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Mediterranean Crossbills *Loxia curvirostra* sensu lato (Aves, Passeriformes): new data and directions for future research

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Abstract - Mediterranean Crossbills are as much differentiated as *L. scotica* and *L. pytyopsittacus*. They are sedentary, linked to pine trees and have evolved a thicker bill to extract the seeds from Pine cones. Their decolorization could be due to dietary causes. The authors studied biometrics, breeding phenology, and primary food of Italian populations living in Calabria and Etna (Sicily) and compared them with the other Mediterranean populations. A coevolutive radiation between the different populations of Mediterranean Crossbills presently living in the three main peninsulas, adjacent islands and North Africa occurred separately and this may be demonstrated by their morphometrics, their sedentariness, as well as by songs and some genetic results recently published. They conclude that the same criteria followed to raise *L. curvirostra scotica* to the species rank as *scotica* occur also for the different Mediterranean populations.

Keywords: Pine cones, Biometrics, Sedentariness, Breeding phenology.

Riassunto - Crocieri mediterranei *Loxia curvirostra* sensu lato (Aves, Passeriformes): nuovi dati e direzioni per la ricerca futura.

I crocieri mediterranei sono tanto differenziati quanto *L. scotica* e *L. pytyopsittacus*. Sono sedentari, legati ai pini e hanno evoluto un becco più spesso per estrarre i semi dalle pigne dei pini. La loro decolorazione potrebbe essere dovuta a cause alimentari. Gli autori hanno studiato la biometria, la fenologia riproduttiva e la risorsa alimentare delle popolazioni italiane che vivono in Calabria e sull'Etna (Sicilia) e le hanno confrontate con le altre popolazioni mediterranee. Tra le diverse popolazioni di crocieri mediterranei che vivono attualmente nelle tre principali penisole, nelle isole adiacenti e nell'Africa settentrionale è avvenuta separatamente una radiazione coevolutiva e questo può essere dimostrato dalla loro morfometria, dalla loro sedentarietà, così come dai canti e da alcuni risultati genetici recentemente pubblicati. Essi concludono che gli stessi criteri seguiti per elevare *L. curvirostra scotica* al rango di specie come *L. scotica* si verificano anche per le diverse popolazioni mediterranee.

Parole chiave: pigne, biometria, sedentarietà, fenologia di riproduzione.

INTRODUCTION

Crossbills are very popular birds; according to Whitaker (1905) "In Bohemia a curious popular superstition exists among the lower classes, the Crossbill being supposed to ward off illness from the house in which it is kept in confinement. Moreover, should any member of that household be taken hill, the poor bird is said to contract the illness in the patient's stead, and to die of it!". This bird has attracted the curiosity of many researchers, and a lot of papers on this odd finch have been published. It has been always popular for its crossed bill and nomadic movements; many authors have treated its peculiar bill-shape and variability, with rounded and crossed mandibles. Following Bezzel (1977) Crossbills use their bill with crossed jaws as a special pincer to extract coniferous seed from beneath the scales covering cones. This feature allows them a food specialization, which is to extract the seeds from the coniferous pine cones, through a lateral movement of the jaws that moves the cone scales. In addition, Crossbills have another unique character within the Fringillidae, namely their stout tarsi, which are proportionally shaped to the bill, and they are likely used during the extraction of seeds from cones exactly as in parrots.

Crossbills have an inter-population variation in the bill size; birds with bigger bill have the upper mandible more curved (Eck, 1981). They can have a more or less robust bill, those with the thinnest bill eat the seeds of different species of conifers, mostly larches and spruces, while those with the more massive bills feed on the pine seeds, which produce larger cones than the other conifers. The central-northern populations of European Crossbills feed

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on *Larix* and *Picea* seeds, those of southern Europe are an exception feeding on *Pinus* seeds; they are also characterized by larger bills than north European individuals. Thicker scales require deeper bills, because deeper bills can exert a greater force to separate the overlapping scales. They are considered an example of an ongoing evolutionary process (Edelaar *et al.*, 2003, 2012).

The interest in these birds lies also in the fact that some northern populations have an irregularly nomadic behavior, possibly depending on the variability of the fruiting of coniferous trees. Further, much of the recent and past studies have been carried out on the relationship between the bill shape of Crossbills and the cone scales size of the coniferous plants, on which they feed on, in terms of coevolutionary adaptive radiation. The populations of Crossbills that have settled in the Mediterranean live in coniferous forests that guarantee a more regular availability of seeds, while the northern populations find themselves in certain years in the need to emigrate to look for areas with fruiting conifers. It is a true emigration because they can stay for a few years in the places they are going to colonize, breed outside their usual range, and then return to their places of origin, when they expect to find trophic availability again.

In the present paper we analyze for the second time (the first was the paper by Massa, 1987) some aspects of populations of the Crossbills living in the southern parts of the Italian peninsula and Sicily (Etna) and feeding on pine seeds, this in light of the interesting and conclusive research carried out in the Iberian peninsula (see for example Alonso *et al.*, 2006, 2020; Edelaar *et al.*, 2003, 2012), in order to compare them with other Mediterranean populations and to try some general conclusions and a taxonomical proposal.

In the present paper we follow the Biological Species Concept (BSC), which consider species 'genetically cohesive groups of populations that are reproductively isolated from other such groups'; according to BSC, geographic isolation leads to genetic change and potentially to the reproductive isolation of sister taxa (Hill & Powers, 2021); however, genetic change is not always present and cases of reproductively isolated species without evident genetic differences are known in other finches (e.g., Citril and Corsican Finches: Pasquet & Thibault, 1997; Gill *et al.*, 2020; or the much debated *Corvus cornix/corone*).

Etymology of crossbill scientific names cited in this paper

Loxia was described by Linnaeus (1758) as follows: rostrum conico-gibbum, fronte subcalvum, mandibula inferior margine laterali inflexa. *Loxia* derives from the Greek Λοξή (*curvus*, oblique); the species *curvirostra* means curved bill (*curvum rostrum*), and Linnaeus (1758) in its short description wrote '*rostro forficato*' which means 'bill crossed'. The following Palaearctic taxa are known, some names are geographical or distinctive adjectives, others are eponymous: *L. c. balearica* (von Homeyer, 1862) (after the Latin term *balearicus*, from Balearic Islands), *L. curvirostra poliogyna* Whitaker, 1898 (*poliogyna*, from Πολιός, polios = grey and γυνή, gyne = female, female grey colored), *L. c. guillemardi* Madarász, 1903 (after the British geographer and ornithologist Francis Henry Hill Guillemard, 1853-1933), *L. curvirostra hispana* Hartert, 1904 (after the Latin term *hispanus*, living in Hispania), *L. curvirostra caucasica* Buturlin, 1907 (after the Latin term *caucasicus*, from the Cacucasus), *L. curvirostra mariae* Dementiev, 1932 (after the Grand Duchess Maria, 1819-1876, daughter of tzar Nicholas I of Russia), *L. pytyopsittacus* Borkhausen, 1793 (from the Greek words πιτυς, pitus = pine, and ψιττακος, psittakos = parrot, and means parrot of pines), *L. scotica* Hartert, 1904 (after the Latin term *scoticus*, living in Scotia).

MATERIAL AND METHODS

Specimens studied

In the Table 1 the number of specimens examined, their geographic origin and subspecies identification are listed; most of them were included within the material examined by Massa (1987) in the Natural History Museum, London, American Museum of Natural History, New York, Museum National d'Histoire Naturelle, Paris, Museo Civico di Storia Naturale, Milan, plus some specimens preserved in the Museo Regionale di Terrasini (Palermo).

Tab. 1 - Number of specimens and origin of *Loxia curvirostra* sensu lato examined. / Numero di esemplari esaminati di *Loxia curvirostra* sensu lato e loro origine

Origin	**Males**	**Females**
Sicily (Etna) and Calabria (S Italy)	21	7
Corsica (ssp. *corsicana*)	5	3
N Italy (Alps)	18	13
N Africa (Tunisia and Algeria) breeding (ssp. *poliogyna*)	42	29
Cyprus (ssp. *guillemardi*)	22	13
Balearic Islands (ssp. *balearica*)	17	8
TOTAL	125	73

The following measurements were taken with a caliper (with a 0.01 precision) on all the specimens: flattened wing, tarsus, bill length from the feathering to tip, and bill depth at the base. All statistical analyses were performed separately on males and females. Preliminarily, based on the low distance between them, we decided to merge the two samples from Calabria and Sicily, after assessing that no significant differences were present for all the considered variables (Student's t-test, males: wing $F_{1,20} = 0.45$, $p = 0.51$; tarsus $F_{1,20} = 2.29$, $p = 0.15$; bill length $F_{1,20} = 0.01$, $p = 0.99$; bill height $F_{1,20} = 0.47$, $p = 0.50$; females: wing $F_{1,6} = 1.31$, $p = 0.30$; tarsus $F_{1,6} = 0.27$, $p = 0.62$; bill length $F_{1,6} = 0.18$, $p = 0.69$; bill height $F_{1,6} = 0.12$, $p = 0.74$).

Afterwards, analysis to assess differences among means of morphometric characters among the crossbill populations was performed with a 1-way ANOVA, after data normalisation by means of a Box-Cox transformation. All significant analyses were concluded with Tukey post hoc tests to compare the populations for each character. Moreover, a discriminant analysis was performed using the correlation matrix, aimed at evaluating the predictive multivariate capability of the recorded morphometric parameters for population identity. Minitab software has been used throughout for all statistical analyses.

Finally, the general condition of the plumage and the extent of the primary moult was also noticed.

Field observations

Apart from food availability, the best sites where Crossbills breed and are sedentary are sites with a regular presence of fresh water. In the 'Nuova Gussonea' Botanical Garden, covering about 10 hectares and located in Ragalna, at an altitude of 1700-1750 m a.s.l. on the southern slope of the Etna Natural Park (Sicily), the regular presence of water has accustomed the crossbills to human presence to the point that they may be approached up to a few meters away (T. Puma, F. Turrisi, *pers. comm*.). A considerable amount of field work has been carried out on Mt. Etna (Sicily) and Sila (Calabria) to establish the food source of Crossbill populations and the possible arrival of northern individuals in the irruption years. In addition, during the 1990 influx of Crossbills from northern populations, a few pairs settled in the afforestation of *Pinus halepensis* on Mt. Pellegrino (Palermo, Sicily); their habits were followed for some years, but in 2005 they were missing from that breeding site, probably because they migrated back to their original country.

Pine cones (Tab. 2)

The Black Pine *Pinus nigra* J.F.Arnold is distributed with different subspecies in the Mediterranean (Isajev *et al*., 2004; Enescu *et al*., 2016). However, according to Enescu *et al*. (2016) more than 100 Latin specific, varietal, and formal names have been recorded by different authorities and as yet, there is no general consensus.

Following Lucas-Borja & Vacchiano (2018) and references herein, European Black Pines show a highly variable fecundity through time, although *P. nigra* subsp. *laricio* has the capacity to produce seeds every year, good seed years only average every 3-5 years. Furthermore, fluctuations in cone and seed production are reported for Spanish Black Pine. Sometimes few trees per stand are highly productive.

Concerning the size of cones of the Black Pines, Enescu *et al*. (2016) wrote "cones are sessile, 4-8 (9) cm long, 2-4 cm wide… They ripen in the autumn of the second year, and open in the third year. Cones contain 30-40 seeds". The cones of Aleppo's Pine *Pinus halepensis* open in September (Ayari & Larbi Khouja, 2014) but many cones are serotinous and seed release by fire (pyriscence) or by drying atmospheric conditions (xeriscence) (Daskalakou & Thanos, 2010) so the seeds are available all time.

However, we obtained precise measurements from specialist literature and directly from cones collected by the authors. Concerning the cones of *Pinus nigra* present in Calabria (South Italy) and Etna (Sicily), and *Pinus halepensis* from Sicily, during seed production a sample was collected from both woods and the following measurements were taken from each cone using a caliper (precision 0.01 mm): total length, maximum depth in the middle, length x width of scales in the middle of the cone.

The following cones of Black Pines *Pinus nigra laricio* were collected and measured: 20 on 7th December 2020 in Calabria (south Italy), at San Giovanni in Fiore (Cosenza), loc. Colle Ciuccio, from a tree ca. 25-30 years old; cones were collected at ca. 2 m from the soil, exposure south-east, altitude 1191 m a.s.l., UTM 33T, 4349188.92N, 644174.95E. The plant was not infested by the Pine Processionary *Thaumetopoea pityocampa* moth, in the area there are present both Crossbills and Calabrian Black Squirrel *Sciurus meridionalis*. A further 20 cones were collected on 11th December 2020 at San Giovanni in Fiore, loc. Cuturelle, from a tree ca. 40 years old, at ca. 3.5 m from the soil, exposure south-west, altitude 1200 m a.s.l., UTM 33T, 4348993.52N, 643641.37E. The plant housed winter nests of the Pine Processionary, with some signs of erosion on the needles caused by the caterpillars; this area holds both Crossbills and Squirrels. Other 12 cones were collected on 15th December 2020 at Casali del Manco, loc. Carlomagno (Cosenza), from a tree ca. 60 years old, at ca. 2 m from the soil, exposure north, altitude 1560 m a.s.l., UTM 33T, 4352035.63N, 634280.32E. The Pine Processionary was not present on this tree, and both Crossbills and Squirrels are present. Twenty more cones were collected on 15th December 2020 at Casali del Manco, loc. San Nicola (Cosenza), from a tree ca. 80 years

Tab. 2 - Subspecies of *Pinus nigra* in the Mediterranean area. References for taxonomical aspects and distribution/ Sottospecie di *Pinus nigra* nel Mediterraneo. Riferimenti bibliografici per gli aspetti tassonomici e la distribuzione: Isajev *et al*., 2004; Enescu *et al*., 2016; Caudullo *et al*., 2018; von Raab-Straube, 2014.

Subspecies	**Distribution**
Pinus nigra subsp. *nigra*	Balkans, Austria, N-E Italy
Pinus nigra subsp. *salzmannii*	France, Spain
Pinus nigra subsp. *mauretanica*	Algeria, Morocco
Pinus nigra subsp. *pallasiana*	S-E Balkan Peninsula, Turkey, Cyprus, Crimea
Pinus nigra subsp. *dalmatica*	Some small islands of Croatian coast
Pinus nigra subsp. *laricio*	Corsica, South Italy, Sicily

old, at ca. 2.5 m from the soil, exposure west, altitude 1430 m a.s.l., UTM 33T, 4352035.63N, 634280.32E. The plant housed winter nests of the Pine Processionary, in the area both Crossbills and Squirrels are present.

Forty-five cones of Black Pines *Pinus nigra laricio* were collected and measured on 21st December 2020 in Sicily (Etna), at Ragalna (Catania), Pine Wood Serra La Nave, 37.687756N, 14.951778E, exposure south-west, altitude; in this site Crossbills were present. Squirrels are absent from Sicily.

A further 15 cones of *Pinus halepensis* were collected and measured in March 2021 from one locality (Marettimo, Egadi Is., Sicily), where crossbills arrived and bred for some years at the end of 1990s; finally 30 *Pinus halepensis* cones were collected and measured from five trees in the Nature Reserve 'Pinewood of Vittoria' (Sicily) in March 2021, where this species is considered autochthonous.

RESULTS

Biometrics

The mean of the considered variables and results of statistical analysis are reported in Table 3. In males, no statistical differences were found in tarsus length ($F_{5,124}$ = 1.75, p = 0.129), while for the other variables significant differences were recorded (wing $F_{5,124}$ = 10.82, p < 0.01; bill length $F_{5,124}$ = 14.38; bill height $F_{5,124}$ = 6.92; length/height of bill $F_{5,124\,=}$ 4.39, in all analyses p < 0.01). In females, no statistical differences were found in bill height ($F_{5,72}$ = 1.74, p = 0.138), while for the other variables significant differences were recorded (wing $F_{5,72}$ = 3.88; tarsus $F_{5,72}$ = 7.02; bill length $F_{5,72}$ = 4.73; length/height of bill $F_{5,72\,=}$ 3.19, in all analyses p < 0.01). Females resulted to be always smaller than males in wing length, with differences more evident in North Italy, Corsica and Cyprus. On the other hand, the other morphometric characters showed to be quite similar in males and females from the same population (Tab. 3).

Red Crossbills from Balearics are smaller than all other populations, and significant differences were always found in males for wing length and bill length and height in comparison with birds from Cyprus. Males from Cyprus differed from males from North Africa in bill length and height, and from the Alps and southern Italy in their bill height, while no significant differences in all measurements were found in comparison with Corsica (Figs. 1-3; Tab. 3). No statistical differences for all morphometric variables were found in males from the Alps, southern Italy, Corsica and North Africa. Finally, the bill ratio of length/height was significantly higher in males from the Alps compared to North Africa and Balearic Islands, while all other populations showed intermediate values. Of some interest is the difference between males and females in wing length (Fig. 4). Overall, females showed fewer clear differences among the different populations. Wing length in females from North Africa and southern Italy was significantly higher than in the Balearics, while those from Cyprus, Corsica and the Alps did not differ from them. Tarsus length was significantly higher in females from Cyprus compared with the Alps, Corsica, North Africa, and the Balearics, while females from southern Italy had inter-

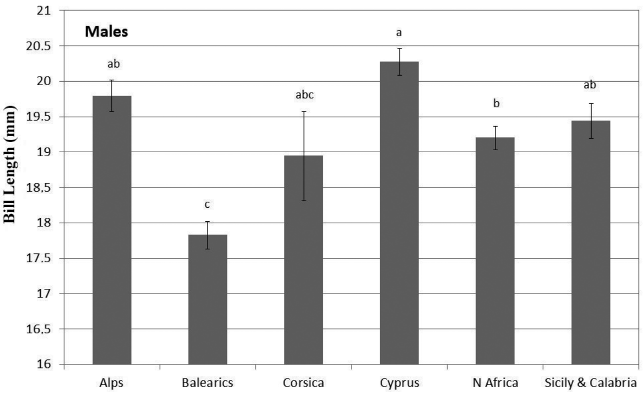

Fig. 1 - Bill length in the Mediterranean samples (adult males) of Crossbills. Different letters indicate the statistical differences among the different populations (1-way ANOVA followed by Tukey post hoc test). / Lunghezza del becco nei campioni mediterranei (maschi adulti) di crociere. Lettere diverse indicano le differenze statistiche tra le diverse popolazioni (ANOVA a 1 via seguita da test post hoc di Tukey).

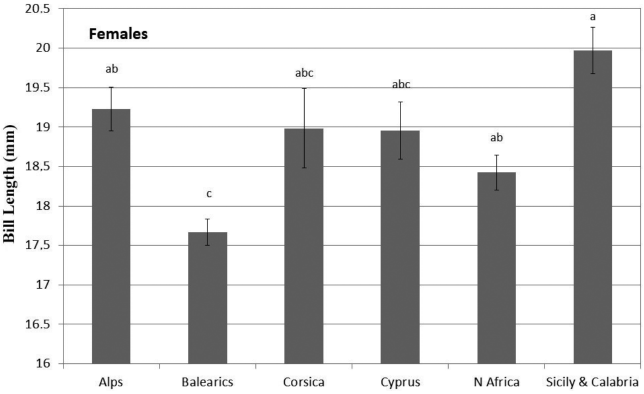

Fig. 2 - Bill length in the Mediterranean samples (adult females) of Crossbills. Different letters indicate the statistical differences among the different populations (1-way ANOVA followed by Tukey post hoc test). / Lunghezza del becco nei campioni mediterranei (femmine adulte) di crociere. Lettere diverse indicano le differenze statistiche tra le diverse popolazioni (ANOVA a 1 via seguita da test post hoc di Tukey).

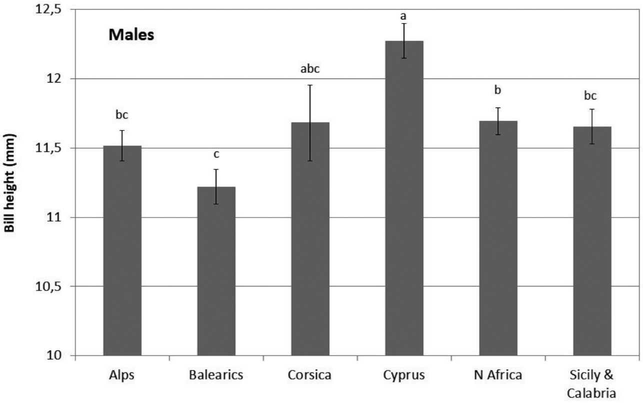

Fig. 3 - Bill height in the Mediterranean samples (adult males) of Crossbills. Different letters indicate the statistical differences among the different populations (1-way ANOVA followed by Tukey post hoc test). / Altezza del becco nei campioni mediterranei (maschi adulti) di crociere. Lettere diverse indicano le differenze statistiche tra le diverse popolazioni (ANOVA a 1 via seguita da test post hoc di Tukey).

Tab. 3 - Biometrics of male and females Crossbills from different areas of the Mediterranean. Letters within columns indicate the statistical differences among the different populations for each morphometric character (1-way ANOVA followed by Tukey post hoc test). / Biometria di maschi e femmine di crocieri di differenti aree del Mediterraneo. Le lettere all'interno delle colonne indicano le differenze statistiche tra le diverse popolazioni per ciascun carattere morfometrico (ANOVA ad 1 via, seguita da test post hoc di Tukey)

	No. Samples	Wing ± S.E. (min-max)	Tarsus ± S.E. (min-max)	Bill length ± S.E. (min-max)	Bill height ± S.E. (min-max)	Bill l/h ± S.E. (min-max)
MALES						
Cyprus	22	95.95±0.50 **a** (92-103.5)	18.48±0.31 (15.88-21)	20.27±0.19 **a** (18.72-21.9)	12.27±0.12 **a** (11.65-13.9)	1.65±0.02 **ab** (1.49-1.82)
Sicily & Calabria	21	96.56±0.46 **a** (91.9-100)	17.97±0.18 (16-19.65)	19.44±0.25 **ab** (17.65-22.62)	11.65±0.13 **bc** (10.55-12.65)	1.67±0.07 **ab** (1.54-1.85)
Corsica	5	96.46±0.92 **a** (93-98)	17.69±0.41 (16.7-19.1)	18.94±0.63 **abc** (17.4-20.6)	11.68±0.27 **abc** (11-12.5)	1.62±0.03 **ab** (1.53-1.70)
Alps	18	96.27±0.58 **a** (90.9-99.7)	17.94±0.29 (16.88-21.65)	19.79±0.22 **ab** (18.31-21.55)	11.52±0.11 **bc** (10.5-12.11)	1.72±0.02 **a** (1.59-1.92)
N Africa	42	95.91±0.41 **a** (91-103.5)	17.72± 0.22 (15-21)	19.20±0.17 **b** (17.5-22.3)	11.69±0.1 **b** (10.5-12.75)	1.64±0.01 **b** (1.43-1.84)
Balearics	17	91.31±0.72 **b** (86-95)	17.37±0.22 (15.9-19)	17.83±0.20 **c** (16.4-19.62)	11,22±0.13 **c** (10.2-12.2)	1.59±0.02 **b** (1.45-1.75)
FEMALES						
Cyprus	13	92.57±0.69 **ab** (89-97.38)	18.95±0.28 **a** (18-21)	18.96±0.36 **abc** (16.9-21.5)	12,273±0.12 (11.65-13.9)	1.61±0.03 **b** (1.43-1.82)
Sicily & Calabria	7	95.45±1.06 **a** (92.09-101)	17.67±0.26 **ab** (16.82-18.5)	19.97±0.30 **a** (18.85-21)	11.65±0.13 (10.55-12.65)	1.77±0.05 **a** (1.61-1.96)
Corsica	3	91.63±2.15 **ab** (89-95.9)	16.34±0.69 **b** (15-17.3)	18.98±0.51 **abc** (18.1-19.85)	11.53±0.23 (11.3-12)	1.65±0.02 **ab** (1.60-1.68)
Alps	13	92.05±0.84 **ab** (85.75-96.55)	17.38±0.25 **b** (16-18.65)	19.23±0.28 **ab** (17.60-20.8)	11.36±0.20 (10-12.67)	1.69±0.03 **ab** (1.61-1.87)
N Africa	29	94.04±0.48 **a** (87-98.81)	17.21± 0.19 **b** (15-19)	18.43±0.22 **bc** (15-19.95)	11.28±0.1 (9.5-12.42)	1.63±0.02 **b** (1.39-1.78)
Balearics	8	90.74±0.45 **b** (88.4-92)	17.29±0.25 **b** (16-18.65)	17.67±0.17 **c** (16.8-18.3)	11,05±0.22 (10.3-12.18)	1.60±0.03 **b** (1.46-1.71)

mediate values, not significantly different from all other populations. The bill ratio of length/height was significantly higher in females from southern Italy when compared to Cyprus, North Africa and the Balearic Islands, while all other populations showed intermediate values.

The result of the discriminant analysis revealed that the overall proportion of correct attribution is not very high, being 0.33 for males and 0.52 for females. Bill height and tarsus length were the most relevant parameters in the population attribution for males and females, respectively, whereas bill length had the lowest influence for both sexes. Nevertheless, the proportion of correct attribution in males from Cyprus and the Balearics (0.68 and 0.77, respectively) was higher compared to all other populations, for which it ranged from 0.10 (southern Italy) to 0.28 (Alps) (Tab. 4).

Regarding females, all Crossbills from the Balearics were correctly assigned, whereas the proportion of correct attribution for specimens from Cyprus and southern Italy was 0.62 and 0.71, respectively. The lowest proportion was that from the Alps (0.23). These results lead to the conclusion that the recorded morphometric characters

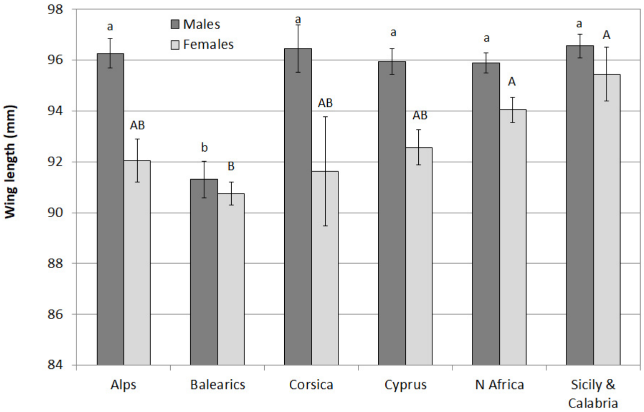

Fig. 4 - Wing length in the Mediterranean samples (adult males and females) of Crossbills. Different letters indicate the statistical differences within males (lower-case letters) and females (capital letters) among the different populations (1-way ANOVA followed by Tukey post hoc test). / Lunghezza delle ali nei campioni mediterranei (maschi e femmine adulti) di crociere. Le lettere diverse indicano le differenze statistiche all'interno dei maschi (lettere minuscole) e delle femmine (lettere maiuscole) tra le diverse popolazioni (ANOVA a 1 via seguita da test post hoc di Tukey).

Tab. 4 - Classification of males and females Crossbills from different populations compared with the groups determined by the discriminant analysis performed on all morphometric parameters. Coeffcients show the impact of the different morphometric parameters in the correct attribution to the different populations. / Classificazione di maschi e femmine di crocieri di differenti popolazioni confrontate con i gruppi determinati con l'analisi discriminante eseguita sui parametri morfometrici. I coefficienti mostrano l'importanza dei differenti parametri morfometrici nella corretta attribuzione alle differenti popolazioni.

	MALES					
Put into Group	Alps	Balearics	Corsica	Cyprus	N Africa	Sicily & Calabria
Alps	5	0	1	3	10	4
Balearics	1	13	1	2	5	1
Corsica	2	4	1	1	11	6
Cyprus	2	0	1	15	5	6
N Africa	4	0	0	0	5	2
Sicily & Calabria	4	0	1	1	5	2
Total N	18	17	5	22	41	21
N correct	5	13	1	15	5	2
Proportion	0.28	0.77	0.20	0.68	0.12	0.10
Linear Discriminant Function for Groups						
	Alps	Balearics	Corsica	Cyprus	N Africa	Sicily & Calabria
Constant	-1101,4	-1007	-1105	-1134,4	-1097,6	-1110,9
Wing	15.1	14.4	15.2	15	15.1	15.2
Tarsus	18.8	18.4	18.8	19.5	18.8	19
Bill height	34.1	34.8	35.6	37	35.4	35.1
Bill length	1.1	-0.6	-0.2	0.9	0.2	0.5
	FEMALES					
Put into Group	Alps	Balearics	Corsica	Cyprus	N Africa	Sicily & Calabria
Alps	3	0	0	0	6	1
Balearics	3	8	1	2	2	0
Corsica	2	0	1	0	3	1
Cyprus	2	0	0	8	0	0
N Africa	1	0	0	2	13	0
Sicily & Calabria	2	0	1	1	5	5
Total N	13	8	3	13	29	7
N correct	3	8	1	8	13	5
Proportion	0.231	1	0.333	0.615	0,448	0.714
Linear Discriminant Function for Groups						
	Alps	Balearics	Corsica	Cyprus	N Africa	Sicily & Calabria
Constant	-882,7	-852,68	-859,63	-927,33	-899,55	-935,29
Wing	12.42	12.29	12.32	12.45	12.75	12.94
Tarsus	19.29	19.51	18.27	21.33	19.33	19.42
Bill height	16.19	16.51	16.58	18.39	16.17	15.13
Bill length	5.37	3.99	5.29	4.3	4.58	6.04

reliably described only the populations from Cyprus and Balearics, while all the other populations have intermediate values in most of the different morphometric characters, and seem to be more homogeneous; thus, a higher level of misidentification occurs.

Breeding season and moult

Breeding populations from Etna and Calabria generally breed in winter, in some years from November-December. Moult in adults occurs after fledging and independence of young, between April-May and September.

Cone size (Tab. 5)

Cones of both species, *P. nigra* and *P. halepensis*, resulted very variable in size (Tab. 5). Seventy-two cones of *Pinus nigra* collected in Calabria resulted 6.86±1.03 cm (min-max: 5.2-10.0) long, and 2.74±0.23 (min-max: 2.2-3.3) wide; their scales resulted 1.13±0.16 cm (min-max: 0.8-1.6) wide, and 0.63±0.13 (min-max: 0.4-1.0) long. However, a small difference was noticed between the plants of Colle Ciuccio and Cuturelle. There was a statistically significant difference in the length of the two groups of cones (t of Student; t=10.236, P<0.001, N=38), while the width did not result statistically different (t=0.507, P=0.61, N=38); accordingly, there was a significant difference in the length of scales (t=3.318, P=0.002, N=38), but their width was not significant (t=0.371, P=0.71, N=38). The 45 cones collected in Sicily (Etna) resulted 7.0±0.9 cm (min-max: 5.1-10.6) long, and 3.7±0.5 (min-max: 3.0-6.1) wide; their scales resulted 1.11±0.16 (min-max: 0.8-1.6) wide, and 0.9±0.1 (min-max: 0.7-1.1) long. There was no statistical difference between the values of cone size from Calabria and Sicily (t of Student; t=-0.718, P=0.474, N=114).

Finally, concerning the cones of *Pinus halepensis*, 15 samples collected in Marettimo resulted 7.6±0.5 (min-max: 6.8-8.4) long, and 4.5±1.0 (min-max: 3.0-6.0) wide; their scales resulted 1.7±0.1 (min-max: 1.6-1.8) wide, and 1.1±0.1 (min-max: 1.1-1.3) long, 30 samples collected at Vittoria resulted 7.2±1.0 (min-max: 5.5-9.3) long, and 3.2±0.3 (min-max: 2.6-3.8) wide; their scales resulted 1.5±0.1 (min-max: 1.1-1.7) wide, and 1.1±0.1 (min-max: 0.8-1.4) long.

Sedentariness

Interestingly, in Sicily the population of Crossbills living on Mt. Etna did not mix with individuals coming from northern populations during the irruption of 1990; the population of Mt. Pellegrino (Sicily) arrived in 1990, remained for many years breeding there, but from 2005 onwards no birds were recorded, most probably they returned back to their original breeding area. On the other hand, they very likely starved to death, as they were observed feeding on seed of planted *Eucalyptus* (G. Guadagna, *pers. comm.*). The population of Sila (Calabria, S Italy) has shown a considerable sedentariness, and in the last years has numerically increased, feeding also on exotic planted spruces (Congi, 2021).

DISCUSSION

Biometrics

The most complete monograph on the Crossbills remains that by Ludlow Griscom (1937), a very interesting personage much ahead of the time he lived (1890-1959), in the USA he is known as the ‘Dean of the birdwatchers’. He examined 546 skins of Crossbills from Europe and emphasized that the debatable breeding areas are the mountains of Spain and Corsica in W Europe, the Crimea, the Caucasus and the mountains of Turkey in the east. He assumed that there are three strongly marked subspecies, about the characters of which there is no dispute whatever: *L. c. balearica* (von Homeyer, 1862), *L. curvirostra poliogyna* Whitaker, 1898 and *L. c. guillemardi* Madarász, 1903. In these subspecies the bill becomes notably stouter, heavier and thicker, even if Whitaker (1898) did not find biometric differences between *L. c. poliogyna* and *L. c. curvirostra*.

The bill height of the different groups of Crossbills differs along a West-East gradient (12.3 for male Crossbills using *Pinus nigra* in Cyprus, 11.7 for Crossbills using *Pinus halepensis* in North Africa, 11.6-11.7 for Crossbills using *Pinus nigra*/*laricio* in Corsica, S Italy and Etna (Sicily), 11.2 for Crossbills using *Pinus halepensis* in Majorca (Balearics), 10.76 for Spanish Crossbills using *P. uncinata*, 10.54 for Crossbills feeding on *P. sylvestris*, 10.31 for those eating seeds of *P. halepensis* in Spain) (Edelaar *et al.*, 2012; present study), which is very similar to the difference in bill height among some ecologically highly specialized North American Crossbills (Groth, 1993). Since Balearic and eastern Spanish birds eat seeds of the Aleppo Pine *Pinus halepensis*, whereas those of the north Iberian peninsula feed on other pines, the biometric differences might well reflect ecological differences between the populations involved (Edelaar *et al.*, 2003); the same appears to occur in other parts of the Mediterranean. According to Clouet (2003) crossbills from Corsica have a less decurved upper mandible than other crossbills in the Mediterranean; Benkman & Parchman (2009) consider that this reflects local adaptation to the tin-scaled cones on Corsica. Sedentary Crossbills of Mt. Etna (Sicily) have a stouter (higher but no longer) bill than individuals coming from north-European populations, arrived during periodical influxes. For example Herremans (1988) reports Belgium males with bills measuring 19.5 (mean length) and 10.3 (mean height) and females 18.7 (mean length) and 10.1 (mean height), with an index bill length/height of 1.9 (see also Summers *et al.*, 1996), while in south Italy, Sicily and North Africa male bills measure 19.2-19.4 (mean length), 11.6-11.7 (mean height), bill females 18.4-20.0 (mean length), 11.3-11.6 (mean height), with an index bill length/height of 1.6-1.8 (present data).

Overall, it seems that central Mediterranean Crossbills belong to the same population, at least biometrically speaking. Even the measurements of migratory Crossbills (detected during the various influxes that periodically occurred in the Mediterranean) indicate that they are coming from central-north European areas. They show thinner bills, adapted to different species of conifers, but not to *Pinus*. Conversely, in Spain all the populations of Crossbills are pine-feeding, have wings shorter than north Eu-

Tab. 5 - Sizes of cones of *Pinus nigra* and *Pinus halepensis*. **Pinus nigra pallasiana* var. *yaltirikiana* is distinguishable from other varieties by the fact that its cones are bigger (Alptekin, 1987; Oral, 2019). **According to Boulli *et al*. (2001) cone length varied among populations from 6.35 cm (Nkor population) to 9.01 cm (Boug population), the cone width varied from 3.13 cm (Jlak population) to 3.8 cm (Boug population). The longest and largest cones come from the South-West populations. / Dimensione degli strobili di *Pinus nigra* e *Pinus halepensis*. **Pinus nigra pallasiana* var. *yaltirikiana* è distinguibile dalle altre varietà per il fatto che gli strobili sono più grossi (Alptekin, 1987; Oral, 2019). **Secondo Boulli *et al*. (2001) la lunghezza degli strobili varia tra le popolazioni da 6,35 cm (popolazione di Nkor) a 9,01 cm (popolazione di Boug), la larghezza degli strobili varia da 3,13 cm (popolazione di Jlak) a 3,8 cm (popolazione di Boug). Gli strobili più lunghi e più larghi provengono dalle popolazioni sud occidentali.

Pinus nigra				
Locality	Length cones cm	Width cones cm	Length scales cm	Width scales cm
North Spain (Tíscar, 2019)	6.1±0.5	3.0±0.2		
Central Spain (Tíscar, 2019)	5.5±0.4	2.8±0.2		
South Spain (Tíscar, 2019)	5.7±0.3	2.9±0.1		
Spain (Alejano *et al*., 2019)	5.4±0.3	2.7±0.1		
Turkey (Sivacioglu & Ayan, 2010)	6.4±0.9	3.0±0.4		
Turkey (Oral, 2019)*	9.2 (7.7-10.2)	3.9 (3.6-4.3)		
Greece (Panayiotopoulos & Thanos, 2002)	5.3-6.2	2.5-3.2		
Italy, Abruzzo, Villetta Barrea (Giacobbe, 1933)	6-7 (4.0-8.5)			
Italy, Calabria, Sila (Giacobbe, 1933)	3.2-9.0			
Corsica (Giacobbe, 1933)	3.4-7.5			
Italy, Calabria, Sila (Benkman & Parchman, 2009)	6.35	3.2	0.3	1.8
France, Corsica (Benkman & Parchman, 2009)	6.0	3.0	0.3	1.7
Italy, Sicily, Etna (Benkman & Parchman, 2009)	6.4	3.3	0.3	1.8
Cyprus, Troodos (Benkman & Parchman, 2009)	7.7	3.6	0.4	2.1
Italy, Colle Ciuccio, Calabria (n = 20)	7.39±0.25 (min-max: 6.9-7.7)	2.9±0.14 (min-max: 2.7-3.2)	0.62±0.05 (min-max: 0.5-0.7)	1.14±0.09 (min-max: 1.0-1.4)
Italy, Cuturelle, Calabria (n = 20)	6.09±0.51 (min-max: 5.2-7.5)	2.74±0.17 (min-max: 2.2-3.0)	0.55±0.08 (min-max: 0.4-0.7)	1.13±0.08 (min-max: 0.9-1.2)
Italy, Carlomagno, Calabria (n = 12)	8.48±0.93 (min-max: 6.9-10.0)	2.89±0.24 (min-max: 2.5-3.3)	0.88±0.08 (min-max: 0.8-1.0)	1.35±0.17 (min-max: 1.1-1.6)
Italy, San Nicola, Calabria (n = 20)	6.14±0.20 (min-max: 5.8-6.5)	2.51±0.12 (min-max: 2.2-2.8)	0.57±0.08 (min-max: 0.4-0.7)	0.99±0.08 (min-max: 0.8-1.1)
Italy, Etna (n = 44)	7.0±0.9 (min-max: 5.1-10.6)	3.7±0.5 (min-max: 3.0-6.1)	0.9±0.1 (min-max: 0.7-1.1)	1.11±0.16 (min-max: 0.8-1.6)
Pinus halepensis				
Morocco (15 localities) (Boulli *et al*., 2001)**	min: 6.3±1.1 max: 9.0±1.4	min: 3.1±0.3 max: 3.8±0.4		
Tunisia sub-humid (Ayari *et al*., 2011)	7.6±0.6	3.3±0.7		
Tunisia upper semiarid (Ayari *et al*., 2011)	6.3±1.3	2.9±0.9		
Tunisia middle semiarid (Ayari *et al*., 2011)	6.7±1.0	3.1±0.6		
Tunisia lower semiarid (Ayari *et al*., 2011)	6.9±1.3	3.2±0.7		
Italy (Giordano, 1961; Ancillotti & Giannini, 1975)	min: 7.6±0.1 max: 9.5±0.1; 6.3-10.2	min: 3.2±0.03 max: 3.7±0.03; 2.8-3.8		
West coast Algeria (8 stands) (Harfouche *et al*., 2003)	8.3±1.6	5.0±1.4		
Greece (Amphilochia) (Matziris, 1998)	9.2±0.9	3.9±0.3		
Greece (from 5 regions) (Panetsos, 1975)	min: 7.3±1.0 max: 8.1±1.0	min: 3.3±0.3 max: 4.1±0.4		
Greece, Rhodos (Panetsos, 1975)	7.3±1.0	3.7±0.5		
Italy, Marettimo (Egadi Is., Sicily, Italy)	7.6±0.5 (min-max: 6.8-8.4)	4.5±1.0 (min-max: 3.0-6.0)	1.1±0.1 (min-max: 1.1-1.3)	1.7±0.1 (min-max: 1.6-1.8)
Italy, Vittoria, Sicily, Italy	7.2±1.0 (min-max: 5.5-9.3)	3.2±0.3 (min-max: 2.6-3.8)	1.1±0.1 (min-max: 0.8-1.4)	1.5±0.1 (min-max: 1.1-1.7)

ropean ones, are mostly sedentary and show a stouter bill (Alonso *et al*., 2006). Also, Crossbills in the Pyrenees and Corsica are pine-feeders and show a stouter bill.

Wing length reflects well the flight performance with migrant populations having a longer wing than resident ones. Assuming that the length of the wing corresponds to a larger size, it seems that southern Crossbill populations are more sedentary than northern ones and are smaller in size (shorter wing). Furthermore, the apparent clinal variation that was suggested by Massa (1987) does not appear to exist, even though northern populations, like those living in central-north Europe, are characterized by a larger size (e.g.: Herremans, 1988) and the southernmost populations are represented by smaller individuals (the minimum is that of the insular population of the Balearics, as shown in the present study).

Colouration in males and females

In *L. c. balearica*, *L. c. poliogyna* and *L. c. guillemardi*, as well as in the other Mediterranean populations, adult red males are rare to very rare, the majority being permanently xanthochroistic; adult females tend to lose the olive green and yellowish tones and become mostly grey or brownish ashy grey (Griscom, 1937). Figs. 5-8 show some skins coming from Italy, North Africa, the Balearics and Cyprus. Xanthochromism is an unusually yellow pigmentation often associated with the lack of usual red pigmentation and its replacement with yellow. The cause is usually genetic but may also be related to the bird's diet; the scarcity of coloration in Mediterranean Crossbills may depend on the insufficient carotenoids in their diet (Cantarero *et al*., 2020). Whitaker (1898) describing *L. c. poliogyna*, wrote that 'it is paler and greyer, this character being more conspicuous in the female, which is almost entirely grey, and not green or greenish, as is the female of the Common Crossbill'. Handrinos & Akriotis (1997) report that the male Crossbills breeding in Greece are duller and yellowish, with only a small percentage of red individuals, and females are greyer, less greenish than northern birds. Interestingly, among the specimens studied those obtained during irruptions from northern populations had a general discolored plumage; this may depend on the age class or the origin of irruptive population, which may be linked to pine seeds. Fig. 9 shows some males photographed in the field and Fig. 10 the original plate by Whitaker (1905) of *Loxia curvirostra poliogyna*.

Massa (1987) calculated the percentage of red in the breast and rump with the Munsell method (Smithe, 1975), and found that male and female specimens from N Europe resulted to be 66.1±10.7 and 65.3±6.6, in specimens from N Italy resulted 65.0±10.2 and 63.7±8.4, respectively, while in specimens from South Italy and Mt. Etna (Sicily) resulted 54.1±18.4 and 53.2±17.9, in specimens from N Africa 46.4±23 and 41.1±22.8, in those from Cyprus 25.0±15.8 and 20.8±13.3, and in specimens from the Balearics 44.0±20.4 and 38.3±23.0, respectively. Overall, it seems evident that all the Mediterranean populations show a high rate of xanthochromism, with extreme limits in the east population of Cyprus, in the west population of Majorca (Balearics), and in the southernmost population in North Africa.

Moult

The moult of all the Mediterranean Crossbills occurs between April-May and September (Massa, 1987; present study), showing that these birds breed in winter, presumably to allow the overlap of the hatching of chicks and the highest availability of pine seeds. According to Whitaker (1905), Tunisian Crossbills breed in the first months of the year. The birds breeding in the Alps are reported to breed between April and June (Spina & Licheri, 2003; Spina & Volponi, 2008). Generally, the northern populations of Crossbills breed following an irregular phenological calendar depending on food availability.

Studies on the bioacoustics

We recorded samples of songs, calls, and excitement calls of Crossbills in Calabria and Sicily, but they resulted to be insufficient to be presented in this paper. Differences in vocal types to recognize different populations of Crossbills were proposed by Clouet & Joachim (1996), who used the flight calls to discriminate Corsican, French Alpine and French Pyrenean populations; later Robb (2000) found out six different vocal types in North Europe. Since some years the American Crossbills were divided into nine 'sister taxa' or 'vocal types', sometimes living sympatrically, but separated by different vocalizations (Groth, 1993). Crossbills living in the Mediterranean area differ morphologically and vocally (Summers & Jardine, 2005). The vocal types of Mediterranean crossbills show at least some similarities to the vocal types of the rather sedentary crossbills of North Europe *L. pytyopsittacus* and *L. scotica*, which are also adapted to pine seeds; a peculiar 'flight call' has been observed in Corsica, called 'type H' by Förschler & Kalko (2009). The sedentary populations of Majorca, Cyprus and Morocco show some similarities in terms of shapes of the calls (Summers & Jardine, 2005). Overall, flight calls from Morocco, south Italy and Sicily sound like the flight call of Scottish Crossbill *Loxia scotica*. Interestingly, the song of crossbills vaguely resembles the song of the Greenfinch *Chloris chloris*, which was described by Linnaeus (1758) as *Loxia chloris*.

In recent times the song recordings and their sonograms have made it possible to appreciate that ethological barriers exist even among some populations of European Crossbills, although similar genetic barriers are not evident (Robb, 2000). Martin *et al*. (2019, 2020) found at least 18 different call types in the western Palaearctic, but interestingly, they found more call types than tree species, thus excluding the one-to-one specialization of individuals belonging to different call types in a particular tree species. They consider the possible hypothesis that populations characterized by different call types are not specialized in extracting seeds of specific conifer species cones. In addition, the bill depth, considered as a good measure of the specialization to the pine trees, is widely overlapping between the call types, even though at least most call types represent geographically clustered populations (Martin *et al*., 2020). However, many of these populations do not hybridize with each other, thanks to mechanisms still unknown to us (Edelaar, 2008; Edelaar *et al*., 2008).

Fig. 5 - Skins of male Crossbills preserved in the Civic Museum of Natural History of Milan collected in North Italy and Sila (Calabria, Italy); above dorsal view, below ventral view. / Pelli di crociere maschi conservati nel Museo Civico di Storia Naturale di Milano raccolti nel Nord Italia e in Sila (Calabria, Italia); sopra vista dorsale, sotto vista ventrale.

Fig. 6 - Skins of male Crossbills preserved in the Natural History Museum (Tring, UK), collected in Tunisia; above dorsal view, below ventral view. / Pelli di crociere maschi conservati nel Natural History Museum (Tring, UK), raccolti in Tunisia; sopra vista dorsale, sotto vista ventrale.

Fig. 7 - Skins of male Crossbills preserved in the Natural History Museum (Tring, UK), collected in the Balearic Islands; above dorsal view, below ventral view. / Pelli di crociere maschi conservati nel Natural History Museum (Tring, UK), raccolti nelle isole Baleari; sopra vista dorsale, sotto vista ventrale.

Fig. 8 - Skins of male Crossbills preserved in the Natural History Museum (Tring, UK), collected at Cyprus; above dorsal view, below ventral view. / Pelli di crociere maschi conservati nel Natural History Museum (Tring, UK), raccolti a Cipro; sopra vista dorsale, sotto vista ventrale.

Pine seeds as primary food

Crossbills eat seeds in both mature and green pine cones, forcing the scales to open with their bill to reach the seeds. Often when they eat on the pine cones, they are silent, and you can only hear the noise of crunching pine cones that they emit when using their bill. The lack of a fluctuation in the availability of coniferous seeds may have influenced selection in the Mediterranean Crossbill. Regular seed crops allowed Mediterranean Crossbills to establish resident populations and to increase numerically in isolated areas. Some *Pinus* taxa, mainly *P. halepensis*, are considered serotinous species, that is they release their seeds over a long period of time. Many populations of Mediterranean Crossbills eat the seeds of *Pinus nigra*, a circum-mediterranean species (Rodriguez-Sánchez *et al*., 2010; Tiscar, 2018), which also has regular crops. *P. halepensis* has been present in Spain for about 6000 years, *P. sylvestris* and *P. uncinata* have been present since the Tertiary. According to Rodriguez-Sánchez *et al*. (2010) during the last glacial maximum (21,000 years BP) the Iberian Peninsula acted as a refuge for *P. nigra* (other than for *P. sylvestris* and *P. uncinata*), while *P. halepensis* appears to be a recent addition to the Iberian flora that arrived from the northeast after the last glaciation. Expanding this consideration to the whole Mediterranean area, then *Pinus nigra* would have arrived before *P. halepensis*, and the Crossbills (whose common ancestor dates back to 11,000 years before present: Björklund *et al*., 2013; Parchman *et al*., 2018) would have adapted first to eating seeds of *P. nigra*, then to those of *P. halepensis*. Following Tiscar (2018), however, the geographical variation in cone and seed traits of *P. nigra* is mainly due to spatio-temporal variability in the pine interaction with Crossbills.

Because cones of *P. halepensis* are generally believed larger than those of *P. nigra* (but see Tab. 5), Crossbills that specialized to feed on seeds of *P. nigra*, when *P. halepensis* spread over the Mediterranean had to adapt to feeding on cones of *P. halepensis*. In this sense the populations adapted to *P. halepensis* are the result of a more recent adaptation. North African populations could represent an example. Extensive genetic work on western Palaearctic crossbills has been carried out by Parchman *et al*. (2018) who found a strong genetic support for separating Iberian and North African populations. Also Edelaar *et al*. (2012) found that bioacoustics, morphometrics and mitochondrial DNA of Crossbills differ among populations living in forest of different trees. Correctly, Parchman *et al*. (2018) consider that, given the right conditions, population genetic divergence in Crossbills occurred rapidly.

Individuals with a larger bill can access a food source, such as the pine cone, in advance of individuals with a thinner bill and this allows them to be present in space at the same time, but food segregate them over time; the selective pressures must have allowed a morphological evolution and a local adaptation to the resources, producing subtle and imperceptible reproductive barriers between the different populations.

Mezquida *et al*. (2018) observed that the period between seed fall of one generation of cones and the production of seeds by the new generation of cones is much greater in the south than in the north Europe, which could lead to the starvation of a specialist population of Crossbills. However in Mediterranean pines, such as *Pinus halepensis*, serotiny is much more developed and therefore more cones remain in plants that open due to high temperatures or fire; moreover the Aleppo's Pine produces cones very early (Tapias *et al*., 2001).

The food availability by Mediterranean Crossbills feeding on seeds of *Pinus* spp. is more regular than in central-north Europe, where they feed on less regularly seed producing *Picea* and *Larix* species (Martin *et al*., 2020). For this reason Mediterranean populations of Crossbills are sedentary.

Cones

The cones of *Pinus nigra* resulted as much variable in length, but not in width; from the beak crossbill's point of view, what is important is the size of cone scales, and is generally assumed that the Crossbills' beak is adapted to them. In Calabria we found two different sizes of cones with different scale size, but statistical difference was noticed only in the length of both cones and scales, but not in their width. Crossbills extract the seeds from the pine cones through a lateral movement of the jaws that moves the cone scales; thus, it is more important the width than the length of the scales for the jaw's movement of the bill.

It is well documented that seed predation by Red Squirrels *Sciurus vulgaris* causes selection for larger cone scales (Mazquida & Benkman, 2005); according to De Pace (2016) the clearest example of geographic variation in species assemblage that causes difference in forest tree fitness and direction of disruptive selection involves competition between squirrels and crossbills for North American Rocky Mountains *Pinus ponderosa* cone seeds. *Sciurus aberti* feeds mainly on the inner bark of Ponderosa pine twigs and exerts selection on resin characteristics but not directly on cone structure. In the absence of *S. aberti*, captive Crossbills had significantly longer seed extraction times when feeding on cones. However, cone scale provides resistance to Crossbills spreading cone scales apart, and increases scale thickness in response to Crossbill predation. Furthermore, *Sciurus griseus* has a selective impact on western Ponderosa pine by preferring seeds from cones with a high ratio of seed mass to cone mass which tends also to be small. Selection exerted by *S. griseus* favors trees with large cones and a low ratio of seed mass to cone mass, and these are the traits that characterize cones in which Grey squirrels are present and Crossbills absent (De Pace, 2016).

Thus, where Crossbills and Squirrels live together, cone scales size and bill morphology of Crossbills may change accordingly (Alonso *et al*., 2006). In the Balearic Is., where Squirrels are absent, cone scales are smaller and bill morphology of Crossbills results different from that of continental Spain (Alonso *et al*., 2006), may be as consequence of this. Interestingly, the cones measured in Calabria were collected in one area with co-occurrence of Crossbills and Squirrels, while in Sicily Squirrels are absent and consequently only Crossbills were present in

Veneto (N Italy)

Etna (Sicily, Italy)

Etna (Sicily, Italy)

Sila (Calabria, S Italy)

Fig. 9 - Some individuals of Crossbills photographed in the wild; Veneto: photo by L. Sattin; Sicily (Etna): photo by T. Puma; Calabria (Sila): photo by G. Congi. / Alcuni individui di crociere fotografati in natura; Veneto: foto di L. Sattin; Sicilia (Etna): foto di T. Puma; Calabria (Sila): foto di G. Congi.

Fig. 10 - The plate of *Loxia curvirostra poliogyna* depicted by H. Grönvold for Whitaker (1905) Birds of Tunisia. / La tavola di *Loxia curvirostra poliogyna* raffigurata da H. Grönvold per Birds of Tunisia di Whitaker (1905).

the Pine wood of Mt. Etna, like on the Balearic Is. However, from the measurements of cones of *Pinus nigra* we failed to demonstrate a difference due to the presence/absence of Squirrels; it seems that in southern Italy the presence of Squirrels is not a cause of change in size of the cones compared to Sicily, where Squirrels do not exist. Also, Beckman & Parchman (2009) observed that geographic patterns of cone variation suggest that Squirrels are not uniformly important selective agents on Black pine.

Sedentariness

Various arguments have been made to show that the size of the bill is an adaptive trait that allows the Crossbill to extract the seeds from the pine cones. While the populations living in central European conifers, with thinner bill, are characterized by a high nomadism, mainly due to the irregularity of the fructification of the larches and spruces, the populations linked to the pines, with more massive bill, become sedentary. Invasions originating from Europe north of Pyrenees (mainly from Russia) reach Spain every 3-6 years (Edelaar *et al*., 2012); in the Italian territory Crossbill irruptions are known from north Europe, but more distant from each other in years. Some of these birds may breed locally, but it is not demonstrated that they mix with local Crossbills. In fact, the interaction between ecology, breeding phenology, local performance and sexually selected traits can reduce gene flow among differentiating populations (Edelaar *et al*., 2012). Even if some authors wrote that it is not demonstrated that sedentary Crossbills exist (e.g., Eck, 1981), really there are some sedentary populations that live in different areas of the Mediterranean (e.g., Whitaker, 1905; Massa, 1987; Alonso *et al*., 2006). In accordance with Griscom (1937), it is unquestionable proved that Crossbills are resident in the Pyrenees, the mountains of Spain, Corsica and Cyprus, that Crossbills from North Europe have reached Spain in irruption years, but the resident Crossbills of the Iberian peninsula are notably isolated from the typical stocks in boreal Europe, and they are nearer to *L. c. balearica* than to *L. c. curvirostra*. Sedentariness is the condition to allowing divergence among populations. No Mediterranean populations have migrated northwards and have been detected in central Europe, the movement of nomadic Crossbills has been always unidirectional (Förschler & Kalko, 2009).

According to Hill & Powers (2021) these populations may be considered as ecomorphs, that is regional populations of a more widespread taxon that under strong selection adapts to a local environment but remains connected by gene flow to the parent population. Similarly, Summers & Piertney (2003) considered that crossbill species are not reproductively isolated and do not satisfy the species status under the BSC. We do not agree with these opinions, because at least in the Mediterranean populations of Crossbills the gene flow with northern populations has never been demonstrated, they have different bill morphology, show different breeding phenology, different moult strategy; overall, they may be considered reproductively isolated.

Biogeographic considerations

Griscom (1937) was convinced that *L. pytyopsittacus* Borkhausen, 1793 is a subspecies of *Loxia curvirostra*, even if within its breeding range *L. pytyopsittacus* lives promiscuously with *L. curvirostra*, and the two birds give every evidence of being two distinct species with a marked ecological distinction, *L. curvirostra* preferring spruce and larch, *L. pytyopsittacus* pines. Following Knox (1975, 1976, 1990) and Voous (1978), *L. scotica* is a valid species and the southern forms of Crossbills with a robust bill should deserve the same treatment as valid species. Murray (1978) and Eck (1981) agree with this opinion. According to Knox (1990) there have been many reports of two or more 'subspecies' of Crossbills breeding alongside one another, apparently without hybridizing; such evidence would indicate that separate species are involved (but see Summers & Piertney, 2003).

The Mediterranean Crossbills are a clear example where an integrated approach combining ecology, vocalizations and genetics is both needed and expected to be successful (Edelaar *et al*., 2003). Genetic studies performed on the three species of European crossbills *Loxia curvirostra*, *L. scotica* and *L. pytyopsittacus* did not find clear differences in microsatellites and mitochondrial DNA sequences (Piertney *et al*., 2001), and some overlap was observed in the bill size, which is considered as the morphological character that allows adaptive segregation (Massa, 1987). Some studies have reported a lack of clear genetic differences among most European populations of Crossbills (Questiau *et al*., 1999); conversely some genetic differences have been found in Mediterranean pine feeding populations (Borrás *et al*., 2008; Björklund *et al*., 2013; Arizaga *et al*., 2015; Parchman *et al*., 2018). According to Newton (2006) the lack of genetic evidence may be due to relatively young and ongoing speciation events. However, Crossbills live segregated in the form of different ecotymorphs in body size, vocalisations, bill size, color and food preferences (Clouet & Joachim, 1996; Edelaar, 2008; Edelaar *et al*., 2003, 2008, 2012; Alonso *et al*., 2020). Summers *et al*. (2007) have shown that the assortative mating indicates that *L. pytyopsittacus*, *L. scotica* and *L. curvirostra* behave as good species when breeding in sympatry (see also Robb, 2000).

Concerning *L. c. guillemardi*, according to Flint & Stewart (1992) it is endemic to Cyprus. Handrinos & Akriotis (1997) consider that Crossbills breeding in Greece tend to be smaller; they have been classified as *L. c. curvirostra* grading into *L. c. guillemardi*. According to Roselaar in Cramp & Perrins (1994) *L. c. guillemardi* should be distributed in Turkey, Crimea, Caucasus area and Cyprus. However, Griscom (1937) considered that the Crimea, Caucasus and Turkey specimens do not show any of the subspecific characters so strongly developed in *L. c. guillemardi* from Cyprus. Also, Benkman & Parchman (2009), reporting the biometric data from Roselaar, highlight that Cyprus crossbills have bill depths and widths 0.3 and 0.4 mm larger, respectively, than those from Turkey. Presently, no recent and exhaustive studies on Balkan Crossbills have been carried out; thus, it is impossible to identify them as belonging to the subspecies *guillemardi*, more probably birds in the Balkan peninsula are exactly the same of those of the other two Mediterranean peninsulas where they occur: Crossbills feed on pine seeds, consequently they have a more robust bill, and as a possible consequence of their diet, the males are less red and females less green than Crossbills of central-north Europe, generally classified as *Loxia c. curvirostra*. Like in the other Mediterranean areas they have a marked sedentariness and do not mix with north European *L. curvirostra*.

According to Griscom (1937) Crossbills reached Cyprus from the west or northwest and not from the north or northeast, and that *L. c. guillemardi* and the other Mediterranean subspecies are relics of an ancestral stock, which reached this area during a Pleistocene glaciation. Nethersole-Thompson (1975) and Murray (1978) proposed that *L. scotica* and *L. pytyopsittacus* evolved from a common ancestor that became isolated in pine forests in western Europe during the last glaciation. Following Murray (1978), the Crossbills were first divided into the western Palaearctic pine-feeding and the central and eastern Palaearctic spruce-feeding populations during glacial periods. Subsequently, the western Palaearctic populations were subdivided, during the postglacial, into three isolated groups that later evolved into the full species *scotica*, *pytyopsittacus* and the 'less well differentiated' Mediterranean forms. The spruce-feeding *curvirostra* populations then re-invaded the western Palaearctic as their main food source colonized the area (in the last 3-4,000 years). Eck (1981) proposed the hypothesis of a centrifugal spread from the central European populations northwards and southwards, producing forms with stronger bills. However, Knox (1990) considered that heavier bills evolved several times in pine feeding Crossbills, and it seems more likely that the west Palaearctic large-billed populations each arose separately. Tyrberg (1991) proposed that in the Pleistocene, Mediterranean Crossbills very likely followed the advancing of Pine forest distribution northwards. Differentiation following independent colonization by irrupting Crossbills could have led to the populations now found on some of the Mediterranean islands, in scattered areas of the Mediterranean peninsulas and in North Africa.

The geographic isolation of Mediterranean seed pines feeding populations of Crossbills has certainly contributed to the morphological divergence, as well as to genetic divergence (at least of some studied populations, like *balearica* and *poliogyna*; cf. Parchman *et al*., 2018). Very likely, all Mediterranean populations of Crossbills remained isolated and underwent a divergent selection from the north European *L. curvirostra*. The populations of the Mediterranean area, characterized by individuals with more massive bills than the central European ones, are probably descending from the Pleistocene ones which lived in the coniferous forests that then dominated the landscape; they had to feed on pine seeds, as other conifers were absent or rare west of the Urals. A possible diffusion towards the south had to be occurred from central European populations, which gave rise to forms with a large bill, such as *L. scotica*, *L. pytyopsittacus* and the Mediterranean populations; the specialization in feeding on pine seeds had to produce various adaptations, including a relatively longer tongue, which increased the ability to extract seeds from conifers that fruit regularly for long periods, as well as a tendency to be sedentary. Possibly, the ancestors of the most east-Mediterranean population, presently living in Cyprus, were Crossbills coming from the north-east, south of the Ural Mts. The most differentiated forms are peripheral to the whole European distribution, namely in the north (*L. scotica* and *L. pytyopsittacus*) and in the south (the Mediterranean populations) and possibly the rate of speciation has been accelerated by the development of sedentary populations. According to Martin *et al*. (2020) the interaction of the driving forces affecting differentiation differs between the Mediterranean sedentary populations and northern European nomadic ones.

We agree with the opinion of Knox (1990), heavier bills evolved several times in pine feeding Crossbills; thus, it is very likely that populations living in Mediterranean islands, Iberian, Italian, Balkan peninsulas and North Africa are the present result of the colonization occurring in different times, and the ancestors of the present populations have distant relations with each other. *Loxia curvirostra* could be a superspecies (rassenkreis or ring species) in the sense of Mayr (1931), that is a monophyletic group of very closely related and largely or entirely allopatric species; superspecies are geographical representatives of a common stock, but have attained reproductive isolation and are not merely subspecies of a single polytypic species. The term '*superspecies*' is not the same as the rank genus, it is only a concept to explain an evolutionary process in progress. The different populations of Crossbills are presently the result of allopatric isolation, and it is highly presumed they do not interbreed with each other.

CONCLUDING PROPOSALS

We think that the Mediterranean Crossbills are as much separate as *L. scotica* and *L. pytyopsittacus*, not less, as claimed by Murray (1978). The same criteria followed to raise *L. curvirostra scotica* to the species rank as *Loxia scotica* occur also for the different Mediterranean populations. We are convinced that a coevolutive radiation between the different populations of Mediterranean Crossbills presently living in the three main peninsulas, nearby islands and North Africa occurred separately and this may be demonstrated by their morphometrics, their sedentariness, as well as by songs and some genetic results, while the decolorization could be due to dietary causes.

We assume that the directions for future research on this bird must include studies on the very poorly examined Asian populations, east of Turkey. Further, it should be also considered treating at species level the following taxa: 1) *L. balearica* (von Homeyer, 1862) living in the Balearic Islands, and represented by some possible subspecies in the Iberian peninsula; among them *L. curvirostra hispana* Hartert, 1904 has been described, but see Griscom (1987) about the controversial types of this taxon; 2) *Loxia poliogyna* Whitaker, 1898, living in North Africa, and possibly in Corsica, South Italy, Calabria, Sicily (Mt. Etna) and central Italian Apennines; *L. curvirostra corsicana* Tschusi, 1912 could be a geographical subspecies of this taxon, but possibly other subspecies will be described from south Italy; 3) *Loxia guillemardi* Madarász, 1903, living in Cyprus, and represented by some subspecies in the Balkan peninsula; among them the following have been described: *L. curvirostra caucasica* Buturlin, 1907 from Caucasus, feeding on pine seeds, and *L. curvirostra mariae* Dementiev, 1932 from Crimea, feeding on *Pinus nigra*.

Some Crossbill populations are numerically very small and endangered, but they are not recognized as distinctive taxa. This is clearly a relevant problem from the conservation point of view (Edelaar *et al*., 2003). A practical aspect of a choice to treat the Mediterranean populations as valid species would be a major guarantee of their protection and future conservation.

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