

Geographic diversification in the call repertoire of the genus *Pyrrhonorax* (Aves, Corvidae)

Paola Laiolo, Antonio Rolando, Anne Delestrade, and Augusto De Sanctis

Abstract: We analysed the call repertoires of the Red-billed Chough (*Pyrrhonorax pyrrhonorax*) and the Alpine Chough (*Pyrrhonorax graculus*) across three continents (Europe, Asia, and Africa) for intraspecific and interspecific differences in call-repertoire size and discuss the factors that could have promoted its evolution. The overall call repertoire of the Red-billed Chough was twice as large as that of the Alpine Chough, but the number of calls recorded in each population did not differ significantly between the two species. The greater fragmentation of the range of the Red-billed Chough possibly induced its remarkable call-repertoire diversification. Some populations (i.e., those from Ethiopia, Central Asia, Canaries) had a peculiar call repertoire that overlapped very little with those from other regions; consequently, the overall numbers of call types within the species were heavily influenced by these unusual populations and were very large. The call-repertoire size and call-repertoire similarity of populations of both species were affected and constrained by geographic distance. More closely situated or continental populations tended to have a more similar pool of calls (this is probably due to mingling among close populations).

Résumé : Nous avons analysé le répertoire des cris chez le Crave à bec rouge (*Pyrrhonorax pyrrhonorax*) et le Chocard à bec jaune (*Pyrrhonorax graculus*) sur trois continents (Europe, Asie et Afrique) par estimation des différences intraspécifiques et interspécifiques dans l'importance du répertoire des cris et par examen des facteurs qui peuvent avoir favorisé son évolution. Dans l'ensemble, le répertoire des cris du Crave à bec rouge est deux fois plus important que celui du Chocard à bec jaune, mais le nombre de cris enregistrés chez chacune des populations ne diffère pas significativement chez les deux espèces. La fragmentation plus importante de l'aire de répartition du Crave à bec rouge est sans doute responsable de la diversification remarquable de son répertoire. Certaines populations (i.e., celles de l'Éthiopie, de l'Asie centrale et des îles Canaries) ont des répertoires bizarres avec très peu de chevauchement avec des oiseaux d'autres régions; en conséquence, le nombre global de types de cris au sein de l'espèce est fortement influencé par ces populations particulières et est donc très élevé. L'importance du répertoire et la similarité du répertoire chez les populations des deux espèces sont affectées et restreintes par la distance géographique. Les populations proches les unes des autres ou les populations continentales ont tendance à avoir un répertoire plus semblable (probablement à cause des mélanges entre populations rapprochées).

[Traduit par la Rédaction]

Introduction

Many studies have focused on micro- and macro-geographical changes in song repertoire and song complexity in songbirds (Kroodsmas 1981; Mundinger 1982; Lynch and Baker 1994; Lang and Barlow 1997). Studies of avian vocal communication usually distinguish between songs (which are long, complex utterances) and calls (which are briefer and simpler sounds) (Thielcke 1970).

To date, patterns and processes of call variation and evolution (either genetic or cultural, i.e., developed through a learning process) have been given little consideration in corvids (Martens 1996). Remarkably, no study has pointed to call "regiolects", i.e., the geographical dialects or call variants that encompass extensive subpopulations within a large range (Tembrock 1984). The repertoire of corvids is normally partitioned into rather discrete call categories, and different call types are used in different contexts; the multisyllable song typical of most oscines is normally lacking (Goodwin 1986; Cramp and Perrins 1994).

The term repertoire usually refers to a set of song variants that are often functionally analogous (Kroodsmas 1982). Dealing with calls, some problems in terminology can arise. In the interest of clarity, our use of repertoire (or call repertoire) describes the list of call types uttered by a species. Throughout this paper we assume that most factors which have been found to affect song divergence would be responsible for call variation as well, although few studies have addressed the latter. We hypothesize (and would expect) that calls exhibit patterns of diversification similar to those of single syllables in songs, which have been proved to be the most conservative unit of a song (Lynch et al. 1989; Burnell 1998). In fact, longer songs (multisyllables) are more likely

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P. Laiolo¹ and A. Rolando. Dipartimento di Biologia Animale e dell'Uomo, Via Accademia Albertina 17, 10123 Turin, Italy.

A. Delestrade. Centre de recherches sur les Ecosystèmes d'Altitude, 400 Route du Tour, Montroc, 74400 Chamonix, France.

A. De Sanctis. Abruzzo Centre for Faunal Research (C.A.R.F), c/o World Wildlife Fund – Abruzzo, C.P. 317, 65100 Pescara, Italy.

¹Corresponding author (e-mail: laiolo@dba.unito.it).

to be broken down and recombined than single-syllable ones (Lynch et al. 1989). Based on early experiments on ontogeny, the hypothesis was developed that songs are learned, while calls form independently of learning (Thorpe 1958). This assumption has now become outmoded, since cases of learned calls have been documented for various taxa (for a review see Baptista 1996)

In this paper we analyse the patterns of geographical differentiation in the call repertoire of the Red-billed Chough (*Pyrrhocorax pyrrhocorax*) and the Alpine Chough (*Pyrrhocorax graculus*), focusing on intraspecific and interspecific differences in call-repertoire size. We also analysed the relationship between call-repertoire similarity and geographic distance among populations, testing the prediction that call types of closer populations are more similar than those of remote ones.

Both species are highly gregarious and occur in open rocky and grassy habitat, chiefly in mountainous regions, although the Red-billed Chough also inhabits coastal cliffs (Madge and Burn 1994). They are widely distributed throughout the Palearctic Region but have many disjunct populations in isolated continental areas or on islands, an attribute that might promote geographic differentiation. Isolated populations of the Red-billed Chough, for instance, occur in Ethiopia, Canaries, British Isles, Brittany, and most Mediterranean islands. In the case of the Alpine Chough, secluded geographical nuclei are found on some Mediterranean islands and in Tunisia (Madge and Burn 1994; Maumary et al. 1998). Previous studies carried out on these species proved that geographical variation does occur, both in morphometrics and in the acoustic features of the commonest call types. A clinal change in morphometric traits and a variation in body size conforming to Bergmann's and Allen's rules were demonstrated (Laiolo and Rolando 2001), as well as a parallel divergence in the spectrotemporal features of the commonest calls, supporting the reverse relationship between body size and frequencies (Laiolo et al. 2001). There is evidence that some calls in these species are learned and follow a particular developmental pathway (Cramp and Perrins 1994; Laiolo et al. 2000): such nongenetic transmission across generations can become a powerful source of variation.

The cultural-evolution model predicts that errors during the learning process are among the main factors causing song differentiation (Lynch and Baker 1994). Cultural mutations are imperfect song copies, probably resulting from limited exposure to the models (Jenkins 1978; Lynch 1996). Such changes might occur during the learning processes and, if they persist, divergence among populations will eventually be enhanced. Populations that are separated tend to diverge provided that the level of migration and its homogenizing effect are limited. Other factors, not included in the previous model, can become important sources of variation. For instance, differences in social and acoustic environment experienced by birds can result in differentiation through a different adaptive response in their vocal behaviour (Wiley and Richards 1982).

In the Red-billed Chough and the Alpine Chough, call diversification is not likely to be affected by environmental factors, since these species inhabit roughly the same habitat (open fields interspersed with cliffs) throughout their ranges. Altitude might affect the spectrotemporal features of calls,

but we suppose that its effect on the whole call repertoire is weaker. Conversely, social factors cannot be ruled out: population density, which was different in the areas we sampled (Bignal 1994, P. Laiolo, personal observation), could have influenced the social environment and, in turn, call-repertoire complexity (Kroodsma 1982).

Methods

From 1996 to 1999, we recorded Red-billed Chough and Alpine Chough calls from 12 and 11 localities, respectively, spanning the Palearctic range of the species from north to south and from east to west (Fig. 1). Most recordings were made in late spring – summer, with the exceptions of Sardinia (October), Canaries (November), and Ethiopia (December). Birds were recorded in the open field and only when they were within view (5–20 m). During fieldwork we used a SONY TC-D7, a SONY TC-D8, or a TASCAM DA-P1 (TEAC Professional Division) tape recorder and a SONY ECM 672 (frequency response 20 – 20 000 Hz (± 1.0 dB)), a SENNHEISER ME67 (frequency response 50 – 20 000 Hz (± 2.5 dB)), or a SENNHEISER ME88 (frequency response 50 – 15 000 Hz (± 2.5 dB)) microphone. Calls from Ethiopian populations were recorded with a AIWA CM-S32 microphone.

In each locality more than one recording site was usually chosen (20–150 km apart) in order to record calls from as many birds as possible. Since all recordings were obtained from unidentified birds and individual calls could not be identified when uttered by birds in large flocks, we considered each single call to be an independent unit. However, given that the sample size was often much less than the local largest flock size and the estimated population size, the problems of pseudoreplication may be regarded as negligible.

Calls were analysed using Avisoft-SASLab Pro 3.4b software of Raimund Specht (Berlin, Germany), performing a fast Fourier transform (FFT) (sampling frequency 44.1 kHz, bandwidth 223 Hz, FFT length 512, time resolution 11.6 ms, frequency resolution 86.1 Hz). Call types were classified by inspecting sonograms by eye. A major drawback of visual classifications is their subjectivity, as different observers might disagree on which calls look similar to each other (Lynch 1996). However, in this study the visual inspection of sonograms was carried out by the same investigator (P.L.), using the same strict criteria, thus avoiding any inter-observer bias. Calls of the two species fell into discrete categories, and the variation within categories was minimal compared with the variation between categories.

Call-repertoire size

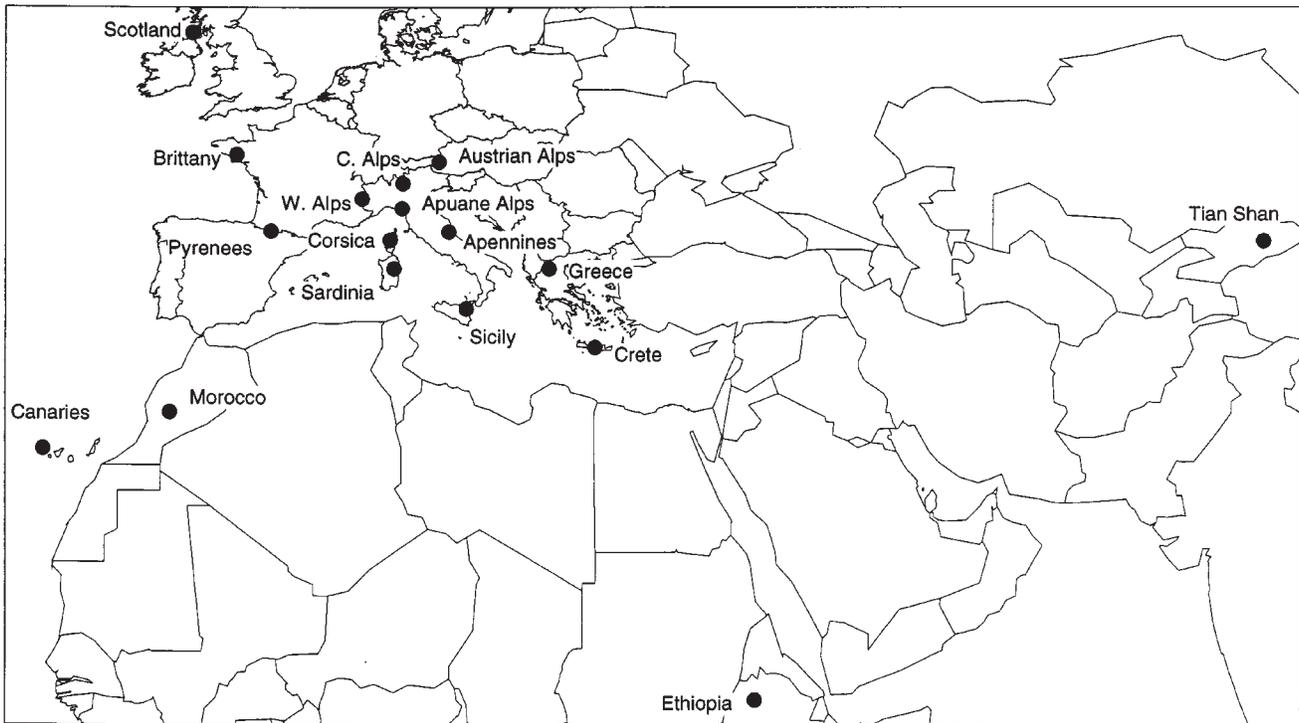
Since some populations were recorded in different seasons, we excluded from the call repertoire those vocalizations linked to a particular time of the year, such as the begging and courtship calls typical of the breeding season. Excluding the above calls, we surveyed the calls sampled in the Alps throughout the study: the call repertoire did not vary significantly among seasons, as the calls we considered were contact, excitement, aggression, and alarm calls that occurred throughout the year (P. Laiolo, unpublished data). Only calls from adult birds were considered.

Call-repertoire variation within species

A problem that could arise in comparing call-repertoire sizes of populations is that they are deduced from different sample sizes. We used two methods to estimate the expected call-repertoire size.

The first method involved a correction for sample coverage, Θ , which is an estimate of the probability that the next sampled call will be of a type already encountered (Good 1953; Fagen and Goldman 1977; Kroodsma and Canady 1985). We estimated the call-repertoire size, R , by $R = N/\Theta$, where Θ is $1 - (S/N)$; N is the number of call types sampled and S is the number of calls occur-

Fig. 1. Map showing the geographical locations of the populations. Red-billed Choughs (*Pyrrhocorax pyrrhocorax*) were recorded in Scotland, Brittany, Canaries, Morocco, Ethiopia, Sardinia, Sicily, Apennines, Western Alps, Apuane Alps, Crete, and Tian Shan (Central Asia, Kyrgyzstan). Alpine Choughs (*Pyrrhocorax graculus*) were recorded in Pyrenees, Morocco, Corsica, Western Alps, Central Alps, Austrian Alps, Apuane Alps, Apennines, Greece, Crete, and Tian Shan (Central Asia, Kyrgyzstan).



ring only once in the sample (Kroodsma and Canady 1985). The limit of this first estimate is that no range or variance measure is associated with the estimate of the call-repertoire size. The second method was based on the statistical approach of rarefaction, which involves the standardization of all samples to a common size (Simberloff 1972; Krebs 1989). Using the rarefaction algorithm, we calculated the expected R value in a random sample of 10 calls in the case of the Alpine Chough and 58 calls in the Red-billed Chough (i.e., the smallest sample under consideration in each species, in keeping with Krebs 1989). The large sample variance of this estimate was also computed using the expected call-repertoire size for 10 and 58 calls. The latter estimate also provides the variance of the expected call-repertoire size thus allowing the statistical comparisons among populations. Hence, we computed a one-way ANOVA to test for differences in call-repertoire size of the populations sampled within each species.

Call-repertoire variation among species

We also compared the call-repertoire size between species with a Mann–Whitney U test (every population entered in the model) and a Wilcoxon's paired t test (only the regions with both species entered in the model: Western Alps, Apennines, Apuane Alps, Crete, Morocco, and Tian Shan). These analyses between species were performed using the observed and expected sample sizes computed with the first method, since the second method was based on a different number of calls for the two species. Furthermore, we compared the call-repertoire variability in the two species by computing the variation within each species by means of three coefficients of variation (CVs of the observed call-repertoire size and its two estimates). The CVs of the two corvids were compared using the Sokal and Baumann (1980) method.

Patterns of population differentiation

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, which resulted in a binary matrix. In keeping with Lynch and Baker (1994), we used Jaccard's coefficient (Sneath and 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. We did not compare frequencies of occurrence of call types, since bias could rise from differing call sample sizes.

The multidimensional scaling analysis (MDS, Guttman–Lingoes starting configuration) based on the matrix of call-repertoire distance was used to describe the pattern of differentiation between populations. MDS involves the construction of an ordination space in which the population positions are rearranged until a good correspondence between population separation and call-repertoire dissimilarities is generated. The measure of goodness of fit is called the stress value and, although there is no sampling distribution for the stress value, a "good" fit is generally obtained with a value less than 0.1 (Kruskal and Wish 1978).

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 association between geographic distance and call-repertoire size dissimilarity was tested by Spearman's rank-order correlation and Mantel's randomization test (Manly 1991). These tests evaluated the prediction that call-repertoire similarity is negatively correlated with geographic distances. Significance of Mantel's statistic was estimated by performing a randomization simulation wherein rows and columns were randomly rearranged 10 000 times; distances were standardized to zero mean and unit standard deviation.

Results

Call-repertoire size

Overall 3540 sonograms of Red-billed Chough and 1249

of Alpine Chough calls were inspected, revealing 20 call types in the former species and 9 in the latter, despite the fact that the local call repertoires were much smaller than this (Figs. 2 and 3). In both species, despite local differences in call-repertoire sizes, the estimates over all populations determined by the sample coverage and rarefaction methods were equal to the observed sizes (20 calls in the Red-billed Chough and 9 in the Alpine Chough). Observed sample size, sample coverage, and expected sample size and its variance for each population are shown in Tables 1 and 2. For three populations of the Alpine Chough (Apennines, Apuane Alps, and Crete) and three of the Red-billed Chough (Crete, Sardinia, and Brittany) sample coverage was rather low. A one-way ANOVA computed on the second estimate of call-repertoire size (i.e., using the expected call-repertoire size and its variance for the smallest sample under consideration in each species, 10 calls in the Alpine Chough and 58 in the Red-billed Chough; Krebs 1989) showed that populations of both species significantly differed in the number of call types uttered (Red-billed Chough: $F_{[11,685]} = 782.9$, $P < 0.001$; Alpine Chough: $F_{[10,110]} = 7.69$, $P < 0.001$). In the case of the Red-billed Chough, the Ethiopian and Central Asiatic (Tian Shan) populations proved to have the largest call repertoire (both observed and estimated) (Table 1). In the case of the Alpine Chough, the greatest variety of calls was uttered by the Moroccan population (Table 2).

No significant difference resulted between call-repertoire sizes of the populations of the two species, using both all populations (observed call repertoire: Mann–Whitney U test = 35.5, $Z = -1.88$, $n = 23$ populations, not significant; estimated call repertoire: Mann–Whitney U test = 36.0, $Z = -1.85$, $n = 23$ populations, not significant) and populations inhabiting the same regions (observed call repertoire: Wilcoxon's t test = 3, $Z = 0.73$, $n = 6$ populations per species, not significant; estimated call repertoire: Wilcoxon's t test = 5, $Z = 0.67$, $n = 6$, not significant). The Red-billed Chough showed a greater interpopulation variability in call-repertoire size than its congener (40–47 vs. 20–30%) (Tables 1 and 2) and, accordingly, the differences among the two species CVs were significant (comparison among CVs of the observed call-repertoire size: $F_{[1,21]} = 4.81$, $P < 0.05$; of the first estimate: $F_{[1,21]} = 4.46$, $P < 0.05$; of the second estimate: $F_{[1,21]} = 30.4$, $P < 0.001$).

Patterns of population differentiation

Figure 4 shows the results of MDS based on the call repertoire dissimilarity matrix. In the case of the Red-billed Chough, the remote Ethiopian and Central Asiatic populations are quite separate from the European and North African ones, which in turn share most calls. It is worth noting that in every Red-billed Chough population but the Ethiopian one, the most recurring call was the contact call “chwee-ow”. Notably, the signal with the function of a contact call in Ethiopia was not chwee-ow, but a call resembling it. The chwee-ow call in the Ethiopian population occurred in the call repertoire with a frequency of only 4% (Laiolo 1999).

In the case of the Alpine Chough, Pyrenean, Alpine, and Moroccan populations differed from those of southeastern Europe and Corsica (Fig. 5).

Mantel's tests showed a significant covariation between call-repertoire dissimilarity and geographic distance in the

case of both the Red-billed Chough ($r = 0.5$, $P < 0.001$) and the Alpine Chough ($r = 0.6$, $P < 0.001$). A positive correlation between geographic and call-repertoire distance was confirmed in both species by Spearman's rank-order correlations (Red-billed Chough: $r_S = 0.61$, $t_{64} = 6.2$, $P < 0.01$ (Fig. 6); Alpine Chough: $r_S = 0.30$, $t_{53} = 2.3$, $P < 0.05$). Figure 6 shows that in the Red-billed Chough the call repertoire did not change qualitatively if populations were less than 3500 km apart, whilst from 4000 km onwards dissimilarity greatly increased and new call types appeared.

Discussion

The overall call repertoire of the Red-billed Chough was twice as large as that of the Alpine Chough, but the numbers of calls recorded in each population did not differ significantly between the two species. This result can be attributed to the higher variability within the Red-billed Chough's pool of calls. Some populations (i.e., those from Ethiopia, Central Asia, Canaries) had a peculiar local call repertoire that overlapped very little with those from other regions; consequently, the overall number of call types within the species was heavily influenced by these unusual populations and, hence, was very large. The high richness of the overall call repertoire of the Red-billed Chough may be due to the greater fragmentation of its range (Goodwin 1986). Habitat boundaries are often distinct and 7 out of 12 populations are actually isolated (Canaries, Ethiopia, Crete, Sicily, Sardinia, Brittany, British Isles).

If migration is effectively absent, genetic or cultural (due to learning errors) mutations could have accumulated thus enhancing population divergence. As Lynch (1996) pointed out, cultural mutations are a common phenomenon, which might occur at any stage of the vocal learning pathways (Jenkins 1978; Slater and Ince 1979). The evidence for these dynamic changes may be found in the Ethiopian Red-billed Choughs, in which the typical contact call (chwee-ow) has been replaced with a poor copy of it.

Drift might also have fixed divergence. An important type of drift occurs during severe bottlenecks or founder events, such as in the colonization of new areas by a small number of individuals (Baker and Jenkins 1987). In such geographic isolation, novelties can persist or even develop further, especially if the migrants are young birds that did not complete their acoustic imprinting (“withdrawal of learning” hypothesis; Thielcke 1973). According to Martens (1996), however, such a rapid modification of vocalizations is likely to occur only during the colonization of remote islands or isolated continental areas, whilst in continental regions conditions are less favourable for rapid changes in vocalizations. Even peripheral populations on continents will often not be sufficiently isolated, thus the process of differentiation is likely to be very slow. Furthermore, the relatively small repertoire of calls of each species suggests that call-mutation rate is quite slow. It is worth noting that calls are expected to be much more constrained in their variability than are syllables of a complex song, due either to phylogenetic constraints (the syrinx structure) or to the greater ease of copying a simple call than a multisyllable song.

The Alpine Chough provided no examples of clear-cut intraspecific differences. This might be attributed to the lack

Fig. 2. Spectrograms of the call repertoire of the Red-billed Chough.

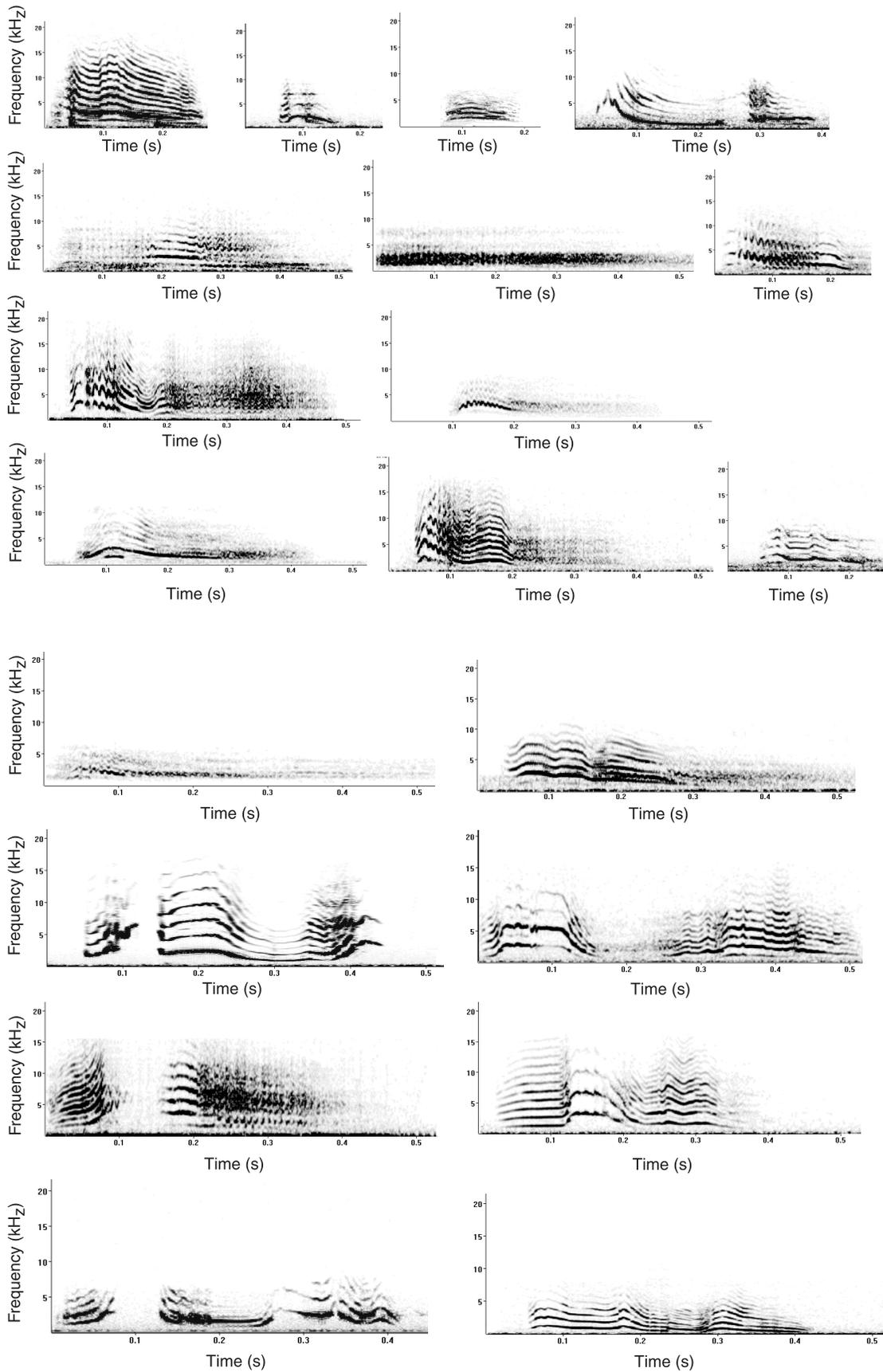
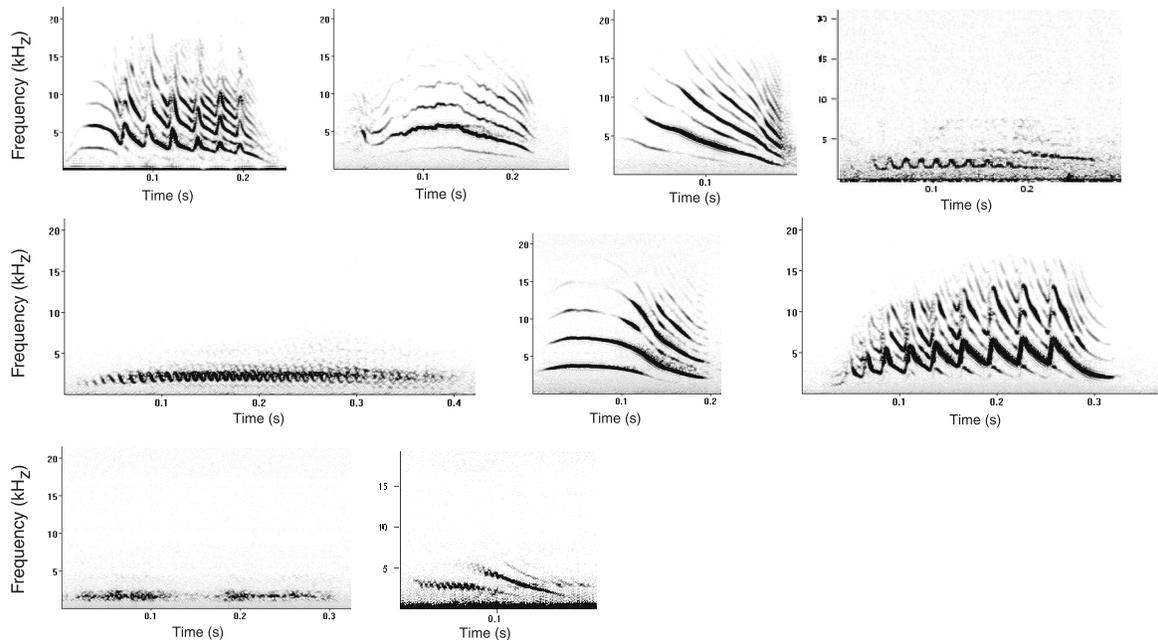


Fig. 3. Spectrograms of the call repertoire of the Alpine Chough.**Table 1.** Call-repertoire data for the Red-billed Chough (*Pyrrhocorax pyrrhocorax*) populations.

Populations	No. of calls examined	Observed call-repertoire size	Sample coverage	Estimated call-repertoire size*	Estimated call-repertoire size [†]	Variance [‡]
Apennines	203	4	1.00	4.00	3.88	0.11
Western Alps	293	5	1.00	5.00	4.30	0.42
Apuane Alps	58	5	1.00	5.00	5.00	0.00
Crete	248	5	0.40	12.5	4.12	0.29
Sicily	284	6	1.00	6.00	5.26	0.44
Sardinia	77	6	0.67	9.00	5.53	0.36
Brittany	71	7	0.71	9.80	6.64	0.31
Scotland	689	5	0.80	6.25	4.08	0.08
Morocco	414	5	1.00	5.00	4.68	0.27
Canaries	555	8	0.88	9.14	6.41	0.39
Ethiopia	323	14	0.93	15.1	10.60	1.38
Tian Shan	325	13	1.00	13.0	11.00	1.07
Total	3540	20	1.00	20		
Intraspecific CV [‡] in call-repertoire size		47.14		44.38	40.75	

*Call-repertoire size estimated by dividing the observed call-repertoire size by the sample coverage (Kroodsmma and Canady 1985); see text for further explanation.

[†]Call-repertoire size and variance estimated by means of the rarefaction statistic considering a sample of 58 calls for every populations (Krebs 1989); see text for further explanation.

[‡]CV, coefficient of variation.

of isolation of its populations, given that this species shows a rather continuous continental distribution and only 2 out of the 11 populations sampled were geographically secluded (Crete and Corsica). Alternatively, the lesser divergence of local call repertoires in the Alpine Chough might also be due to its greater vagility. As Goodwin (1986) pointed out, the Red-billed Chough is remarkably sedentary, thus its fragmented populations are relatively more isolated from one another.

The differences in local call-repertoire size within each species are difficult to interpret. Why should Ethiopian and

Central Asiatic Red-billed Choughs and Moroccan Alpine Choughs have the largest call repertoires? The emergence of song repertoire variation, as hypothesized by Kroodsmma (1982, 1988), can be related to the social environment. Increases in population density, which are likely to be correlated with increases in the frequency of interactions, may lead to an increase in song output; the latter, in turn, might result in correlated increases in song variation and call-repertoire size. Hence, larger populations might be expected to utter more call types. This might be the case with the Asian Red-billed Chough populations, which are larger than most European

Fig. 4. Three-dimensional plot of multidimensional scaling analysis (MDS) based on the dissimilarity matrix of the Red Billed Chough. The stress value is 0.0117 and the alienation value is 0.189. The call repertoire dissimilarity matrix is reproduced through the three axes (dimensions), with the greatest call-repertoire dissimilarity resulting in the greatest separation among populations in the plot.

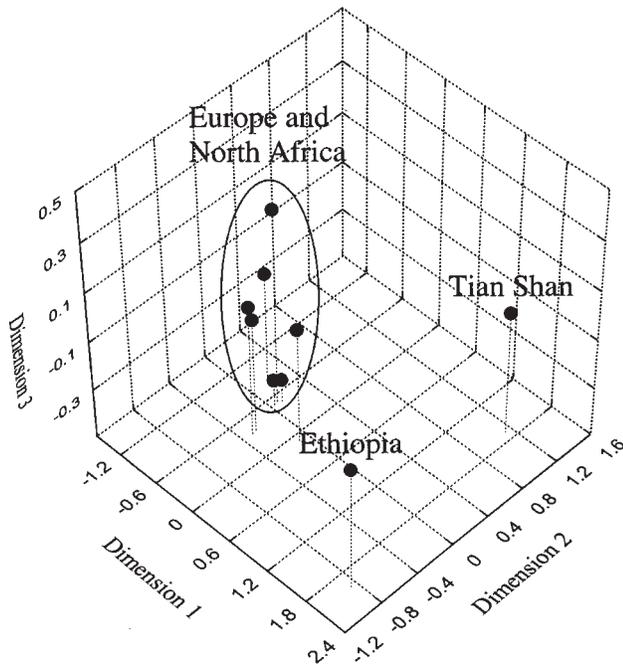


Fig. 5. Three-dimensional plot of MDS based on the dissimilarity matrix of the Alpine Chough. The stress value is 0.037 and the alienation value is 0.056. The call repertoire dissimilarity matrix is reproduced through the three axes (dimensions), with the greatest call-repertoire dissimilarity resulting in the greatest separation among populations in the plot.

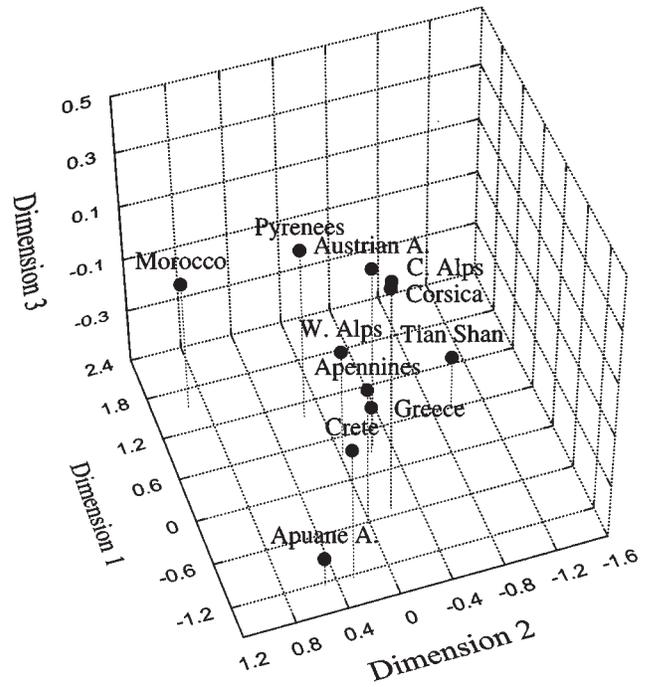


Table 2. Call-repertoire data for the Alpine Chough (*Pyrrhocorax graculus*) populations.

Populations	No. of calls examined	Observed call-repertoire size	Sample coverage	Estimated call-repertoire size*	Estimated call-repertoire size [†]	Variance [‡]
Apennines	23	4	0.50	8.00	2.45	0.17
Western Alps	250	5	1.00	5.00	2.73	0.52
Central Alps	147	4	1.00	4.00	2.58	0.37
Apuane Alps	10	3	0.67	4.50	2.00	0.00
Austrian Alps	114	5	1.00	5.00	3.17	0.00
Corsica	50	4	1.00	4.00	3.38	0.35
Crete	30	3	0.67	4.50	1.84	0.14
Greece	59	5	0.80	6.25	3.16	0.55
Morocco	363	8	0.88	9.14	3.14	0.72
Pyrenees	111	6	1.00	6.00	3.49	0.72
Tian Shan	92	6	1.00	6.00	3.71	0.61
Total	1249	9	1	9		
Intraspecific CV [‡] in call-repertoire size		30.53		29.11	21.12	

*Call-repertoire size estimated by dividing the observed call-repertoire size by the sample coverage (Kroodsma and Canady 1985); see text for further explanation.

[†]Call-repertoire size and variance estimated by means of the rarefaction statistic considering a sample of 10 calls for every populations (Krebs 1989); see text for further explanation.

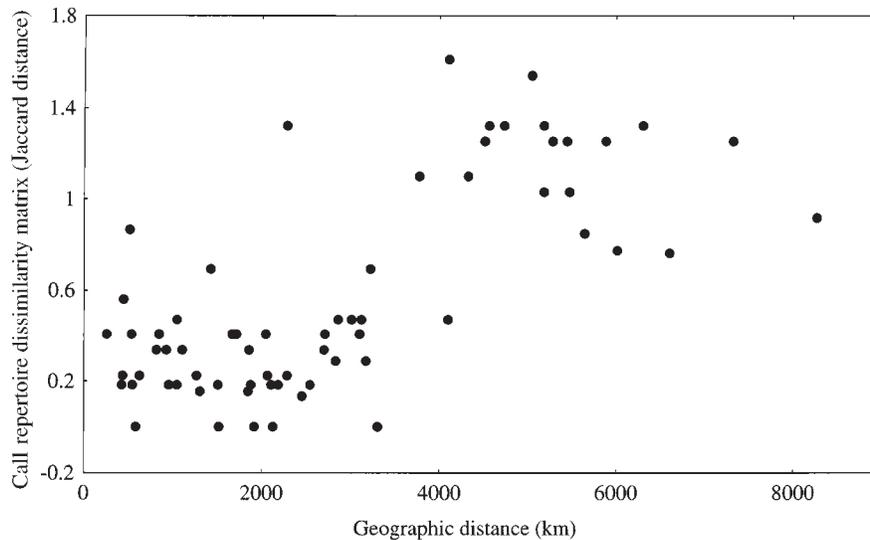
[‡]CV, coefficient of variation.

ones (Bignal 1994, P. Laiolo, personal observation), but further work is needed to confirm or reject this hypothesis.

The analysis of the pattern of population differentiation seemed to reveal a great diversification among the Ethiopian, Central Asiatic, and European – North African populations

in the Red-billed Chough and much less diversification among the Alpine Chough populations. The same pattern was observed in the spectrotemporal features of the commonest call types (Laiolo et al. 2001). Such changes in space might be interpreted as changes over time: European – North African,

Fig. 6. Pairwise relationship between geographic distance and the call repertoire dissimilarity matrix in the Red billed Chough.



Asiatic, and Ethiopian Red-billed Choughs have probably been segregated for a long time. Given that the distance separating these areas largely exceeds the present dispersal capabilities of the species, birds have probably had enough time to evolve variants over large areas, or, in a word, regiolects (sensu Tembrock 1984). Conversely, the clustering of European and North African populations was random with respect to geography in both species. Presumably, the period of isolation among these populations has not been long enough to loosen the acoustic tradition. European ranges might have fragmented only after the last ice age, and at this time North Africa was probably colonized by European birds.

Our analyses have suggested a strict relationship between the call repertoire dissimilarity matrix and geographic distances. In the Red-billed Chough, dissimilarity greatly increased when populations were wide apart (more than 3500 km). In both species a high degree of scatter was found between the plotted pairwise points of the call repertoire dissimilarity matrix and geographic distance. Closer populations do have a more similar call repertoire, but scattering, enhanced by variability in pairwise dissimilarity values, suggest that a certain degree of random differentiation has occurred.

We conclude by suggesting that local call-repertoire size and call-repertoire similarity of both species was affected and constrained by geographic distances. As dispersal is most likely to occur between close or continental populations, more closely situated or continental populations tend to have a more similar pool of calls. Drift might have been an important cause of variation in the Red-billed Chough, since its range is fragmented into isolated and sometimes small populations. The variability in pairwise dissimilarity values and point scattering in the plots confirm the importance of drift in both species and imply that call types have drifted somewhat independently from geographic distance.

Both the subject (calls) and the family (Corvidae) have been neglected in studies of geographic variation. More work is needed (i) to investigate the evolution of call types (which call derives from which) and, above all, (ii) to analyse the “nature–nurture” influences on each call. All of these are

difficult questions but need to be addressed to build on the current knowledge of the microevolutionary phenomena and to reach a more profound understanding of the processes involved.

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