Breeding biology during establishment of a reintroduced Griffon Vulture *Gyps fulvus* population

FRANÇOIS SARRAZIN[1,*], CONSTANT BAGNOLINI[2],
JEAN LOUIS PINNA[3] & ETIENNE DANCHIN[1]
[1] *Université Pierre et Marie Curie, Laboratoire d'Ecologie, CNRS-URA258., Bât. A, 7e étage,
7 quai Saint Bernard, Case 237, F-75252 Paris cedex 05, France*
[2] *Fonds d'Intervention pour les Rapaces, Mairie, 12720 Peyreleau, France*
[3] *Parc National des Cévennes, Château de Florac, BP15 48400 Florac, France*

We studied the breeding parameters of a reintroduced population of individually marked Griffon Vultures *Gyps fulvus* in the Grand Causses region of southern France from the time of first reintroduction in 1982 to 1992. Among nesters, 65% of the birds released as immatures or born in the wild recruited into the breeding population when 4 years old, i.e. 1 year earlier than previously described. The proportion of birds nesting each year was relatively high and increased with time, suggesting that conspecific attraction favoured recruitment. We detected a permanent adverse effect of long-term captivity on the nesting success of birds released when more than 2 years old: compared to the natural population, birds which had been kept in captivity showed a reduced breeding success during the whole study period. The breeding success of released immatures and wild-born birds was similar to the highest values observed in a natural population in the Spanish and French Pyrenees. Breeding failures did not usually result in mate change but affected nest-site fidelity. Birds not born in the wild were more likely to recruit to the largest subcolonies available, which highlights the role of social attraction. The observed philopatry of wild-born birds probably resulted from such a social attraction since most of them were born in the largest subcolony. Conspecific attraction maintained the spatial aggregation of nests, whereas nest changes after a breeding failure favoured the spatial expansion of the colony.

The present biodiversity crisis has led to an increasing number of reintroduction programs (Griffith *et al.* 1989, Wilson & Stanley Price 1994) which provide opportunities for large-scale monitoring of long-lived species that have previously received little study in the field. Reintroduced birds are, however, likely to show some anomalies due to the period of captivity experienced by the released individuals, and studying such birds permits an assessment of the ability of these species to recover their normal breeding behaviour following translocation.

The establishment of a new population in a vacant habitat (i.e. colonization) has been infrequently documented in the field, in experimental or natural conditions (see Ebenhard 1991) and rarely on birds (Fritz 1979, O'Connor 1986, Kress & Nettleship 1988, Podolsky & Kress 1989). Most studies on this topic were about survival or extinction probabilities of newly established populations (Griffith *et al.* 1989, Ebenhard 1991) in the theoretical context of island invasion as proposed by MacArthur and Wilson (1967). These studies simulated or compared the demography of several species with or without interspecific competition in order to determine the best colonizer (Armstrong 1978, Mehlhop & Lynch 1978, O'Connor 1986, Mangel & Tier 1993). To our knowledge, the intraspecific demographic and behavioural variations of individuals during colonization have rarely been explored in animals (e.g. Wyllie & Newton 1991, Massot *et al.* 1994), although demographic parameters and population dynamics of colonial birds have been well studied on established populations. Here again, reintroduction programs can provide information on the process of colonization provided that the bias induced by release and management methods are taken into account.

In this paper, we consider these factors in the study of the reproductive biology of the reintroduced Griffon Vulture *Gyps fulvus* population in the Grand Causses region of southern France. We discuss the demographic parameters and behaviour in the context of reintroduction and colonization.
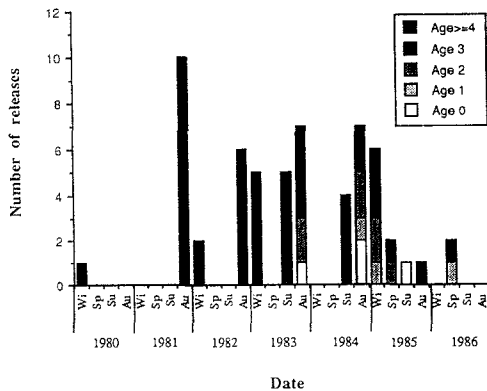
* Corresponding author.

Figure 1. Timing of releases of Griffon Vultures according to age classes. One bird escaped from the aviary in 1980 and came back 3 years later. Win = winter, from 1 January to 31 March; Spr = spring, from 1 April to 30 June; Sum = summer, from 1 July to 30 September; Aut = autumn, from 1 October to 31 December.

METHODS

Reintroduction and monitoring

Because of direct and indirect persecution all over southern Europe (Houston 1982, Elosegui 1989, Donazar & Fernandez 1990), Griffon Vultures became extinct in the Causses region in 1945. In 1968, the restoration of this population was proposed, and from 1980 to 1986, 61 individuals (59 marked) were released in the Causse Méjean. Contrary to practice in other raptor reintroduction programmes (e.g. White-tailed Eagle *Haliaeetus albicilla*, Love 1983, Evans *et al.* 1994; Bearded Vulture *Gypaetus barbatus*, Frey & Bijleveld van Lexmond 1994), at first, only adult birds were released (age ≥ 4 years, n = 39). Starting in 1983, 20 immatures and subadults (0–3 years old) were released (Fig. 1) (Bonnet *et al.* 1990, Terrasse 1990, Terrasse *et al.* 1994). Introduced birds started nesting in the wild in 1982, and up to 1992 the released birds established a colony from which a total of 95 young had been reared. The colony currently contains slightly more than 100 birds. Birds feed mainly on sheep carcasses from local farms which are taken to three feeding sites, although in recent years birds have been locating an increasing number of carcasses elsewhere (Terrasse *et al.* 1994). All birds were ringed with metal and engraved or coloured plastic rings either in captivity, before fledging or during recapture sessions (Sarrazin *et al.* 1994). This allowed individual recognition of all birds in the field and regular monitoring of their movement and activity. Griffon Vultures are cliff-nesting birds whose breeding cycle lasts almost 9 months (from December to September). Thus. observations were made during the whole year, mainly in an area within a 10-km radius of the release centre. Because they are monomorphic (Fry 1983, Elosegui 1989, Mundy *et al.* 1992), individuals are not readily sexed, and sex was not considered in our study. Age classes corresponded 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 1974a).

Analyses

The minimal behavioural criterion to be considered a nesting bird was the transport of nesting material. All birds building a nest for the first time were considered to be recruits to the breeding population (Danchin *et al.* 1991, Newton 1991, Cooke & Francis 1993). Local survival estimates for the population (Sarrazin *et al.* 1994) allowed us to estimate the proportion of birds having already recruited in each age class for released immatures and wild-born birds or per time since release for released adults. These values are minimal since some birds could have been missed as first nesters because of loss of the coloured ring or difficulty in observing some nests. This proportion of recruits r_a for the age class a, is given by

$$r_a = \frac{\sum_{i=1}^{d-a} r_{ia}}{\sum_{i=1}^{d-a} n_i \cdot \prod_{j=1}^{a} s_j}, \tag{1}$$

where d is the duration of the monitoring period limiting the range of possible age; r_{ia}, the number of birds of age a among cohort i which have bred at least once; n_i, the size of cohort i; s_j, the survival rate from age j to age $j+1$ (constant with time; Sarrazin *et al.* 1994).

Age-specific proportions of nesting birds (α_a) can be estimated for each year from the ratio of the observed number of identified nesting birds at a given age (o_a) to the total number of identified birds of the same age (n_a) observed in the population. Because of problems in reading rings at some nests, we corrected the proportion of nesters in our population by taking into account the probability that a marked bird could be observed during the reproductive period (1 January to 30 September) but missed as a nester. Thus, we estimated

$$\alpha_a = e_a/n_a, \tag{2}$$

where e_a is the estimated number of potentially identifiable nesters (see Appendix for the method of estimating e_a).

Productivity parameters were defined using different criteria. Nesting success was the number of fledged young per nesting pair per year. Since clutch size was one, nesting success was the proportion of successful pairs among all nesting pairs. It was split into three components: laying success (proportion of laying pairs among nesting pairs), hatching success (proportion of eggs hatching) and fledging success (proportion of hatchlings that fledge). Breeding success was the proportion of successful pairs among laying pairs. In estimating these parameters for the whole population, pairs detected belatedly were not taken into account because
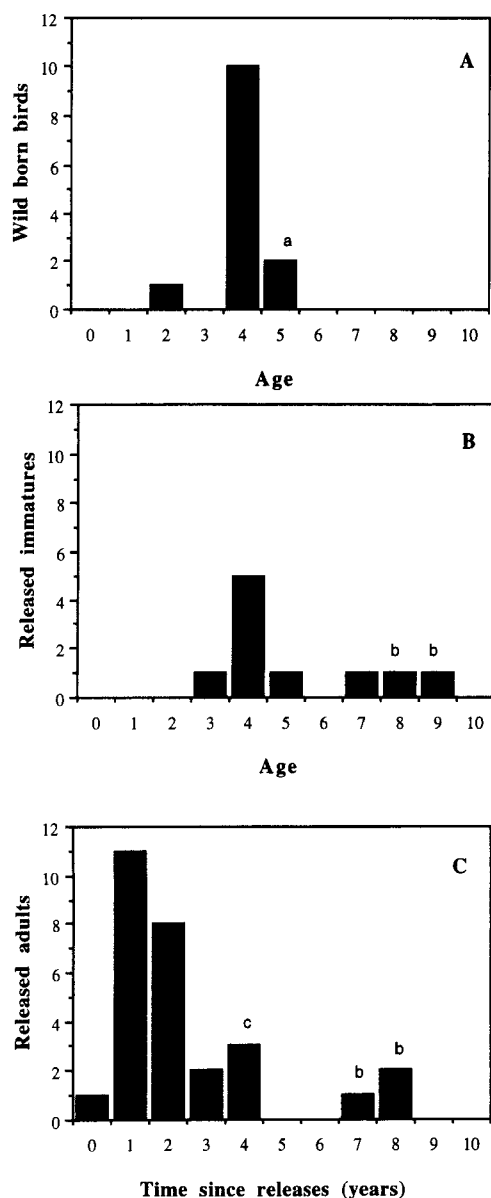
Figure 2. Number of breeding recruits in the Griffon Vulture population according to origin and age or time since release. (a) These two birds were not resighted during the previous year and could have recruited when 4 years old; (b) These four birds were not resighted some years before recruitment but were observed as non-breeders the year before apparent recruitment; (c) One bird escaped in 1980 and came back in 1983. It obviously could not recruit since it was alone. It recruited 1 year after its return to the colony.

Figure 3. Proportion of Griffon Vultures which had nested at least one time (i.e. recruited). (A) Per age class for released immatures and wild-born birds; (B) Since release for released adults. Figures above the bars are the total number of birds which could potentially attain the age (or time) defined in the x axes during the study period.

of possible early nest desertions. The chicks which disappeared after 100 days of age were considered to have fledged. Any deaths after that date affected first-year survival and not breeding success.

Logistic regressions were computed with SAS using the Catmod and Logistic procedures.
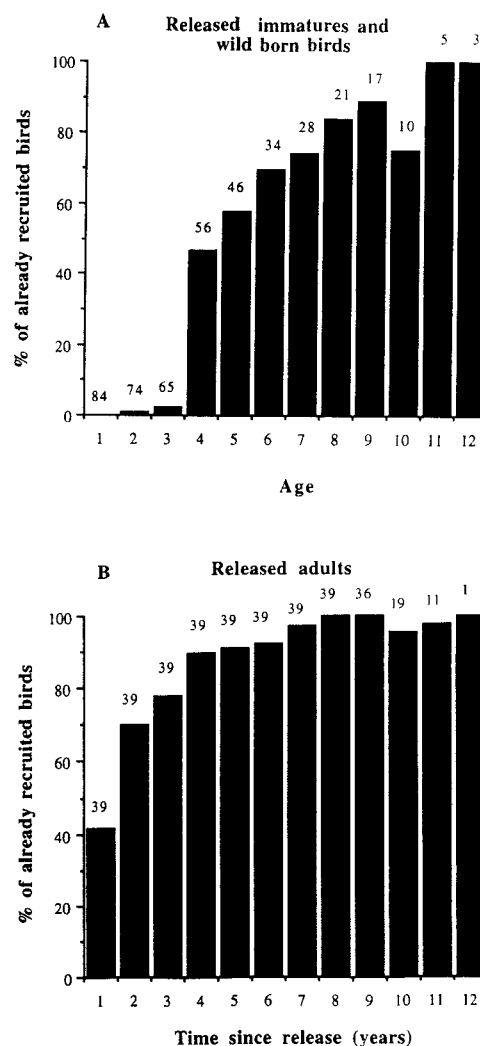
RESULTS

Recruitment

Age at first nesting was not significantly different between wild-born birds and birds released as immatures (Wilcoxon Rank Sum test, $n = 23$ n.s.; Figs 2A and B). They were thus pooled together, and, of the birds which bred for the first time, 65% did so when 4 years old. Two cases of nest building by younger birds were recorded, but no eggs were produced. The proportion of already recruited birds per age class displayed a marked increase at the age of 4 and increases more slowly thereafter (Fig. 3A). The slight decrease noted for

Table 1. *Annual proportions of nesting Griffon Vultures per age classes in the whole colony (p_t: number of pairs; v: probability to nest in an easily observable site; u: probability that a nesting bird is marked; n_4: number of observed 4-year-old birds; $n_{>4}$: number of observed >4-year-old birds; o_4: observed number of 4-year-old nesters; $o_{>4}$: observed number of >4-year-old nesters; o_t: total number of observed nesters; α_4: estimated percentage of 4-year-old nesters; $\alpha_{>4}$: estimated percentage of >4-year-old nesters)*

Year	p_t	v	u	n_4	$n_{>4}$	o_4	$o_{>4}$	o_t	α_4	$\alpha_{>4}$
1982	3	1.00	1.00	0	12	0	6	6	—	50
1983	4	1.00	1.00	0	14	0	7	7	—	50
1984	9	1.00	1.00	3	22	2	15	17	66	68
1985	12	1.00	0.96	0	28	0	23	23	—	82
1986	13	1.00	0.92	1	32	0	24	24	0	75
1987[a]	17	0.96	0.86	3	26	2	25	28	69	99
1988	18	0.96	0.87	1	35	1	29	30	100	85
1989	23	0.89	0.86	4	39	4	31	35	100	88
1990	26	0.78	0.86	5	45	3	32	35	74	88
1991	30	0.84	0.77	4	42	2	34	36	57	93
1992[b]	33	0.84	0.68	2	41	2	34	37	100	96

[a] One 3-year-old bird recruited in 1987.
[b] One 2-year-old bird recruited in 1992.

ages 9 and 10 is due to the first wild-born bird, which never recruited.

Forty-one percent of the recruitment of released adults occurred during the first year after release (Fig. 2C). Moreover, the proportion of birds which had nested at least once, i.e. recruits, since release quickly increased to 100% after 6 years (Fig. 3B).

Some unringed Griffon Vultures immigrated into our colony. Two unringed birds were captured in 1988, and during the study period up to nine unringed birds were observed. One of them bred in 1990 and 1991.

Proportion of nesters

Because recruitment before age 4 was exceptional and because the age of some released adults was assumed to be more than 5 years based on their plumage, we considered the annual proportion of nesters at age 4 and older than 4, whatever the origin of the birds (Table 1).

Over the entire study period, there was a slight but non-significant increase in the proportion of nesters between 4-year-old and older birds ($\chi^2_1 = 3.58$, n.s.), but the time effect was significant (two-way logistic regression; $\chi^2_{10} = 32.70$, $P < 0.001$). The low sample size and the fact that once recruited some birds did not nest each year may explain the non-significance of the age effect on the proportion of nesters. In all adults (age $\geq$ 4), the proportion of nesters increased with time (logit(α) = $-20.48+0.25$*year, $\chi^2_1 = 25.5$, $P < 0.001$). This was due to the delayed recruitment

of some released adults (Figs 2C and 3B) which constituted the majority of the releases from 1982 to 1984 (Fig. 1).

Mate choice and fidelity

Mate choice was constrained by artificial releases and early recruitment. In 22 pairs with two identified nesters, 11 consisted of released adults, six of released immatures and wild-born birds, three of released adults and released immatures and two of one released adult and one wild-born bird.

Griffon Vultures showed a strong mate fidelity. Pooling years and pairs, 95% of the identified pairs in any year remained unchanged in the following year ($n = 107$). The few divorces ($n = 5$) followed one or more successive nesting failures. No identified nester died during the study period; thus, remating after the death of one partner could not be studied.

Productivity

Ninety-five young were fledged from the beginning of the reintroduction in 1982 up to 1992 (Table 2). Clutch size was a single egg, and a replacement egg was laid in 39% of the cases when an egg was lost during incubation ($n = 31$). Only one was recorded after a failure early during the chick stage ($n = 5$). One pair of released adults laid clutches of two eggs in 4 years but failed in all years but one, in which they fledged one chick.

In order to estimate the effect of captivity on nesting success of released birds, we compared nesting success of identified pairs of birds released after the first half of immaturity (i.e. age 3 or more) and nesting success of birds released as young and wild-born birds. In order to avoid confounding effects, year and pair effects were tested on the most important group, pairs of birds released at age 3 or more. There was no significant annual variation in nesting success ($\chi^2_{10} = 7.76$, $n = 87$, n.s.), but the effect of pairs was significant ($\chi^2_{11} = 34.8$, $n = 103$, $P < 0.001$). This was due to one pair which did not lay during 9 consecutive years and to two pairs which did not lay for 8 years. After removing them, the heterogeneity of nesting success among remaining pairs ($\chi^2_8 = 10.9$, $n = 78$, n.s.) or between years ($\chi^2_{10} = 8.14$, $n = 78$, n.s.) was not significant.

Nesting success was significantly lower for birds released when older than 3 (i.e. 0.42 fledged young per laying pair [$n = 103$] against 0.82 [$n = 11$] for released young and wild-born birds [$\chi^2_1 = 5.18$, $P < 0.05$, $n = 114$; Fig. 4A]). Breeding success was not significantly lower for released adults than for pairs which had not experienced long-term captivity ($\chi^2_1 = 2.31$, $n = 87$, n.s.; Fig. 4A). However, released adults laid more replacement clutches to produce one young ($\chi^2_1 = 4.69$, $P < 0.05$, $n = 102$; Fig. 4B). No significant effect of captivity on laying, hatching or fledging success alone was detected, although these parameters were lower in birds having experienced long-term captivity (Fig. 4C). Whatever

Table 2. *Annual nesting success components in Griffon Vulture (L.S.: laying success; H.S.: hatching success; F.S.: fledgling success)*

Year	No. pairs	L.S.	First clutches			Replacement clutches			No. fledglings
			No. eggs	H.S.	F.S.	No. eggs	H.S.	F.S.	
1982	3	0.66	2	0.50	1.00	0	—	—	1
1983	4	0.75	3	0.33	1.00	1	0.00	—	1
1984	9	0.66	6	0.33	0.50	2	0.00	—	1
1985	12	0.75	9	0.55	1.00	0	—	—	5
1986	13	0.77	10	0.60	1.00	3	0.00	—	6
1987[a]	17	0.75	13	0.84	1.00	0	—	—	12
1988[a]	18	0.82	14	0.64	0.88	2	0.50	1.00	10
1989[a]	23	0.85	21	0.42	0.77	0	—	—	9
1990[a]	26	0.84	21	0.80	0.76	4	0.25	1.00	15
1991	30	0.90	23	0.71	0.80	1	1.00	1.00	17
1992[b]	33	0.88	30	0.56–0.71	1.00–0.78	2	0.50	1.00	18

[a] In order to avoid artificial maximization of nesting success, only early recorded nesting events were taken into account in estimating number of eggs, laying, hatching and fledging success.

[b] The timing of 5 failure events was undetermined. Thus minimum and maximum values of hatching and fledging success are given.

the origin of the breeders, most of the failures occurred during incubation (Table 2).

The cause of breeding failure was difficult to determine since the egg usually disappeared between visits. Ravens *Corvus corax*, however, disturbed several pairs and were observed to take one egg. Most of the chick mortality at the nest occurred just after hatching. However, in 3 consecutive years, a chick was found dead under the same nest when about 2 months old.

Choice of a nesting site

During the 10 years following first releases, the colony expanded and the aggregation of nests remained high relative to the numerous unoccupied but suitable areas of the Jonte and Tarn Gorges (Fig. 5). In 1982, the first released pairs settled where nest sites had been painted in order to mimic vultures faeces close to the release point in the Jonte Gorges (Fig. 5, area A). These cliffs had been last used by vultures 60 years earlier (Bonnet *et al.* 1990). New nests were built close to other nesters (Fig. 5, area A) until a pair established a site in the Tarn Gorges in 1984 (Fig. 5, area C). In 1985, a pair which had failed in 1984 used the same nest site in the Tarn and fledged one young; in 1986, other nesters joined them. Meanwhile, the pair that had first bred in the Tarn in 1984 established a new nesting ground 3 km up the river Tarn on cliffs known to have been used before extinction (Solanet 1894 in Bonnet *et al.* 1990; Fig. 5, area D). Once a cliff had been successfully colonized, it was not deserted.

Philopatry was strong: 85% ($n = 13$) of wild-born recruits settled at their natal gorges. However, conspecific attraction could be an alternative explanation; since the population is recent, the largest colony at recruitment was also likely to have been the largest one when the chicks were hatched. This could lead one to interpret as philopatry what is, in fact, conspecific attraction.

We tested the effect of conspecific attraction on recruitment at the subcolonial scale. Among the 35 birds able to prospect during the year before recruitment (i.e. wild-born birds, released immatures or adults released before the end of summer in any year, only one settled in a following year on a previously unoccupied cliff (Fig. 5, area B). The 34 other birds chose to nest in the largest subcolonies (χ^2_3 = 8.59, $P < 0.05$) or in the areas with the largest number of fledglings (χ^2_3 = 8.70, $P < 0.05$) in the previous year.

In order to avoid the confounding effect of philopatry, we checked the subcolony choice in birds that were not born in the wild ($n = 21$). They were strongly attracted to the largest subcolony (in terms of its number of nests or fledglings) in each year ($\chi^2_1 = 5.15$, $P < 0.05$). Finally, among eight adults released after September and known to recruit thereafter, six delayed their recruitment for 1 year or more and recruited in the previous year's largest colony. The two others bred the year after release, also in the largest subcolony.

The possible confounding effect of a particularly attractive cliff (area A, Fig. 5, had the largest number of nests over the whole study period) was examined by removing the 23 recruits in that area. The tendency for conspecific attraction remained true.
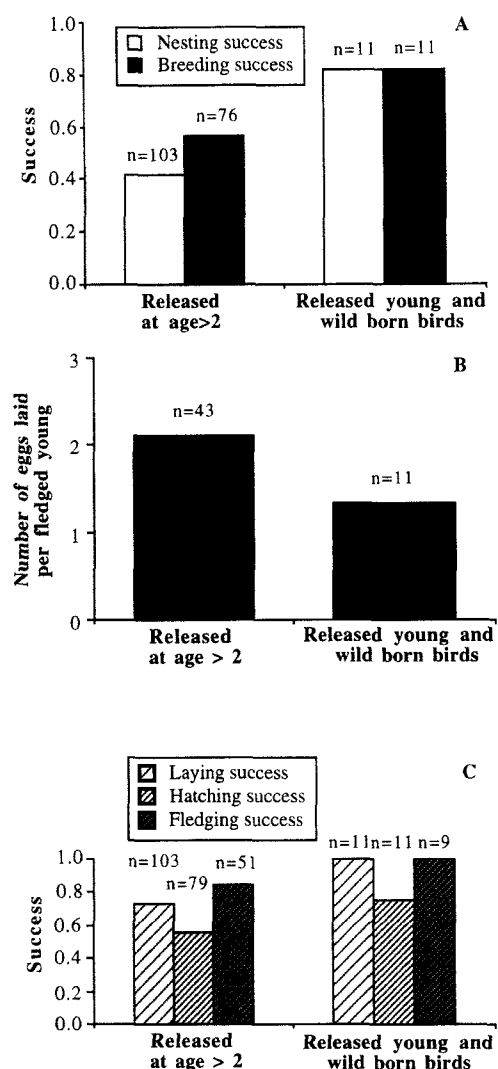
Figure 4. Productivity parameters for the Griffon Vulture during the overall study period according to the origin of nesters. (A) Nesting success (i.e. proportion of successful pairs among nesting pair) and breeding success (i.e. proportion of successful pairs among laying pairs); (B) Number of eggs laid per fledged young; (C) Laying, hatching and fledging success.

Nest fidelity

Individual marked birds allowed us to link nesting success in any year to nest-site fidelity in the following year. In order to avoid any confounding effect of divorce on nest-site fidelity and nesting success, only pairs that did not divorce were used.

There were no significant differences in site fidelity after a failure occurring during the first or second clutches (Fisher's exact test, n.s., $n = 51$), so the data were pooled. No year effect was detected ($\chi^2_9 = 3.90$, $n = 92$, n.s.), and years were also pooled together. Taking into account the effect of
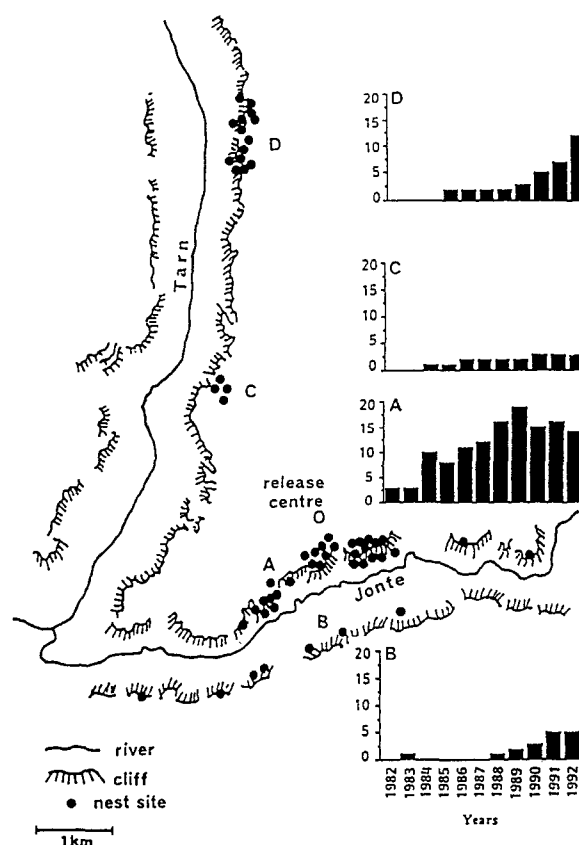

Figure 5. Annual number of Griffon Vulture nest sites in subcolonies in the Tarn and Jonte Gorges.

captivity on nesting success, birds were shown to be more faithful to their nests after a success (76% fidelity) than after a failure (45% fidelity; effect of birds' origins: $\chi^2_1 = 2.45$, n.s.; effect of nesting success in year t given birds' origins: $\chi^2_1 = 6.40$, $P < 0.02$, $n = 92$). Moreover, among pairs which laid no replacement egg in year t, the larger the reproductive effort (i.e. no egg laid, breeding failure or breeding success), the stronger the nest-site fidelity in year $t+1$ (effect of birds' origins: $\chi^2_1 = 0.36$, n.s.; effect of reproductive effort given birds' origins: $\chi^2_1 = 7.73$, $P < 0.05$, $n = 74$, Fig. 6). This was reinforced by behavioural observations: unsuccessful pairs were often seen prospecting active nest sites after their breeding failure, whilst this was not observed among successful breeders. Nest-site fidelity between first and replacement clutches in the same year ($n = 14$) was not significantly different from nest-site fidelity between year t and year $t+1$ ($n = 51$, $\chi^2_1 = 0.07$, n.s.).

To what extent is this movement of nest site an adaptive behaviour? We compared the breeding success of birds that changed or did not change sites after experiencing a breeding failure. Such movement behaviour can be maintained only if changing nest sites after a failure gives an advantage. For this, pairs which never laid were removed because the ca-

pacity to lay an egg could not be restored by changing nest sites. Breeding success was higher (0.76) in pairs that changed sites after a breeding failure than in pairs that did not (0.29; $\chi^2_1 = 7.11$, $P < 0.01$, $n = 31$).

DISCUSSION

Little is known about the demographic characteristics of Old World vultures despite, and sometimes because of, their endangered status (Newton 1979, Elosegui 1989, Mundy et al. 1992). Breeding success is the best-known demographic parameter in Griffon Vultures because it is easily observable and often deceptively considered the most important parameter in its dynamics. Some estimates are available from Spain (Donazar 1987, Arroyo et al. 1990) and the French Pyrenees (Leconte 1985, Elosegui 1989). However, other reproductive parameters, such as the age at first nesting, recruitment rates and the proportions of nesters, have been neglected because they require individual marking. For the same reason, behavioural aspects of nesting and colony formation, such as mate and nest-site fidelity or conspecific attraction inside the colony, have been little studied or only described (Elosegui 1989, Mundy et al. 1992).

Data analyses in the case of reintroduced populations

Reintroduced populations are often characterized, at least during establishment, by low numbers, which may limit the range of testable hypotheses but can lead to maximum efficiency in monitoring.

In bird populations, few attempts at estimating age-specific recruitment rate and proportions of nesters have been made (Clobert & Lebreton 1991, Cooke & Francis 1993). New methods using capture-mark-recapture of nesters have been described (Lebreton et al. 1990, Clobert et al. 1993, Clobert et al. 1994), but the small number of wild-born birds prevented us from using them. However, the small size of this population and the extensive monitoring of the whole population allowed us to use the more basic methods. In the same way, although we were unable to test the real effect of nest-site quality on nesting success, the present results on nest-site fidelity and conspecific attraction constitute, to our knowledge, the first information on individual nest-choice strategies for this type of species.

Costs of captivity in released adults

The effect of captivity was greater on nesting success than on breeding success. However, the breeding success of the birds released when older than two (0.57 $n = 76$) corresponded to the lower values recorded in natural populations in the French Pyrenees (Leconte 1985, Elosegui 1989). Although the causes of breeding failure were generally unknown, predation on eggs by ravens has been observed in
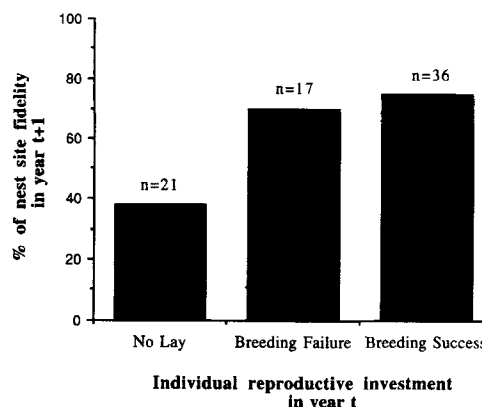

Figure 6. Nest-site fidelity of Griffon Vulture in year $t + 1$ according to investment of nesters in year t whatever the origin of nesters.

Rüppell's Griffon *Gyps rueppellii* (Houston 1976) and seems not to be due to the previous captivity of breeders. This depression seemed permanent since breeding success did not improve with time, at least during the study period. Released adults also paid a cost in survival in the year after their release (0.74 with 95% asymmetric confidence interval [CI] 0.59-0.85) but thereafter showed a high survival rate (0.987, CI = 0.965-0.995, Sarrazin et al. 1994). Thus, natural selection acted mainly in the first months following release. After that period, birds having experienced long-term captivity survived as well as adults born in the wild but did not seem to be able to attain normal breeding success. The breeding success of pairs consisting of released immatures or wild-born birds (0.82, $n = 11$) was similar to the highest breeding success estimated in Spanish (Arroyo et al. 1990) and French colonies (Leconte 1985, Elosegui 1989). This illustrates some of the negative effects of captivity on the behaviour of reintroduced animals emphasized by Shepherdson (1994).

Early recruitment of released immatures and wild-born birds

The age of first nesting was about a year lower than expected from anecdotal information previously recorded in the wild (Terrasse 1977) or in captivity (Mendelssohn & Leshem 1983). Similar early nesting has, however, been recorded in Cape Vulture *Gyps coprotheres* (Robertson 1984). At least 45% of the birds which had not experienced long-term captivity and wild-born birds recruited when 4 years old. No laying occurred in birds younger than 4, confirming that physiological maturity could be at this age.

Local recruitment results from immature survival and dispersal (Clobert et al. 1993). In the study population, the annual survival rate was lower during the first 3 years after fledging (0.86, CI = 0.761-0.919, against 0.987, CI = 0.965-0.995, for adults; Sarrazin et al. 1994). Thus, Griffon Vultures recruited once they reached the local adult survival

rate, corresponding to low dispersal and, of course, mortality.

In birds a period of delayed maturity is linked to high adult survival rate, low fecundity and large body size (Newton 1989, Gaillard et al. 1989). However, the age of first nesting shows some plasticity, and low density is known to reduce the age of first nesting in species such as Herring Gull *Larus argentatus* (Coulson et al. 1982), Kittiwake *Rissa tridactyla* (Porter & Coulson 1987), Puffin *Fratercula arctica* (Kress & Nettleship 1988) and Sparrowhawk *Accipiter nisus* (Wyllie & Newton 1991). This could explain the early age of recruitment in the Causses Griffon Vulture population since its recent foundation implies low density and relaxed intraspecific competition. Moreover, conspecific attraction (Stamps 1988, Smith & Peacock 1990, Ray & Gilpin 1991, Reed & Dobson 1993) encourages settlement in colonial species. After the early phase of colonization of an empty habitat, the presence of pairs rearing chicks can favour recruitment by informing potential breeders about the possibilities of nesting in a given area (Shields et al. 1988, Brown et al. 1990, Danchin et al. 1991), which increases the viability of the newly founded population. At the metapopulation scale, the fact that natural immigration occurred during the study period and the increase of the annual proportion of nesters among released birds can be interpreted as effects of conspecific attraction on recruitment.

Philopatry or conspecific attraction

The establishment of the population was marked by aggregation of nests, and birds not born in the wild tended to recruit in the current largest subcolonies (in terms of the number of nests or chicks). Since most of the wild birds were born in the largest subcolonies, the observed philopatry to the natal cliffs may simply result from conspecific attraction alone. The ultimate function of conspecific attraction may be to use conspecifics as a cue to assess the quality of a local area. The delayed nesting of adults released after the end of a fledging season corroborates the hypothesis of the necessity of a prospecting phase before recruitment.

In other artificial colonization experiments, conspecific attraction was used to attract birds to the target area (Parnell et al. 1988, Kress & Nettleship 1988, Podolsky & Kress 1989). Tape lure or man-made nests increased the probability of a colony being established. Our results show that during reintroduction, first-released birds can be efficient attractors for secondarily released and wild-born individuals. The necessity of releasing individuals immediately able to breed (i.e. adults) thus appears to be strong.

Nest site fidelity

Because dispersal to different nest sites is reduced in long-lived colonial birds (Greenwood 1980, Johnson & Gaines 1990), nest-site fidelity was considered within the colony, within a range of 10 km around the release centre. The

foraging abilities of Griffon Vultures (Houston 1974b, Robertson & Boshoff 1986) allows us to assume that all birds nesting within that range exploited the same food resources. Many species are known to be more likely to change nest sites after a nesting failure (Brooke 1978, Newton & Marquiss 1982, Gavin & Bollinger 1988, Schieck & Hannon 1989, Thompson & Hale 1989, Desrochers & Magrath 1993, Beletsky & Orians 1991). However, differential nest-site fidelity according to sex, partner survival and divorce may cause confusion between nest-site and mate fidelity (Schieck & Hannon 1989, Desrochers & Magrath 1993). In the present study, low competition for nest sites during the early colonization probably decreased the cost of nest changes compared to mate changes, and mate fidelity was stronger than nest-site fidelity (only 4.6% of 107 pair-years divorced, while 41.5% of 89 pair-years changed nest sites). Because unchanged pairs changing nests after a nesting failure had a higher breeding success in the following year, breeding dispersal on a local scale seemed to be a good strategy.

Thus, the spatial organization of our colony resulted from two opposite forces, conspecific attraction, which maintained aggregation of nests, and nesting failures of some released adults, which favoured movements.

Reintroduction as a settlement experiment

In order to be successful, a reintroduction program has to take into account some of the aspects of natural colonization, but it often overrides some others. Indeed, birds must be artificially attracted to the target area (e.g. in this case by imprinting captive birds to the release area and through food management). Since the reintroduced individuals were not natural colonizers, they could not mimic all the aspects of natural propagules (Massot et al. 1994). Part of the lower survival rates in the first year after release observed in adults may result from such features. However, some of the aspects of this program led us to consider this reintroduction as a source of information on colony settlement in a long-lived bird.

First, captivity and translocation did not definitively alter the biology of the newly founded population over the long term. Second, even though breeding dispersal is lower than natal dispersal (Greenwood 1980) and recently formed colonies of seabirds have a high proportion of first-time nesters and immatures (Kharitonov & Siegel-Causey 1988), releasing adults was a good way to simulate the settlement of a colony in this Griffon Vulture population. Indeed, the secondary subcolonies were all founded by old nesters, whereas young recruits joined previous nesters. Third, the annual number of released birds was similar to the number of propagules likely to occur in nature. The Spanish natural Griffon Vulture colonies vary from less than ten to more than 90 pairs (Arroyo et al. 1990), so the maximum influx of ten releases per year (Fig. 1) was a sensible choice. Finally, the increase of local food resources and the disappearance of predation risks in unoccupied patches (Taylor 1990) favours

the fixing of active dispersers (Pulliam 1988, Hanski 1991, Ebenhard 1991). These conditions were fulfilled in the Causses area since natural sheep mortality on local farms used to supply artificial feeding places plus a decrease in human persecution had led to the restoration of a favourable habitat (Friedman & Mundy 1983, Houston 1987).

These results show that monitoring reintroduced populations allows us not only to test conservation methods but also to study aspects of the behavioural ecology and population dynamics of species which are often poorly studied in the wild because of their endangered status.

REFERENCES

Armstrong, R.A. 1978. A note on the demography of colonisation. Am. Nat. 112: 243–245.

Arroyo, B., Ferreiro, E. & Garza, V. (eds) 1990. Il censo nacional de buitre leonado (Gyps fulvus): Poblacion, Distribucion, Demographia y Conservación. Ministerio de agricultura pesca y alimentacion. Madrid: Instituto Nacional para la Conservación de la Naturaleza.

Beletsky, L.D. & Orians, G.H. 1991. Effects of breeding experience and familiarity on site fidelity in female Red-winged Blackbirds. Ecology. 72: 787–796.

Bonnet, J., Terrasse, M., Bagnolini, C. & Pinna, J.L. 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 Revue Française d'Ornithologie. 60: 181–206.

Brooke, M.L. 1978. Some factors affecting the laying date, incubation and breeding success of the Manx shearwater, Puffinus puffinus. J. Anim. Ecol. 47: 477–495.

Brown, C.R., Stutchbury, B.J. & Walsh, P.D. 1990. Choice of colony size in birds. TREE 5: 398–403.

Clobert, J. & Lebreton, J.D. 1991. Estimation of demographic parameters in bird populations. In Perrins C.M., Lebreton J.D. & Hirons G.J.M. (eds) Bird Population Studies; Relevance to conservation and management: 75–104. Oxford: Oxford University Press.

Clobert, J., Julliard, R. & McCleery, R.H. 1993. The component of local recruitment. In Lebreton J.D. & North P.M. (eds) Marked Individuals in the Study of Bird Population: 281–293. Basel: Birkhauser Verlag.

Clobert, J., Lebreton, J.D., Allaine, D. & Gaillard, J.M. 1994. The estimation of age specific breeding probabilities from recaptures or resightings in vertebrate populations. II. Longitudinal models. Biometrics 50: 375–387.

Cooke, F. & Francis, C.M. 1993. Challenges in the analysis of

recruitment and spatial organisation of populations. In Lebreton J.D. & North P.M. (eds) Marked Individuals in the Study of Bird Population: 295–308. Basel: Birkhauser Verlag.

Coulson, J.C., Duncan, N. & Thomas, C. 1982. Changes in the breeding biology of the Herring Gulls (Larus argentatus) induced by reduction in the size and density of the colony. J. Anim. Ecol. 51: 739–756.

Danchin, E., Cadiou, B., Monnat, J.Y. & Estralla, R.R. 1991. Recruitment in long-lived birds: Conceptual framework and behavioural mechanisms. Proc. Int. Orn. Congr. XX: 1641–1656.

Desrochers, A. & Magrath, R.D. 1993. Environmental predictability and remating in European blackbirds. Behav. Ecol. 4: 271–275.

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

Donazar, J.A. & Fernandez, C. 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.

Ebenhard, T. 1991. Colonization in metapopulations: A review of theory and observations. In Gilpin M. & Hanski I. (eds) Metapopulation Dynamics: Empirical and theoretical investigations: 105–121. London: Academic Press.

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

Evans, I.M., Love, J.A., Galbraigh, C.A. & Pienkowski, M.W. 1994. Population and range restoration of threatened raptors in the United Kingdom. In Meyburg, B.U. & Chancellor, R.D. (eds) Raptor Conservation Today: 447–457. Mountfield, East Sussex: World Working Group on Birds of Prey and Owls.

Frey, H. & Bijleveld van Lexmond, M. 1994. The reintroduction of the Bearded Vulture Gypaetus barbatus aureus into the Alps. In Meyburg, B.U. & Chancellor, R.D. (eds) Raptor Conservation Today: 459–464. Mountfield, East Sussex: World Working Group on Birds of Prey and Owls.

Friedman, R. & Mundy, P.J. 1983. The use of "restaurants" for the survival of Vultures in South Africa. In Wilbur, S.R. & Jackson, J.A. (eds) Vulture Biology and Management: 345–355. Berkeley: University of California Press.

Fritz, R.S. 1979. Consequences of insular population structure: Distribution and extinction of Spruce grouse populations. Oecologia 42: 57–65.

Fry, D.M. 1983. Techniques for sexing monomorphic vultures. In Wilbur, S.R. & Jackson, J.A. (eds) Vulture Biology and Management: 185–196. Berkeley: University of California Press.

Gaillard, J.M., Pontier, D., Allainé, D., Lebreton, J.D., Trouvilliez, J. & Clobert, J. 1989. An analysis of demographic tactics in birds and mammals. Oikos 56: 59–76.

Gavin, T.A. & Bollinger, E.K. 1988. Reproductive correlates of breeding-site fidelity in Bobolinks (Dolichonyx oryzivorus). Ecology 69: 96–103.

Greenwood, P.J. 1980. Mating systems, philopatry and dispersal in birds and mammals. Anim. Behav. 28: 1140–1162.

Griffith, B., Scott, J.M., Carpenter, J.W. & Reed, C. 1989. Translocation as a species conservation tool: Status and strategy. Science 245: 477–480.

Hanski, I. 1991. Single-species metapopulation dynamics: Concepts, models and observations. Biol. J. Linn. Soc. 42: 17–38.

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

Houston, D.C. 1974b. Food searching in Griffon Vultures. E. Afr. Wildl. J. 12: 63–77.

Houston, D.C. 1976. Breeding of the White-backed and Rüppell's Griffon Vultures, Gyps africanus and G. Rueppelli. Ibis 118: 14–40.

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. In Hill, D.J. (ed.) Breeding and Management in Birds of Prey: 15–29. Bristol: University of Bristol.

Johnson, M.L. & Gaines, M.S. 1990. Evolution of dispersal: Theoretical models and empirical tests using birds and mammals. Ann. Rev. Ecol. Syst. 21: 449–480.

Kharitonov, S.P. & Siegel-Causey, D. 1988. Colony formation in seabirds. In Johnston, J.F. (ed.) Current Ornithology, Vol. 5: 223–272. New York: Plenum Press.

Kress, S.W. & Nettleship, D.N. 1988. Re-establishment of Atlantics puffins (Fratercula arctica) at a former breeding site in the Gulf of Maine. J. Field Ornithol. 59: 161–170.

Lebreton, J.D., Hemery, G., Clobert, J. & Coquillart, H. 1990. The estimation of age-specific breeding probabilities from recaptures or resightings in vertebrate populations. I. Transversal models. Biometrics 46: 609–622.

Leconte, M. 1985. Present Status of the Griffon Vulture on the Northern Slopes of the Western Pyrénées. ICBP Technical Publication No. 5: 117–127. Cambridge: International Council for Bird Preservation.

Love, J. 1983. The Return of the Sea-eagle. Cambridge: Cambridge University Press.

MacArthur, R.H. & Wilson, E.O. 1967. The Theory of Island Biogeography. Princeton: Princeton University Press.

Mangel, M. & Tier, C. 1993. Dynamics of metapopulations with demographic stochasticity and environmental catastrophes. Theor. Pop. Biol. 44: 1–31.

Massot, M., Clobert, J., Lecomte, J. & Barbault, R. 1994. Incumbent advantage in common lizards and their colonising ability. J. Anim. Ecol. 63: 431–440.

Mehlhop, P. & Lynch, J.F. 1978. Population characteristics of Peromyscus leucopus introduced to islands inhabited by Microtus pennsylavnicus. Oikos 31: 17–26.

Mendelssohn, H. & Leshem, Y. 1983. Observations on reproduction and growth of Old World vultures. In Wilbur, S.R. & Jackson, J.A. (eds) Vulture Biology and Management: 214–241. Berkeley: University of California Press.

Mundy, P., Butchart, D., Ledger, J. & Piper, S. 1992. The Vultures of Africa. London: Academic Press.

Newton, I. 1979. Population Ecology of Raptors. Berkhamsted: T, & A. D. Poyser.

Newton, I. 1989. Lifetime Reproduction in Birds. London: Academic Press.

Newton, I. 1991. The role of recruitment in population regulation. Proc. Int. Orn. Congr. XX: 1689–1699.

Newton, I. & Marquiss, M. 1982. Fidelity to breeding area and mate in Sparrowhawks Accipiter nisus. J. Anim. Ecol. 51: 327–341.

O'Connor, R.J. 1986. Biological characteristics of invaders among bird species in Britain. Phil. Trans. R. Soc. Lond. B Biol. Sci. 314: 583–598.

Parnell, J.F., Ainley, D.G., Blokpoel, H., Cain, B., Custer, T.W., Dusi, J.L., Kress, S., Kushlan, J.A., Southern, W.E., Stenzel, L.E. & Thompson, B.C. 1988. Colonial waterbird management in North America. Colonial Waterbirds 11: 129–169.

Podolsky, R.H. & Kress, S.W. 1989. Factors affecting colony formation in Leach's Storm-Petrel. Auk 106: 332–336.

Porter, J.M. & Coulson, J.C. 1987. Long-term changes in recruitment to the breeding group, and the quality of recruits at a Kittiwake Rissa tridactyla colony. J. Anim. Ecol. 56: 675–689.

Pulliam, R.H. 1988. Sources, sinks, and population regulation. Am. Nat. 132: 652–661.

Ray, C. & Gilpin, M. 1991. The effect of conspecific attraction on metapopulation dynamics. Biol. J. Linn. Soc. 42: 132–134.

Reed, J.M. & Dobson, A.P. 1993. Behavioural constraints and conservation biology: Conspecific attraction and recruitment. Trends Ecol. Evol. 8: 253–255.

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

Robertson, A.S. & Boshoff, A.F. 1986. The feeding ecology of Cape Vulture (Gyps coprotheres) in a stock farming area. Biol. Conserv. 35: 63–86.

Sarrazin, F., Bagnolini, C. Danchin, E. & Clobert, J. 1994. High survival estimates of Griffon Vultures Gyps fulvus fulvus in a reintroduced population. Auk 111(4): 853–862.

Schieck, J.O. & Hannon, S.J. 1989. Breeding site fidelity in Willow Ptarmigan: The influence of previous reproductive success and familiarity with partner and territory. Oecologia 81: 465–472.

Shepherdson, D. 1994. The role of environmental enrichment in the captive breeding and reintroduction of endangered species. In Olney, P.J.S., Mace, G.M. & Feistner, A.T.C. (eds) Creative Conservation: Interactive management of wild and captive animals: 167–177. London: Chapman & Hall.

Shields, W.M., Crook, J.R., Hebblethwaite, M.L. & Wiles-Ehmann, S.S. 1988. Ideal free coloniality in the Swallows. In Slobodchikoff, C.N. (ed.) The Ecology of Social Behavior: 189–228. London: Academic Press.

Smith, A. & Peacock, M.M. 1990. Conspecific attraction and the determination of metapopulation colonisation rates. Conserv. Biol. 4: 320–323.

Stamps, J.A. 1988. Conspecific attraction and aggregation in territorial species. Am. Nat. 131: 329–347.

Taylor, A.D. 1990. Metapopulations, dispersal, and predator-prey dynamics: An overview. Ecology 71: 429–433.

Terrasse, J.F. 1977. Maturité sexuelle du vautour fauve, premières données obtenues dans la nature. L'Oiseau et la Revue Française d' Ornithologie 47: 214–218.

Terrasse, M. 1990. Réintroduction du Vautour fauve dans les grands Causses et renforcement de population de Vautour percnoptère. In Réintroductions et renforcements de populations animales en France. Compte rendu du colloque de Saint Jean du Gard, Revue d'Ecologie. Terre Vie 5(Suppl): 213–226.

Terrasse, M., Bagnolini, C., Bonnet, J., Pinna, J.L. & Sarrazin, F. 1994. Reintroduction of the Griffon Vulture Gyps fulvus in the Massif Central, France. In Meyburg, B.U. & Chancellor, R.D. (eds) Raptor Conservation Today: 479–491. Mountfield, East Sussex: World Working Group on Birds of Prey and Owls.

Thompson, P.S. & Hale, W.G. 1989. Breeding site fidelity and natal philopatry in the Redshank Tringa totanus. Ibis 131: 214–224.

Wilson, A.C. & Stanley Price, M.R. 1994. Re-introduction as a reason for captive breeding. In Olney P.J.S., Mace G.M. & Feistner A.T.C. (eds) Creative Conservation: Interactive management of wild and captive animals: 243–264. London: Chapman & Hall.

Wyllie, I. & Newton, I. 1991. Demography of an increasing population of sparrowhawks. J. Anim. Ecol. 60: 749–766.

APPENDIX

In order to estimate the actual number of nesters of age a (e_a), we considered that each nester had two possibilities to be missed: it could have lost its identification marks, or its nest could have been difficult to observe. So, we can define two probabilities, u and v, as the probability of being a marked bird (u) and the probability of nesting in a site that was easy to observe (v).

By using the proportions of pairs with two, one or no identified birds, we estimated the annual probability of a bird being missed as a nester because of inadequate nest observations. If

p_2 = number of pairs with two identified nesting birds,
p_1 = number of pairs with one identified nester,
p_0 = number of pairs with no identified nester,
$p_t = p_0 + p_1 + p_2$,
n_t = total number of observed birds in the population and
o_t = total number of observed nesters,

then, the probabilities m and o are estimated by

$$p_2/p_t = v \cdot u^2,$$

$$p_1/p_t = v \cdot 2u(1 - u)$$

and

$$p_0/p_t = v \cdot (1 - u)^2 + (1 - v).$$

When $p_0 = 0$, we assume that $v = 1$. When $p_0 > 0$,

$$u = (p_1 + 2 \cdot p_0 - 2 \cdot p_t)/(-2 \cdot p_t \cdot v)$$

and

$$v = [-(p_1 + 2 \cdot p_0 - 2 \cdot p_t)]2/(p_2 \cdot 4 \cdot p_t),$$

so

$$e_a = o_a + [p_t \cdot (1 - v) \cdot 2 \cdot (n_a/n_t) \cdot (o_a/o_t)].$$

Finally,

$$e_a = o_a[1 + (2 \cdot p_t n_a \cdot (1 - v))/(n_t \cdot o_t)].$$