The Auk 111(4):853-862, 1994

HIGH SURVIVAL ESTIMATES OF GRIFFON VULTURES (*GYPS FULVUS FULVUS*) IN A REINTRODUCED POPULATION

François Sarrazin,[1,2] Constant Bagnolini,[2]
Jean Louis Pinna,[3] Etienne Danchin,[1]
and Jean Clobert[1]

[1]*Ecole Normale Supérieure, Université Pierre et Marie Curie, Laboratoire d'Ecologie, CNRS, URA 258, 46 rue d'Ulm, 75230, Paris Cedex 05, France;*
[2]*Fonds d'Intervention pour les Rapaces—Grands Causses, Mairie, 12720 Peyreleau, France; and*
[3]*Parc National des Cévennes, Château de Florac, BP 15, 48400 Florac, France*

Abstract.—Little is known of the life history of vultures. The reintroduction program of Griffon Vultures (*Gyps fulvus fulvus*) in the Causses (south of the Massif Central, France) and extensive monitoring by capture-mark-resighting of the released birds allowed us to obtain the first estimates of their survival. Adult survival rates are high ($\bar{x}$ = 0.987 ± SE of 0.006). A release effect on adult survival was detected (only 0.743 ± 0.006 survival during the first year after release). Young born in the wild (less than three years old) had an annual survival rate of 0.858 ± 0.039. Mortality causes and erratic behavior of immature birds are considered in order to assess the effectiveness of this reintroduction program. Our results indicate that reintroductions of vultures and similar species should use adults that have bred in captivity within the target area rather than juveniles or immatures. *Received 9 February 1993, accepted 19 August 1993.*

Old world vultures such as Griffon Vultures (*Gyps fulvus fulvus*) are long-lived birds that are highly sensitive to environmental changes (Houston 1987). Being exclusively scavengers, they depend on the availability of large carcasses. Loss of this food resource and direct persecution of birds by hunting and indirect poisoning led to the decline of southern European vulture populations over the last few hundred years (Houston 1982). Griffon Vultures in the Causses (south of the Massif Central, France) were extirpated in 1945 (Berthet 1946). In 1968, a successful reintroduction project was instigated and more than 100 Griffon Vultures now occupy the Causses colony composed of both captive-bred birds and their wild-born offspring (Bonnet et al. 1990, Terrasse 1990). We report on two aspects of the recently established population.

Our first aim was to gain a better understanding of the biology and especially of the demographic parameters of this poorly studied species (Donazar 1987, Elosegui 1989). In particular, survival is the demographic parameter to which population growth is most sensitive for such long-lived animals (Lebreton and Clobert 1991). Few survival estimates have been made because they require long-term studies and extensive field observation; only recently have suitable adapted and standardized analysis methods been available to achieve such estimates (for review, see Pollock 1991, Lebreton et al. 1992, Nichols 1992). Crude estimates of survival have been made for only one *Gyps* species, the Cape Vulture (*G. coprotheres*; Piper et al. 1981, Robertson 1984). In our study, we monitored every individual in the population from 1981 to 1991 and used these data to calculate survival rates. Our second objective was to compare survival rates of wild-born and released captive birds to evaluate techniques for the reintroduction program. Overall, our purpose was to use capture-resighting data to model and compare survival estimates in three categories of individuals of this population: (1) wild-born individuals, (2) birds released as adults, (3) birds released as immatures.

Initially, we analyzed our three data sets separately. First, the wild-born individuals were studied since they were not likely to be affected by any reintroduction effect. These results were then compared with the survival estimates for released adults in order to test the release effect. We then estimated the survival rates of birds released as young. Finally, the three classes were grouped together to compare parameters of the different data sets and to obtain the best-possible estimates.

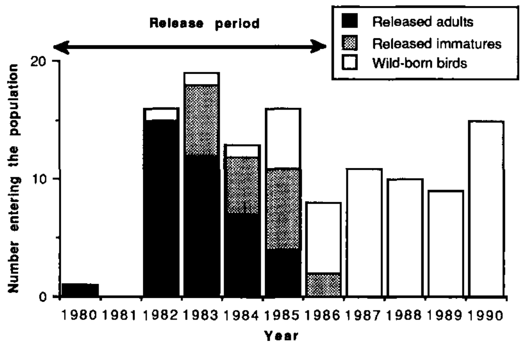

Fig. 1. Number of marked Griffon Vultures entering Causses population per year. Numbers of yearly released birds differ from those given by Bonnet et al. (1990) and Terrasse (1990) because vultures released after mid-November were considered here as released during following year. One bird escaped from aviary in 1980 and came back three years later. The 17 individuals born in 1991 were not taken into account in survival analyses.

METHODS

Reintroduction and management technique.—The study area covers all the Grands Causses of south-central France where the Tarn, Jonte, and Dourbie rivers flow into deep canyons. The release site was located on the southern rim of the Causse Méjean (44°12′N, 3°15′E), where aviaries for captive breeding were built at the top of a cliff overlooking the gorges of the Jonte River. In 1970, a first attempt to release four juveniles failed because the young birds rapidly left the area. A stock of captive adults was then acquired with the intention of establishing breeding pairs in the aviaries (Bonnet et al. 1990, Terrasse 1990). The release of these adults began in December 1981 and was carried on with younger birds until 1986 (Fig. 1). During these five years, 61 Griffon Vultures were released (one banded and two unbanded birds escaped unintentionally in 1980 and 1985, respectively). Food resources in the area mainly consisted of sheep and cattle carcasses resulting from natural mortality. In addition, there was an active education program for local farmers and hunters, sites for supplementary feeding were established, nest cliffs were protected from climbers, and power lines were converted to prevent birds being electrocuted (Bonnet et al. 1990, Terrasse 1990).

Monitoring.—We conducted detailed monitoring of the population. Each marked individual wore a metal band on one tarsus and an identification system on the other. This system changed during the monitoring period. The first birds to be released were equipped with a combination of two plastic color bands. Because of the loss of some of these bands, engraved DARVIC white bands were used from 1988. However, problems of legibility from distances over 300 m led us to use a code of more resistant four-layer DARVIC color bands. Banding occurred on different occasions: (1) before release ($n = 59$); (2) at nest for wild-born chicks when 60 to 80 days old ($n = 59$); (3) at nest for tame adults ($n = 3$); (4) during recapture sessions to compensate for band losses or to change the identification system (in 1988 $n = 29$; in 1991 $n = 31$). Observations were essentially made by three people. Birds were observed with a 20–60× telescope year-round to obtain information on their overall activities (breeding, feeding, etc.). All resightings were entered into a dBase III+ database, and individual capture-resighting histories were constructed from the observations made during the breeding period (between 1 January and 30 September of each year).

Analyses.—Although banding recoveries have been used to estimate survival of the Cape Vulture (Houston 1974, Piper et al. 1981, Piper 1990), we did not use them because of their limited importance in the context of our study (Lakhani and Newton 1983, Anderson et al. 1985, Lebreton 1985 unpubl. report). As our population was considered to be an open population (Pollock et al. 1990, Pollock 1991, Nichols 1992), survival and resighting rates (respectively noted Φ and P) were computed with capture resightings models (Clobert et al. 1985, Clobert et al. 1987, Lebreton et al. 1992). Models combining survival and resighting parameters were noted models Φ P. These parameters were estimated using SURGE 4 (Pradel and Lebreton 1991, Lebreton et al. 1992), a program that allows use of user defined models. The constancy of Φ and P, as well as the effects of release (r), age (a), and time (t) on Φ and P, could be tested as in standard analysis of variance or of covariance. Models with interactions ($a + t + a{\cdot}t$) were noted $a{\cdot}t$, whereas models without interactions were noted $a + t$ (see Table 1 for model notations). Details of models structure are available in Pradel et al. (1990), Pradel and Lebreton (1991), Lebreton et al. (1992).

Because we were led to consider numerous models, we used Akaike's procedure, which allows comparison of non-necessarily nested models. This new statistical method is recommended in multivariate analysis (Lebreton et al. 1992). It gives a penalty to models with too many parameters. Thus, it is useful to retain the most-parsimonious models. The lower the Akaike's information criterion value (AIC), the more appropriate is the model for the data. The similarity of Φ and P parameters across groups and the dependence of these parameters on capture-resighting history were tested with TEST1 and TEST3, respectively, of the computer program RELEASE (Burnham et al. 1987, Lebreton et al. 1992). Because Griffon Vultures are monomorphic (Newton 1979, Fry 1983, Elosegui 1989), sex was not taken into account in our analyses.

Some Griffon Vultures started to breed when they were four years old, so we considered birds to be adults from that age onwards. These age classes cor-

TABLE 1. Number of parameters (*np*) and Akaike's information criterion values (AIC) for different models of survival (Φ) and resighting (P) parameters tested on capture-resighting histories of wild-born individuals. Letters indicate the effect: (*a*) age; (*c*) constant over time; (*t*) time (i.e. one parameter per year). Subscript numbers correspond to range of different age classes described in models (e.g. $\Phi[a_{3.6}]$ is model of survival rate with two age classes three and six years long, respectively). When no subscript included, each age is fully identified. The lower the AIC value, the more appropriate is the model for the data. Selected model for Φ and P parameters is in bold.

Survival models (Φ)		Resighting model (P)										
		c	***t***	$a_{1.1.1.6}$	$a_{1.1.7}$	$a_{1.8}$	$a_{2.7}$	$a_{3.6}$	$a_{4.5}$	$a_{3.6}*t$	$a_{3.6}+t$	$a_{2.6}+t$
c	*np*	2	10	5	4	3	3	3	3	16	11	11
	AIC	248.58	248.03	251.46	250.07	250.30	248.28	248.03	249.95	248.91	246.56	247.74
t	*np*	10	17	13	12	11	11	11	11	23	18	18
	AIC	258.98	257.20	261.33	259.85	260.81	258.34	258.34	260.01	258.70	256.07	251.06
a	*np*	10	18	13	12	11	11	11	11	24	19	19
	AIC	258.98	257.86	263.00	261.13	260.25	259.14	259.58	260.66	261.10	258.05	258.69
$a_{1.1.1.6}$	*np*	5	13	8	7	6	6	6	6	19	14	14
	AIC	249.22	247.86	254.01	252.01	250.71	250.02	250.58	251.22	253.08	248.71	248.69
$a_{1.1.7}$	*np*	4	12	7	6	5	5	5	5	18	13	13
	AIC	248.20	246.91	252.77	250.96	249.60	248.96	249.12	250.16	251.10	247.32	247.77
$a_{1.8}$	*np*	3	11	6	5	4	4	4	4	17	12	12
	AIC	250.13	249.47	253.37	252.00	252.07	250.27	249.95	265.68	250.82	248.37	249.64
$a_{2.7}$	*np*	3	11	6	5	4	4	4	4	17	12	12
	AIC	246.23	245.53	251.64	249.91	248.73	248.00	247.88	248.80	249.60	246.02	246.71
$a_{3.6}$	*np*	3	**11**	6	5	4	4	4	4	17	12	12
	AIC	246.11	**245.04**	264.75	248.75	248.01	246.94	247.49	248.11	249.89	245.66	245.72
$a_{4.5}$	*np*	3	11	6	5	4	4	4	4	17	12	12
	AIC	248.20	247.09	252.08	250.29	250.02	248.50	248.67	250.11	249.23	246.25	247.25

responded to the calendar year, except the first one, which was shorter (from fledging in July and August to 31 December of the same year, as in Houston 1974). All wild-born individuals were banded as nestlings. Therefore, their age was known precisely and cohorts included only birds of the same age. Other vultures that were born in our aviary were also aged precisely. This was not the case for some captive birds of unknown origin. A minimal age for such individuals was estimated from plumage characteristics. We recognized five age classes (zero, one, two, three, and four or more years old). Cohorts of released birds were constituted of birds released at the same time, but probably not born in the same year.

RESULTS

Group splitting.—The first successful reproduction in the wild occurred in 1982 (Fig. 1). By 1990, 60 Griffon Vultures had been born in the wild (59 of whom were marked); these were in addition to the 59 marked birds that had been released. Therefore, 118 individual histories were analyzed.

TEST1 showed significant differences between capture-resighting histories of wild-born and released birds (TEST1 = 67.38, df = 14, $P = 0.0001$). Similarly, there was significant heterogeneity in the histories of birds released as adults and birds released as young (TEST1 = 27.01, df = 9, $P = 0.0014$). Thus, capture-resighting histories of individuals depended on their origin and these three groups were studied separately.

Model selection for wild-born individuals.—This group contained 59 individuals whose capture-resighting histories stretched over nine cohorts (1982-1990; Fig. 1). TEST3 did not reveal any heterogeneity among individual capture-resighting histories (TEST3 = 5,946, df = 9, $P = 0.745$).

We tested for constancy and for age and/or time effect in both survival and capture rate. For the age effect on survival rate, different age classes were evaluated, looking for maximal parsimony of parameters. In the same way, we tested an age effect and a time effect on the different age classes on resightings rates. Models with interactions (P$a*t$) and without interaction (P$a + t$) were evaluated. Table 1 describes the models and their AIC values.

The model $[\Phi a_{3.6}, Pt]$ was accepted (AIC = 245.04, number of parameters *np* = 11), although closest models had similar AIC values (Table 1). Therefore, the resighting rate de-

TABLE 2. Number of parameters (*np*) and Akaike's information criterion (AIC) values for different models Φ P tested on capture-resighting histories of birds released as adults (see text and Table 1 for notations). The lower the AIC value, the more appropriate is the model for the data. Selected model for Φ and P parameters is in bold.

Survival model (Φ)		Resighting model (P)		
		r	***t***	*c*
t	*np*	22	21	12
	AIC	174.06	153.96	165.58
c	*np*	12	12	2
	AIC	181.36	163.55	173.02
r	*np*	21	22	12
	AIC	167.43	151.17	160.97
$\mathbf{r_{1.10}}$	*np*	13	**13**	3
	AIC	156.16	**137.56**	147.83
$r_{1.1.9}$	*np*	14	14	4
	AIC	156.80	138.43	148.46
$r_{2.9}$	*np*	13	13	3
	AIC	161.31	143.56	152.93

pended on time and the survival rate Φ only depended on age (i.e. Φ was constant from zero to three years old and constant over the following ages). Parameter values will be discussed after the last analysis with the three groups together.

Model selection for birds released as adults.—We released 39 adult Griffon Vultures from 1980 to 1985 (Fig. 1). TEST3 revealed heterogeneity in capture-resighting histories (TEST3 = 9.33, df = 3, $P = 0.009$). Nevertheless, because this test compares, for each resighting occasion, the capture-resighting histories of birds never seen before and those of birds seen before this occasion (according to a Jolly-Seber time effect; Burnham et al. 1987), a strong age effect could cause this apparent heterogeneity. Unfortunately, the small number of individuals prevented us from making a batch-by-batch analysis (Burnham et al. 1987).

As these birds were released when at least four years old, their survival should have been constant according to the model for wild-born individuals. Cohorts contained birds of different ages so it was not possible to test any age effect. However, the release effect was estimated using models that described an "age-since-release" effect (Φ*r*). Different types of delayed effect were tested (Table 2).

The selected model was [$\Phi r_{1.10}$, P*t*] (AIC = 137.56, *np* = 13). Thus, there was a time effect on resighting rate. Moreover, survival rate was different during the first year after release.

TABLE 3. Number of parameters and Akaike's information criterion values for different models Φ P tested on capture-resighting histories of birds released as immatures (see text and Table 1 for notations). The lower the AIC value, the more appropriate is the model for the data. Selected model for Φ and P parameters is in bold.

Survival model (Φ)		Resighting model (P)		
		c	*t*	$\mathbf{a_{2.6} + t}$
c	*np*	2	9	10
	AIC	998.92	858.66	768.19
t	*np*	9	15	16
	AIC	854.71	737.21	653.04
$r_{1.1.6}$	*np*	4	11	12
	AIC	906.97	777.58	690.13
$r_{2.6}$	*np*	3	10	11
	AIC	905.98	779.58	698.65
$r_{1.7}$	*np*	3	10	11
	AIC	973.46	844.19	762.46
$\mathbf{\Phi^a}$	*np*	10	17	**18**
	AIC	828.94	712.83	**642.14**
Φ^b	*np*	7	14	15
	AIC	852.68	731.87	648.16
Φ^c	*np*	6	13	14
	AIC	928.81	802.99	725.57

[a] Age since release and time effect on first two years followed by constant survival.

[b] Time effect on first two years followed by a constant survival.

[c] Time effect on first year followed by a constant survival.

Model selection for birds released as immatures.—From 1983 to 1986, 20 Griffon Vultures were released when less than four years old (Fig. 1). According to the survival estimates for the two previous groups, the survival rate of these birds released as young should have been subject to a release and age effect. However, because of the low number of birds of each age class released, we could not define a group for each age class and we used only one group. Heterogeneity should have been important in this data set, although it was not detected by TEST3 (TEST3 = 9.365 df = 5, $P = 0.095$). The models with release effect (Φ*r*) should be considered as rough approximations because they described histories of birds released at different ages (e.g. when fledgling or when two years old). According to the models tested for wild-born vultures, the hypothesis of difference in resighting rates during immaturity and maturity ($Pa_{2.6} + t$) was tested (see Table 3 for tested models and AIC values).

The model [Φ^a, $Pa_{2.6} + t$] (Table 3) was selected (AIC = 642.14, *np* = 18). In resighting rate, a

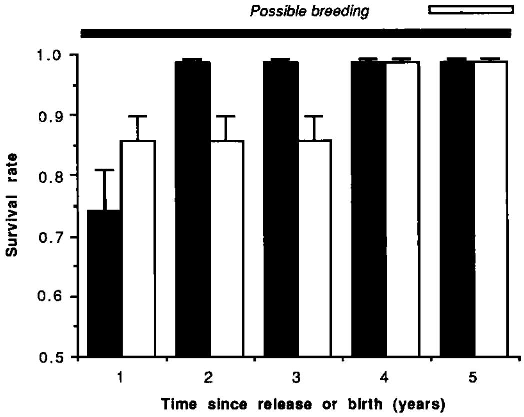

Fig. 2. Increase of survival rates (wisker indicates SE) with time in released adults (full bars) and wild-born birds (open bars). Released adults can breed immediately, whereas fledglings cannot breed before four years of age.

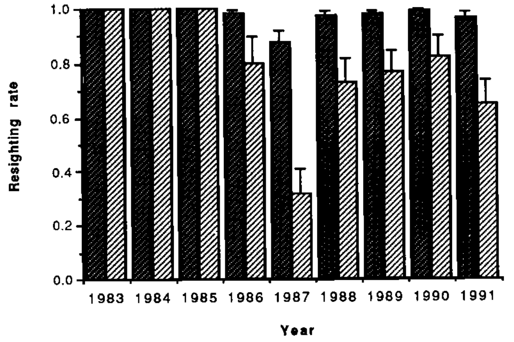

Fig. 3. Annual resighting rates (wisker indicates SE) of Griffon Vultures according to their origin: released adults and released immatures after the first two years following releases (dark bars); wild-born birds and released immatures during the first two years following releases (light bars).

time effect with a parallelism over two "age" classes (the first two years following release and the rest of life) was detected. Survival rate depended on the interaction of time and "age since release" during the first two years following release and was constant over age and time thereafter. This result was due to the impossibility of selecting a more-parsimonious model, probably because of the influence of age at release.

Model selection for the three data sets.—To develop the most-parsimonious model, the three previous groups were studied together. Four models were compared. Model A was the sum of the three previously accepted models without parameter equality between groups (AIC = 479.23, *np* = 42). Model B was the same model with equality of adult resighting rates of released birds (released adults and released immatures after the first two years following releases; AIC = 470.18, *np* = 26). Model C equalized wild-born birds resighting rates and those estimated during the first two years after releases of immatures, with a parallelism over time with adult resighting rates of released birds (AIC = 455.80, *np* = 25). Finally, model D that equalized adult survival rates over the three groups was accepted (AIC = 452.88, *np* = 23) and gave the final estimates of resighting and survival parameters.

Survival and resighting rates.—The values obtained were exceptionally high, particularly for adult survival (0.987 with 95% asymmetric confidence interval [*CI*] = 0.965–0.995; Fig. 2). Annual survival was lower during the first three years of life for wild-born individuals (0.858, *CI* = 0.761–0.919). The effect of release on adult survival rates was strong during the first year after release (adult survival rate after release is 0.743, *CI* = 0.594–0.851). In the same way, annual survival rates of released immatures varied during the first two years following releases and had a mean value of 0.755.

Resighting rates changed over time, but were the same for adults of released birds and generally were significantly lower for wild-born birds and released immatures during the two first years following releases (Fig. 3). Before 1986, high observation pressure on a small number of individual explains that resighting rates reach 1.0.

Causes of mortality and removal from population.—From 1981 to 1991, 27 marked Griffon Vultures were recovered dead (*n* = 18) or deliberately removed (*n* = 9; Table 4). Electrocution was the most important known cause of mortality. From December 1981 to May 1992, 10 banded and 1 unbanded juvenile and immature Griffon Vultures (unknown origin) were killed in the Grands Causses. Most of these birds were found electrocuted at the bottom of transformer pylons. In the Grands Causses, no case of shooting or poisoning has been proved since the beginning of the reintroduction program. However, 1 of 17 fledglings born in 1991 was found poisoned in Senegal (Kaffrine department, 14°N, 16°W) in February 1992. This re-

TABLE 4. Summary of deaths and reasons why birds were deliberately removed from wild from 1981 to 1991. Sample size (n) indicates initial number of birds.

	No. immatures		No. adults		
	Released ($n = 20$)	Wild-born ($n = 59$)	Released ($n = 39$)	Wild-born ($n = 25$)	Total
		Death			
Electrocution	3	7	2	0	12
Exhaustion	0	1	1	0	2
Unknown	1	2	1	0	4
		Removal			
Exhaustion	0	0	4	0	4
Starvation	0	4	0	0	4
Injury	0	0	1	0	1
Total	4	14	9	0	27

covery gives evidence of long-distance migration and the risks run by Griffon Vultures outside our study locality.

Human intervention to help birds in difficulties often occurred just after releases and after fledging each year. The large number of birdwatchers in the area during the summer increases the chance that fledging birds that get into difficulties along roads or rivers can be recaptured, fed, and released. However, this effort only led to saving 2 released adults of 11 recaptured birds, and no wild-born fledgling, so it did not have any artificial effect on the survival estimates.

DISCUSSION

Methodological aspects.—The present method of sampling data violated two of the five main assumptions of the capture-recapture models in open populations (Lebreton 1985 unpubl. report, Clobert et al. 1987, Pollock 1991, Lebreton et al. 1992, Nichols 1992): (1) existence of band losses; (2) relatively long duration of the sampling period (nine months) in comparison to the intersampling period (three months). However, different elements allowed us to give robustness to our results.

Some plastic identification bands were lost, but none of the metal bands were. Five of the birds that lost plastic identification were identified when recaptured. This could have induced some heterogeneity, although moderate heterogeneity in capture rates has little effect on survival estimates (Nichols et al. 1982, Clobert et al. 1993). Moreover, as resighting rates were higher than 0.5, except in 1987 (Fig. 3), the bias on survival estimates arising from unequal resighting probabilities of individuals could be neglected (Carothers 1973). However, ignoring definitive tag loss (i.e. loss of both plastic and metal bands, or loss of plastic bands only, if individuals are not recaptured during the study period) can entail a severe underestimate of survival rates (Kremers 1988). Nevertheless, because of their high values, survival estimates were obviously not affected in a substantial way by band loss in our study.

Also, we cannot consider that the duration of sampling periods was instantaneous, because it was three times longer than the interperiod, and mortality and emigration could have occurred during this time. For example, most of the removals or observed death of released adults occurred less than two months after release. Thus, the temporal location of mortality had no biological significance according to the intersampling period. Since most of annual first resightings of individuals (89.46% ± SE of 1.26) were made during the first half of the sampling period, we assumed that the short duration of the intersampling period did not change the statistical background of this study, but only caused us to moderate the interpretation of our results.

Finally, the time effect on resighting rates was due essentially to variations in observation activity. It has declined after 1984 because the main observer began to spend time collecting carcasses. The lower values of resighting rates in wild-born birds and released immatures during the first two years following releases could have different methodological or biological causes (see below). Resighting pressure could have been higher on adult breeders because of the intensive monitoring of nests. Nonbreeders were occasionally resighted at roost or feeding places in the proximity of nesting cliffs, but were not subject to the intensive observations of the breeding birds.

Biological aspects.—Overall, the survival rates observed in this study are high. Our estimate of adult survival rate from one year after release onwards, or after three years for wild-born birds (0.987, *CI* = 0.965–0.995), is higher than those obtained by Piper et al. (1981) for Cape Vultures using banding recoveries. High adult survival is confirmed by the absence of any recoveries of dead adults among wild-born birds (Table 4).

Different biological factors can explain this very high adult survival rate in the Griffon Vultures. First, high survival rate can be related to the other life-history characteristics of this species, which produces a maximum of one offspring per year after the four to five years needed to reach maturity (Simmons 1986). Our estimates are similar to those obtained by capture-recapture methods in other large soaring birds that forage extensively for spatiotemporally unpredictable resources: Wandering Albatrosses (*Diomedea exulans;* mean adult survival 0.968); and Light-mantled Albatrosses (*Phoebetria palpebrata;* 0.973; Weimerskirch et al. 1987). Second, adult breeding birds are not known to have dispersed once they start reproduction and breeding dispersal has not been described in other *Gyps* species. Therefore, emigration could not affect adult survival estimates. Third, Griffon Vultures have no predators or competitors in this study region, and their low density minimizes intraspecific competition. Furthermore, the number of sheep carcasses constituting the main food resource was substantial and could support a population of about 300 Griffon Vultures in summer and 1,200 in winter (Briquet 1987). Finally, the life span of the Griffon Vulture (37 years in captivity; Newton 1979) exceeds the total duration of this study. Thus, no senescence is to be expected. However, it is likely that such survival rates are not peculiar to our population. Long-lived species are extremely sensitive to small variations in survival rates (Lebreton and Clobert 1991). Thus, the rapid increase in Spanish Griffon Vulture populations (Donazar 1987, Donazar and Fernandez 1990) may be due to a slight increase in survival rates reaching values similar to those reported here.

The effect of release on adult survival in the first year could be due to some consequences of captivity: the energetic cost of learning to fly; the necessity to learn how to feed; and behavioral problems for the most imprinted birds (Table 4). However, the birds that successfully withstood this period had no more problems, as shown by the steep increase in their survival rate.

The annual survival rate of wild-born birds is significantly lower during the first three years of life (0.858 ± 0.039 vs. 0.987 ± 0.006), which includes the period up until one year before the earliest first breeding (Fig. 2). This age effect observed on survival rates of wild-born birds can have various explanations concerning postfledging dependence period and natal dispersal.

In fact, the period of learning to fly following fledging seems to be a critical period for a Griffon Vulture. Despite the observations of two fledglings feeding on sheep carcasses a few days after fledging, juveniles still depend on adult feeding for several weeks after fledging, as in Cape Vultures (Robertson 1985). Perhaps competition with adults at feeding sites prevents them obtaining sufficient food. In the Causses, juvenile Griffon Vultures were fed at the nest by their parents up to 90 days after fledging. Newly fledged Griffon Vultures often use flapping flight, which is of high energetic cost for these soaring birds (Pennycuick 1972). Furthermore, some juveniles face considerable difficulties returning to the nest after their first flight. Intraspecific competition at feeding sites and inefficient flight probably leads some newly fledged Griffon Vultures to exhaustion (Table 4). As only a small number of fledglings was released ($n = 4$), we could not estimate the impact of release on their survival.

Some unbanded immature Griffon Vultures immigrated to our colony (two unbanded birds were captured in 1988 and, during the study period, five to nine unbanded birds were seen; one of them bred in 1990 and 1991). Thus, although no bird born in the Causses was recorded in the nearest Griffon Vulture colonies in Spain or in the Pyrenees, they may belong to the same metapopulation. Natal dispersal favoring gene flow between populations (for review, see Johnson and Gaines 1990) could occur in this population. The erratic behavior of immatures that came back some years later to the colony may be responsible for the lower resighting rates of wild-born birds (Fig. 3). Erratic behavior of young birds has been shown to take them to North and West Africa in autumn (Elosegui 1989, Berthold et al. 1991). The juvenile recovered in Senegal shows that birds born in the Causses have restored this migration pattern. However, we could not detect any effect of age on resighting rates of wild-born birds despite the fact that the model [$\Phi a_{3.6}$, $Pa_{3.6} + t$] was very close to the selected one [$\Phi a_{3.6}$, P_t] (Table 1). This could be due to variations in the age at first breeding together with few temporary band losses in wild-born adults.

Nevertheless, the juvenile survival rate estimated in the Causses is much higher than that estimated by Piper et al. (1981), or by Robertson (1984) for the Cape Vulture. Even though the methods used by these authors had many biases that could explain such a discrepancy, the immature survival rate observed in the Causses is probably higher than in other populations. Both an increase of the population density and a decrease of human effort to make resources predictable in the future are likely to affect immature survival rates. This encourages us to study natural populations in order to discriminate between intrinsic characteristics of survival rates and those due to the management of reintroduced Griffon Vulture populations.

Conservation aspects.—The reintroduction program strictly followed the recommendations of the International Union for Conservation of Nature concerning preparatory measures, introduction schedule, and monitoring. From a conservation point of view, the education program was successful: no human persecution (shooting, poisoning) was recorded (Table 4). Only one case of disturbance at the nest by climbers was reported. Until now, the efficient collaboration of local farmers has provided an abundant food resource at feeding stations (Bonnet et al. 1990, Terrasse 1990). Moreover, farmers now tend to leave carcasses in the field more often so that Griffon Vultures can forage by themselves. As for Cape Vultures in South Africa (Markus 1972) and other large raptors such as Spanish Imperial Eagles (*Aquila adalberti;* Ferrer and Hiraldo 1991), electrocution is the main cause of death (Table 4). It increases juvenile mortality of Griffon Vultures in Causses as in Israel (Leshem 1985). A collaboration with Elecricité De France from 1988 permitted us to modify about 300 pylons near the release center to reduce the possibility of electrocution.

The present reintroduction schedule differed from previous reintroduction programs by releasing adult pairs in order to establish a breeding group. In former reintroduction projects involving raptors such as the Bearded Vulture (*Gypaetus barbatus;* Coton and Esteve 1990), the White-tailed Sea Eagle (*Haliaeetus albicilla;* Love 1983), and the Peregrine Falcon (*Peregrinus anatum;* Holroyd and Banash 1990), only immature birds were released. Taking into account the biological cost of our method (during the first year after release the apparent mortality of adults was higher [0.257] than later on [0.013], the survival rate from release to first breeding is higher with adults (0.743) than with juveniles ($0.858^3 \times 0.987 = 0.623$; Fig. 2), even ignoring a possible release effect on juveniles. In addition, immatures are much more likely to emigrate, especially when there is no established natural population, which is always the case for reintroduction projects. Thus, we propose that reintroduction protocols for Griffon Vultures and similar species should involve adults that have bred in captivity within the target area rather than fledglings or even immatures. Two new reintroduction projects of Griffon Vulture in Friuli (northeastern Italy) and the southern French Alps will use our method. Because natal dispersal rapidly developed from Spain to the Causses colonies, these projects are expected to reinforce the exchange possibilities between subpopulations in order to restore a southern European Griffon Vulture metapopulation.

ACKNOWLEDGMENTS

We are very grateful to M. Terrasse of the Fonds d'Intervention pour les Rapaces and J. Bonnet of the Parc National des Cevennes, who designed the field reintroduction and monitoring. Data were used in the framework of the agreement between the Parc National des Cevennes, the Fonds d'Intervention pour les Rapaces, and the Laboratoire d'Ecologie of the Ecole Normale Supérieure. The Centre de Recherche sur la Biologie des Populations d'Oiseaux supported banding. We also thank M. S. Gaines, D. C. Houston, and J. D. Nichols for their reviews and J. M. Thiollay and I. Swingland for improving an earlier draft of the manuscript. T. Boulinier and G. Sorci provided fruitful discussions. This study was supported by a SRETIE grant (n°90088) of the French Ministry of the Environment.

LITERATURE CITED

ANDERSON, D. R., K. P. BURNHAM, AND G. C. WHITE. 1985. Problems in estimating age-specific survival rates from recovery data of birds ringed as young. J. Anim. Ecol. 54:89–98.

BERTHET, G. 1946. Les derniers Vautours fauves du Massif Central. Rev. Soc. For. Franche-Comté, 1–6.

BERTHOLD, P., J. GREISINGER, E. NOWAK, AND U. QUERNER. 1991. Satellite tracking of a migrating Griffon Vulture in Spain. J. Ornithol. 132:327–329.

BONNET, J., M. TERRASSE, C. BAGNOLINI, AND J. L. PINNA. 1990. Installation et extension d'une colonie de Vautours fauves (*Gyps fulvus fulvus*) réintroduite dans les Grands Causses du Massif Central. L'Oiseau et la R.F.O. 60:181–206.

BRIQUET, R. 1987. Les ressources alimentaires des Vautours fauves dans la région des Grands Causses. Paris, Rapport stage enseignement optionnel de 4ème année-E.N.V. Maisons-Alfort.

BURNHAM, K. P., D. R. ANDERSON, G. C. WHITE, C. BROWNIE, AND K. H. POLLOCK. 1987. Design and analysis methods for fish survival experiments based on release-capture. Am. Fish. Soc. Monogr. 5.

CAROTHERS, A. D. 1973. The effects of unequal catchability on Jolly-Seber estimates. Biometrics 29: 79–100.

CLOBERT, J., R. JULIARD, AND R. H. MCCLEERY. 1993. The components of local recruitment. Pages 281–293 *in* Marked individuals in the study of bird population (J. D. Lebreton and P. M. North, Eds.). Birkhauser Verlag, Basel.

CLOBERT, J., J. D. LEBRETON, AND D. ALLAINE. 1987. A general approach to survival estimation by recaptures or resightings of marked birds. Ardea 75:133–142.

CLOBERT, J., J. D. LEBRETON, M. CLOBERT-GILLET, AND H. COQUILLARD. 1985. The estimation of survival in bird populations by recaptures or sightings of marked individuals. Pages 197–213 *in* Statistics in ornithology (B. J. T. Morgan and P. M. North, Eds.). Springer, Berlin.

COTON, C., AND R. ESTEVE. 1990. La réintroduction du Gypaète barbu dans les Alpes. *In* Reintroductions et renforcements de populations animales en France. Compte rendu du colloque de Saint Jean du Gard Supl. 5, Revue d'Ecologie, La Terre et la Vie:227–241.

DONAZAR, J. A. 1987. Apparent increase in a Griffon Vulture (*Gyps fulvus*) population in Spain. J. Raptor Res. 21:75–77.

DONAZAR, J. A., AND C. FERNANDEZ. 1990. Population trends of the Griffon Vultures *Gyps fulvus* in northern Spain between 1969 and 1989 in relation to conservation measures. Biol. Conserv. 53: 83–91.

ELOSEGUI, I. 1989. Vautour fauve (*Gyps fulvus*), Gypaete barbu (*Gypaetus barbatus*), Percnoptère d'Egypte (*Neophron percnopterus*): Synthèse bibliographique et recherches. Acta Biologica Montana 3. Série Document de Travail.

FERRER, M., AND F. HIRALDO. 1991. Evaluation of management techniques for the Spanish Imperial Eagle. Wildl. Soc. Bull. 19:436–442.

FRY, D. M. 1983. Techniques for sexing monomorphic vultures. Pages 185–196 *in* Vulture biology and management (S. R. Wilbur and J. A. Jackson, Eds.). Univ. California Press, Berkeley.

HOLROYD, G., AND U. BANASH. 1990. The reintroduction of the Peregrine Falcon, *Falco peregrinus anatum*, into southern Canada. Can. Field Nat. 104:203–208.

HOUSTON, D. C. 1974. Mortality of the Cape Vulture. Ostrich 45:57–62.

HOUSTON, D. C. 1982. The status of European vultures and their ranges in the Soviet Union. Vulture News 8:4–6.

HOUSTON, D. C. 1987. Management techniques for vultures feeding and releases. Pages 15–29 *in* Breeding and management in birds of prey (D. J. Hill, Ed.). Univ. Bristol, Bristol.

JOHNSON, M. L., AND M. S. GAINES. 1990. Evolution of dispersal: Theoretical models and empirical tests using birds and mammals. Annu. Rev. Ecol. Syst. 21:449–480.

KREMERS, W. K. 1988. Estimation of survival rates from a mark-recapture study with tag loss. Biometrics 44:117–130.

LAKHANI, K. H., AND I. NEWTON. 1983. Estimating age-specific bird survival rates from ring recoveries—Can it be done? J. Anim. Ecol. 52:83–91.

LEBRETON, J. D., AND J. CLOBERT. 1991. Bird population dynamics, management and conservation: The role of mathematical modelling. Pages 105–125 *in* Bird population studies. Relevance to conservation and management (C. M. Perrins, J. D. Lebreton, and G. J. M. Hirons, Eds.). Oxford Univ. Press, Oxford.

LEBRETON, J. D., K. P. BURNHAM, J. CLOBERT, AND D. R. ANDERSON. 1992. Modeling survival and testing biological hypothesis using marked animals: A unified approach with case studies. Ecol. Monogr. 62:67–118.

LESHEM, Y. 1985. Griffon Vultures in Israel: Electrocution and other reasons for a declining population. Vulture News 13:14–20.

LOVE, J. 1983. The return of the Sea-eagle. Univ. Press, Cambridge.

MARKUS, M. 1972. Mortality of vultures caused by electrocution. Nature 238:228.

NEWTON, I. 1979. Population ecology of raptors. T. & A. D. Poyser, Berkhamsted.

NICHOLS, J. D. 1992. Capture-recapture models using marked animals to study population dynamics. BioScience 42:94–102.

NICHOLS, J. D., S. L. STOKES, J. E. HINES, AND M. J. CONROY. 1982. Additional comments on the assumption of homogeneous survival rates in modern bird banding estimation models. J. Wildl. Manage. 46:953–962.

PENNYCUICK, C. J. 1972. Soaring behaviour and performance of some East African birds, observed from a motor-glider. Ibis 114:178-218.

PIPER, S. E. 1990. Dispersal, nomadism and conservation in the Cape Vulture. Ring 13:217-218.

PIPER, S. E., P. J. MUNDY, AND J. A. LEDGER. 1981. Estimates of survival in the Cape Vulture *Gyps coprotheres.* J. Anim. Ecol. 50:815-825.

POLLOCK, K. H. 1991. Modeling capture, recapture, and removal statistics for estimation of demographic parameters for fish and wildlife populations: Past, present, and future. J. Am. Stat. Assoc. 86:225-237.

POLLOCK, K. H., J. D. NICHOLS, C. BROWNIE, AND J. E. HINES. 1990. Statistical inference for capture-recapture experiments. Wildlife Monogr. 107.

PRADEL, R., J. CLOBERT, AND J. D. LEBRETON. 1990. Recent developments for the analysis of capture-recapture multiple data set. An example concerning two Blue Tit populations. Ring 13:193-204.

PRADEL, R., AND J. D. LEBRETON. 1991. User's manual for program SURGE version 4.1 Mimeographed document. C.E.F.E./C.N.R.S. BP 5051, 34033 Montpellier, CEDEX, France.

ROBERTSON, A. S. 1984. Aspects of the population dynamics of Cape Vultures in the Cape province. Ostrich 55:196-206.

ROBERTSON, A. S. 1985. Observations on the post fledging dependence period of Cape Vultures. Ostrich 56:58-66.

SIMMONS, R. 1986. Delayed breeding and the non-adaptive significance of delayed maturity in vultures: A fruit fly perspective. Vulture News 15: 13-18.

TERRASSE, M. 1990. Réintroduction du Vautour fauve dans les grands Causses et renforcement de la population de Vautour percnoptère. Pages 213-226 *in* Reintroductions et renforcements de populations animales en France. Compte rendu du colloque de Saint Jean du Gard Supl. 5, Revue d'Ecologie, La Terre et la Vie.

WEIMERSKIRCH, H., J. CLOBERT, AND P. JOUVENTIN. 1987. Survival in five southern albatrosses and its relationship with their life history. J. Anim. Ecol. 56:1043-1055.