, the mean life expectancy (Seber 1982) of the pen-reared adults (3.01 months, SE = 0.26) is less than half that of the other groups (7.16 month, SE = 1.48). This difference is biologically important, because longer-living individuals accumulate more experience and are therefore more likely to reproduce successfully, or if not, may at least serve as foster parents.

Because the main cause of mortality in partridges is predation (this study, e.g. Potts 1986), the different survival skills of the three treatment groups is probably due to differential experience in avoiding predators (Dowell 1990). While pen-reared adults have not normally encountered predators prior to release and are not familiar with their release habitat, translocated wild birds have the advantage of being familiar with predators. Chicks reared in captivity and fostered to wild counterparts benefit from the behavioural skills of their experienced

Table 4. Hypothetical number of individuals that need to be released in each group (in the control group it is the number of hatchlings of re-established pairs) to obtain a population of 20 individuals at time of reproduction (May in year t). Indicated is also the number of individuals alive at the beginning of the second breeding season. Calculations are based on the survival estimates from the best model (see Table 2) and refer to untagged individuals. The standard errors are in brackets.

Group	Release month	Number to be released	Number alive in May (year t+1)
Translocated wild adults	April (year t)	24.3 (1.8)	1.9 (1.7)
Pen-reared adults	December (year t-1)	116.5 (9.8)	0.3 (0.3)
Fostered chicks	August (year t-1)	65.2 (18.5)	3.0 (1.4)
Wild-hatched chicks	June (year t-1)	147.5 (47.9)	5.3 (2.1)

parents by acquiring knowledge of both predator avoidance and local habitat. Survival rates of our wild-hatched chicks were similar to wild (not re-introduced) partridge populations (Panek 1992, Potts & Aebischer 1994, Panek 1997, Putaala 1997, Bro et al. 1998).

The radio-tags may have had a minor negative effect on partridge survival (8-19% lower; inference based on the best model). However, the summed QAIC weight of models with and without radio transmitters is nearly the same when $\hat{c} > 2$, reflecting considerable uncertainty about radio-tag effect on survival (see Table 3). Bro et al. (1999) found a negative impact of necklace mounted radio-tags on partridge survival and Putaala et al. (1997) showed that flight abilities of grey partridges were reduced when they were equipped with a backpack radio-tag. To avoid those reported adverse effects we used a Rappole-harness (Rappole & Tipton 1990). Further studies with larger sample sizes are required to clearly demonstrate the effect of radio-tags on survival. Survival may also be affected by other factors such as environmental variation among years or gender; neither of which was considered here.

To compare the efficiency of our three different release techniques we calculated the number of individuals that need to be released in each treatment group for obtaining a population of 20 individuals in May, based on the estimated group-specific survival rates (Table 4). Only 24 translocated wild adults have to be released in April (one month before the breeding season starts) to reach the goal. However, translocations are often problematic because they can have negative effects on the source population (IUCN Re-introduction Specialist Group 2004). This is of special concern because partridges are considered vulnerable throughout Europe (Tucker & Heath 1994). Despite its efficiency, we therefore regard translocation of many partridges as not advisable.

The efficiency of the two release techniques using pen-reared individuals is remarkably different. Although pen-reared adults are released later than fostered chicks, about twice as many individuals must be used to obtain the same number of potential breeders the next year (see Table 4). Importantly, when compared to the fostered birds, the low survival rates of the pen-reared adults indicate that approximately 90% fewer birds are still alive at the beginning of the second breeding season. Therefore, we conclude that fostering captive reared chicks is the best release regime given that it has no negative impact on existing wild partridge populations.

The establishment or re-establishment of self-sustaining populations is the basic aim of reintroduction projects (Scott & Carpenter 1987). To evaluate the self-sustainability of populations created by different release regimes it is necessary to study the breeding performance of the different groups of birds in addition to survival. We monitored breeding success of the released and wild-hatched grey partridges of the founder population and found that individuals of all treatment groups were able to reproduce successfully. However, because of the small sample size, we could not test for differences in breeding performance among the treatment groups. Therefore, further studies that assess, in more detail, whether the reproductive skills of the treatment groups differ would be highly valuable. Having this information, the next step would be to include information about the economic costs to identify the most efficient release strategy.

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