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Vocalizations and morphology: interpreting the divergence among populations of Chough *Pyrrhocorax pyrrhocorax* and Alpine Chough *P. graculus*

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Capsule Differences in vocalizations among populations are mostly explained on morphological bases, but historical factors may have played a significant role in differentiation processes.

Aims To investigate the relationships among vocal and morphological variation in two corvids: Chough and Alpine Chough.

Methods We used data from 11 populations of Chough and seven populations of Alpine Chough spanning the Palearctic distribution of the two species. Three data sets (morphometry, spectrotemporal parameters of trill calls and acoustic repertoire) were analysed and their variation compared with uni- and multivariate techniques.

Results In both species, morphological differences among populations were correlated to spectrotemporal variation of trills; in particular, frequencies of calls were negatively correlated to wing length (an indicator of body size). By considering only co-existing populations of the two species, the magnitude of morphological and spectrotemporal divergence was similar.

Conclusions In both species, birds from populations with similar morphology uttered similar call types and trills with close spectrotemporal features. In particular, larger-sized populations, as expressed by wing length, emitted lower pitched calls. However, the fact that dissimilarities in repertoire and morphology were correlated cannot be explained only by appealing to functional explanations, as the observed intraspecific morphological variability does not seem to be high enough to promote consistent changes in the pool of calls. In this case, historical factors might have contributed to the present pattern of differentiation.

Morphology and vocalizations are often used and combined to evaluate the degree of geographic differentiation of natural populations of passerines (James 1983, Mundinger 1982, Kroodsma *et al.* 1984, Merilä & Björklund 1999). Here, we consider and compare patterns of morphological and acoustic divergence in two species of Corvids: Chough *Pyrrhocorax pyrrhocorax* and Alpine Chough *P. graculus*. Both are distributed throughout the Palearctic, with many disjunct populations in isolated continental areas or on islands. Isolated populations of Chough, for instance, occur in Ethiopia, Canaries, Britain, Ireland, Brittany and most Mediterranean islands; in the case of Alpine Chough, secluded geographical nuclei are found on some Mediterranean islands and in Tunisia (Madge & Burn 1994, Maumary *et al.* 1998). Several factors might have contributed to the present pattern of trait geographical variation in the *Pyrrhocorax* species. Natural selection might have favoured morphological divergence of population through local adaptation to differing environmental conditions: a clinal change in size and shape was found, and larger birds with shorter extremities inhabited colder and more arid regions possibly because the low ratio of respiratory surface to body size reduces heat loss (Laiolo & Rolando 2001).

The spectral parameters of the commonest calls in both *Pyrrhocorax* species also varied across latitude and

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longitude (Laiolo *et al.* 2001a). A negative relationship between body mass and frequencies of signals has been demonstrated below and above the species level in several bird species: larger birds are supposed to emit calls with a lower fundamental frequency because of their larger syrinxes (Ryan & Brenowitz 1985). It has also been shown that the length of oropharyngeal tubes and that of its distal part (the bill) can affect call pitch (Hoese *et al.* 2000, Podos 2001, Laiolo & Rolando 2003).

We compare morphometry, the spectrotemporal features of trill calls and the repertoire of 11 populations of Chough and seven populations of Alpine Chough in Europe, Asia and Africa. Data from some of these populations have already been analysed separately (Laiolo & Rolando 2001, Laiolo *et al.* 2001a, Laiolo *et al.* 2001b) but the data sets have not been compared. We aim (1) to assess whether populations with similar morphometry were also similar in bioacoustics, (2) to test for the correlation between body size, bill length and call frequencies, (3) to compare the magnitude of morphometric and acoustic differentiation within and between species.

METHODS

Sampling and measurements

Morphological measurements from 195 museum study skins of adult Choughs and 161 skins of adult Alpine Choughs were used in this study. Bill length (BL), bill depth (BD), bill width (BW), tarsus (TRS), tail length (TL) and wing length (WL) were measured using the standard methods described by Laiolo & Rolando (2001). Spectrotemporal measurements from 1736 Chough and 468 Alpine Chough trill calls were obtained; all trills were recorded by the authors with the instruments described in Laiolo *et al.*(2001a). We measured six acoustic parameters in the trill call of the Chough and 20 in the trill call of the Alpine Chough. All morphometric and acoustic measurements were taken by the same researcher (P.L.).

The term vocal repertoire is used to describe the list of call types uttered. We included in the analysis only call types recorded over five times. Call types were classified by inspecting sonograms by eye. Visual inspection of sonograms was carried out by the same investigator (P.L.) using strict criteria, thus avoiding any interobserver bias. See Laiolo *et al.* (2001b) for sonograms of call types from the two species and for confidence limits of repertoire size.

Only populations contributing at least four individuals were included in the analyses. Overall, data from the following 11 populations of Chough were considered: Himalayas (northeastern Nepal), central Asia (Tian Shan, Kyrghyzstan), Ethiopia (Bale and Simien mountains), Morocco (High Atlas), Canaries (La Palma), Sicily, Crete, Apennines, western Alps, Scotland (Islay), Spain (Los Monegros).

In the case of Alpine Chough, seven populations were considered: Himalayas (northeastern Nepal), central Asia (Tian Shan, Kyrghyzstan), Morocco (High Atlas), Pyrenees, Apennines, eastern Alps, west-central (hereafter western) Alps.

Comparing calls recorded in the fields with morphological measurements taken on museum skins, we supposed that the morphological features we looked at have not changed in such a short time to produce a bias in the comparison between morphometry and call parameters. To avoid problems of pseudoreplication, all analyses were carried out using population mean values of morphometry and spectrotemporal data set (Appendix). In this study the sex of the calling bird was rarely known, but there is no reason to suspect that recordings were sex-biased since many recordings were generally obtained in each locality, mostly from mates alternating their calls. In the case of museum skins, females comprised 51% of Chough and 48% of the congener (range within populations of Chough: 25–67%, Alpine Chough: 30–70%).

Data analysis

Relationships between body size, bill length and call frequencies

In both species, the relationships between trill frequencies (we chose the peak fundamental (FF) and the peak carrying frequency (FM) as representative of spectral features) versus wing length (indicator of body size) and bill length were analysed through partial correlation tests on log-transformed data. These correlation analyses were carried out to eliminate the effects of possible inter-correlations between variables (namely between bill and wing length). There was one mean value for each population sampled.

Comparisons among morphometry and bioacoustic dissimilarities

In both species, three dissimilarity matrices were produced, one for each data set (morphometrical measurements, spectrotemporal measurements, acoustic repertoire). In the case of continuous measurements (morphometry and spectrotemporal variables) differences between each pair of populations were expressed as Euclidean distances (Sneath & Sokal 1973). In the case of call repertoire, similarity was calculated for each species by scoring the presence (1) or absence (0) of a call type in the pool of a population: a binary matrix thus resulted. In keeping with Lynch & Baker (1994), we used Jaccard's coefficient (Sneath & Sokal 1973) to calculate the level of call sharing and then converted it to a distance measure by the equation $D_{ij} = -\ln(J_{ij})$, where J_{ij} is the Jaccard's coefficient from populations i and j, and D_{ij} is their respective distance. Because pairwise elements of distance matrices are not independent, and thus violate the basic assumptions associated with standard tests of significance (Smouse *et al.* 1986), the relationships between morphometric and acoustic dissimilarities were tested by Spearman's rank-order correlations on dissimilarity matrices. These tests evaluated the prediction that distances of the three data sets were correlated.

Magnitude of morphometric and acoustic differentiation within and between species

To test for inter-specific differences in the magnitude of population differentiation in trills and morphometry (data sets with quantitative variables), we analysed the pattern of variability using the populations of the two species that co-existed in the same regions. The analysis was therefore restricted to the western Alps, Apennines, High Atlas, Himalayas and Tian Shan populations. Regarding the physical properties of trills, we limited analyses to the variables that were measured in both species' trills: duration of the call D, duration of a sinusoidal modulation cycle (DP in Chough, DH1 in Alpine Chough), peak fundamental frequency (FF), peak carrying frequency (FM), rate of sinusoidal modulation (S). By considering the same variables of both species, we reduced bias deriving from the use of different sets of acoustic properties. The coefficient of variation CV (SD/mean × 100) was used as a measure of variation among populations. CVs were computed for the six morphological measures and for the five measures of time and frequency characters in the trill call. Inter-specific differences in each data set were tested with Wilcoxon matched pairs test, whereas intra-specific differences between data sets were tested with Mann–Whitney *U*-tests.

RESULTS

The acoustic variables measured are shown in Figs 1–2. The mean values of the variables and the number of call types per population are given in the Appendix.

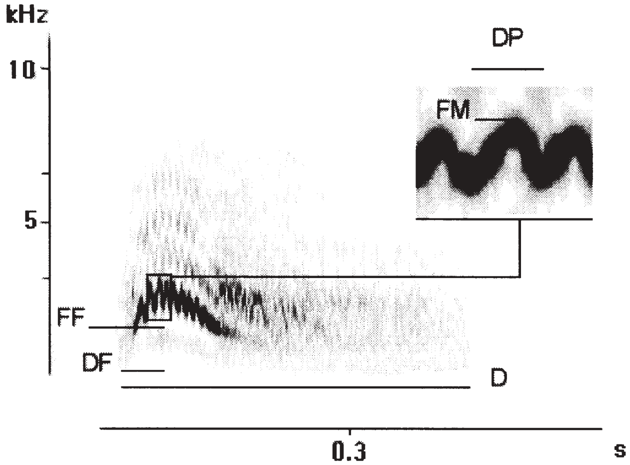

Figure 1. Spectrograms of Chough trill. Spectrotemporal parameters measured: D, duration of the whole call; DF, duration of the ascending limb of the call; DP, duration of the sinusoidal frequency modulation cycle; FF, fundamental frequency, measured at the highest peak; FM, carrying frequency, measured at the highest peak; S, frequency of sinusoidal modulation (number of frequency peaks/s).

Chough

Relationships between body size, bill length and call frequencies

The peak carrying frequency and bill length (partial correlation $r = -0.61$, $n = 11$ populations, $P = 0.06$) and wing length (partial correlation $r = -0.60$, $n = 11$, $P = 0.06$) approached a significant negative correlation.

Comparisons among morphometry and bioacoustic dissimilarities

Intra-specific differences in the spectro-temporal features of trill were significantly correlated to morphometrical differences (Spearman's $r = 0.35$, $n = 55$ pairwise comparisons, $P < 0.01$; Fig. 3). Repertoire dissimilarities were significantly and positively correlated to differences in trills ($r = 0.53$, $n = 55$ comparisons, $P < 0.001$) and morphometry (Spearman's $r = 0.45$, $n = 55$ pairwise comparisons, $P < 0.001$; Fig. 3).

Relationships among populations

Populations significantly differed in all their acoustic parameters (one-way ANOVAs, all P values < 0.001) and in five out of six morphological variables ($P > 0.05$ for tail length, $P < 0.01$ for the other variables). Population relationships were highlighted by means of cluster analysis (UPGMA method). We derived a single matrix of Euclidean distances from morphometry and trills; data on repertoire were not included because their matrix was qualitative (presence/absence of call

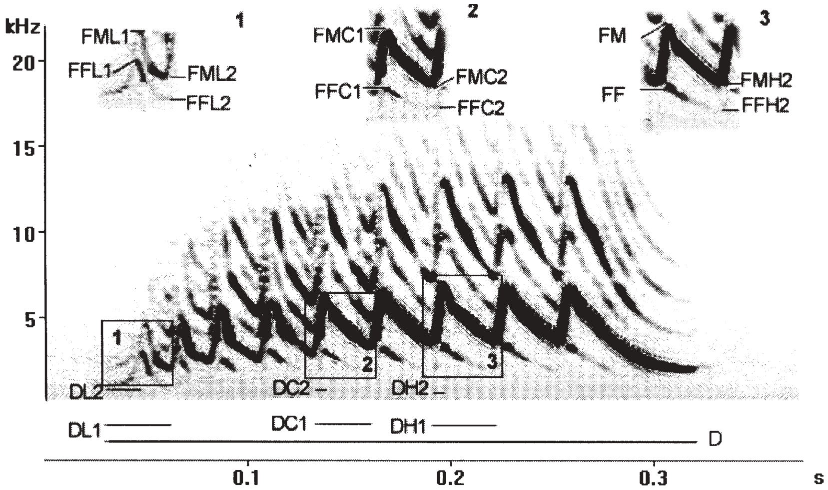

Figure 2. Spectrograms of Alpine Chough trill. Boxes 1, 2 and 3 indicate the lowest, central and highest peak of the trill. Spectrotemporal parameters measured: D, duration of the whole call; DC1, duration of the central frequency peak; DC2, duration of the ascending limb of the central frequency peak; DL1, duration of the lowest frequency peak; DL2, duration of the ascending limb of the lowest frequency peak; DH1, duration of the highest frequency peak; DH2, duration of the ascending limb of the highest frequency peak; FFL1, peak fundamental frequency measured at the lowest frequency peak of the signal (box 1); FFL2, minimum fundamental frequency after the lowest frequency peak of the signal (box 1); FML1, peak carrying frequency measured at the lowest frequency peak of the signal (box 1); FML2, minimum carrying frequency after the lowest frequency peak of the signal (box 1); FFC1, peak fundamental frequency measured at the central frequency peak of the signal (box 2); FFC2, minimum fundamental frequency after the central frequency peak of the signal (box 2); FMC1, peak carrying frequency measured in the central frequency peak of the signal (box 2); FMC2, minimum carrying frequency after the central frequency peak of the signal (box 2); FF, peak fundamental frequency measured at the highest frequency peak of the signal (box 3); FFH2, minimum fundamental frequency after the highest frequency peak of the signal (box 3); FM, peak carrying frequency measured at the highest frequency peak of the signal (box 3); FMH2, minimum carrying frequency after the highest frequency peak of the signal (box 3); S, frequency of modulation (number of frequency peaks/s).

types). As shown in Fig. 4, populations from Ethiopia and Asia were well separated from the cluster of Europe and north Africa. This latter group split into two: southern Italy populations clumped with Atlas ones, whereas Canary Island, Scotland and Crete joined the group of continental Europe (Spain plus Alps).

Alpine Chough

Relationships between body size, bill length and call frequencies

Peak carrying frequency was significantly and negatively correlated to wing length (partial correlation $r = -0.76$, $n = 7$ populations, $P < 0.05$) and nearly significantly correlated to bill length (opposite to Chough, we found a positive trend: $r = 0.64$, $n = 7$, $P = 0.06$). The correlations between peak fundamental frequency versus wing and bill length only approached significance ($P = 0.055$ and 0.09 respectively).

Comparisons among morphometry and bioacoustic dissimilarities

Intra-specific differences in the spectrotemporal features of trill were significantly correlated to morphometric differences (Spearman's $r = 0.51$, $n = 21$ pairwise comparisons, $P < 0.05$; Fig. 3). Repertoire dissimilarity was significantly and positively correlated only to morphometric dissimilarity (Spearman's $r = 0.78$, $n = 21$ pairwise comparisons, $P < 0.001$; Fig. 3).

Relationships among populations

Populations significantly differed in 16 acoustic parameters (one-way ANOVAs, 16 P values < 0.01; differences were not significant in the case of the duration measures DL1, DL2, DH1, DH2, see Fig. 2) and in five out of six morphological variables ($P > 0.05$ for tail length, $P < 0.01$ for the other variables). As in the case of Chough, we clumped the two continuous and correlated data sets to produce a single dendrogram with cluster analysis (Fig. 4). A clear longitudinal gradient appeared and three groups were formed: eastern populations (Tian Shan-Himalayas), western populations (Pyrenees-High Atlas) and central Europe populations (two Alpine populations and Apennines).

Pattern of variation in syntopy: magnitude of morphometric and acoustic differentiation within and between species

Considering the six populations of Chough and Alpine

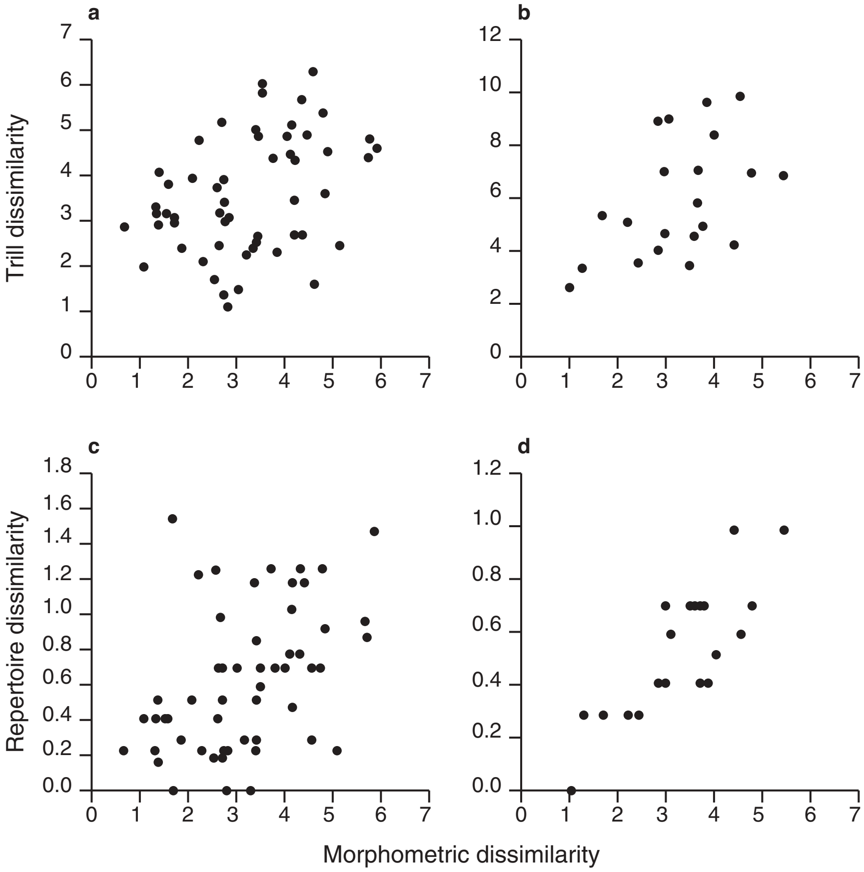

Figure 3. Pairwise relationships between trill and repertoire dissimilarity versus morphometric dissimilarities. a, c, Chough; b, d, Alpine Chough.

Choughs co-existing in the same localities, no significant inter-specific difference resulted in the degree of variation of morphometry and trills (Wilcoxon tests not significant). In both species, trill acoustic features varied to a greater extent than morphological characters (Chough: CV of acoustic parameters = 17.3% ± 7.0 sd, $n = 5$ parameters; CV of morphometry parameters = 5.5% ± 1.7 sd, $n = 6$ parameters; comparison between data set: Mann–Whitney $U = 0$, $z = -2.9$, $P < 0.05$; Alpine Chough: CV of acoustic parameters = 14.2% ± 6.2 sd, $n = 5$ parameters; CV of morphometry parameters = 4.8% ± 0.70 sd, $n = 6$ parameters; comparison between data set: Mann–Whitney $U = 1$, $z = -2.7$, $P < 0.05$).

DISCUSSION

This study compares morphology and bioacoustics of several populations of Chough and Alpine Choughs in an effort to describe the patterns of intra- and inter-specific variability. In both species, birds from populations with similar morphology utter similar call types and trills with close spectrotemporal features. In particular, in both species larger-sized populations, as expressed by wing length, emit lower pitched calls (although in Chough the relationship only approaches significance). This finding supports the hypothesis of body size–frequency correlation shown in many studies (Bowman 1979, Ryan & Brenowitz 1985). Laiolo & Rolando (2001) hypothesized that the evolution of body size in these corvids might have been driven by natural selection favouring larger birds in colder climates. In the light of this assumption, selective forces acting on morphology and deriving from local ecological conditions could have enhanced trill variation, at least in its spectral features. The relationships between frequencies and bill length are less clear, as nearly significant but opposite trends occurred in the two species; a larger sample of populations is needed to produce clearer results.

The fact that dissimilarities in repertoire and morphology were correlated cannot be explained only by appealing to functional explanations, as an intra-specific morphological variability averaging 5% does

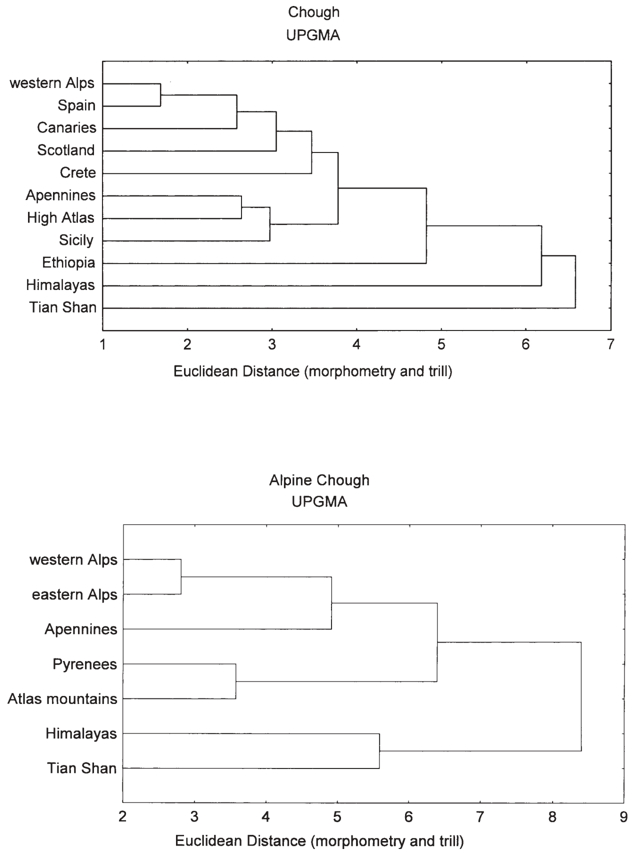

Figure 4. Cluster analysis based on morphology and trill spectrotemporal features.

not seem to be high enough to promote consistent changes in the pool of calls, and cause the origin/loss of call types. In this case, historical factors (i.e. origin from a common ancestor) might have contributed to the present pattern of differentiation. Laiolo & Rolando (2001) and Laiolo *et al.* (2001a, 2001b) showed that intra-specific divergences both in morphometry and bioacoustics were significantly correlated to geographical distances among populations, which could indicate that dispersal probably occurred between close populations, and thus more closely situated populations tend to have a more similar morphology and communication systems. This is also confirmed by the grouping of populations produced by cluster analysis: Europe–North African, Asiatic and Ethiopian Choughs have probably been segregated for a long time, and their morphometry and acoustic communication systems had time to diverge to a great extent.

The lack of interspecific differences in the magnitude of divergence of the different data sets suggests that the rate of populations' divergence was comparable in the two species. This could be the effect of chance or, alternatively, the two species might have responded in a similar way to equivalent forces promoting differentiation (natural selection, constraints, drift, etc.). The fact that the degree of variation of morphometric features was lower than that of acoustic ones might be the consequence of stronger eco-physiological constrains acting on the first set of characters.

In the case of Chough, poor genetic differentiation among populations was recorded (Giannino 1999). In particular, no clear pattern of geographical variation was highlighted, as differences in mtDNA sequences were not associated to geographical location of populations. This finding does not agree with the patterns observed in morphometry (Laiolo & Rolando 2001), trills (Laiolo *et al.* 2001a) and repertoire (Laiolo *et al.* 2001b). Several studies have documented disconnection between haplotypes and morphological–vocal evidence (Zink & Dittmann 1993, Questiau *et al.* 1999). It has been suggested that morphology might evolve faster than mtDNA, as selection, or rapid adaptation to the local environment, can act rapidly in the differentiation of morphs (Questiau *et al.* 1998, Questiau *et al.* 1999). In the case of acoustic communication systems, whose variation seems to be higher than that of other traits (this study, Laiolo *et al.* 2001b), cultural evolution (i.e. non-genetic trait transmission) might also have enhanced differentiation.

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APPENDIX

Mean values of population morphometric and acoustic measures. For acronyms see Figs 1 & 2.

Chough

		Morphometric variables						Repertoire	Trill acoustic variables					
Population	No. of museum specimens	BL (cm)	BD (cm)	BW (cm)	TRS (cm)	TL (cm)	WL (cm)	No. of call types*	D (s)	DF (s)	DP (s)	FF (kHz)	FM (kHz)	S (No. of peaks/s)
Scotland	7	4.79	1.40	1.63	5.01	13.60	26.74	4	0.43	0.048	0.011	1.474	2.803	93.16
Western Alps	23	4.51	1.40	1.61	5.05	14.16	28.52	4	0.35	0.026	0.012	1.524	2.953	95.09
Apennines	4	4.96	1.54	1.72	5.41	14.40	29.55	3	0.37	0.027	0.012	1.384	2.666	92.27
Sicily	4	4.89	1.62	1.61	5.31	13.68	27.88	5	0.38	0.029	0.012	1.303	2.461	85.28
Crete	6	3.93	1.28	1.70	5.02	14.38	27.62	4	0.34	0.031	0.012	1.444	2.921	90.71
Canaries	8	4.84	1.41	1.63	5.01	13.85	27.58	7	0.34	0.032	0.011	1.333	2.550	93.90
Spain	12	4.53	1.40	1.65	5.24	13.87	28.18	6	0.37	0.025	0.012	1.395	2.857	102.9
High Atlas	25	4.74	1.47	1.66	5.14	14.42	28.99	4	0.30	0.028	0.015	1.362	2.496	84.10
Ethiopia	5	5.01	1.46	1.74	5.30	14.98	31.24	14	0.33	0.052	0.011	1.363	2.350	90.28
Himalayas	73	4.77	1.46	1.66	5.44	16.25	30.86	8	0.15	0.037	0.013	1.015	2.304	69.21
Tian Shan	28	4.25	1.30	1.56	4.49	15.96	29.13	13	0.29	0.047	0.018	1.330	2.709	56.46

Alpine Chough

		Morphometric variables						Repertoire	Trill acoustic variables					
Population	No. of museum specimens	BL (cm)	BD (cm)	BW (cm)	TRS (cm)	TL (cm)	WL (cm)	No. of call types*	D (s)	DC1 (s)	DC2 (s)	DL1 (s)	DL2 (s)	DH1 (s)
Eastern Alps	39	2.20	1.12	1.43	4.21	15.86	25.75	4	0.21	0.030	0.009	0.031	0.008	0.023
Western Alps	70	2.22	1.11	1.40	4.25	16.46	26.30	4	0.23	0.028	0.008	0.030	0.008	0.022
Apennines	4	2.18	1.05	1.33	4.07	16.15	25.25	3	0.20	0.030	0.008	0.031	0.008	0.030
High Atlas	11	2.42	1.19	1.48	4.56	16.47	26.55	8	0.21	0.029	0.008	0.029	0.009	0.027
Pyrenees	7	2.37	1.14	1.49	4.54	16.86	26.42	6	0.25	0.031	0.008	0.030	0.008	0.032
Himalayas	17	2.29	1.06	1.45	4.33	18.06	28.36	8	0.20	0.027	0.011	0.032	0.009	0.025
Tian Shan	13	2.29	1.08	1.39	4.12	18.32	28.12	6	0.20	0.031	0.010	0.033	0.010	0.038

	Trill acoustic variables													
	DH2 (s)	FFC1 (kHz)	FMC1 (kHz)	FFC2 (kHz)	FMC2 (kHz)	FF (kHz)	FM (kHz)	FFH2 (kHz)	FMH2 (kHz)	FFL1 (kHz)	FML1 (kHz)	FFL2 (kHz)	FML2 (kHz)	S (No. of peaks/s)
Eastern Alps	0.008	2.27	4.60	1.22	2.49	2.62	5.02	1.32	2.61	1.68	3.16	1.01	1.74	36.31
Western Alps	0.008	2.36	4.74	1.39	2.66	2.64	5.04	1.46	2.69	1.84	3.48	1.05	1.79	38.32
Apennines	0.009	1.90	3.98	1.17	1.96	2.32	4.31	1.19	2.05	1.54	3.00	0.89	1.46	34.53
High Atlas	0.008	2.63	5.14	1.54	2.82	2.75	5.34	1.52	2.77	2.02	3.72	1.29	2.17	36.81
Pyrenees	0.008	2.60	5.26	1.44	2.77	2.92	5.60	1.47	2.68	2.16	3.85	1.28	1.94	34.69
Himalayas	0.010	2.04	3.63	1.10	1.83	2.26	3.96	1.10	1.75	1.59	2.79	0.94	1.50	35.35
Tian Shan	0.009	1.78	3.60	1.12	2.01	1.98	3.85	1.11	1.94	1.27	2.55	0.81	1.36	29.66

*Only calls recorded more than five times were included.