

## ROLES OF SURVIVAL AND DISPERSAL IN REINTRODUCTION SUCCESS OF GRIFFON VULTURE (*GYPS FULVUS*)

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**Abstract.** The success of reintroduction programs greatly depends on the amount of mortality and dispersal of the released individuals. Although local environmental pressures are likely to play an important role in these processes, they have rarely been investigated because of the lack of spatial replicates of reintroduction. In the present study, we analyzed a 25-year data set encompassing 272 individuals released in five reintroduction programs of Griffon Vultures (*Gyps fulvus*) in France to examine the respective roles of survival and dispersal in program successes and failures. We use recent developments in multi-strata capture–recapture models to take into account tag loss in survival estimates and to consider and estimate dispersal among release areas. We also examined the effects of sex, age, time, area, and release status on survival, and we tested whether dispersal patterns among release areas were consistent with habitat selection theories. Results indicated that the survival of released adults was reduced during the first year after release, with no difference between sexes. Taking into account local observations only, we found that early survival rates varied across sites. However when we distinguished dispersal from mortality, early survival rates became equal across release sites. It thus appears that among reintroduction programs difference in failure and success was due to differential dispersal among release sites. We revealed asymmetrical patterns of dispersal due to conspecific attraction: dispersers selected the closest and the largest population. We showed that mortality can be homogeneous from one program to another while, on the contrary, dispersal is highly dependent on the matrix of established populations. Dispersal behavior is thus of major interest for metapopulation restoration and should be taken into account in planning reintroduction designs.

**Key words:** capture–mark–recapture; dispersal; Griffon Vulture; *Gyps fulvus*; habitat selection; reintroduction; release cost; survival.

### INTRODUCTION

Survival and dispersal of released individuals are the most crucial processes for the establishment phase of reintroduction (Tweed et al. 2003). Understanding the factors affecting these parameters is thus necessary to improve release methods and management of reintroduced populations (Armstrong et al. 1999). High mortality after release has been revealed in previous studies of translocation or reintroduction experiments (Massot et al. 1994, Green et al. 2005). Moreover, dispersal from the release site has also been noticed (Clarke and Schedvin 1997, Pierre 1999, Tweed et al. 2003). Two main types of factors may influence survival and dispersal of released individuals: (1) the release method, including soft vs. hard release (Green et al.

2005), captive-reared vs. wild-reared individuals (Maxwell and Jamieson 1997, Mathews et al. 2005), the pre-release experience (Biggins et al. 1999), or familiarity (Armstrong 1995, Armstrong and Craig 1995); and (2) individual characteristics, such as age, sex, and origin (Wauters et al. 1997, Doligez et al. 2004b, Schaub et al. 2004, Hardman and Moro 2006). Some studies agree that animals that have spent a long time in captivity suffer a demographic cost in survival and may tend to over-disperse, mainly because of stress and inexperience in the new habitat (Curio 1996, Caro 1999, Hellstedt and Kallio 2005, Mathews et al. 2005; but see Berry 1998, White et al. 2005). Effects of release methods and individual characteristics are, contrarily, more variable and species-dependent (Armstrong 1995, Maxwell and Jamieson 1997, Ellis et al. 2000, Hardman and Moro 2006; vs. Hellstedt and Kallio 2005, Mathews et al. 2005). Although local environmental pressures are likely to play an important role in this variability, they have

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rarely been investigated because of the lack of spatial replicates of reintroduction.

Release costs in survival and reproduction have been estimated in a Griffon Vulture (*Gyps fulvus*) population reintroduced in the Causses (south of Massif central, France [Sarrazin et al. 1994, 1996]). This long-lived scavenger raptor went extinct in this area in 1945, and a reintroduction program was successfully conducted with the release of 61 captive individuals from 1980 to 1986 (Terrasse et al. 2004). By studying capture–mark–recapture histories of released individuals the first 10 years after release, Sarrazin et al. (1994) estimated a 24% additional mortality during the first year following release for individuals released as adults, while their survival after the first year was equivalent to the one of adult wild-born individuals. Subsequent modeling work using those estimates permitted an examination of the effect of different age ratio release strategies on the reintroduction success. Projective models indicated that releasing adults is a more efficient strategy than releasing immature birds, even when taking into account the demographic cost of individuals released as adults (Sarrazin and Legendre 2000).

The studies cited above allowed optimizing the release methods of future programs. Nevertheless, they suffered from biases, which can, at present, be partly resolved. First, sex-specific survival was not investigated. As the Griffon Vulture is monomorphic, and as the two sexes participate equally in chick rearing (Mendelssohn and Leshem 1983), no differential survival rate was expected, an expectation supported by the study of Bosé et al. (2007) on mortality. Nevertheless, this assumption remains to be verified taking resighting rate into account, in case of any differential behavior between males and females that could affect survival (Prévot-Julliard et al. 1998). Second, previous survival estimates did not take into account tag loss. These events are yet known to cause underestimation of survival rates and to induce some heterogeneity in resighting rates among individuals (Bradshaw et al. 2003). Recent developments in multi-strata capture–recapture model provide insight in taking into account tag losses in survival estimates (Brownie et al. 1993, Lebreton and Pradel 2002, Conn et al. 2004, Kendall et al. 2006). Third, the lack of comparison of the demographic estimates obtained for the Causses population with other reintroduction projects prevents from generalizing the durations and the values of estimated demographic costs (Sarrazin and Legendre 2000). Since the Causses reintroduction, four additional reintroduction programs took place in the South of France at different times and places. Two of them failed, whereas the population successfully settled and bred in the other projects. In accordance with the gregarious behavior of the Griffon Vulture, we suspect that the presence and performance of conspecifics is used by individuals to choose a place to settle (Wagner and Danchin 2003). A previous study confirms this hypothesis at the within-colony level in the Griffon Vulture (P.

Le Gouar, A. Camina, E. Danchin, N. Lecomte, C. Arthur, P. Lécuyer, M. Surroca, C. Tessier, and F. Sarrazin, *unpublished manuscript*), but breeding habitat behavior among colonies is still a question of great fundamental interest in long-lived species (Cam et al. 2004, Breton et al. 2006). Besides, it is important to distinguish dispersal from mortality as a cause of failure of establishment, as it influences management actions (Tweed et al. 2003). Furthermore, if dispersal is costly, quantifying dispersal rates among populations can potentially explain observed patterns of mortality (Armstrong et al. 1999).

In the present study, we analyzed a 25-year data set encompassing five reintroduction programs. Multi-strata capture–recapture models allowed us to (1) consider and estimate dispersal among release areas (Brown et al. 2003); and (2) take into account tag losses in survival estimates (Kendall et al. 2006). Our work was motivated by fundamental and applied questions: (1) Is there any effect of sex, in interaction with age, time, tag loss, or release status, on survival or dispersal? (2) Is the survival of released individuals equivalent in the different release areas, and what are the respective roles of survival and dispersal in program successes and failures? (3) Are dispersal patterns among release areas consistent with habitat selection theories?

## MATERIALS AND METHODS

### *Reintroduction projects*

The overall protocol of release was common to the five projects and was developed by the Fonds d'Intervention pour les Rapaces (Terrasse et al. 2004). First, aviaries for captive breeding were built close to the release site on a cliff overlooking the gorges where birds were expected to settle after release. Captive colonies were constituted of Griffon Vultures from Spanish and French rescue centers and zoos. Birds were kept several years in captivity so that breeding pairs could be formed. Concurrently, an active education program on the benefits of the Griffon Vulture was led for local people (especially farmers and hunters), nest cliffs were protected from climbers, and power lines were equipped to prevent bird electrocutions. Releases occurred during several years. Several feeding places were installed within the area, some of them through a program of farmers' involvement in the Griffon Vulture restoration program. Among projects, size and age ratio of founding groups, as well as years of release, were different. In the Causses (44°12' N, 3°15' E), 61 birds were released from 1980 to 1986 by the Ligue pour la Protection des Oiseaux and the Parc National des Cévennes. At present, more than 130 pairs breed in this colony. The founding group was constituted of 41 adults (i.e., birds of age  $\geq 4$  years) and 20 immature birds. Age ratio of the first released individuals was biased toward adults, whereas it was skewed toward immature individuals at the end of the program. In Navacelles (43°52' N, 3°36' E), at 45 km from the Causses release

site, 50 birds were released from 1993 to 1997 by the GRIVE association. The age ratio of the founding group was highly biased toward adults: 47 adults and three immature birds. Up to two breeding pairs were observed in this colony from 1993 to 1998. After 1998, no breeding pairs have been observed in this colony, and some individuals released in Navacelles were frequently seen in the Causses. Thus, resighting and recovery rates of individuals released to Navacelles were distinctly modeled from 1993 to 1998 and from 1998 to 2004. In the Baronnies (44°24' N, 5°20' E), more than 150 km away from Causses and Navacelles, 56 vultures were released from 1996 to 2001 by the Vautour en Baronnies association. A mix of immature and adult birds was released each year excepted the last year in which a majority of adults were released. Overall, 21 adults and 25 immature individuals were reintroduced to the wild. In 2004, 45 breeding pairs were observed in this colony. In the Diois (44°50' N, 5°27' E), at 45 km from the Baronnies release site, 43 birds (28 adults and 23 immature) were released between 1999 and 2001 by the Parc regional du Vercors. No successful reproduction has been observed in this area since releases. In the Verdon (43°47' N, 6°26' E), more than 200 km from Causses and Navacelles and 110 km away from Baronnies, 90 individuals were released from 1999 to 2004 by the Ligue pour la Protection des Oiseaux. To estimate survival and dispersal, we took into account the releases from 1999 to 2003, i.e., two adults and 71 immature birds. In 2004, 13 breeding pairs were present in this colony.

#### *Sex assignment*

In the Causses, founders from zoos were sexed by laparoscopy or karyotype analysis. Observations of copulation behavior in aviaries allowed determining the sex of some other birds before release. Tissue samples collected on founders recaptured after release were used for molecular sexing analysis and these results were used to complete information on sex ratio of the release group. However, the sexing of individuals after release should be interpreted carefully because it could be biased toward individuals with high survival rates. In the other projects, blood samples were collected on captive individuals before release and individuals were sexed with molecular techniques. The sex ratio of founding groups was 1:1 as in native populations (Bosé et al. 2007).

#### *Banding*

Banding of birds occurred before release and rebanding of individuals having lost their band occurred during recapture sessions (in 1986, 1988, 1989, 1990, 1992, 1996, 1998, 1999, 2003, 2004 only in Causses). Marking was achieved by assigning two bands to each individual. Birds wore a small metal band on one tarsus (hereafter "metal band"), allowing their identification and classification by the Centre de Recherche sur la Biologie des

Populations d'Oiseaux. Additionally, a band allowing long-distance identification was carried on the other tarsus. Two long-distance recognition systems have been used. Bands displaying a combination of different colors ("color bands") were used for most of released individuals in Causses ( $n = 47$  birds) and for some released birds in Navacelles ( $n = 3$  birds). Bands with letters ("code bands") were used for some individuals in Causses ( $n = 8$  birds), most of the founders in Navacelles ( $n = 43$  birds), and almost all released individuals in Baronnies ( $n = 56$  birds), in Verdon ( $n = 90$  birds), and in Diois ( $n = 38$  birds). All birds had a distance recognition band, except two birds in Causses, four in Navacelles, and one in the Diois that escaped and had only one metal band and four birds in the Diois that escaped without any bands. Additionally, most released birds were equipped with short-lived radio transmitters with an operating life of three months. Juvenile wild-born birds were marked at the nest in all programs with successful reproduction ( $n = 494$  birds) but these data were not considered in the present study.

#### *Monitoring*

In each site, released individuals were monitored by technicians of the association or park in charge of the local reintroduction program. Most resighting occurred through the monitoring of nests, and during collective feeding events at artificial places. The monitoring of nests was exhaustive at the beginning of programs, and became less intensive with the expansion of the colonies. Resighting rates, consequently, were potentially heterogeneous over time.

#### *Statistical methods*

Survival and recapture models were computed with a capture-resighting approach (Lebreton et al. 1992), using the program MARK (White and Burnham 1999). We considered a time step of one year, and all observations made during the breeding period of each year (i.e., between 1 January and 30 September) in all monitored areas were used to construct individual capture-resighting histories. Incorporating information on recoveries (i.e., birds found dead) into mark-recapture models may lead to improved precision of estimates (Barker 1997, Kendall et al. 2006). Such information was available in the case of the Griffon Vulture ( $n = 42$  recovery events) and was used in all analyses.

*General notations.*—We used both mono-stratum and multi-strata models including information on live recapture and dead recovery (LRDR). Mono-stratum models were based on the formalism of Burnham (1993) including survival ( $s$ ), live recapture ( $p$ ), dead recovery ( $r$ ), and fidelity ( $F$ ) parameters and were used only to test the sex effect and for goodness-of-fit testing. More complex models were developed using the LRDR multi-strata approach designed in MARK in which the different strata corresponded either to the type of band

carried by individuals (tag loss models) or to the possible locations of the individuals (dispersal models). These models included local survival ( $\phi$ ), live recapture ( $p$ ), dead recovery ( $r$ ), and strata transition probability ( $\psi$ ) parameters.

Subscripts indicated whether parameters were constant (e.g.,  $\phi_c p_c$ ), time dependent (e.g.,  $\phi_t p_t$ ), age dependent (e.g.,  $\phi_{a1,2} p_{a1,2}$  for two age classes), or vary according to sex (e.g.,  $\phi_s p_s$ ), age at release (e.g.,  $\phi_{ar} p_{ar}$ ), or site of release (e.g.,  $\phi_{sr} p_{sr}$ ). Because the ages of individuals released as immature and as adult were heterogeneous, "age-dependent" models could only reveal a "time-since-release" effect (i.e., the age-dependent model for survival  $\phi_{a1,2}$ , actually assumes one estimate for the first year following release and another estimate for all following years).

Interactions between effects were denoted with  $\times$  (for example,  $\phi_{t \times s}$  when survival is considered to vary among years and sexes in a nonadditive fashion. Additive effects were denoted with  $+$ ).

*Model selection approach.*—We used Akaike's procedure (Burnham and Anderson 1998) that allows comparisons of non-nested models according to their Akaike information criterion (QAIC<sub>c</sub>), calculated as  $QAIC_c = -2\log(L)/\hat{c} + 2n_p + 2n_p(n_p + 1)/(n_{ess} - n_p - 1)$ , with  $L$  being the likelihood of the considered model,  $\hat{c}$  being a measure of the data's overdispersion,  $n_p$  being the number of parameters of the model, and  $n_{ess}$  being the effective sample size. The choice of the model having the lowest QAIC<sub>c</sub> value therefore allows the best compromise between parsimony and explanation. When difference between models was lower than 2, the model with fewer parameters was retained (Festa-Bianchet et al. 2003).

Several groups were distinguished in the analysis: sex (two sexes), age at release (two age levels), and site of release (five sites). We assessed potential differences in  $\phi$ ,  $p$ ,  $r$ , and  $\psi$  by comparing different models, some of which separately modeled the effect of each group, whereas others considered the groups as a common pool. Age groups with fewer than five individuals were not included in the analysis; hence eight age-at-release groups were studied (adults in Causses,  $n = 39$  birds; immature in Causses,  $n = 20$ ; adults in Navacelles,  $n = 47$ ; adults in Baronnies,  $n = 21$ ; immature in Baronnies,  $n = 35$ ; adults in Diois,  $n = 28$ ; immature in Diois,  $n = 11$ ; immature in Verdon,  $n = 71$ ).

As we were limited by computer memory, we could not investigate both tag loss and dispersal in a same multi-strata model, which would have implied 792 transition matrixes. Thus, we used two different multi-strata parameterizations to assess first the tag loss problem and then the dispersal question. In order to limit the number of groups for each analysis, we first tested the effect of sex, year, time since release, and age at release on demographic parameters considering each project separately and then the effect of release site pooling all individuals in one data set. Due to the large

number of potential models (more than 5000 possible models if all combinations of time, age, sex, age at release, and site of release on  $\phi$ ,  $p$ ,  $r$ , and  $\psi$  were tested), we examined only those models that tested explicit hypotheses regarding the biology and the monitoring of Griffon Vulture ( $n = 1480$  birds for analysis of sex effect in each site,  $n = 603$  for model selection for each site separately, and  $n = 25$  for model selection when pooling individuals of all sites).

*Mono-stratum parameter designations: sex effect.*—Previous work on French populations of Griffon Vulture (Bosé et al. 2007) suggested that there is no sex bias in mortality and movement whatever the site and age at release. In the present paper, we verified the absence of sex effect by first testing a priori a set of predefined mono-stratum models with survival ( $s$ ), live recapture ( $p$ ), dead recovery ( $r$ ), and fidelity ( $F$ ) parameters constant ( $c$ ) or varying with year ( $t$ ) and a set of models with survival ( $s$ ) varying with time since release with two classes ( $a1,2$ ), and the other parameters constant ( $c$ ) or varying with year ( $t$ ), differing between sex or not (i.e., a set of 296 models for each release site). As a complement to this analysis, we tested a posteriori the effect of sex on all parameters using the best multi-strata model selected for each site.

*Multi-strata parameter designations: tag loss models.*—

1. *Data and notations.*—Loss of the long-distance recognition band was frequent. In consequence, the type of band on which recognition was based was heterogeneous between individuals and for a given individual at different times. Because the expected probabilities of identifying an individual carrying these different types of bands are not necessarily equal, this may potentially affect resighting and survival estimates. In order to cope with this problem, we used multi-strata models (Brownie et al. 1993) in which each stratum represents a particular type of band that can be carried by individuals. For individuals carrying two types of bands at a given time (i.e., one metal band and one long-distance recognition band), only the long-distance recognition band was considered, because identification was assumed to be occurring only through the reading of this band for such individuals. For individuals carrying two different long-distance recognition bands (code and color) only the code band was considered. However, such individuals were exceptional.

Hence, our model assumed three different strata, according to the system of recognition worn by each individual at a given time: code band, color band, and metal band. The multi-strata models allowed us to compute transition probabilities corresponding to tag loss rates (e.g., the transition  $\psi[\text{color} \rightarrow \text{metal}]$  [ $\psi[\text{losscol}]$  concerns individuals losing their color ring in a given year, and subsequently only detectable through their metal ring) and to account for rebanding events (e.g.,  $\psi[\text{metal} \rightarrow \text{color}]$ ). Several plausible models for tag loss were investigated in each site (i.e., constant, year-dependent, or time-since-release-dependent loss rates

[details presented in the Appendix]). Transitions corresponding to rebanding were constrained according to known rebanding events in Causses (i.e., transitions were fixed to zero for years for which no rebanding occurred, and unique nonzero parameters were considered for years with rebanding). The probability of metal band loss could not be estimated. However, it is considered extremely low because of the robustness of metal bands.

2. *Model selection.*—We assumed that the probabilities of recapture  $p$  were different for different types of band in a given site. Several plausible models for  $p$  (e.g., constant, year-dependent, or time-since-release-dependent models; see the Appendix for details) were compared for each type of band (i.e.,  $p_{\text{met}}$ ,  $p_{\text{col}}$ ,  $p_{\text{code}}$ ).

In all multi-strata tag loss models, we assumed that recovery rates  $r$  and survival  $\phi$  of individuals were not influenced by the type of bands that they carried and we tested several plausible models for  $r$  and  $\phi$  (e.g., constant, year-, or time-since-release-dependent; Appendix).

Because it was impossible to explore all possible models for the combined site data set (three strata, eight groups), we first looked for the best model for  $\phi$ ,  $p$ ,  $r$ , and  $\psi$  in each site by starting with the less-constrained model and by making it simpler. This was achieved by first considering nuisance parameters ( $r$  and  $p$ ), second transition probabilities ( $\psi$ ), and finally survival parameters ( $\phi$ , see the Appendix). In a second step, we pooled data from all sites while keeping the best model structure previously determined for each site to test (1) if survival rates were equal among released areas (successful vs. unsuccessful programs) and (2) if bands loss were equal among monitored areas. The last test allowed us to correct survival rates estimated with dispersal models if differences in tag loss occurred among released areas.

*Multi-strata parameter designations: dispersal.*—

1. *Data and notations.*—The task of estimating dispersal among release areas also required multi-strata modeling. The area in which each single observation was made was taken into account in the analysis as the strata. When a given bird was observed alive in different areas from 1 January to 30 September of the same year, we considered that the bird was fixed in the area where most of observations were made on the longer period. The information on location of individuals recovered dead in monitored areas was also considered to compute transition rates among strata. In cases where an individual was recovered outside monitored areas ( $n = 5$  birds, mostly immature individuals), the stratum (location) of the individual at the time of its death was assumed to be the same as its last stratum (last observation of the living individual). As a result, dispersal to unmonitored areas was a component of apparent survival.

2. *Model selection.*—Our model assumed five strata according to the five release areas considered. As a first step, we studied each colony separately, focusing on

parameters estimated for released individual in their release site rather than in dispersal areas. We tested several plausible models for  $r$ ,  $p$ ,  $\psi$ , and  $\phi$  of individuals in their released area whereas we considered these parameters constant in their dispersal area. Model selection was achieved by starting from the less constrained models and making them simpler for  $r$ ,  $p$ ,  $\psi$ , and  $\phi$  sequentially (see the Appendix).

As for tag loss models, we used the best model structure determined for each site in the combined site data set to investigate variation in parameters among sites. We first tested (1) if the survival rate of dispersing individuals was different from the survival of resident individuals, in order to test for some dispersal cost in survival; (2) if the survival rates of released individuals were different among release areas (successful vs. unsuccessful programs).

3. *Habitat selection theories testing.*—We then assessed several hypotheses about dispersal in relation with distance and habitat selection theories (Cam et al. 2004, Breton et al. 2006): (1) dispersal rates were equal among released areas, (2) dispersal rates was negatively correlated with the distance between released areas, (3) dispersal rates depended on the relative sizes of the source and destination colonies (“conspecific attraction/avoidance hypothesis”), (4) dispersal rates depended on the relative breeding success in the source and destination colonies (“conspecific performance based hypothesis”), (5) dispersal rates varied both with distance and colony sizes, and (6) dispersal rates varied both with distance and performance of conspecifics. For hypotheses 2, 5, and 6, we used the distances in kilometers and natural logarithm transformations of distances. For hypotheses 3 and 5, we correlated dispersal from site A to site B with the ratio of the mean number of breeders in site A over the 25 years ( $N_A$ ) on the mean number of breeders in site B over the 25 years ( $N_B$ ). For hypotheses 4 and 6, we correlated dispersal from site A to site B with the ratio of mean breeding success in site A over the 25 years ( $BS_A$ ) on the mean breeding success in site B over the 25 years ( $BS_B$ ). In order to avoid errors due to division by 0, we added 1 to each mean. A negative correlation between dispersal rates and the considered ratios is expected for hypotheses 3, 4, 5, and 6. To test these covariates, we used an analysis of deviance (ANODEV; White and Burnham 1999).

#### *Goodness-of-fit testing*

We used mono-stratum models to assess the fit of our data set to the assumptions inherent to CMR models. Different potential sources of heterogeneity in survival and recapture parameters were first investigated using the Cormack-Jolly-Seber (CJS) model (live recapture only) with the program RELEASE (Burnham et al. 1987). The overall fit of mono-stratum models using both live recapture and dead recovery was also examined, by using the Median  $\hat{c}$  approach proposed in program MARK (White and Burnham 1999). This

approach allowed us to compute the variance inflation factor,  $\hat{c}$ , which was used to scale the deviance of all subsequent models and to inflate parameter variances (see QAIC<sub>c</sub> formula in *Materials and methods: Statistical methods: Model selection approach* [Burnham et al. 1987]). Unfortunately no similar approach for multi-strata models with recapture and recovery data is currently available. Nevertheless, data sets that met the single stratum assumption were probably robust for multi-strata analysis (Brown et al. 2003).  $\hat{C}$  values were computed using time-dependent models for each site (five data sets) separately, and for the data set including all sites.

## RESULTS

### *Goodness-of-fit testing and $\hat{c}$ estimates*

By using our entire data set ( $n = 272$  released individuals divided into eight groups), we found that Griffon Vulture data met the CJS single-strata assumption on survival homogeneity under the model  $\phi_t p_t$ , for live recapture data only (test 3:  $\chi^2 = 36.21$ ,  $df = 27$ ,  $P = 0.11$ ). However, we found significant heterogeneity of capture probability among individuals (test 2:  $\chi^2 = 107.7$ ,  $df = 42$ ,  $P < 0.001$ ) certainly due to tag loss.

For LRDR data, using model ( $s_{t \times sr}$ ,  $p_{t \times sr}$ ,  $r_{sr}$ ,  $F_{t \times sr}$ ) as the general starting model we obtained a  $\hat{c}$  value equal to 1.35. We used this variance inflation factor to compute all subsequent QAIC<sub>c</sub> values for multi-site models.

When considering each site separately (model  $\{s_{t \times ar}$ ,  $p_{t \times ar}$ ,  $r_{ar}$ ,  $F_{t \times ar}\}$  for Causses, Baronnies, and Diois and model  $\{s_t$ ,  $p_t$ ,  $r_c$ ,  $F_t\}$  for Navacelles and Verdon),  $\hat{c}$  values were respectively 1.13, 1.08, 1.33, 1.36, and 1.21.

### *Model selection: independent analysis of each site*

*Sex effect.*—In all sites, comparisons among models with and without sex provided no support for an effect of sex on survival, recapture, reporting rates, and fidelity probabilities. Indeed, the analysis of 296 models for each site including different combinations of constant, year and sex groups on  $s$ ,  $p$ ,  $r$ ,  $F$  parameters, as well as time-since-release effect on the  $s$  parameter, revealed no evidence of an effect of sex on a QAIC<sub>c</sub> basis. These results supported the contention that few behavioral differences occur between sexes. Dispersal rates of released individuals were also not different between males and females, which confirms previous work on movement frequencies and distances between all colonies (Bosé et al. 2007). Therefore, subsequent analyses were conducted using all individuals (males and females) with no sex group.

As mentioned in *Materials and methods*, the effect of sex was further investigated in a posteriori analysis of the best multi-strata model selected for each site (i.e., best models in Table 1). Once again, all models including sex effect had higher QAIC<sub>c</sub> values than the ones without sex effect.

*Tag loss model selection for each site.*—In each site, several combinations of age at release, year and time

since release effects for the survival, recapture, recovery, and transition parameters have been compared. Results of model selection are summarized in Table 1 (more details available in the Appendix).

For all populations, the best survival model assumed that survival varies with time since release (Table 1). In Causses, Baronnies, Diois, and Verdon, for birds released as immatures, the best survival model was  $\phi_{a1,1,2}$ , involving two distinct survival rates: one for the first two years after release, and a constant survival rate for birds released for more than two years. However, this result is difficult to interpret from a biological viewpoint, due to the high heterogeneity of the class of birds released as immature. In Causses, Navacelles, Baronnies, and Diois, for birds released as adult, the best survival model was  $\phi_{a1,2}$ , involving two distinct survival rates depending on the time since release (one for the first year following release and one for the following years), and no year effect. This model is consistent with the existence of a short-term release effect (i.e., a temporary reduction in survival rates) for individuals released as adults.

Best models for resighting probability, recovery rate and tag loss probability were different among colonies and type of band (Table 1).

*Dispersal model selection for each site.*—Structure of best dispersal model selected for survival ( $\phi$ ) was similar to that of best tag loss model (i.e., time since release and age at release effects, Table 1) in each site. We assessed dispersal rates as a function of the age at release only in the Diois as no individual released in Causses or Baronnies has dispersed. In the Diois, the model assuming an effect of the age at release on both survival and dispersal had the lowest QAIC<sub>c</sub> (Table 1).

Dispersal among monitored colonies has been observed only for individuals released in Navacelles, Diois, and Verdon. In Navacelles, dispersal occurred only to the Causses. The best model assumed that dispersal varied with year from 1993 to 1998 and was null after 1998 (Table 1). Dispersal from Navacelles to Causses varied with time; 18% (SE = 11%) of the individuals present in Navacelles dispersed to Causses during the first year of the program, 7% (SE = 7%) the second year, 24% (SE = 8%) the last year; and all living individuals released in Navacelles had dispersed the year after the last release.

In Diois, dispersal occurred mainly to the Baronnies and Verdon. The best model included dispersal from Diois to Baronnies varying with time since release (one dispersal rate for the first year and one for the following years) and constant dispersal from Diois to Verdon (Table 1). Dispersal from Diois to Baronnies and Verdon differed between individuals released as immature and those released as adult. Dispersal from Diois to Baronnies the first year after release was low for immature ( $\psi_{im}[\text{DIOIS} \rightarrow \text{BAR}]$  first year after release = 0.11, 95% CI = 0.017–0.495) whereas it was high for adult ( $\psi_{ad}[\text{DIOIS} \rightarrow \text{BAR}]$  first year after release = 0.78,

TABLE 1. Akaike's information criterion values (QAIC<sub>c</sub>) and numbers of parameters (n<sub>p</sub>) for starting (less constrained) and best models for survival (φ), resighting (p), recovery (r), and strata transition (ψ) parameters, for each release site for the Griffon Vulture (*Gyps fulvus*).

Site and model type (no. models tested)	φ	p	ψ	r	QAIC <sub>c</sub>	n <sub>p</sub>
<b>Causses</b>						
Tag loss (n = 140)						
Less constrained	φ <sub>t×ar</sub>	p <sub>met<sub>t×ar</sub>; p<sub>col<sub>t×ar</sub>; p<sub>cod<sub>t×ar</sub></sub></sub></sub>	ψ <sub>losscol<sub>t×ar</sub>; ψ<sub>losscod<sub>t×ar</sub></sub></sub>	r <sub>t×ar</sub>	2191.43	330
Best model	φ <sub>im<sub>a1,1,2</sub>†; φ<sub>ad<sub>a1,2</sub>†</sub></sub>	p <sub>met<sub>c</sub>; p<sub>col<sub>c</sub>; p<sub>cod<sub>a1,2</sub></sub></sub></sub>	ψ <sub>losscol<sub>a1,1,1,1,1,1,1,1,2</sub>; ψ<sub>losscod<sub>c</sub></sub></sub>	r <sub>a1,2</sub>	1021.9	37
<b>Baronnies</b>						
Tag loss (n = 78)						
Less constrained	φ <sub>t×ar</sub>	p <sub>met<sub>t×ar</sub>; p<sub>cod<sub>t×ar</sub></sub></sub>	ψ <sub>losscod<sub>t×ar</sub></sub>	r <sub>t×ar</sub>	453.49	84
Best model	φ <sub>im<sub>a1,1,2</sub>†; φ<sub>ad<sub>a1,2</sub>†</sub></sub>	p <sub>met<sub>c</sub>; p<sub>cod<sub>c</sub></sub></sub>	ψ <sub>losscod<sub>t</sub></sub>	r <sub>c</sub>	279.06	14
<b>Navacelles</b>						
Tag loss (n = 120)						
Less constrained	φ <sub>ad<sub>t</sub></sub>	p <sub>met<sub>t</sub>; p<sub>col<sub>t</sub>; p<sub>cod<sub>t</sub></sub></sub></sub>	ψ <sub>losscol<sub>t</sub>; ψ<sub>losscod<sub>t</sub></sub></sub>	r <sub>t</sub>	496.07	86
Best model	φ <sub>ad<sub>a1,2</sub></sub>	p <sub>met<sub>c</sub>; p<sub>col<sub>c</sub>; p<sub>cod<sub>c</sub></sub> (0 from 1998 to 2004)</sub></sub>	ψ <sub>losscol<sub>c</sub>; ψ<sub>losscod<sub>c</sub></sub></sub>	r <sub>c</sub> (0 from 1998 to 2004)	305.95	15
Dispersal (n = 40)						
Less constrained	φ <sub>ad[NAV]<sub>t</sub></sub>	p[NAV] <sub>t</sub>	ψ[NAV→CAU] <sub>t</sub>	r[NAV] <sub>t</sub>	369.4	49
Best model	φ <sub>ad[NAV]<sub>a1,2</sub></sub>	p[NAV] <sub>a1,2</sub>	ψ[NAV→CAU] <sub>t</sub> (0 from 1998 to 2004)	r[NAV] <sub>a1,2</sub>	279.85	17
<b>Verdon</b>						
Tag loss (n = 41)						
Less constrained	φ <sub>im<sub>t</sub></sub>	p <sub>met<sub>t</sub>; p<sub>cod<sub>t</sub></sub></sub>	ψ <sub>losscod<sub>t</sub></sub>	r <sub>t</sub>	291.24	30
Best model	φ <sub>im<sub>a1,1,2</sub></sub>	p <sub>met<sub>t</sub>; p<sub>cod<sub>t</sub></sub></sub>	ψ <sub>losscod<sub>c</sub></sub>	r <sub>c</sub>	258.8	14
Dispersal						
Less constrained	φ <sub>im[VER]<sub>t</sub></sub>	p[VER] <sub>t</sub>	ψ[VER→BAR] <sub>t</sub>	r[VER] <sub>t</sub>	291.23	29
Best model	φ <sub>im[VER]<sub>a1,1,2</sub></sub>	p[VER] <sub>t</sub>	ψ[VER→BAR] <sub>a1,1,2</sub>	r[VER] <sub>c</sub>	265.06	17
<b>Diosis</b>						
Tag loss (n = 78)						
Less constrained	φ <sub>t×ar</sub>	p <sub>met<sub>t×ar</sub>; p<sub>cod<sub>t×ar</sub></sub></sub>	ψ <sub>losscod<sub>t×ar</sub></sub>	r <sub>t×ar</sub>	297.22	54
Best model	φ <sub>im<sub>a1,1,2</sub>†; φ<sub>ad<sub>a1,2</sub>†</sub></sub>	p <sub>met<sub>t</sub>; p<sub>cod<sub>c</sub></sub></sub>	ψ <sub>losscod<sub>c</sub></sub>	r <sub>c</sub>	130.56	11
Dispersal (n = 81)						
Less constrained	φ[DIOIS] <sub>t×ar</sub>	p[DIOIS] <sub>t×ar</sub>	ψ[DIOIS→BAR] <sub>t×ar</sub> ; ψ[DIOIS→VER] <sub>t×ar</sub>	r[DIOIS] <sub>t×ar</sub>	429.28	65
Best model	φ <sub>im[DIOIS]<sub>a1,1,2</sub>†; φ<sub>ad[DIOIS]<sub>a1,2</sub>†</sub></sub>	p[DIOIS] <sub>c</sub>	ψ <sub>im[DIOIS→BAR]<sub>a1,2</sub>; ψ<sub>ad[DIOIS→BAR]<sub>a1,2</sub>; ψ<sub>im[DIOIS→VER]<sub>c</sub>; ψ<sub>ad[DIOIS→VER]<sub>c</sub></sub></sub></sub></sub>	r[DIOIS] <sub>c</sub>	196.52	22

Notes: All QAIC<sub>c</sub> values have been computed using a multi-strata model (tag loss or dispersal) including live recaptures and dead recoveries. Details on intermediate models tested are provided in the Appendix. Abbreviations are: im, parameter for individuals released as an immature; ad, parameter for individuals released as an adult; met, metal band; col, color band; cod, code band; losscol, loss of color band; losscod, loss of code band; A→B, dispersal from release site A to site B; c, constant; t, year effect; a<sub>1,2</sub>, time since release (age) effect with first class for the first year after release and second class for the following years; a<sub>1,1,2</sub>, time since release effect with first class for the first two year after release and second class for the following years; ar, age at release effect, i.e., parameters differ between individuals released as immatures vs. adults.

† The long-term survival rates of individuals released as immatures vs. adults are equal.

95% CI = 0.53–0.91). On the contrary, from the second year after release, dispersal from Diois to Baronnies was higher for immature (ψ<sub>im</sub>[DIOIS→BAR] after second year = 0.688, 95% CI = 0.68–0.69) than for adult (ψ<sub>ad</sub>[DIOIS→BAR] after second year = 0.30, 95% CI = 0.04–0.81). In the same way, dispersal from Diois to Verdon was higher for immature (ψ<sub>im</sub>[DIOIS→VER] = 0.31, 95% CI = 0.309–0.313) than for adult (ψ<sub>ad</sub>[DIOIS→VER] = 0.10, 95% CI = 0.02–0.32).

In Verdon, dispersal occurred mainly to the Baronnies. The best model assumed that dispersal depends on the time since release, with two distinct dispersal rates: one for the first two years after release, and a constant

dispersal rate for birds released for more than two years (Table 1). Dispersal from Verdon to Baronnies occurred only the first two years after release but was quite low (less than 10% per year).

*Model selection: all sites of release considered together*

In this section, results are presented for the analysis including all individuals divided into eight groups according to age at release and released site.

*Tag loss model selection for all sites together.*—As monitoring was site specific, we did not consider model assuming equal “monitoring” parameters (r, p) among sites and these parameters were modeled as in the single

TABLE 2. Effect of constraining survival rates of individuals released in different sites to be equal on Akaike’s information criterion values (QAIC<sub>c</sub>) and numbers of parameters (n<sub>p</sub>) of tag loss models integrating individuals released in all colonies.

Complete model	QAIC <sub>c</sub>	n <sub>p</sub>
A) Sum of the best models (all parameters different)	22251.2	74
B) Constraining tag loss among sites to be equal but different between color and code band	2239.6	69
C) Constraining tag loss among band types to be equal	2246.9	68
D) Same as B, with equality of first-year survival for immature	2266.4	64
E) Same as B, with equality of released cost for adults	2250.3	64
F) Same as B, with constraining survival rate among sites to be equal with age at release effect conserved	2249.4	58
<b>G) Same as B with constraining survival rates among birds released in successful programs (Causses, Baronnies, Verdon) to be equal</b>	<b>2233.9</b>	<b>64</b>
H) Same as G with constraining long-term survival of individuals to be equal among successful and unsuccessful programs	2261.7	61

Note: In each case, QAIC<sub>c</sub> values have been computed using a multi-strata model (tag loss model) including live recaptures and dead recoveries, and best models are described in Table 1. The selected model is in boldface type.

site models. The model assuming that tag loss was equal among monitored areas was better than the model assuming heterogeneous tag loss (Table 2). However, tag loss rates were different for color ( $\psi_{losscol} = 0.079$ , 95% CI = 0.05–0.127) and for code bands ( $\psi_{losscod} = 0.046$ , 95% CI = 0.031–0.068). The best model assumed that survival rates were equal among birds released in successful reintroduction programs (Causses, Baronnies, and Verdon) and that survival rates estimated in unsuccessful programs (Navacelles and Diois) were different for both immediate survival (first year following release) and long-term survival. The survival rate estimate for immature released in successful programs during the first two years after release (Table 3) was higher than for immature released in Diois (unsuccessful program). The survival rate of adults released in successful programs (Causses and Baronnies) estimated for the first year after release (Table 3) was also higher than the one estimated for the adults released in unsuccessful programs (Navacelles and in Diois). The long-term survival rate for individuals released as immatures and as adults in successful programs (Table 3) was higher than the one estimated for individuals released in unsuccessful programs.

*Dispersal model selection for all sites together.*—When pooling all individuals from the different release areas in a multi-strata dispersal type model, the best selected model implied no difference in long-term survival within one colony among settled individuals from different origins (Table 4); suggesting that there was no survival difference between resident and immigrant individuals. The best model assumed that the first-year survival rates for released as immatures and adults were the same in all areas (i.e., successful and unsuccessful programs, Table 3). The long-term survival rate was the same for all individuals in all released areas, except in Navacelles (Table 3).

The hypothesis of equal dispersal rates among released areas was highly rejected (Table 5). Including correlation with the distance or with the ratio  $N_A/N_B$  or with the ratio  $BS_A/BS_B$  resulted in substantial reductions of model deviances, although the model in which all dispersal rates were different between release areas remained the best one on a QAIC<sub>c</sub> basis. The best model including covariables was the one testing for the hypothesis of interaction between distance and conspecific attraction (Table 5, Hypothesis 5). ANODEV results indicated that 77% of the among-site variation

TABLE 3. Short-term and long-term survival rates (with 95% confidence interval) estimated in each release site with best tag loss and dispersal models integrating individuals released in all colonies (multi-strata model including live recaptures and dead recoveries).

Multi-strata model and age at release	Release area	Status	Short-term survival rate	Long-term survival rate
<b>Tag loss</b>				
Immature	Cau, Bar, Ver	success	0.807 (0.73–0.86)	0.97 (0.96–0.98)
Immature	Diois	failure	0.69 (0.26–0.93)	0.15 (0.02–0.5)
Adult	Cau, Bar	success	0.80 (0.69–0.87)	0.97 (0.96–0.98)
Adult	Nav	failure	0.56 (0.09–0.72)	0.68 (0.45–0.84)
Adult	Diois	failure	0.087 (0.02–0.29)	0.71 (0.13–0.97)
<b>Dispersal</b>				
Immature	Cau, Bar, Ver, Diois	success	0.90 (0.86–0.94)	0.955 (0.94–0.97)
Adult	Cau, Bar, Diois	success	0.74 (0.66–0.81)	0.955 (0.94–0.97)
Adult	Nav	failure	0.74 (0.66–0.81)	0.72 (0.59–0.82)

Notes: Best models are described in Tables 2 and 4. Abbreviations are: Cau, Causses; Bar, Baronnies; Ver, Verdon; Nav, Navacelles.



TABLE 4. Effect of constraining parameters of individuals released in different sites to be equal on Akaike’s information criterion values (QAIC<sub>c</sub>) and numbers of parameters (*n*<sub>p</sub>) of dispersal models integrating individuals released in all colonies.

Complete model	QAIC <sub>c</sub>	<i>n</i> <sub>p</sub>
A) $\phi_{dc}$ , <i>p</i> , <i>r</i> different within one colony depending on the origin of individuals	1703.5	146
B) <i>p</i> , <i>r</i> equal within one colony but $\phi_{dc}$ depending on the origin of individuals	1585.1	77
C) Same as B, with equality of $\phi_{dc}$ among origins	1580.8	72
D) Same as C, with equality of survival rates among birds released in successful reintroduction programs (Causses, Baronnies, Verdon)	1576.9	67
<b>E) Same as D, with constraining survival rates of birds released in Diois (failure) to be equal with survival rate of birds released in successful programs</b>	<b>1570</b>	<b>63</b>
<b>F) Same as E, with constraining released cost for adults released in Navacelles (failure) to be equal with released cost for successful programs</b>	<b>1571</b>	<b>62</b>
G) Same as F, with constraining long-term survival of individuals released in Navacelles to be equal with the other individuals.	1590.7	61

Notes: In each case, QAIC<sub>c</sub> values have been computed using a multi-strata model (dispersal model) including live recaptures and dead recoveries. Release costs in survival for released individuals are modeled for their release site; survival of these individuals in another site ( $\phi_A$ ) is assumed constant ( $\phi_{dc}$ ). Selected models are in boldface type.

in dispersal was explained by these covariates (distance +  $N_A/N_B$  + interaction; ANODEV,  $F_{3,16} = 18.21$ ,  $P < 0.0001$ ).

dispersal did not differ with sex and year but they differed with age at release and time since release.

DISCUSSION

Comparison with previous survival estimates

Using resighting of Griffon Vulture reintroduced in five areas, we estimated and compared survival and dispersal rates among release sites. Survival and

Sarrazin et al. (1994) showed that the long-term survival of released and wild-born individuals in Causses were not significantly different. Current work of collaborators on re-estimation of survival of wild-born

TABLE 5. Tests of hypotheses on the relationship between dispersal, distance, and habitat selection theories, through comparison of QAIC<sub>c</sub> values of dispersal models integrating individuals released in all colonies.

Complete model	QAIC <sub>c</sub>	<i>n</i> <sub>p</sub>	$\beta$ (SE)
Hypothesis 1: simple model All dispersal rates are equal	1803.9	46	
Hypothesis 2: distance Dispersal correlated with distance (km)	1776.6	47	-0.014 (0.003)
Dispersal correlated with ln(distance)	2053.6	47	0.08 (0.16)
Hypothesis 3: conspecific attraction Dispersal correlated with $N_A/N_B$	1770.6	47	-0.83 (0.13)
Hypothesis 4: performance-based habitat selection Dispersal correlated with $BS_A/BS_B$	1796.2	47	-2.06 (0.37)
Hypothesis 5: interaction between conspecific attraction and distance Logit(Dispersal) = $\beta_1 \times \text{distance} + \beta_2 \times (N_A/N_B) + \beta_3 \times (\text{distance} \times [N_A/N_B])$	1633.4	49	$\beta_1 = -0.02 (0.004)$ $\beta_2 = -0.47 (0.33)$ $\beta_3 = -0.006 (0.004)$
Logit(Dispersal) = $\beta_1 \times \ln(\text{distance}) + \beta_2 \times (N_A/N_B) + \beta_3 \times (\ln[\text{distance}] \times [N_A/N_B])$	1663.6	49	$\beta_1 = -2.98 (0.27)$ $\beta_2 = -3.6 (1.16)$ $\beta_3 = 0.65 (0.21)$
Hypothesis 6: interaction between performance based selection and distance Logit(Dispersal) = $\beta_1 \times \text{distance} + \beta_2 \times (BS_A/BS_B) + \beta_3 \times (\text{distance} \times [BS_A/BS_B])$	1660.9	49	$\beta_1 = -0.06 (0.01)$ $\beta_2 = -10.5 (1.24)$ $\beta_3 = 0.04 (0.01)$
Logit(Dispersal) = $\beta_1 \times \ln(\text{distance}) + \beta_2 \times (BS_A/BS_B) + \beta_3 \times (\ln[\text{distance}] \times [BS_A/BS_B])$	2206.4	49	$\beta_1 = 8.6 (2.42)$ $\beta_2 = -2.08 (0.55)$ $\beta_3 = -2.66 (2.32)$
Hypothesis 7: global model <b>All dispersal rates differ between release areas</b>	<b>1616.3</b>	<b>65</b>	

Notes:  $N_A$  is the mean number of breeders in site A over the 25 years;  $N_B$  is the mean number of breeders in site B over the 25 years;  $BS_A$  is the mean breeding success in site A over the 25 years;  $BS_B$  is the mean breeding success in site B over the 25 years;  $\beta$  is the slope of the linear regression of dispersal rate on each covariable considered estimated by the model (with standard error, SE, in parentheses). In each case, QAIC<sub>c</sub> values have been computed using a multi-strata model (dispersal model) including live recaptures and dead recoveries. The selected model is in boldface type.

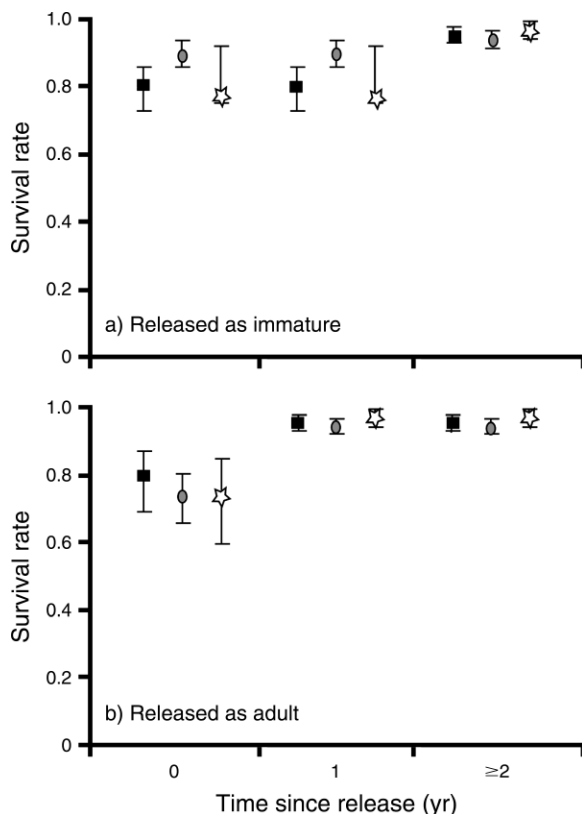


FIG. 1. Comparison of survival estimates of the Griffon Vulture (*Gyps fulvus*) in Causses, France, obtained over the 1980–2004 period with complete tag loss model (black squares) and complete dispersal model (gray ovals) with the estimates of Sarrazin et al. (1994) obtained over the 1981–1991 period (open stars) for vultures released (a) as immatures and (b) as adults. Bars indicate the 95% confidence interval.

individuals in Causses indicates that adult survival is equal to 0.967 (95% CI = 0.944–0.981 [A. Gault, A. Robert, M. Bosé, P. Lécuyer, J.-L. Pinna, C. Arthur, and F. Sarrazin, *unpublished manuscript*). This estimate is very similar to our estimate (Table 3) although we were not able to test the difference with the QAIC<sub>c</sub> method. However, the survival rates estimated in our study were slightly different from those estimated by Sarrazin et al. (1994). The early survival of released individuals was generally higher in our study, whereas long-term survival rate was a bit lower (Fig. 1). The discrepancy between the two studies may be due to methodological aspects. In our study, the incorporation of different recapture probabilities according to the bands carried by individuals (tag loss model) and the use of data on recoveries of dead individuals (tag loss and dispersal models) may have limited the overestimation of mortality due to band loss and heterogeneous banding. Another source of discrepancy is the temporal variation in survival over the 25-year period covered by the analysis. Lowest long-term survival rates over the 25-year period compared with the 10-year period suggest

indeed a reduction in the survival of the individuals released in the Causses during the 1990s. Such reduction is likely to be the consequence of senescence (notably for individuals released as adults), or of density-dependent regulation following the rapid increase of population size. However, previous studies (Ferrière et al. 1996) have uncovered a high sensitivity of the population growth rate to changes in adult survival in the Griffon Vulture, as expected for long-lived species (Gaillard et al. 2000). Since theory predicts that traits with high proportional sensitivities may have low variances (Stearns and Kawecki 1994), a negative density-dependent effect on adult survival is little probable and is more expected on juvenile and immature survival. Consequently, the hypothesis of senescence of released individuals seems more probable, although we were unable to detect any effect of senescence, probably due to an insufficient amount of data. An effect of senescence on reproductive performance has been previously shown in a long-lived raptor species (Nielsen and Drachmann 2003), but senescence on survival has never been revealed because of lack of long-term studies.

#### Early survival rate estimates and comparison among sites

In all colonies, we found that the early survival rates of released individual (from one to two years after release) are different from the long-term survival rate and dependant on the age at release. The reduction of survival of individual released as immature is however difficult to interpret from a biological viewpoint, due to the high heterogeneity of age at release for this class of individuals. On the contrary, the temporary reduction in survival rates for individual released as adults is clearly consistent with the existence of a short-term release effect. Mortality during the establishment phase of the reintroduction is often suspected to be higher than normal due to the stress and inexperience of the released birds (Armstrong et al. 1999, Tweed et al. 2003). However, the intensity of survival reduction is likely to depend on environmental conditions. In our study, although the protocol of release was the same in all programs, some variability in history, origin, and age of founders, as well as heterogeneous geographical and historical contexts of release sites, may explain the observed differences in mortality during the establishment phase.

With tag loss models including local observations only, early survival rates varied across sites, with two groups being distinguished: successful programs (Causses, Baronnies, and Verdon) on one hand, and programs that failed (Navacelles and Diois) on the other hand. However, when using “dispersal” model including observations of individuals in all monitored areas, early survival rates became equal across release sites. It thus appears that among-site differences observed with local observation models are due to differential dispersal among release areas. When taking into account dispersal, short-term release cost in adult survival seems to be

spatially replicable and predictable: 21% additional mortality is expected when releasing adults that have experienced several years of captivity.

#### *Long-term estimates and comparison among sites*

With the tag loss model, individuals released in successful programs (Causses, Baronnies, and Verdon) have an equivalently high long-term adult survival, which is consistent with results on reintroduced (Bustamante 1996, 1998, Green et al. 1996) and natural (Brown 1997, Real and Manosa 1997, Bustamante 1998, Piper et al. 1999) populations of raptor species. Long-term survival rates estimated for individuals released in unsuccessful programs (Navacelles and Diois) were lower, especially for immature birds released in Diois.

Again, the results obtained with dispersal models were slightly different: long-term survival rates were equal in all areas, except in Navacelles, where survival was lower. Three main hypotheses could explain this pattern: (1) a lower quality of individuals released in Navacelles; (2) some difference in threats against vultures in Navacelles; and (3) a high dispersal from Navacelles to unmonitored areas. The first hypothesis could easily be rejected, as the survival of individuals from Navacelles that have dispersed to Causses was the same as other released individuals. Moreover, there was no difference in genetic diversity of released groups in Navacelles and in the Alps (Le Gouar et al., *in press*). The second hypothesis is difficult to support as well, as a  $\chi^2$  test of the distributions of main mortality causes (electrocution, clash with wire cable, starvation, unknown, and other causes) reported in each colony for all individuals (wild-born and released) was not significant ( $n = 178$ ,  $\chi^2 = 22.03$ ,  $df = 16$ ,  $P = 0.14$ ). The dispersal hypothesis is therefore the most likely, as dispersal to Pyrenees and Spain has probably occurred from the Navacelles area. Unfortunately, because of the low number of observations of banded birds in these regions, we could not confirm this hypothesis.

#### *Habitat selection theories*

We found asymmetrical patterns of dispersal among reintroduced colonies. Indeed, the Causses and Baronnies sites attracted birds, contrary to Navacelles, Diois, and Verdon. We found that no individual from Causses or Baronnies dispersed to newly established colonies, certainly because dispersal by established breeders is uncommon (Lebreton et al. 2003). These results are in accordance with recent estimates of gene flow among native populations of Griffon Vultures (Le Gouar et al., *in press*).

Dispersal rates differed between ages at release, at least in Diois. On one hand, dispersal from Diois to Verdon was higher for immature birds than for adults. On the other hand, dispersal from Diois to Baronnies was delayed for immature birds, whereas it was higher in the first year following release for adults. These results contrast with previous studies on erratic behavior of

immature birds and site fidelity of adults for vulture species (Mundy et al. 1992). However, we were interested in effective dispersal, i.e., the settlement of individuals in a colony during the breeding period, whereas previous studies focused on migration or movement. Our results suggest that intra-annual prospecting movements of immature birds released in Diois into established colonies in the first year following release were actually frequent, but birds often came back to Diois to feed (J. P. Choisy, *personal communication*). When birds released as immatures become sexually mature, they choose a colony in which to breed. In contrast, individuals released as adults choose their breeding colony in the first year following release.

Among the habitat selection hypotheses we tested, the one that best explained dispersal among colonies integrated distance, conspecific attraction, and their interaction. Dispersers selected the closest and the largest population. It should be noted, however, that the best dispersal model on a QAIC<sub>c</sub> basis was the least constrained one (i.e., the model allowing different dispersal rates between all pairs of sites; see Table 5). This suggests that the simple function used to assess the effects of distance and colony densities on dispersal (additive effects with interaction term) insufficiently reflects their actual complex effects (e.g., threshold effect, depending on the maximum foraging distance of birds). Nevertheless, it clearly appears that distance and colony size have a strong effect on dispersal, and explain a large amount of variance (77%) when compared with the most constrained model (i.e., in which all dispersal rates are equal).

In contrast, an effect of the breeding success on dispersal was not supported by the data. This result contrasts with our previous analysis on habitat selection within population, which showed that individuals use performance of conspecifics to select their habitat. Average breeding success over the last 25 years might not be the best covariable to use as an index of performance. A more accurate relationship could certainly be uncovered by using the correlation of dispersal extent in each year with the breeding success of the previous year. As it would add 500 parameters to the model, it was not possible to compute such an index with our computer capacities. However, using the performance cue assumes an intensive prospecting of breeding colonies during the rearing phase of reproduction (Boulinier et al. 1996, Pärt and Doligez 2003), which could be easily done by individuals within their daily foraging movements (radius between 30 and 40 km), but which is more difficult at larger scales. Although density of conspecifics reflects habitat quality poorly (Reed 1999, Doligez et al. 2003), using the presence cue to select habitat at a large scale certainly represents a trade-off between the predictive value of the cue and the costs of gathering this cue (Doligez et al. 2004a). In addition, breeder density is a useful cue for evaluating potential mate availability. Finally, in the

case of reintroduced populations, as releases occur at the beginning of the reproduction period, the performance cue is unavailable for released individuals, unlike the presence cue.

In accordance with the conspecific attraction behavior theory (Serrano et al. 2005), asymmetric movements are not rare among populations of colonial species. The genetic and demographic consequences of this phenomenon have been investigated through modeling (Smith and Peacock 1990, Ray and Gilpin 1991, Kawecki and Holt 2002). However, spatially explicit viability analyses are lacking due to difficulty of validation and parameterization of the movement processes (Macdonald and Johnson 2001, Harrison et al. 2006). These models could yet improve restoration strategies by taking into account the matrix of remnant populations, and thus dispersal among populations of various densities.

#### Management implications

The analyses of settlement failures in Navacelles and Diois allowed us to discriminate between survival and dispersal effects, uncovering dispersal as the main cause of local extinction. Dispersal from some release sites is associated with local failure, in spite of reinforcement of close reintroduced populations. Optimization of release protocols thus should be achieved to compromise between limiting loss of investment and maximizing the viability of reintroduced populations. Hence, we need to define global restoration strategies in fragmented habitats. The Single-Large or Several-Small (SLOSS) debate on reserve design (Diamond 1975) could be applied to restoration design of endangered species populations. Many species (such as the Griffon Vulture) have a naturally patchy distribution due to specific habitat requirements. Metapopulation theory suggests that a minimum level of connection is necessary to ensure long-term persistence of these species, for demographic (Hanski 2001) and genetic (Whitlock 2001) reasons. In this context, the restoration design should be a compromise between local viability during the critical establishment phase following reintroduction (minimization of the effects of demographic stochasticity and permanent emigration), and long-term metapopulation viability (sufficient degree of connection to allow genetic exchanges). In this context, we showed that the age of released individuals, the distance to established populations, and the density of these populations were the main factors to control. Dispersal into Baronies of individuals released in Verdon (110 km) was lower than dispersal of individuals released during the same period in Diois (45 km). Reintroduction within a radius of 40–45 km of an established colony seems to favor reintroduction failure due to dispersal for this species. The distance of 100 km seems to be the good compromise to restore gene flow among populations while avoiding the deleterious effects of attraction. In this aim, we recommend releasing adults first in a suitable area much farther than 100 km from dense

populations. Then, immature birds should be released once several pairs have settled in the release area, to favor genetic exchanges with other populations. Measures to favor adult settlement should be considered in accordance with knowledge of habitat selection behavior (Reed and Dobson 1993).

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#### APPENDIX

Selection of the best tag loss and dispersal models in each site (*Ecological Archives* A018-030-A1).