

NEW FOSSIL RECORDS OF CHOUGHS GENUS *PYRRHOCORAX* IN THE CANARY ISLANDS: HYPOTHESES TO EXPLAIN ITS EXTINCTION AND CURRENT NARROW DISTRIBUTION

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SUMMARY.—*New fossil records of choughs genus Pyrrhocorax in the Canary Islands: hypotheses to explain its extinction and current narrow distribution.*

Aims: To describe the new fossil records of the genus *Pyrrhocorax* in the Canary Islands. The main goal will be to use these data to discuss about the possible scenario of colonization and extinctions events of this genus in the canary archipelago. Specifically, the possible causes affecting the current narrow distribution of the red-billed chough in the Canary Islands are discussed. Actually this species only breeds in La Palma, the most north-westerly island of the archipelago.

Location: Four caves in three islands (La Palma, Tenerife and La Gomera) of the Canary archipelago.

Methods: Fossil bones were identified through the combination of biometric and morphologic traits, and using Discriminant Function Analysis (DFA).

Results: Bones of both red-billed chough *Pyrrhocorax pyrrhocorax* and an alpine chough *P. graculus* were identified. Bones of the alpine chough were found on both Tenerife and La Palma, the highest islands in the Canary archipelago. These are the first records for this bird in the Canary Islands. On the other hand, the fossil record shows that red-billed chough was distributed at least on La Palma, Tenerife and La Gomera.

Conclusions: It is suggested that the colonisation of choughs could be related to climatic changes affecting to the distribution of mainland biota during the Upper Pleistocene period. Alteration of island ecosystems by human arrival is also suggested as an hypothesis to explain local extinctions in the Canaries, such as has been proposed in other insular environments. Two main hypotheses to explain the current narrow distribution of red-billed chough are discussed: (i) It is the result of the survival of a part of the ancestral pool of choughs living in the Canary Islands; (ii) It is a direct consequence of new colonisation and/or reintroduction event.

Key words: Island biogeography, Canary Islands, extinction, palaeontology, *Pyrrhocorax graculus*, *Pyrrhocorax pyrrhocorax*.

RESUMEN.—*Nuevos hallazgos de fósiles de chovas del género Pyrrhocorax en las islas Canarias: hipótesis para explicar su extinción y su restringida distribución actual.*

Objetivos: Describir los nuevos hallazgos del género *Pyrrhocorax* en las islas Canarias. La principal intención ha sido usar estos datos para discutir sobre el posible escenario de colonización y los eventos de extinción de este género en el archipiélago canario. Específicamente, se discuten las posibles causas que pueden explicar la restringida distribución actual de la chova piquirroja en Canarias. Actualmente esta especie sólo nidifica en La Palma, la isla más noroccidental del archipiélago.

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Localidad: Cuatro tubos volcánicos localizados en tres islas (La Palma, Tenerife y La Gomera) del archipiélago canario.

Métodos: Los huesos fósiles fueron identificados a través de la combinación de caracteres morfológicos y biométricos, así como con el uso de Análisis Discriminante.

Resultados: Los huesos estudiados fueron identificados como pertenecientes a la chova piquirroja *Pyrhocorax pyrrhocorax* y chova piquigualda *P. graculus*. Los huesos de chova piquigualda fueron encontrados en Tenerife y La Palma, las islas más altas del archipiélago. Estos registros constituyen los primeros restos de esta especie hallados en Canarias. Por otro lado, el registro fósil indica que la chova piquirroja en el pasado estuvo distribuida, al menos, en las islas de La Palma, Tenerife y La Gomera.

Conclusiones: Se sugiere que la colonización de las grajas pudo estar relacionada con los cambios climáticos que afectaron la distribución de la biota continental durante el Pleistoceno Superior. La alteración de los ecosistemas insulares a causa de la llegada de los humanos, se propone como posible causa para explicar las extinciones locales en Canarias, tal y como ha sido sugerido para otros ambientes insulares. Se discuten dos hipótesis principales para explicar la restringida distribución actual de la chova piquirroja: (i) es el resultado de la supervivencia de parte de las poblaciones ancestrales de chovas que vivieron en Canarias; (ii) es consecuencia directa de una nueva colonización y/o reintroducción.

Palabras clave: Biogeografía insular, islas Canarias, extinción, paleontología, *Pyrhocorax graculus*, *Pyrhocorax pyrrhocorax*.

INTRODUCTION

Insular faunas are the result of several processes: colonization, diversification (with subsequent evolution) and extinction. These processes are related to the degree of isolation, the age or the diversity of habitats in islands (MacArthur and Wilson, 1967; Whitacker, 1998; Brown and Lomolino, 2000). However, the extinction process has recently been accelerated by human colonization and activities. The immediate consequences of these extinctions are reflected in the huge differences between the island vertebrate faunas in the Upper Pleistocene-Holocene and those found nowadays (see Quammen, 1996; Worthy and Holdaway, 2002; Steadman, 2006, for a general view).

Other important factors affecting the arrival of species to island is the distribution of continental biota through geological time. So, current distribution of continental Western Palearctic fauna is in part consequence of a post-glacial re-colonization northward from southern refuge (Hewitt, 2000). Nevertheless, taxa such as alpine birds could be considered as relict populations of an older and wider distri-

bution (Tyrberg, 1991). Indeed, there is extensive fossil evidence for a continuous lowland distribution during the last glacial period (Tyrberg, 1991).

The current distribution of different taxa in the Canary Islands have been used to suggest new hypotheses on speciation processes (Emerson and Kolm, 2005), distribution pattern of reptile species (Guerrero *et al.*, 2005) or bird species richness (Carrascal and Palomino, 2002). These approaches were carried out taking advantage of current checklists on distribution of species in the Canary Islands. However, it is not known how the inclusion of the fossil data (i.e. extinct species or past wider distributions) could change these interpretations. So, extinction processes are obviously influencing current biogeographic patterns. Indeed, the study of fossil data has been used to recognise episodes of range expansion or geo-dispersal in several different lineages (Lieberman, 2003). Likewise, the study of paleobiogeography could have important implications for conservation of species. For instance, the fossil record of the giant lizards in the Canary Islands (some species are included in the red list at "Critically Endangered")

suggests a wider island distribution some centuries ago (Martín, 2006).

The Holocene pre-human vertebrate fauna from the Canary Islands show huge differences from the actual. These differences are mainly based on: 1) the existence of endemic vertebrate species now extinct (3 rodents, 2 shearwaters, 1 quail, 2 passerines, and at least 1 giant lizard); 2) several extinctions of non endemic species (see Rando, 2003). In all cases, bones have been found in Quaternary deposits. Indeed, several bones have dated or found in archaeological sites with an age of less than 2,500 years old.

The most widely held hypotheses on the Holocene island extinctions include a strong component of human impact, but the climatic variation hypothesis and collateral effect can not be excluded (James, 1995). In the Canary Islands, main available data on Holocene fauna extirpations would suggest an anthropogenic cause (Alcover and McMinn, 1995; Rando, 2003).

Actually the red-billed chough *Pyrhcorax pyrrhcorax* lives exclusively in La Palma (Canary Islands), the most north-westerly island of

the archipelago, where it is a common breeding bird (Martín and Lorenzo, 2001). The narrow range distribution of this species has been very difficult to explain due to the extent of apparently similar habitats available on the other Canary Islands. Data on the putative historical existence of this bird on other islands are very poor and limited to occasional observations. However the fossil record shows that red-billed chough lived, at least, in La Gomera and Tenerife (Jaume *et al.*, 1993; Rando and López, 1996).

The goal of this paper is: 1) to describe the new fossil records of this genus at the Canary Islands; 2) to discuss about the possible scenario of colonization and extinctions events of both species in the archipelago; and 3) to suggest hypotheses on the current narrow distribution of red-billed chough in the Canary Islands.

MATERIAL AND METHODS

Fossil bones examined in this study have been collected at four caves on three islands: Cueva de Los Murciélagos (La Palma), Bujero del Silo (La Gomera), Cueva de Cosme and Cueva del Viento (Tenerife) (see Fig. 1).

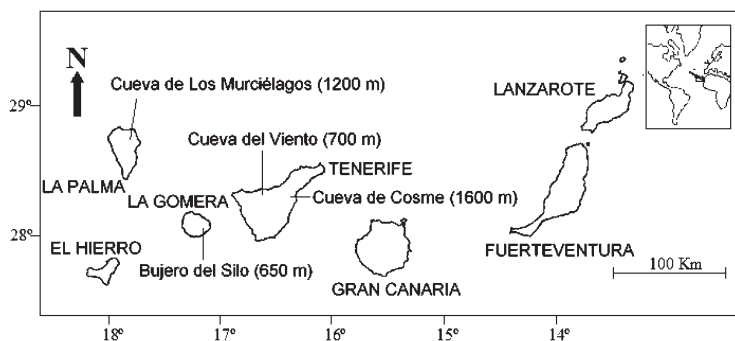


FIG. 1.—Geographic situation of the Canary Islands showing the fossil sites with bones of choughs, genus *Pyrhcorax*, and their altitude.

[Situación geográfica de las islas Canarias mostrando los yacimientos fósiles con huesos de chovas género *Pyrhcorax* y su altitud].

Cueva de Los Murciélagos (UTM 28R X: 223896; Y: 3184960) is a volcanic tube of 100 meters long situated at 1200 meters high at the north east of the island. It is one of the older caves of La Palma with an estimated age of more than 100.000 years old (Oromí *et al.*, 2001).

Bujero del Silo (UTM X: 282916; Y: 3107024) is a volcanic pit with a central hall of 15 meters long and 9 meters high, that is connected to the outside by a narrow chimney 17.5 meters long. It is situated on the south east of La Gomera at 650 meters above sea level (Jaume *et al.*, 1993). It is at least 2.8 My old (Cantagrel *et al.*, 1984).

Cueva de Cosme (UTM X: 355701; Y: 3135771) is a tube of 70 meters long located to 1600 meters high. It is in the recent volcanic series (less than 0.43 My) of Tenerife (Ancochea *et al.*, 1990).

Cueva del Viento is a 17 km long complex system of volcanic galleries, formed 0.17 - 0.13 My ago, situated in the north side of the island (Hernández *et al.*, 1995; Ancochea *et al.*, 1990). The bones were collected from one of these volcanic galleries called Galería de Los Pájaros. The nearest entrance to Galería de Los Pájaros is 700 meters above sea level (UTM X: 333122; Y: 3137145). Bones were collected directly from the cave floor (for further details on this site see, Rando and López, 1996).

Choughs

The material (see Appendix 1) is kept in the Vertebrate Collection at the Departamento de Biología Animal (Zoología) of La Laguna University (Canary Islands, Spain) (DZUL). It was compared with specimens of the same collection and with skeletons from Museu de la Naturalesa de les Illes Balears (MNIB). Bones from Cueva del Viento and Cueva de Cosme were in articulated positions.

Measurements were taken with a digital caliper to the nearest 0.05 mm, such as shown

in Figure 2. Anatomical terminology after Baumel (1993), Moreno (1985) and Tomek and Bochenski (2000) was followed. Discriminant function analysis (DFA) was performed for the mandible using the measurements and methods after Tomek and Bochenski (2000) for small and medium-sized corvids. The procedure is as follows: (i) take measurements of mandible; (ii) make calculations applying the formula $P_j = C_j + n \sum_{i=1}^n m_i f_i$ (where: P_j = value of DFA for the "j" species; C_j = constant [value typical for the "j" species]; n = number of measurements taken from a given skeletal element; f = parameter of the DFA for a given species; m = subsequent measurements taken from the bone under study); (iii) compare the results (P_j) from all the calculations. The mandible examined belongs most probably to the species with the highest P_j value.

The bones were always collected from the floor of the caves, and only bones from Bujero del Silo were found buried in clay sediments (Jaume *et al.*, 1993; Rando and López, 1996).

The bone from Bujero del Silo was deposited during the Upper Pleistocene or later (Jaume *et al.*, 1993). Materials from the other sites were probably deposited during the Upper Pleistocene-Holocene as they are not mineralized and do not present a coat of clay.

Red-billed chough bones from Bujero del Silo and Cueva del Viento have previously been mentioned by Jaume *et al.* (1993) and Rando and López (1996).

RESULTS

The fossil records indicate that both chough species, red-billed chough and alpine chough *P. graculus*, were present at several islands in the Canarian archipelago. Bone sizes are shown in Table 1.

Order *Passeriformes*

Family *Corvidae*

Pyrrhocorax pyrrhocorax red-billed chough

Site: Bujero del Silo (La Gomera)

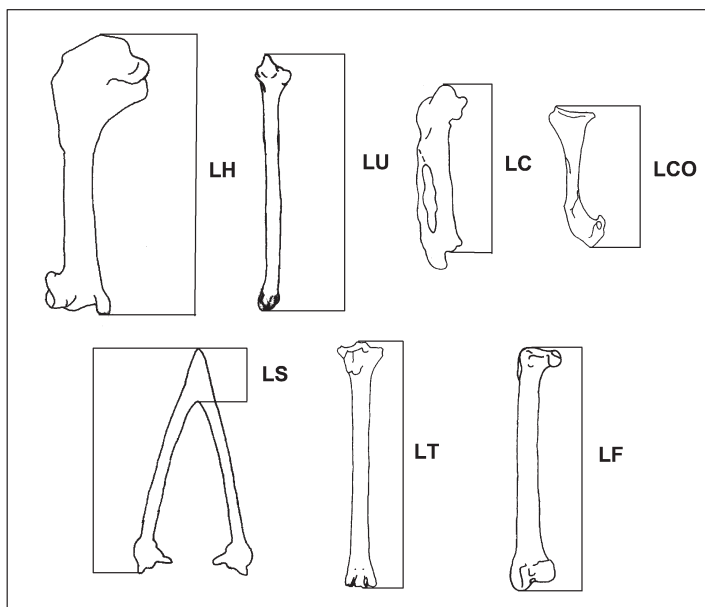


FIG. 2.—Diagram showing the lengths used in this paper. Bones do not belong to the same species and are not to scale. LH: humerus; LU: ulna; LC: capometacarpus; LCO: coracoid; LM: mandible; LS: symphysis; LT: tarsometatarsus; LF: femur.

[Diagrama donde se muestran las longitudes usadas en este artículo. Los huesos no pertenecen a la misma especie y no está a escala. LH: húmero; LU: ulna; LC: carpometacarpo; LCO: coracoides; LM: mandíbula; LS: sínfisis; LT: tarsometatarso; LF: fémur.]

TABLE 1

Lengths (mm) of alpine chough *Pyrrhocorax graculus* and red-billed chough *P. pyrrhocorax* bones found in caves from Canary Islands. LH: humerus; LU: ulna; LC: capometacarpus; LCO: coracoid; LM: mandible; LS: symphysis; LT: tarsometatarsus; LF: femur. Measurements as in Figure 2.

[Longitudes (mm) de los huesos de chova piquigualda *Pyrrhocorax graculus* y chova piquirroja *P. pyrrhocorax* hallados en cuevas de las islas Canarias. LH: húmero; LU: ulna; LC: carpometacarpo; LCO: coracoides; LM: mandíbula; LS: sínfisis; LT: tarsometatarso; LF: fémur. Medidas tomadas como se indica en la figura 2.]

| Cave [Cueva] | Species [Especie] | LM | LS | LH | LU | LC | LCO | LF | LT |
|-----------------|----------------------|-------|-------|-------|-------|-------|-------|-------|-------|
| Los Murciélagos | alpine chough | 52.90 | 10.00 | 44.95 | | | | | |
| Cosme | alpine chough | | | 43.50 | 57.55 | 31.00 | | 38.95 | 46.10 |
| Bujero del Silo | red-billed chough | | | | 64.55 | | | | |
| del Viento | red-billed chough | | | | 66.00 | | 37.70 | | 53.70 |



FIG. 3.—Fossil bones of choughs from Canary Islands: A-D, alpine chough *Pyrrhonorax graculus*; B'-D', red-billed chough *P. pyrrhonorax*. (A) mandible, ventral view; (B-B') ulnae, dorsal view; (C-C') tarsometatarsi, dorsal view; (D- D') coracoid, ventral view. Scale = 3 cm. A = DZUL 3014; B-D= DZUL 3016; B' - D' = DZUL 3015.

[Huesos fósiles de chovas de las islas Canarias: A-D, chova piquigualda *Pyrrhonorax graculus*; B'-D', chova piquirroja *P. pyrrhonorax*. (A) mandíbula, vista ventral; (B-B') ulna, vista dorsal; (C-C') tarsometatarso, vista dorsal; (D- D') coracoides, vista ventral. Escala = 3 cm. A = DZUL 3014; B-D= DZUL 3016; B' - D' = DZUL 3015.]

The length of the only one right ulna of this site (64.55 mm) is coincident with the red-billed chough. This size is out of the range of other species of corvids with of similar size such as alpine chough (54.2 - 62.0 mm) or Eurasian jackdaw *Corvus monedula* (53.6-62.4 mm; Tomek and Bochenski, 2000). Morphological characters are coincident with red-billed chough.

Site: Cueva del Viento (Tenerife)

The combination of biometric and morphologic traits indicates that this specimen belongs to red-billed chough. Biometric data are: ulna length (66.00 mm), coracoids (37.72 mm) and tarsometatarsus (53.7 mm). Likewise, there are two foramens in the distal side of the tarsometatarsus, the first is the *foramen vasculare dorsale* and the second one from the dorsal to the plantar surface (see Fig. 3C', this trait

is present in all choughs specimen examined by Tomek and Bochenski, 2000).

Orden *Passeriformes*

Family *Corvidae*

Pyrrhonorax graculus alpine chough

Site: Cueva de Los Murciélagos (La Palma)

The two bones (mandible and humerus) were found very close together in the same area of the cave, so it is possible that both belong to the same individual. The measurements of the mandible (Table 1) are very close or inside the range of Eurasian jay *Garrulus glandarius*, Eurasian jackdaw, magpie *Pica pica* and alpine chough (Tomek and Bochenski, 2000). The situation of *tuberculum pseudotemporale* (in a distinctive nodule situated in the mid-width of the ramus of the mandible) allows the discard of Eurasian jay and jackdaw. This bone differs

from magpie because in the ventral view the internal edges of the ramus form a narrow, sharp-pointed arch (see Tomek and Bochenski, 2000; and Fig. 3C). In addition, discriminant function analyses indicate that this bone belongs to alpine chough (DFA= 447.8; Tomek and Bochenski, 2000).

The length of the humerus (44.95 mm) is within the range of magpie, nutcracker *Nucifraga caryocatactes* and alpine chough. The former can be discarded because the connection between the *crista pectoralis* and the shaft of the bone is angular. In addition, magpie shows a distinctive bulge on the dorsal side of the *condylus dorsalis* that is absent in the humerus from La Palma.

Site: Cueva de Cosme (Tenerife)

All bones found in this cave were able to be assigned to the alpine chough. All bone lengths are within the range of this species, and the combination of morphologic diagnostic characters indicate that this specimen belong to alpine chough. These traits are: (1) two foramina in the distal side of the tarsometatarsus (the first is the *foramen vasculare dorsale* the second is from the dorsal to the plantar surface, see Fig. 3C); (2) tarsometatarsus do not shows a saddle in the *eminentia intercondylaris*; (3) at the ulna the edge of the *cotyla ventralis* is 45° to the shaft axis; (4) the *processus alularis* (carpometacarpus) does not reach to the base of the bony plate on the shaft; and (5) at the proximal part of the femur the cranial edge of the articular part is visible (Tomek and Bochenski, 2000).

DISCUSSION

The severe human impact on Mediterranean region resulted in dramatic changes in distribution patterns of many species, making the reconstruction of biogeographic scenarios difficult (Covas and Blondel, 1998). To understand current insular biogeographic patterns it is necessary to be aware of human alter-

ations, recent extinction events, the biota inhabiting the nearest mainland areas and any long-term changes that have occurred there.

Colonization

Two main pathways of colonization are plausible: from Northwest Africa or from Southwest Europe (probably via Azores and / or Madeira). Current coexistence of both species in Morocco would favour the African route, albeit, southwest Europe could not be disregarded solely on this basis. Studies using patterns of colonization supported by molecular techniques suggest two different routes of colonization for other Canary Islands bird species. The common chaffinch *Fringilla coelebs* is probably of monophyletic origin from the Iberian Peninsula. However, it seems that the colonisation took place first to the Azores, from which the western Canaries were colonised via Madeira (Marshall and Baker, 1999). In contrast to this, the houbara bustard *Chlamydotis undulata* and the blue tit *Parus caeruleus* probably colonized Fuerteventura and Lanzarote (the nearest islands to the mainland) from an African source (Idaghdour *et al.*, 2004; Kvist *et al.*, 2005).

During last glacial period (Würmian: 115000 BP – 10000 BP) both species of choughs showed a wider distribution. Fossil records suggest a continuous lowland distribution in West Palearctic during that time (Tyrberg, 1991). After the end of the last glacial period insular populations could have been isolated from mainland. The fossil sites in the Canaries as shown in this study of both alpine choughs at 1200 and 1600 meters above sea level, and of the red-billed chough at 700 and 650 meters (see Fig. 1), fits very well with the current breeding altitudinal range for both species. Tenerife and La Palma are the highest islands in the Canary archipelago, with 3718 and 2426 meters, respectively. Moreover, the highlands of these islands have alpine climate conditions (Mar-

zol-Jaén, 2000) similar to the habitats used by alpine chough in continental areas (Snow and Perrins, 1998).

Extinctions

The bones show that the alpine chough inhabited the Canary Islands and that probably it has become extinct recently. Likewise, the fossil record indicates that other local extinction events occurred with the red-billed choughs, at least, in Tenerife and La Gomera. Other extinctions of island corvids are known, for example, there are two species (*Corvus im-pluviatus* and *C. viriosus*) from Hawaiian Islands, *C. antipodum* from New Zealand, and *C. moriorum* from Chatham Islands all of which are now extinct. In these cases a causal link between the alteration of island environments and the arrival of colonising human populations has been suggested (James and Olson, 1991; Gill, 2003). Likewise, the extinction of the red-billed chough from Balearic Islands could be associated with the ecological changes caused by man (Alcover *et al.*, 1992).

The case of the Canary Islands could be different due to the fact that one species of chough was already extant. If the causes of extinction were the same for both species on each island, and taking into account the apparently ecological similarities among western Canaries, the survival of La Palma population is a somewhat unexpected. For this reason, a specific local extinction due to climatic change event is not very plausible, albeit it can not be wholly discarded.

Another alternative hypothesis could be considered. For instance, the re-introduction hypothesis (after the extinction of both species) would imply the arrival and establishment of a breeding population of red-billed choughs only in La Palma (A. Martín, *com. pers.*). This hypothesis would be based on the fondness of people living in La Palma in keeping captive choughs (Martín and Lorenzo, 2001). In this

scenario it is plausible to imagine that some birds escaped or even were released by man and this led to the self-sustaining population of today.

A natural re-colonization event would have probably also involved other islands. It must be noted that both species of choughs are mainly sedentary, except for altitudinal movements in the case of alpine choughs, and the red-billed chough has been recorded far from breeding areas only exceptionally (Snow and Perrins, 1998).

Red-billed chough is currently a common bird species in La Palma. It is well distributed throughout the island with 300 - 400 breeding pairs (Blanco, 2003) with a total population of about 1500 birds, that was even higher until the middle of the 20th century (Martín and Lorenzo, 2001). Introduced plant species are a very important proportion of the diet of the current population of red-billed chough from La Palma (Pais and García, 2000; G. Blanco, *com. pers.*). Moreover, high portion of the insects eaten by choughs in La Palma are associated with pastures used by introduced farm animals, mainly cows (Pais and García, 2000). Overall, these data would suggest that current choughs populations are highly dependent of anthropogenic resources more than mainland populations (Snow and Perrins, 1998; Rolando and Laiolo, 1997).

Original populations of choughs in the Canary Islands were probably small and dependent of the limited resources of insular environments. Furthermore, it is possible that some fraction of the original chough populations of the islands built nests on or nearly the ground due to the absence of mammalian predators, such as have been suggested for Hawaiian Islands and New Zealand corvids (James and Olson, 1991; Gill, 2003). These situations put these species in a highly vulnerable position with regard to non-native predators such as humans, dogs and pigs. Ecosystem alterations could have been marked just after human arrival due to a rapid population expansion and

the activities of their accompanying livestock (Courchamp, 2003).

On the other hand, survival of the ancestral population of Canary choughs in La Palma Island cannot be excluded. Even a combination of both hypotheses is still possible. If so, the current population would be the result of a new colonization/reintroduction and part of the original population. Two bones of adult red-billed choughs collected from levels III and IV of the archaeological site of El Tendal, at the north-west of La Palma, would suggest human exploitation (Navarro *et al.*, 1990; Rando *et al.*, 1996). A radiocarbon date from the upper level II (1270 ± 70 BP; Navarro *et al.*, 1990), 640 - 940 cal. yr. AD, $P = 95.4\%$ program OxCal v3.10 with use of IntCal04 calibration curve (Bronk Ramsey, 2005) allow situation of these materials in the first millennium AD. These bones indicate a survival of the original population at least until that date.

Variation in calls of the red-billed chough populations have been used to separate three groups (Laiolo *et al.*, 2001): Europe and North Africa (including La Palma), central Asia and Ethiopia. European and North African populations tended to cluster together in both species, which suggests that their segregation might be recent. This study shows that proximate geographically populations were more similar than geographically distant ones (Laiolo *et al.*, 2001). Future molecular approaches would be very useful both to ascertain if this result may be related to common ancestry or gene flow effect, likewise, to ascertain the origin, and the approximate arrival date of the current canary population of the red-billed chough.

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BIBLIOGRAPHY

- ALCOVER, J. A., F. FLORIT, MOURER-CHAUVIRÉ, C. and WEESIE, P. D. M. 1992. The avifaunas of the isolated Mediterranean islands during the middle and late Pleistocene. *Scientific Series of Natural History Museum Los Angeles*, 36:273-283.
- ALCOVER, J. A. and MCMINN, M. 1995. Fossil birds from the Canary Islands. *Courier Forschungsinstitut Senckenberg*, 181: 207-213.
- ANCOCHEA, E., FUSTER, J. M., IBARROLA, E., CENDRERO, A., COELLO, J., HERNÁN, F., CANTAGREL, J. M. and JAMOND, C. 1990. Volcanic evolution of the island of Tenerife (Canary Islands) in the light of new K-Ar data. *Journal of Volcanology and Geothermal Research*, 44: 23 1-249.
- BAUMEL, J. J. 1993. *Handbook of avian anatomy: Nomina Anatomica Avium*. Publications of the Nutall Ornithological Club. Cambridge.
- BLANCO, G. 2003. Chova Piquirroja, *Pyrrhocorax pyrrhocorax*. In, R. Martí and J. C. Del Moral (Eds.): *Atlas de las aves reproductoras de España*, pp. 546-547. Dirección General de Conservación de la Naturaleza-Sociedad Española de Ornitología. Madrid.
- BRONK RANSEY, C. 2000. OxCal program v3.10. (www.rlaha.ox.ac.uk/oxcal/oxcal.htm)
- BROWN, J. H. and LOMOLINO, M. V. 2000. Concluding remarks: historical perspective and the future of island biogeography theory. *Global Ecology and Biogeography*, 9: 87- 92.
- CANTAGREL, J. M., CENDRERO, A., FUSTER, J. M., IBARROLA, E. and JAMON, C. 1984. K-Ar chronology of the volcanic eruptions in the Canarian archipelago: island of La Gomera. *Bulletin of Volcanology*, 47: 597-609.
- CARRASCAL, L. M. and PALOMINO, D. 2002. Determinantes de la riqueza de especies de aves en las islas Selvagem y Canarias. *Ardeola*, 49: 211-221.
- COVAS, R. and BLONDEL, J. 1998. Biogeography and history of the Mediterranean bird fauna. *Ibis*, 140: 395-407.
- COURCHAMP, F., CHAPUIS, J. L. and PASCAL, M. 2003. Mammal invaders on islands: impact, control and control impact. *Biological Review*, 78: 347-383.
- EMERSON, B. C. and KOLM, N. 2005. Species diversity can drive speciation. *Nature*, 434: 1015-1017.

- GILL, B. J. 2003. Osteometry and systematics of the extinct New Zealand Ravens (Aves: Corvidae: *Corvus*). *Journal of Systematic Palaeontology*, 1: 43-58.
- GUERRERO, J. C., VARGAS, J. M. and REAL, R. 2005. A Hypothetico-deductive analysis of the environmental factors involved in the current reptile distribution pattern in the Canary Islands. *Journal of Biogeography*, 32: 1343-1351.
- HERNÁNDEZ, J. J., OROMÍ, P., LÁINEZ, A., ORTEGA, G., PÉREZ, A., LÓPEZ, J. S., MEDINA, A. L., IZQUIERDO, I., SALA, L., ZURITA, N., ROSALES, M., PÉREZ, F. and MARTÍN, J. L. 1995. *Catálogo Espeleológico de Tenerife*. OAMC, Cabildo de Tenerife. Santa Cruz de Tenerife.
- HEWITT, G. M. 2000. The genetic legacy of the Quaternary ices ages. *Nature*, 405: 907-913.
- IDAGHDOUR Y., BRODERICK, D., KORRIDA, A. and CHBEL, F. 2004. Mitochondrial control region diversity of the houbara bustard *Chlamydotis undulata* complex and genetic structure along the Atlantic seaboard of North Africa. *Molecular Ecology*, 13: 43-54.
- JAMES, H. E. and OLSON, S. L. 1991. Descriptions of thirty-two new species of birds from the Hawaiian Islands: Part II, Passeriformes. *Ornithological Monographs*, 45: 1-88.
- JAMES, H. F. 1995. Prehistoric extinctions and ecological changes on oceanic islands. *Ecological Studies*, 115: 87-102.
- JAUME, D., MCMINN, M. and ALCOVER, J. A. 1993. Fossil bird from the Bujero del Silo, La Gomera (Canary Islands), with a description of a new species of Quail (Galliformes: Phasianidae). *Boletim do Museu Municipal do Funchal*, 2: 147-165.
- JUAN, C., EMERSON, B. C., OROMÍ, P. and HEWITT, G. M. 2000. Colonization and diversification: towards a phylogeographic synthesis for the Canary Islands. *Trends in Ecology and Evolution*, 15: 104-109.
- KVIST, L., BROGGI, J., ILLERA, J. C. and KOIVULA, K. 2005. Colonisation and diversification of the blue tits (*Parus caeruleus teneriffae*-group) in the Canary Islands. *Molecular Phylogenetics and Evolution*, 34: 501-11.
- LAILOLO, P., ROLANDO, A., DELESTRADE, A., and SANCTIS, A. 2001. Geographical variation in the calls of the choughs. *Condor*, 103: 287-297.
- LIEBERMAN, B. S. 2003. Paleobiogeography: the relevance of fossils to biogeography. *Annual Review of Ecology and Systematics*, 34: 51-69.
- MCCARTHUR, R. H. and WILSON, E. O. 1967. *The Theory of Island Biogeography*. Princeton University Press. Princeton.
- MARSHALL, H. D. and BAKER, A. J. 1999. Colonization history of atlantic island common chaffinches (*Fringilla coelebs*) revealed by mitochondrial DNA. *Molecular Phylogenetics and Evolution*, 11: 201-212.
- MARTÍN, A. and LORENZO, J. A. 2001. *Aves del Archipiélago Canario*. Lemus Editor. La Laguna.
- MARTÍN, A. 2006. 3. Aportaciones de D. Telesforo Bravo al conocimiento de la fauna de vertebrados terrestres de las islas Canarias. In, J. Alfonso-Carrillo (Ed.): *Actas de la Semana Homenaje a Telesforo Bravo*, pp. 71-91. Instituto de Estudios Hispánicos de Canarias. La Orotava.
- MARZOL-JAÉN, V. 2000. El Clima. In, G. Morales and R. Pérez (Eds.): *Gran atlas temático de Canarias*, pp. 87-106. Interinsular Canaria. Santa Cruz de Tenerife.
- MORENO, E. 1985. Clave osteológica para la identificación de los passeriformes ibéricos. I. *Ardeola*, 2: 295-377.
- NAVARRO, J. F., MARTÍN, E., and RODRÍGUEZ, A. 1990. Las primeras etapas del programa de excavaciones en Cuevas de San Juan y su aportación a la diacronía de la prehistoria de La Palma. *Investigaciones Arqueológicas en Canarias*, 2: 189-201.
- OROMÍ, P., ZURITA, N., MUÑOZ, E., DE LA CRUZ, S. and ARECHAULETA, M. 2001. *Conservación de la fauna invertebrada cavernícola de las islas de Tenerife, La Palma y El Hierro*. Departamento de Biología Animal, ULL. La Laguna.
- PAIS, J. L. and GARCÍA, R. 2000. Contribución al estudio del espectro alimentario de *Pyrrhonorax pyrrhonorax barbarus* durante la estación invernal en la isla de La Palma: primeros datos para las Islas Canarias. *UNED La Palma*, 6: 27-37.
- QUAMEN D. 1996. *The song of the Dodo: Island Biogeography in an Age of Extinctions*. Pimlico, London.
- RANDO, J. C. and LÓPEZ, M. 1996. Un nuevo yacimiento de vertebrados fósiles en Tenerife (Islas Canarias). *7th International Symposium on Vulcanospeleology*, 1: 171-173.

- RANDO, J. C. 2003. Protagonistas de una catástrofe silenciosa: los vertebrados extintos de Canarias. *El Indiferente*, 14: 4-15.
- RANDO, J. C., RODRÍGUEZ, A. C., PAIS, E. J., NAVARRO, J. F. and MARTÍN, E. 1996. Los restos de aves del yacimiento arqueológico de El Tendal (La Palma, Islas Canarias). *El Museo Canario*, 51: 87-102.
- ROLANDO, A. and LAIOLO, P. 1997. A comparative analysis of the diets of the Chough *Pyrhcorax pyrrhcorax* and the alpine chough *Pyrhcorax graculus* coexisting in the Alps. *Ibis*, 139: 388-395.
- STEADMAN, D. 2006. *Extinction and Biogeography of Tropical Pacific Birds*. University of Chicago Press. London.
- SNOW, D. W. and PERRINS, C. M. 1998. *The birds of the Western Palearctic. Concise Edition. Vol. 2. Passerines*. Oxford University Press. Oxford.
- TOMEK, T. and BOCHENSKI, Z. M. 2000. *The comparative osteology of European corvids (Aves: corvidae), with a key to the identification of their skeletal elements*. Wydawnictwa Instytutu Systematyki i Ewolucji Zwierząt PAN. Kraków.
- TYRBERG, T. 1991. Artic, montane, and steppe birds as glacial relicts in the west Palearctic. *Ornithologische Verhandlungen*, 25: 29-49.
- WHITTAKER, R. J. 1998 *Island Biogeography: ecology, evolution, and conservation*. Oxford University Press. Oxford.
- WORTHY, T. H. and HOLDAWAY, R. H. 2002. *Prehistoric Life of New Zealand. The lost world of the Moa*. Indiana University Press, Indiana.

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APPENDIX 1 [APÉNDICE 1]

Cueva de Los Murciélagos

Pyrhcorax graculus: one specimen (DZUL 3014) including complete mandible and complete left humerus.

Bujero del Silo

Pyrhcorax pyrrhcorax: complete right ulna (DZUL 1736)

Cueva del Viento

Pyrhcorax pyrrhcorax: associated elements from a single specimen (DZUL 3015) including complete right tarsometatarsus, proximal fragments of left tarsometatarsus, and fragments of both tibiotarsus, left scapula, right coracoids, distal fragment of left humerus, near complete right ulna, two fragments of left radius, left carpometacarpus, anterior portion of sternum including *rostrum sterni*, three fragments of mandible, and eight vertebrae.

Cueva de Cosme

Pyrhcorax graculus: elements from a single specimen (DZUL 3016) both tarsometatarsus, two fragments of left tibiotarsus, proximal fragment of left and near complete right femur, both scapulas, fragment of left and complete right coracoids, near complete right and proximal and distal fragments of left humerus, right and near complete left ulna, proximal fragment of right and near complete of left carpometacarpus, fragment of fifth falanx *digitorum majoris alae*, and three vertebrae.