

## Breeding biology and survival of the Alpine Chough *Pyrrhocorax graculus*

A. DELESTRADE\*† and G. STOYANOV‡ †Centre de Biologie des Ecosystèmes d'altitude, Université de Pau, 64000 Pau, France; ‡21 Golyam Bratan St, Sofia 1618, Bulgaria

*We describe for the first time the breeding biology and survival of the Alpine Chough Pyrrhocorax graculus in different European massifs (Alps and West-Balkan). When all data were pooled, mean clutch and brood sizes were 3.6 eggs (se = 0.1) and 2.6 chicks (se = 0.1), respectively. Fledging success per pair varied between 1 and 4 fledged young per pair (mean 1.9). Survival of the Alpine Chough was estimated with a capture–resighting model using a colour-ringed population (n = 315 adults) which used human food sources. Adult survival rate varied from 83 to 92%, depending on the flock. This difference could be a consequence of differences in flock composition. No significant difference was detected between male and female survival. Survival of first-year birds (77%) was lower than that of adults. In order to analyse the effect of human food supplied by tourist activities, breeding success and flock structure were compared between 2 alpine populations which either did or did not exploit human food supplied by tourist activities. No difference was found in breeding success or flock composition between the 2 populations.*

Reproductive performance in birds is highly dependent on the availability of food.<sup>1–3</sup> Thus, situations where food supply has recently changed (e.g. increased) are interesting to study the impact of food availability on a bird population.<sup>4</sup> Increased tourism in mountainous areas has provided supplemental food for birds (ski stations and their restaurants, refuse dumps, picnic areas). Although Alpine Choughs *Pyrrhocorax graculus* usually forage in alpine grasslands, their opportunistic feeding habits have led them intensively to exploit human refuse.<sup>5</sup> Numerous studies have shown that corvids have benefited from human activities.<sup>6–9</sup> The case of the Alpine Chough, however, has been studied very little.<sup>10</sup> In this paper, we provide new data on the breeding biology, flock composition and

survival of the Alpine Chough in the western Palearctic. Because supplemental food is known to have increased the breeding success of other corvids<sup>6–9</sup> we studied birds at sites with differing levels of human activity.

The Alpine Chough is a social corvid which is distributed throughout the major montane areas of the Palearctic<sup>12</sup> and North Africa.<sup>13</sup> It usually inhabits the alpine zone of high mountains, although it can be found within a wide altitudinal range, i.e. from 500 m in Europe<sup>14</sup> to 4800 m in the Himalayas.<sup>15</sup> The Alpine Chough is a sedentary species, breeding and roosting at night in crevices in cliffs, or in pot-holes.<sup>16</sup>

### MATERIALS AND METHODS

The Alpine Chough is socially monogamous, showing high partner fidelity both in winter and from year to year (unpublished data). Birds always forage in groups, which are larger

\*Correspondence: A. Delestrade, Institut d'écologie, CNRS URA 258, Université Pierre et Marie Curie, 7 Quai St Bernard, 75252 Paris cedex 05, France.

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in winter than in summer, due to the gathering of groups from different massifs at feeding sites.<sup>11</sup> The individual composition of these groups remains stable across seasons.<sup>11</sup> A social dominance hierarchy appears when feeding on clumped resources with adults dominating immatures and males dominating females.<sup>10,17</sup> Different age classes can be distinguished in the Alpine Chough; yearlings and adults differ in leg colour.<sup>18</sup> In this study, birds older than 1 year were classified as adults, yearlings were classified as immatures and birds which were dependent on their parents (for 1 month after fledging) were classified as juveniles.

### Study areas

Three different populations were studied.

1 Ponor massif, Bulgaria (West Balkan), is a calcareous massif (up to 1479 m) where Choughs nest and roost in vertical caves.<sup>19</sup> Phenology of breeding (laying, hatching and fledging), clutch and brood sizes, hatching and fledging success were monitored annually from 1981 to 1987 in 7 vertical caves (total  $n = 33$  nests).

2 Southern Vercors massif (Prealps) is a calcareous karst (up to 2341 m) where a population of *c.* 250 individuals has been studied during the breeding period from 1989 to 1992 and 1994. A large roost frequented by a maximum of 320 birds during the post-fledging period was located in the same cliff as most nest sites.

In these 2 study areas, Alpine Chough fed exclusively on natural resources.

3 Mont-Blanc, Aiguilles Rouges and surrounding massifs in Haute-Savoie (northern French Alps). This is a granitic massif (up to 4807 m) where a population of *c.* 2000 individuals was studied between winter 1988 and summer 1994. This Chough population exploits human refuse provided by tourists. In this population, 488 individuals (425 adults, 44 immatures, 19 juveniles) were caught by canon-net at feeding sites. All these birds were individually ringed with 3 colour rings and 1 metal ring. The loss rate of colour rings was very low (0.3% on 1464 rings). The sex of 40 and 61 adults was determined by laparoscopy<sup>20</sup> or behaviour (only the male feeds the female in spring; see ref 41), respectively. All ringed adults were

then sexed using a discriminant function analysis based on weight, wing and tail lengths, with a resulting 2.1% error.<sup>10</sup>

To determine nest location, breeding success and population structure, we monitored 1 population in particular (*c.* 200 individuals) frequenting the massif of the Aiguilles Rouges (altitude max = 2965 m). In summer, this flock was located at a picnic area (Lac Blanc, 2350 m), where on average 300 tourists per day visited this area.

### Parameters studied

#### *Phenology, nest sites and breeding success*

Laying, hatching or fledging dates were determined either by direct observations at the nest, or from the behaviour of breeders near their nest (e.g. feeding of the female by the male, feeding by the 2 parents at the nest, begging calls of the chicks). However, only 5 nests could be followed over the entire breeding period. When nests were found after the egg stage, we assumed a 20-day incubation period<sup>15</sup> to backdate hatching dates. For the remaining nests we only knew the fledging dates. Median fledging dates were used to compare phenology among the study areas. Also, the nearest-neighbour distance between nests was calculated.

In 1991 and 1992, we recorded all feeding trips to the nest at Vercors and Aiguilles Rouges, for nestlings older than 10 days.

Data on clutch size came from our field studies ( $n = 35$  nests), and from the literature.<sup>14, 16, 18, 21-23</sup> Brood size was recorded at the nest a minimum of 15 days after the laying period. The mean number of fledged young per successful pair was estimated only at French sites by observing chicks near the nest entrance (before fledging) or parents feeding their young on foraging sites (after fledging). Data were randomly recorded and the number of fledged young per successful pair represent a random sample of the population. These 2 methods, which estimate number of fledged young per successful pair, gave similar results at each site: in Haute-Savoie (Kolmogorov-Smirnov test:  $D = 0.12$ ,  $K_s = 0.03$ ,  $n = 283$ , ns) or in Vercors ( $D = 0.15$ ,  $K_s = 0.07$ ,  $n = 123$ , ns), data were therefore pooled at each site. Similarly, in Haute-Savoie no significant dif-

ference could be detected between the median number of fledged young estimated from observations of ringed birds feeding young at foraging sites, and that estimated from observations of non-ringed birds feeding young (median test:  $\chi^2 = 3.4$ , d.f. = 1,  $n_1 = 67$ ,  $n_2 = 244$ , ns). This suggested that possible repeated observations of the same unringed family did not seriously bias counts, so that all count data could be pooled. Means are presented with standard errors.

#### Population structure

The total population was estimated from the largest flock size recorded during the month following the fledging period in Vercors and Aiguilles Rouges. The number of juveniles produced per year was estimated by the maximum number of juveniles recorded at the night roost (at Vercors) or at feeding sites (at Aiguilles Rouges). Then, the number of successful breeders was estimated by the number of juveniles produced each year divided by the mean number of fledged young per successful pair and multiplied by 2. The number of immatures was deduced from the average proportion of immatures obtained by scan sampling during summer before the fledging period.<sup>11</sup> The number of non-breeding adults was deduced from the difference in the total population and the sum of immatures and breeders. All numbers were then transformed to proportions in order to compare results between years and sites.

#### Survival analysis

The estimate of survival rate was based on winter resightings (between December and April) of birds ringed in winter between 1988 and 1992 in Haute-Savoie (315 adults and 25 yearlings). The time between capture and first resighting was at least 8 months. And time between each resighting period (7 months) was greater than the length of the resighting period (5 months: from December to April). This therefore satisfied the requirements of a capture-mark-recapture (CMR) model.<sup>24, 25</sup> We used a capture-mark-recapture model which distinguishes survival and recapture probabilities. We used what Burnham *et al.*<sup>26</sup> called TESTS 2 and 3 for goodness-of-fit to the

Cormack-Jolly Seber model,<sup>27</sup> calculated using program RELEASE.<sup>26</sup> TEST 2 tests the equality of the number of birds released ( $R_i$ ) for release at the different occasions. TEST 3 tests the homogeneity of resighting histories at any release time.<sup>28</sup> TEST 2 could not be used in most cases because of inadequate sample sizes. All models were fitted by the maximum likelihood method using program SURGE (version 4.1).<sup>34</sup> Model selection was based on the smallest Akaike's Information Criterion (AIC) (for more details, see Lebreton *et al.*<sup>32</sup>). When 2 models had the same AIC, the more constrained model was selected.

To analyse adult survival, 2 different winter flocks were studied in Haute-Savoie: (i) a flock which frequented the refuse dump of a ski station (Flaine 1850 m)<sup>17</sup> using resighting histories of 231 adults over 4 winters (1989–92), and (ii) a flock which frequented a ski station (Le Tour 1500 m)<sup>11</sup> using resighting histories of 84 adults over 5 winters (1988–92). To analyse immature survival, we studied one flock in Haute-Savoie which frequented a ski station (Le Tour in 1988–92) using resighting histories of 25 immatures over 5 winters (1988–92). Survival of juveniles could not be tested because of the small sample size ( $n = 16$  ringed birds), thus only the proportion of resighted birds was noted. Survival was estimated for different age classes as follows: juvenile survival was estimated between fledging and the first winter; immature survival was estimated between the first and second winters; adult survival was estimated after the second winter.

## RESULTS

### Nest sites

In Aiguilles Rouges, the mean altitude of nest sites was 2530 m (range 2200–2750 m,  $n = 28$ ). All nests were located in fissures in cliffs. Nearest-neighbour distances varied from 50 to 1000 m ( $n = 16$ ). Nest distribution appeared to be determined principally by site availability. Five additional nests were found in cable car stations during the study period at a lower altitude (mean 2230 m, range 1980–2520 m). These nests were all unsuccessful due to predation, or abandoned because of human disturbance in summer.

In Vercors, nests were located in calcareous cliffs or pot-holes between 1650 and 1950 m (mean 1830 m,  $n = 29$ ). Over 400 m of linear cliff, 23 nests were counted and nearest-neighbour distance varied from 10 to 50 m. The same holes were occupied each year.

In Ponor, nests were found in vertical caves between 5 and 25 m depth. Mean altitude of the entrances was 1220 m (range 1100–1460 m,  $n = 7$ ). The mean number of breeding pairs per pot-hole varied between 1 and 10 (mean  $6.3 \pm 1.5$ ,  $n = 7$ ). Distance between breeding caves varied between 200 and 7000 m. Inside the caves, the nearest-neighbour distance ranged between 2 and 25 m.

### Timing of breeding

All years combined, timing of fledging was similar at the 2 alpine sites (1-way ANOVA:  $F = 0.08$ , d.f. = 1,  $n = 162$ , ns), but delayed compared with Ponor massif (median test:  $\chi^2 = 6.7$ ,  $n = 142$ , d.f. = 1,  $P < 0.01$ ); mean fledging dates being about 1 month earlier in Ponor than in the alpine populations (Table 1). Mean fledging dates appeared to be delayed by 15 days to 1 month in populations in the Alps (Aiguilles Rouges, Vercors), West-Pyrenees and Abruzzes compared with other sites (Corsica, Ponor, Monts Cantabriques, Table

1). No significant relationship was found between mean fledging date and altitude (1-way ANOVA,  $F = 0.54$ , d.f. = 1, ns) or latitude ( $F = 0.66$ , d.f. = 1, ns, data in Table 1), but only a small number of populations had been studied.

The fledging date differed significantly between years (1-way ANOVA,  $F = 10.5$ , d.f. = 5,  $P < 0.001$ , Table 2). No significant interaction was found between years and sites (2-way ANOVA,  $F = 1.39$ , d.f. = 3, ns) suggesting that fledging date follows the same variations between years in the 2 alpine populations. All massifs combined, the nestling period varied between years, from 33 to 41 days ( $n = 6$  nests).

### Breeding success

When data from all massifs were pooled, clutch size varied between 2 and 5 eggs, with a mean of  $3.6 \pm 0.1$  ( $n = 35$ ) or  $3.8 \pm 0.1$  ( $n = 50$ ) when adding data from the literature (Table 3). The modal clutch size was 4 eggs, although a clutch of 6 eggs has been obtained in captivity.<sup>32</sup> No difference was found in clutch size between massifs (Kruskal-Wallis test:  $\chi^2 = 3.0$ , d.f. = 2, ns).

With populations and years combined, brood size varied between 1 and 4 chicks, with a mean of  $2.5 \pm 0.2$  ( $n = 11$  nests, this

**Table 1.** Fledging date (mean and range) of the Alpine Chough, according to latitude and altitude (in parentheses)

Massif	Latitude (alt.)	Fledging (mean)	Range	Source
Morocco (25–50 m)	33°N	> 08–07		Roux <sup>30</sup>
Ponor (1100–1450 m)	42°N	02/07 ( $n = 7$ )	(22/06– 15/07)	This study
Abruzzes (1980 m)	42°N	30/07 ( $n = 2$ )	(30/07– 31/07)	Lovari <sup>18</sup>
Corsica (1500–2200 m)	42°N	16/07 ( $n = 7$ )	(07/07– 29/07)	Delestrade <sup>31</sup>
Monts Cantabriques (600 m)	43°N	07/07 ( $n = 2$ )	(01/07– 15/07)	Garcia-Dori <sup>14</sup>
West-Pyrenees (900–1000 m)	43°N	30/07 ( $n = 4$ )	(18/07– 14/08)	Dendaletche & Saint-Lebe <sup>16</sup>
Vercors (1650–1950 m)	45°N	06/08 ( $n = 67$ )	(20/07– 21/08)	This study
Aiguilles Rouges (2000–2800 m)	46°N	05/08 ( $n = 95$ )	(14/07– 02/09)	This study



**Table 2.** Variations between years of mean fledging dates of the Alpine Chough at 2 alpine massifs

Year	Aiguilles Rouges		Vercors	
	Mean (n)	Range	Mean (n)	Range
1988	30/07 (n = 8)	21/07-10/08	—	—
1989	04/08 (n = 15)	20/07-20/08	04/08 (n = 11)	27/07-06/08
1990	07/08 (n = 5)	29/07-18/08	31/07 (n = 19)	23/07-09/08
1991	14/08 (n = 11)	05/08-02/09	16/08 (n = 10)	09/08-21/08
1992	02/08 (n = 16)	14/07-16/08	04/08 (n = 17)	20/07-10/08
1993	04/08 (n = 23)	23/07-21/08	—	—
1994	06/08 (n = 17)	21/07-29/08	10/08 (n = 10)	27/07-27/08

**Table 3.** Mean clutch size and brood size according to site (data from literature, and this study)

Massifs	Clutch size			Brood size		
	Mean	Range	n	Mean	Range	n
Ponor	3.6*	2-5*	30*	2.5*	2-3*	8*
Alps	4.0 (3.4)*	2-5 (2-4)*	16 (5)*	2.3 (2.3)*	1-4 (1-3)*	6 (3)*
Pyrenées, Monts cantabriques	4.0	4	4	2.6	1-4	28
Total	3.8	2-5	50	2.6	1-4	42

\* Data from this study.

study) or  $2.6 \pm 0.1$  ( $n = 42$  nests) when adding data from the literature. No difference was found in brood size between massifs (Kruskal-Wallis test:  $\chi^2 = 0.4$ , d.f. = 2, ns). An average of  $2.1 \pm 0.3$  ( $n = 12$ ) chicks per nest disappeared between hatching and fledging period, which corresponds to 59% of chicks per nest. Sixty-four per cent ( $n = 64$ ) of nesting pairs produced at least 1 fledgling and were considered as successful breeders.

The number of fledged young per successful pair ranged from 1 to 4. Comparing the 2 alpine populations, on average  $1.7 \pm 0.05$  ( $n = 283$ ) young fledged in Haute-Savoie compared with  $1.9 \pm 0.07$  ( $n = 134$ ) in the Vercors population (Table 4). No significant

difference was found in the number of fledglings per successful pair between the 2 populations (Kolmogorov-Smirnov test:  $D = 0.11$ ,  $K_s = 0.05$ , ns). Combining the 2 populations, no significant difference appeared between years (Kruskal-Wallis test:  $\chi^2 = 10.3$ , d.f. = 6, ns). The fledging period extended over 26-43 days in the Aiguilles Rouges. No significant difference was detected in the number of fledglings per pair between early (young fledged during the first part of fledging period,  $1.8 \pm 0.06$ ,  $n = 199$ ) and late breeding pairs (second part of fledging period,  $1.8 \pm 0.05$ ,  $n = 218$ , Kolmogorov-Smirnov test:  $D = 0.02$ ,  $K_s = 0.01$ , ns). As replacement clutches were never observed, asynchrony of

**Table 4.** Mean number of fledged young ( $\pm$  se) per successful pair according to site and year

Massif	1988	1989	1990	1991	1992	1993	1994
Haute-Savoie	1.8 $\pm$ 0.1 (n = 37)	1.7 $\pm$ 0.1 (n = 59)	1.6 $\pm$ 0.1 (n = 30)	1.85 $\pm$ 0.2 (n = 40)	1.8 $\pm$ 0.1 (n = 44)	1.8 $\pm$ 0.1 (n = 38)	1.5 $\pm$ 0.1 (n = 37)
Vercors	—	1.8 $\pm$ 0.2 (n = 16)	2.0 $\pm$ 0.1 (n = 35)	1.9 $\pm$ 0.1 (n = 32)	2.1 $\pm$ 0.1 (n = 29)	—	1.7 $\pm$ 0.1 (n = 23)

fledging was not induced by laying when the first clutch failed.

Mean feeding trip duration at the nest was 45.8 min (se = 3.6,  $n = 60$ ) in the Aiguilles Rouges against 54.1 min (se = 3.2,  $n = 71$ ) in Vercors. Thus, no significant difference was obtained between the 2 alpine populations ( $t = 1.67$ , d.f. = 129, ns). These results suggest that in Haute-Savoie, feeding on human refuse rather than feeding on natural resources, did not increase the frequency of food deliveries.

### Flock composition

Population structure was estimated before the fledging period in the 2 alpine sites. Flocks contained 20% (Vercors) or 22% (Aiguilles Rouges) immatures (Fig. 1) with no statistically significant difference ( $\chi^2 = 0.01$ , d.f. = 1, ns). Among adults, the proportion of breeders was higher in Haute-Savoie (mean

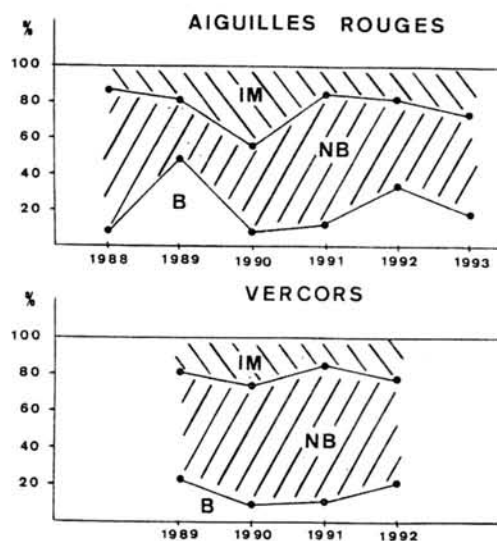
21.9% $\pm$ 0.07,  $n = 6$ ) than in Vercors flocks (16.2% $\pm$ 0.03,  $n = 4$ ) although the difference was not significant (Mann-Whitney test:  $U = 11.5$ ,  $n_1 = 4$ ,  $n_2 = 6$ , ns).

### Survival and dispersal

In all tested data sets, TEST 3 and 2 (when sufficient data were available) were not significant (Table 5) suggesting that the basic assumptions of the Jolly Seber model were met. Thus, no heterogeneity appeared between individual capture-resighting histories.

When all adult resighting histories were taken into account ( $n = 315$ , Table 6), the best model selected depended on the site for adult survival rate with a constant adult resighting rate between sites and years [model ( $\phi_{\text{site}}, p$ ), Table 5]. Resighting rate was high (97% $\pm$ 0.01, Table 5) indicating that adults were highly sedentary. A significantly higher survival rate was obtained in the flock foraging at the ski station Le Tour (92% $\pm$ 0.02,  $n = 84$ ) than for the flock foraging at the refuse dump of Flaine (83% $\pm$ 0.02%,  $n = 231$ ). No significant difference was detected in survival rate between years or sexes at the 2 sites (Table 5).

Survival rate of birds caught in their first winter (immature birds) at Le Tour was lower (76.7% $\pm$ 0.08,  $n = 25$ ) than that of adults. Model selection methods (smallest AIC) with resighting data suggested that there was no effect of time or age (between the first year and subsequent years) for immature survival and resighting rate. It is paradoxical to find a difference in adult survival (older than 2 years) between birds caught as adults (92%) and those caught as immatures (77%) but also to find no difference between age classes of birds caught as immatures. The small number of immatures resighted could explain this difference. In the same way, resighting rate of immatures was lower than that of adults (64.9% $\pm$ 0.1 vs. 97% $\pm$ 0.02), probably as a result of a greater dispersion of young birds.



**Figure 1.** Interannual fluctuations of flock composition (in proportion) in 2 different massifs, before fledging period. B, successful breeders; NB, adults non-breeder; IM, immatures.

**Table 5.** Results of capture-resighting models of adult and yearling and comparison between best models. The best model is noted in bold characters. np = number of parameters. AIC = Akaike's information criterion  $\phi$  = survival rate  $\pm$  se,  $p$  = resighting rate  $\pm$  se. e.g. model ( $\phi$ ,  $p$ ) assumes a constant survival rate and resighting rate across sites and years. Model ( $\phi_{\text{site}}$ ,  $p$ ) varies survival rate by sites but has a constant resighting rate.

Model	deviance	np	AIC	$\phi$	P
<b>Adult</b>					
Flaine + Le Tour: ( $n = 315$ , 5 years)					
(Test 2: $\chi^2 = 0.02$ , d.f. = 1, ns) (Test 3: $\chi^2 = 6.6$ , d.f. = 6, ns)					
( $\phi$ , $p$ )	500.4	2	504.4		$P = 0.97 \pm 0.01$
<b>(<math>\phi_{\text{site}}</math>, <math>p</math>)</b>	<b>494.0</b>	<b>3</b>	<b>500.0</b>	Flaine $\phi = 0.83 \pm 0.02$ ( $n = 231$ )	
( $\phi_{\text{site}}$ , $p_{\text{site}}$ )	494.0	4	502.0	Le Tour $\phi = 0.92 \pm 0.02$ ( $n = 84$ )	
( $\phi_{\text{time}}$ , $p_{\text{time}}$ )	490.4	8	506.4		
( $\phi_{\text{sex}}$ , $p$ )	498.5	3	504.5		
( $\phi_{\text{sex}}$ , $p_{\text{sex}}$ )	498.5	4	506.5		
<b>Yearling</b>					
Le Tour ( $n = 25$ , 5 years)					
(Test 3: $\chi^2 = 6.2$ , d.f. = 5, ns)					
<b>(<math>\phi</math>, <math>p</math>)</b>	<b>97.9</b>	<b>2</b>	<b>101.9</b>	$\phi = 0.767 \pm 0.08$	$P = 0.65 \pm 0.1$
( $\phi_{\text{age}}$ , $p$ )	97.9	3	103.9		
( $\phi_{\text{age}}$ , $p_{\text{age}}$ )	97.7	4	105.7		
( $\phi_{\text{time}}$ , $p$ )	94.2	6	106.2		

**Table 6.** First resighting data each year for adult Alpine Chough at different sites (= SURGE matrix).  $R(i)$  = number of birds released at the year  $i$

Year $i$	Released $R(i)$	First resighting			
		1989	1990	1991	1992
<b>Le Tour</b>					
1988	19	17	16	13	10
1989	6		6	5	5
1990	12			12	12
1991	47				42
<b>Flaine</b>					
1988	0	0	0	0	0
1989	9		8	8	5
1990	141			116	91
1991	81				67

This was partially confirmed by the location of resightings of birds caught as juvenile or immature (unpublished data).

Among birds ringed as juveniles ( $n = 16$ ), 8 disappeared (50%) in their first year. Among the 8 juveniles which survived to their first year, 5 were resighted 1 year later in their natal group which suggested that natal philopatry occurred to some extent. First breeding of birds ringed as juvenile has been observed at 4 years old in their natal massif.

## DISCUSSION

### Breeding strategy of the Alpine Chough: comparison with other corvids

This study describes breeding biology and survival of the Alpine Chough, which have never been studied before in this species. As most other corvids, the Alpine Chough is an opportunistic bird, especially with regard to feeding habits,<sup>5</sup> but also in its nesting. This species was shown to nest either in cliffs or in pot-holes, in colonies or isolated, as well as over a wide altitudinal range [for France, lowest altitude, 600 m (Atlantic Pyrenees),<sup>16</sup> highest, 3800 m (Mont Blanc massif, Alps; personal observation)]. The nesting season appears to be late compared with those of other European corvid species,<sup>15</sup> a likely consequence of delayed spring seasons at high altitude.<sup>33, 34</sup> We suggest that breeding phenology of the Alpine Chough is much constrained by snow melting, because at this season, Chough search for larvae which are numerous around snow patches. The modal clutch size (4 eggs), the incubation length (20 days) and the brooding length (*c.* 30 days) are common characteristics shared with other European corvids (genus *Corvus* or *Pyrrhocorax*).<sup>15, 35, 36</sup> In conclusion, the montane environment ap-



parently affected the starting of breeding more than any other breeding parameter.

The average fledging success (proportion of eggs per nest giving rise to fledged young) was rather low (50%) in the Alpine Chough, with an average of 3.6 eggs which produced 1.8 fledged young, but comparable to data given for the Chough in Britain.<sup>35,36</sup> These figures do not vary apparently according to the massif studied.

Notably, adult survival in Alpine Choughs (83–92%) is the highest known for any corvid species.<sup>36–39</sup> Only in the territorial Carrion Crow *Corvus corone*, has a similar survival rate been found (92%).<sup>40</sup> It should, however, be noted that, contrary to our study, in all other studies on corvids, the survival estimation methods used did not discriminate between resighting rate and survival rate. Thus, survival values previously reported for corvids<sup>35–39</sup> should be interpreted as minimal values. Lastly, we found no difference in survival rates of adults in relation to sex in any studied flock, although females are strongly dominated by males<sup>41</sup> and do not have access to human food sources equally to males.<sup>17</sup> Immature survival (77%) on the other hand is similar to Chough immature survival (74%).<sup>36</sup> Immature survival is typically lower than that of adults as in many other bird species, a likely consequence of their lower foraging abilities<sup>42</sup> and/or their subordinate status with regard to food access.<sup>10,41</sup> Fifty per cent of fledglings survived to their first year and remained in the study area as against 71% in the Chough.<sup>36</sup> Thus, survival rate from fledging to the second winter of their life is rather low in the Alpine Chough (38%), particularly less than that of the Chough in Scotland (50%).<sup>36</sup> Thus, Alpine Chough seems to have higher young mortality than Chough in Scotland. We suggest that these differences are linked to differences in climatic conditions in winter. The Alpine Chough, inhabiting high montane regions, frequents a more variable environment than the Choughs inhabiting Atlantic sea coasts with a mild maritime climate.

### Influence of human food supply

Unlike the Chough, which is an endangered species at least in Europe,<sup>43</sup> the Alpine Chough has adapted well to humans, especially intense

tourist development in mountains.<sup>10</sup> Many Alpine Chough populations actively exploit human food supply, which denotes their more opportunistic habits.<sup>41,44</sup> The spatial distribution of foraging flocks is influenced by human presence.<sup>11</sup> The behaviour of using an artificial food supply is known to have modified breeding parameters in many bird species.<sup>1,9,45–47</sup> Paradoxically, our results suggest that there is no difference between populations which use, or do not use human refuse, either on phenology, breeding success, flock composition or feeding trip durations. The only parameter differing between the 2 alpine populations was the higher variance in the proportion of breeders in Haute-Savoie, possibly induced by higher variability in environmental conditions for the population frequenting higher altitude. It should be noted however, that the human food supply provided by tourism is only available during tourist seasons, i.e. from December to April during winter and in July and August during summer. Thus, supplemental food is not available during 2 critical periods: preceding breeding, and when young become independent from their parents. We have no data to test whether adult survival might be influenced by food supply (in winter), however, we showed that survival was not higher (but in fact lower) among birds which used refuse dumps compared with birds using food available in smaller quantities at ski stations, although it is possible that the differences in adult survival are related to differences in flock composition. For instance, the lower adult survival rate observed in a flock foraging at refuse dumps (82%) could be explained by the presence of a greater proportion of young adults at this site, non-breeders, or birds that are not settled in a group.<sup>48,49</sup>

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