IBIS 136: 91–96

Factors affecting flock size in the Alpine Chough *Pyrrhocorax graculus*

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The Alpine Chough *Pyrrhocorax graculus* is a social corvid which now uses food provided by tourist activities in mountain regions (e.g. at ski stations, refuse dumps, picnic areas). Foraging flock size, flock distribution and flock structure of Alpine Choughs were studied in the northern French Alps between 1988 and 1992. Flock size varied during the year, being larger in winter than in summer. Alpine Choughs were not evenly distributed in space, and their numbers depended principally on site-specific factors, such as seasonal human presence. A significant positive correlation existed between Alpine Chough foraging flock size and the local human population. Immature birds gathered in winter in the largest flocks and principally frequented sites with the greatest food availability (e.g. refuse dump). In summer, immatures dispersed, joined small breeding groups and were more homogeneously distributed.

Seasonal variations of flocking behaviour in birds, and flock distribution, are believed to be closely related to food distribution (Pulliam & Caraco 1984) and to breeding behaviour (e.g. Fischl & Caccamise 1985, Loman 1985, MacDonald & Whelan 1986). Where food is supplied by man (e.g. refuse dumps, cultivated fields), it forms a rich and clumped food source which can be quantified and controlled and thus provides an easy way for understanding the relationships between food distribution and flocking behaviour. Corvids frequently forage in flocks, and many species forage in habitats where humans are also present, benefitting from their waste materials and activities (Feare *et al.* 1974, Dare 1986, Birkhead 1991). The Alpine Chough *Pyrrhocorax graculus*, a social corvid, is well known to use human food sources (Holyoak 1972, Büchel 1983, Delestrade 1989). However, the Alpine Chough has been little studied, and neither the impact of human activity on flocking behaviour nor flock composition has been investigated. The aims of this study were (1) to describe factors affecting Alpine Chough foraging flock size and structure, and (2) to establish that the food sources provided by man have an impact on flocking behaviour in this species.

METHODS

Species and study area

The Alpine Chough is a gregarious montane corvid that forages on alpine grassland where it feeds on berries and invertebrates (Lovari 1981, Dendaletche & Saint-Lebe, 1988, Delestrade 1991). It is known to use human refuse and to frequent many types of man-related sites: ski stations and their restaurants, refuse dumps, picnic areas, huts (Goodwin 1986, Delestrade 1989, 1993) and towns in Switzerland (Strahm 1961, Voisin 1963).

Alpine Choughs were studied in an area of about 400 km^2 in the northern French Alps (Haute-Savoie, Chamonix valley) and its surrounding massifs in the Valais canton (Switzerland). This is a tourist region in both winter and summer (the Mont Blanc massif receives 400,000 visitors/year). All sites frequented by the Alpine Chough (from 400 to 3300 m) were regularly surveyed in winter from 1988 to 1992 (Table 1). The whole population of Alpine Choughs in this area now depends on by-products of human activity in winter. In summer (1988–1992), observations were made in a smaller area because of the wide dispersion of the birds at this season.

A total of 400 birds have been individually marked with Darvic colour rings (Delestrade 1993). The total population of the area was estimated at 1960 birds in January 1991.

Data collection

Alpine Choughs typically frequent feeding sites in groups (Lovari 1976). In winter, they arrive in the morning and leave late in the afternoon (see Strahm 1961, Voisin 1963). I recorded flock sizes at least three times each day. The daily flock size (daily FS) is defined as the maximum of all foraging flock sizes found that day. Census error was estimated at 10% by comparison with photographs. Monthly flock size (monthly FS) is defined as the average of all daily FS during a given month at a given site.

The proportion of immatures (first-year birds) in the observed flock was recorded, as their leg colour differs to that of adults (Lovari 1981, A. Delestrade, pers. obs.). As it is seldom possible to scan the entire group, I sampled a large part of the group and obtained a proportion for 1 day by summing the samples taken during that day.

Human activity was quantified as the number of people visiting a ski station or picnic area and as the number of inhabitants of a town, assuming that this correlated with the quantity of refuse. This should, however, be viewed as a tentative estimate, as availability of food is unlikely to be the same at a refuse dump and in a town.

to snow cover, than in summer. Larger flocks in winter probably resulted from both aggregation of different summer groups and the occurrence of greater movement (Fig. 2). In winter, all sites frequented in this area (refuse dumps, towns, ski stations, picnic areas) were centres of human activity. These different sites are diverse and heterogeneous, which may explain why there is a strong site effect on flock size. For instance, the largest flock sizes were recorded at a refuse dump when the greatest amount of food was available (Pierotti & Annett 1987). Indeed, site quality was more homogeneous in summer when Alpine Choughs exploited alpine grassland, picnic areas or both. Each group frequented only one site (Fig. 2) because birds are restricted to the vicinity of the nest site. At this season, neither year nor site had significant effects on flock size, suggesting that feeding site attendance was determined principally by nest sites, which do not change between years and are more evenly distributed in the area (A. Delestrade, unpubl.). Seasonal variation in flocks occurs in other corvids whose flock sizes and feeding ranges increase with decreasing food availability and patchier distribution (Dunnet *et al.* 1969, Purchas 1980, Loman 1985, MacDonald & Whelan 1986, Eden 1989).

Comparison of foraging behaviour between immatures and adults

The distribution of immatures differed from that of adults. At first, gathered together after fledging and formed immature groups. By winter, the immatures occurred mainly in the largest flocks and exploited sites with the greatest food supply, such as refuse dumps or towns (Table 1). Very few immatures occurred at other sites. Previous studies have shown that young birds congregate at dumps (Spaans 1971, Pierotti & Annett 1987), where food is readily available and can be more profitably obtained by immatures, probably because they are less efficient than adults in searching for food. Thus, there are marked differences in the distributions of different age classes according to their methods of foraging (Greig *et al.* 1983) and competitive abilities (Milinski & Parker 1991). In April, immature birds left their winter sites and joined adult groups for the summer and so became more homogeneously distributed.

Several factors affect the foraging flock size and structure in the Alpine Chough. This study has established that both the breeding cycle and site-specific factors linked to human activity affected flock size in this species. But the fact that site effects induced the strongest variations on flock size and structure suggests that tourist developments at high altitudes have modified the spatio-temporal distribution of the Alpine Chough in this area.

I thank C. Dendaletche and N. Saint-Lebe for showing constant interest throughout my work. I thank particularly R. Voisin for providing all his unpublished counts from Monthey. I am grateful to G. Jarry, the C.R.B.P.O. and many other people for assistance during catching with canon-nets and ringing. The Comité Scientifique des Réserves de Haute-Savoie and the Réserve Naturelle des Aiguilles Rouges provided financial support for the study. I thank The Station Ornithologique Suisse for providing unpublished counts in Swiss towns. I am grateful to V. Bretagnolle for constructive comments and invaluable statistical advice and J. C. Coulson, D. Holyoak and H. Richner for their helpful comments on the manuscript. I thank G. and H. Gartside for improving the English.

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Table 1. *Sites and their characterisitcs and Alpine Chough flock sizes and composition. Flock size and the proportion of immatures are represented by median values with the number of counts in parentheses*

Site	Type	Altitude (m)	Flock size	Proportion of immatures (%)	Human presence per day
A. Winter sites					
Flaine	Refuse dump	1800	500 (85)	16.5 (60)	3000
Les Carroz	Refuse dump	1200	220 (21)	58 (13)	1300
Martigny	Town	460	110 (36)	12.5 (29)	30,000
Monthey	Town	400	230 (77)	—	14,000
St Maurice	Town	400	100 (13)	0.5 (10)	3500
Le Tour	Ski station	1500	90 (283)	6 (165)	700
Lognan	Ski station	2000	50 (65)	7 (36)	2600
Planpraz	Ski station	2000	80 (41)	9 (19)	2000
Gds Montets	Ski station	3300	30 (30)	2.5 (11)	2000
Vallee Blanche	Picnic area	2000	40 (5)	—	1000
B. Summer sites					
Balme	Grassland (in June)	2000	88 (46)	36.5 (22)	0
Lac Blanc	Picnic area	2350	90 (66)	18 (24)	700
Albert ler	Picnic area	2500	80 (11)	—	300
Gds Montets	Lift station	3300	25 (11)	—	250

Statistical analysis

Flock sizes and proportions of immatures in them typically do not fit normal distributions, and the data are presented as median daily FS and median proportion of immatures. However, the variables are normally distributed when log or arcsin transformed. Thus, I tested for the effects of month, season, year and site on daily and monthly FS using one- or two-way ANOVA on transformed data. Other data were examined with appropriate non-parametric tests.

RESULTS

Flock size

Effects of breeding cycle

Mean daily FS averaged for each month is shown in Figure 1 (irrespective of year and site). It was significantly larger in winter (median = 101, $n = 625$) than in summer (median = 67.5, $n = 206$, $t_{829} = 8.7$, $P < 0.001$; Fig. 1). Daily FS also varied significantly with month, within each season (winter: $F_{5,619} = 12.9$, summer: $F_{5,200} = 8.0$, $P < 0.001$ in both cases). In summer, daily FS increased significantly in August (fledging period) compared with July and September ($F_{2,120} = 19.1$, $P < 0.001$; Newman-Keuls test only significant between July and August, and August and September), because the birds gathered in larger flocks after the fledging period.

Site effects

In the study area, the choughs were not evenly distributed, and only ten sites were regularly visited by choughs (Fig. 2). Moreover, flocks were not evenly distributed; when all years and months were combined, there was a strong site effect on daily FS ($F_{12,818} = 65.8$, $P < 0.001$). The same situation arose when analysing the winter ($F_{10,614} = 92.7$, $P < 0.001$) or summer ($F_{11,194} = 6.5$, $P < 0.001$) seasons.

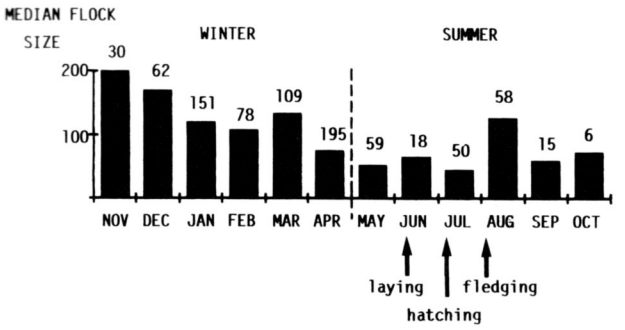

Figure 1. Monthly flock size of Alpine Choughs during the year. Number of counts shown above each column.

Data were analysed by two-way ANOVA, with sites and years or sites and months as the two factors. Significant month effects were detected for daily FS in both winter and summer, but site effects were twice as large as month effects (comparison of F-values in Table 2). A small but significant interaction between these two factors appeared in summer, the result of birds gathering at the fledging period (August) at only a few sites. In winter, both years and sites had highly significant effects on monthly FS (Table 2), with the latter factor again having the strongest effect. Conversely, in summer, neither year nor site had a significant effect (Table 2). Thus, site-specific factors induced more variation in flock size than either month or year (Table 2), especially in winter. In particular, flock sizes were larger at refuse dumps (50–900 individuals) or towns (15–900) than at ski stations (10–300) (Table 1), which suggested that flock size was related to food availability. Indeed, a significant positive correlation appeared between average daily human activity and Alpine Chough flock sizes at a given site (years and months averaged) ($r_{15} = 0.57$, $P < 0.02$). Moreover, an experimental trial conducted between January and April 1992 revealed that an artificial increase of food supply (4–20 kg of apples) attracted 67% more Alpine Choughs (A. Delestrade, unpubl.). Flock size was larger on days with increased food supply than on days without additional food (median = 225 [n = 19] v 120 [n = 32], $t_{49} = 3.26$, $P < 0.01$).

Flock structure

Proportion of immatures

The proportion of immature birds was significantly higher in summer than in winter (median = 21% in summer and

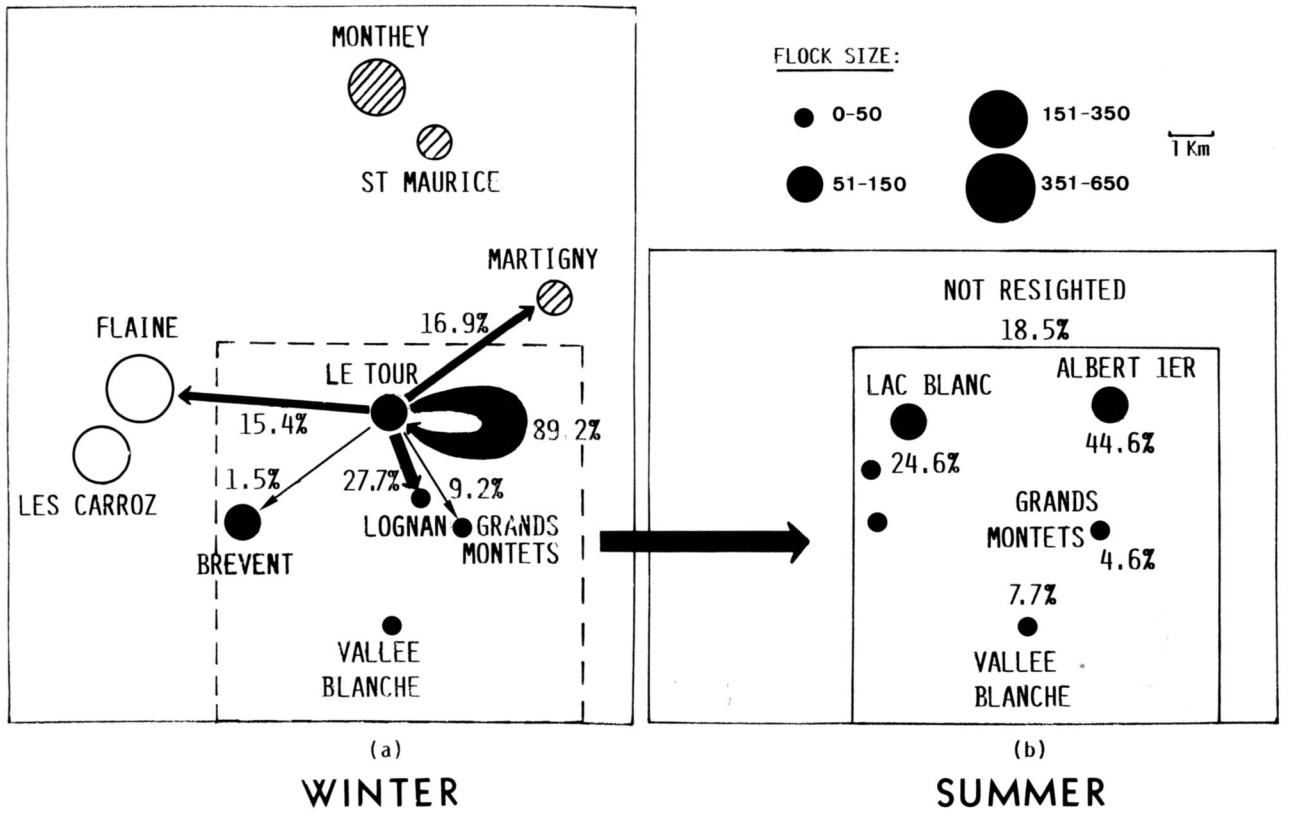

Figure 2. Distribution and size (median value) of foraging flocks of Alpine Choughs in the study area. (a) In winter. The percentage represents the proportion of resighted birds amongst birds caught at Le Tour; (b) In summer. The percentage represents the summer distribution of birds caught at Le Tour in winter. Refuse dumps (open circles), towns (hatched circles) and ski stations or picnic areas (closed circles) are distinguished.

Table 2. *Site, annual and monthly effects on flock size and proportion of immature Alpine Choughs (on daily FS for month × site, on monthly FS for year × site) (two-way ANOVA)*

	Season	Factors	d.f.	*F*	*P*
A. Flock size					
Monthly FS	Winter	Year	3	16.3	<0.001
		Site	4	58.0	<0.001
		Year × site	12	2.8	n.s.
Daily FS	Winter	Month	2	30.2	<0.001
		Site	4	68.2	<0.001
		Month × site	8	5.05	n.s.
Monthly FS	Summer	Year	3	0.42	n.s.
		Site	1	1.92	n.s.
		Year × site	3	0	n.s.
Daily FS	Summer	Month	3	18.3	<0.001
		Site	2	35.3	<0.001
		Month × site	6	7.75	<0.001
B. Proportion of immatures					
	Winter	Year	3	20.3	<0.001
		Site	3	42.3	<0.001
		Year × site	9	11.3	<0.001
	Winter	Month	4	4.22	<0.002
		Site	3	28.0	<0.001
		Month × site	12	0.91	n.s.
	Summer	Year	3	36.6	<0.001
		Site	2	27.4	<0.001
		Year × site	6	0	n.s.
	Summer	Month	3	4.97	<0.004[1]
		Site	2	5.96	<0.004[1]

[1] One-way ANOVA.

8% in winter, $t_{362} = 8.1$, $P < 0.001$), suggesting that many immatures leave the study area in winter. The proportion of immatures differed significantly between month and site in winter and in summer, with stronger site effect in winter (*F*-values in Table 2).

Similarly, both year and site had significant effects on the proportion of immatures in both summer and winter (Table 2), but the situation is more complex in winter, as a significant interaction existed between site and year (Table 2). This resulted from the fact that immatures did not frequent the same sites in different years: 25.5% ($n = 12$) of them were observed at Flaine in 1989, 26% ($n = 19$) in 1992 but only 2% ($n = 20$) in 1991. In 1991, immature proportion increased at Martigny (19%, $n = 10$).

Thus, the proportion of immatures is strongly influenced by site, but in summer there was more year-to-year variation in the proportion. The highest proportions of immatures were observed in winter at refuse dumps or towns (Table 1). Lastly, a positive but weak correlation existed between immature proportion and daily FS in winter ($r_{287} = 0.26$, $P < 0.001$) but not in summer ($r_{75} = 0.185$, n.s.).

Individual fidelity to their groups

Site fidelity was analysed for 65 adult Alpine Choughs that were ringed at Le Tour. In winter, 89% of these birds were resighted at least once each year at Le Tour, indicating that birds are faithful to their main wintering site (Fig. 2a), but only 29% were resighted exclusively at Le Tour. Thus, a significant proportion of birds attended other winter feeding sites (see percentages in Fig. 2a). A completely different situation existed in summer for the same individuals: each bird was resighted exclusively at one site only (see proportions in Fig. 2b), presumably near the nest site. This suggested that the winter groups at Le Tour resulted from the amalgamation of different summer groups (Fig. 2).

DISCUSSION

Site *v* breeding cycle effects on flock size

Larger foraging flocks were observed in winter, when natural food availability was low and patchily distributed due

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Submitted 2 February 1993; revision accepted 29 May 1993