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ORIGINAL ARTICLE

Vocal types in crossbill populations (*Loxia* spp.) of Southwest Europe

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Abstract The evolution of crossbills is one of the most fascinating topics in evolutionary ecology. Recent studies have shown an astonishing divergence in terms of vocalisation between morphologically quite similar crossbill populations in the Red/Common Crossbill complex (*Loxia curvirostra*) of North America and Europe. Some evidence even indicates the existence of "cryptic" species with different vocal types and bill sizes, which are adapted to different conifer species. However, there is so far no strong genetic evidence for the existence of separate species, although assortative mating occurs with respect to bill size. To understand the role of vocalisation in the speciation process of crossbill taxa, basic studies that assess the distribution of vocal types of crossbills and the use of different habitats and resources are needed. In our study, we investigated the occurrence of crossbill vocal types in Southwest Europe. In addition to the well-known vocal types described first by Robb (Dutch Birding 22:61–107, 2000) for the Benelux and Great Britain, we discovered at least six more vocal types in the Mediterranean area. Some vocal types were found exclusively in rather small areas, e.g. in the Pyrenees, the Sierra de Cazorla, Sierra de Javalambre and on Corsica, and appeared to be tightly linked to certain habitat types and pine species. Overall, vocal types in the Mediterranean had a more local occurrence than vocal types from northern populations, which were more widely distributed. This might reflect the nomadic behaviour of northern European crossbills, which feed, in contrast to Mediterranean crossbills, mostly on rather unstable food sources, especially spruce seeds. Furthermore, 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, L. scotica*), which are as well adapted to pine seeds. This might reflect a common ancestry of crossbills adapted for pines. We therefore suggest the existence of two main groups of crossbills in Europe: one group that is rather sedentary and feeds mainly on pine seeds (*L. pytyopsittacus, L. scotica* and the Mediterranean forms), and another group in Central, Northern and Eastern Europe that is highly nomadic and mostly feeds on spruce seeds (*L. curvirostra*). Further studies are needed to unravel the consistency of vocal types and the genetic relationship between the different forms, and to provide more evidence for the degree of assortative mating of crossbills with distinct vocalisation breeding in sympatry.

Keywords Vocal types · Vocalisation · Crossbill · *Loxia* · Speciation · Adaptation · Nomadism

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Introduction

One of the most challenging groups for the study of bird vocalisations and speciation is the species complex of the Red/Common Crossbill, *Loxia curvirostra*. The classification of crossbills has been disputed for a long time (Nethersole-Thompson 1975; Murray 1978; Tyrberg 1991; Groth 1988, 1993), and is still strongly debated (Parkin 2003; Edelaar and Terpestra 2004; Parchmann et al. 2006; Smith

and Benkman 2007; Edelaar et al. 2008; Edelaar 2008). In Europe, until the first half of the last century, three species were recognized based on morphological (bill and body size, wing pattern) and behavioural characteristics (food selection and migratory behaviour): the Common Crossbill *L. curvirostra*, the Parrot Crossbill *L. pytyopsittacus*, and the Two-Barred Crossbill *L. leucoptera bifasciata*. Subsequently, the status of the so-called Scottish Crossbill *L. scotica*, a subspecies of the Common Crossbill which occurs only in the indigenous pine woodlands of Scotland and shows morphological features that are intermediate between Parrot Crossbills and Common Crossbills, was raised to full species status (Knox 1975, 1990). However, other forms with similar intermediate biometry (Massa 1987) inhabiting the pine forests of the Mediterranean are still treated as subspecies of the Common Crossbill, including the subspecies *corsicana* from Corsica, ssp. *balearica* from the Balearics, ssp. *guillemardi* from Cyprus, Greece, and the Southern Balkans and ssp. *poliogyna* from North Africa, Sicily, and Southern Italy (Cramp and Perrins 1994; Dickinson 2003; Newton 2008). This puts the status of the Scottish Crossbill as a full species into question (Parkin 2003), although Summers et al. (2007) found a high degree of assortative mating in the three crossbill taxa breeding in Scotland (Scottish, Parrot, and Common Crossbill).

Recent work on vocalisation indicates that there are a large number of vocal types in the crossbill complexes of North America (Groth 1988, 1993) and Europe (Robb 2000; Constantine and The Sound Approach 2006). Taking the linkage between acoustic characteristics and morphological differences into account, this might point to the existence of more crossbill forms than have previously been recognized. Groth (1988, 1993) and Benkman (1993, 1999, 2003) found striking variation in the flight calls between nine North American Red Crossbill forms which differed only slightly in biometry, namely in body and bill size, and which were rather similar in plumage patterns. They suggested that these acoustically differentiated forms should be treated as "cryptic" species which have evolved adaptations to different types of conifers (Smith and Benkman 2007). Although some of these crossbill forms regularly breed in sympatry, hybridisation appears to be rare due to assortative mating (Groth 1993; Benkman 1993, 1999; Smith and Benkman 2007; Snowberg and Benkman 2007).

The potential use of vocal types as a means to discriminate crossbill populations in Europe was first suggested by Clouet and Joachim (1996), who found a clear divergence of flight calls between three populations in France (Corsica, Alps, and Pyrenees). Subsequently, six distinct vocal types, based mainly on the frequently uttered flight calls, were discovered by Robb (2000) during massive crossbill invasions in the Netherlands. One more vocal type was added later, leading to a total of seven vocal types (Constantine and The Sound Approach 2006): Wandering Crossbill (vocal type A), Bohemian Crossbill (vocal type B), Glip Crossbill (vocal type C), Phantom Crossbill (vocal type D), British Crossbill (vocal type E), Scarce Crossbill (vocal type F), and Parakeet Crossbill (vocal type X).

The occurrence of these seven vocal types in the Benelux, probably representing distinct populations of crossbills, varies considerably from year to year (Edelaar and Terpestra 2004). Biometric data from crossbills captured in different years suggest that birds with different vocal types also differ in functional traits (especially in bill depth) and are apparently mating assortatively (Edelaar 2008; Edelaar et al. 2008). Although it has been argued that this divergence in vocalisation and morphology might be associated with the presence of multiple, cryptic species in Europe, recent genetic analyses did not reveal any evidence for a high degree of differentiation, neither between the European subspecies and vocal types (including Scottish crossbills) nor between the distinct vocal types found in North America (Questiau et al. 1999; Piertney et al. 2001). However, the lack of genetic evidence found so far may result from relatively young and ongoing speciation events (Newton 2008). Furthermore, more sensitive markers may permit the detection of genetic differentiation in the future (Parchmann et al. 2006). In this scenario, we might be witnessing a case of song bird speciation in sympatry. Alternatively, the observed differences in vocalisation pattern may be either not that important or not advanced enough to permit and/or to indicate speciation events among crossbills. In the latter case, vocal types might rather represent groups of crossbills differing in flight call traditions rather than true species.

Crossbill vocalisation has been studied quite extensively in Northwest Europe (Robb 2000; Constantine and The Sound Approach 2006). However, data from the crossbill populations in the Mediterranean, which are mostly sedentary, are rather incomplete (Clouet and Joachim 1996; Summers and Jardine 2005). To fill this gap we recorded calls of various crossbill populations in Central Europe (Black Forest) and in Southwest Europe (Cevennes, Pyrenees, Sistema Central, Sierra de Cazorla, Corsica, Capraia and Sardinia) within a six-year period from 2001 to 2007. Our main aim was to assess and monitor vocal types of crossbill populations in those areas during breeding season. Following Summers and Jardine (2005), we expected flight calls of crossbills in the Mediterranean region to differ from those recorded in Northwest Europe (Robb 2000; Constantine and The Sound Approach 2006) due to the sedentary lifestyle of most of the Mediterranean populations. A second aim was to enlarge our knowledge of the distributions of the vocal types described by Robb (2000) in Southwest Europe. Finally, we searched for evidence for

a higher similarity of vocalizations among Mediterranean crossbills and crossbill forms feeding on pine seeds in northern Europe (*scotica*, *pytyopsittacus*) (Summers and Jardine 2005) than with the crossbills of Central and North Europe feeding on spruce seeds.

Material and methods

Vocalisations of several populations of Common Crossbills across Europe were collected during breeding seasons from 2001–2007. We recorded all birds opportunistically during a study on breeding biology and vocalisation of Citril Finches *Carduelis citrinella* and Corsican Finches *C. corsicanus*, which live in the same habitats (Förschler and Kalko 2006, 2007). Recordings were made at each study site where crossbills were heard and/or observed. Our data constitute a first qualitative overview of the distribution of crossbill vocal types in Southwest Europe, meant as a platform for future quantitative studies. In total we obtained material from eight study areas, including Corsica (Col d'Illerata, Col der Verghio, Haut-Asco, Col de Bavella; April–May 2001; approximately 16 min recordings on 30 excursion days), Cevennes (Causse Méjean, Mont Lozère; April 2002; approx. 53 min recordings on 12 excursion days), Catalonian Pre-Pyrenees (Port del Comte; April–June 2002; approx. 49 min recordings on 50 excursion days), Black Forest (Schliffkopf, Hornisgrinde; March 2002, July 2005; approx. 38 min. recordings on 10 excursion days), Sardinia (Monte Limbara; April 2003; approx. 6 min recordings on 30 excursion days), Capraia (close to the village of Capraia; April 2003; approx. 1 min recordings on 18 excursion days), Southern Spain (Sierra de Cazorla; April 2006; approx. 6 min recordings on 10 excursion days) and Central Spain (Sistema Central: Sierra Gudar and Sierra de Javalambre; May 2006; approx. 6 min recordings on 6 excursion days).

In our study we concentrated on the occurrence of the typical flight calls, which have been shown to be most useful for discriminating between the different crossbill vocal types (Robb 2000; Summers and Jardine 2005; Constantine and The Sound Approach 2006). We followed Robb (2000) for vocal type classification and visually compared the sonograms (frequency vs. time) of our flight call recordings with results of other studies. Additionally we also noted the predominant conifer species in each of our study areas, since there is strong evidence from North America that the occurrence of different crossbill forms is mainly related to the predominant species of conifers (Smith and Benkman 2007).

Vocalisations were recorded with a directional microphone (supercardioid Sennheiser microphone module ME 66 with K6 powering module, including windbreak) on a portable tape recorder (Sony WM-DC6 professional) using chrome dioxide cassettes (Sony UX-S, IEC II/Vocal type II 90 min). To obtain good sound recordings, the birds were approached as closely as possible (mainly between 5–25 m) without disturbing them. Whenever possible, the microphone was pointed on-axis towards the calling bird. Recording level was adjusted manually on the tape recorder and set between 3 and 9 on a scale of 1–10 depending on the distance to the sound source. Recordings were analyzed in the lab with the program Avisoft-SASlab Pro (Version 4.2; Raimund Specht, Berlin). For analysis, signals were processed with a fast fourier transformation (sampling frequency: 22,050 Hz; FFT-length 256; frame 100%; hamming window, FFT with 50% time overlap; frequency resolution 86 Hz, time resolution 5.8 ms) and displayed as colour sonagrams.

Results

We classified a total of 13 vocal types of flight calls in the study area (Fig. 1). Seven corresponded to the vocal types described by Robb (2000) and Constantine and The Sound Approach (2006) (Tables 1, 2; Fig. 2). In addition, at least six more vocal types were present in the Mediterranean crossbill populations (Tables 1, 2; Figs. 3, 4).

Black Forest

In the northern Black Forest, flight calls of the "Phantom Crossbill" (vocal type D) were dominant during our study, while the remaining vocal types corresponded to the "Glip Crossbill" (vocal type C) and the "Wandering Crossbill"

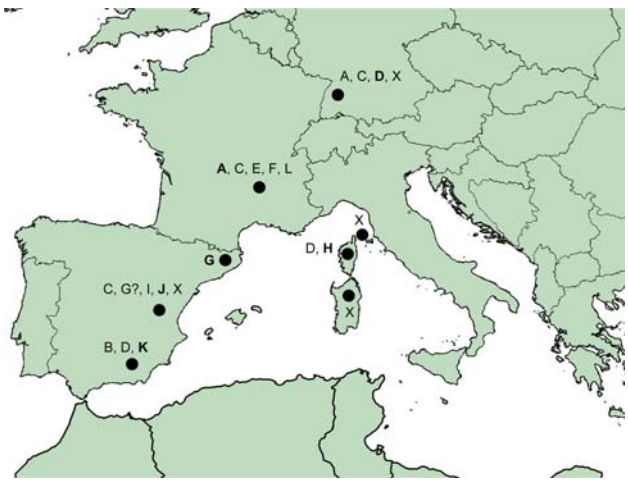

Fig. 1 Distribution of distinct vocal types of flight calls in the eight study areas with Common Crossbills (Black Forest, Cevennes, Pyrenees, Sistema Central, Sierra de Cazorla, Capraia, Corsica, Sardinia). The dominant vocal types are highlighted

Table 1 Vocal types of flight calls in Common Crossbills at eight study sites in Central and Southwest Europe recorded between 2001 and 2007

Vocal type	"Crossbill form"	Black Forest (nomadic)	Cevennes (nomadic)	Sistema Central (sedentary/nomadic)	Cazorla (sedentary/nomadic)	Pyrenees (largely sedentary)	Corsica (largely sedentary)	Sardinia (nomadic)	Capraia (nomadic)
A	Wandering	X	X						
B	Bohemian				X				
C	Glip	X	X	X					
D	Phantom	X			X		X		
E	British		X						
F	Scarce		X						
X	Parakeet	X		X				X	X
G	Pyrenean			X?		X			
H	Corsican						X		
I	Javalambre I			X					
J	Javalambre II			X					
K	Cazorla				X				
L	Cevennes		X						
Number of vocal types		4	5	4–5	3	1	2	1	1

Details on the migratory status in the different areas (nomadic/sedentary) are taken from Génard and Lescourret (1987), Massa (1987), Knox (1990), Cramp and Perrins (1994), Clouet and Joachim (1996), Glutz von Blotzheim and Bauer (1997)

Table 2 Some acoustic parameters of flight calls in Common Crossbills at eight study sites in Central and Southwest Europe recorded between 2001 and 2007

Vocal type	"Crossbill form"	Ind.	*F* low (kHz)	*F* high (kHz)	*F* mean (kHz)	*F* range (kHz)	Duration (s)
A	Wandering	15	2.3–2.8	4.2–5.4	3.6–3.8	2.0–2.6	0.04–0.06
B	Bohemian	15	3.2–3.9	4.3–4.9	4.1–4.3	1.5–1.6	0.02–0.05
C	Glip	12	2.0–2.8	5.0–6.0	3.6–4.3	2.3–3.8	0.03–0.07
D	Phantom	22	1.9–3.0	4.7–5.8	3.7–3.9	2.1–3.3	0.04–0.06
E	British	10	2.9–3.6	5.0–5.6	3.9–4.3	1.4–2.0	0.04–0.06
F	Scarce	1	3.2–3.4	6.2–6.4	4.3–4.4	3–3.1	0.05–0.06
X	Parakeet	20	2.1–3.4	4.2–4.7	3.9–4.1	1.1–2.2	0.06–0.08
G	Pyrenean	20	1.9–2.1	4.4–4.5	3.7–4.3	2.3–3.1	0.03–0.04
H	Corsican	10	2.4–2.8	4.4–4.6	3.4–3.8	1.7–2.1	0.04–0.05
I	Javalambre I	1	2.8	4.9	3.6–3.7	2.1–2.2	0.04–0.05
J	Javalambre II	5	2.5–2.6	5.1–5.2	3.9–4.0	2.6–2.7	0.06–0.07
K	Cazorla	10	3.0–3.1	5.0–5.1	3.8–3.9	1.9–2.0	0.04–0.04
L	Cevennes	10	2.8–3.0	4.0–4.1	4.0–4.1	1.6–1.8	0.04–0.05

F frequency in kHz; *Ind.*, number of birds sampled with the corresponding flight call

(vocal type A). Furthermore, we recorded flight calls of the "Parakeet Crossbill" (vocal type X). Regarding potential food plants, Norway Spruce (*Picea abies*) and Mountain Pines (*Pinus mugo rotundata*) were the predominant conifer species of the Black Forest.

Cevennes

At Mont Lozère we documented flight calls of "Wandering Crossbills" (vocal type A) with fledglings in forests with Scots Pines *Pinus sylvestris* and Mountain Pines *Pinus mugo uncinata*. A large portion of the crossbills recorded in the Causse Méjean in the Cevennes had this vocal type. However, we also recorded "Glip Crossbills" (vocal type C), "British Crossbills" (vocal type E) and one "Scarce Crossbill" (vocal type F) in addition to vocal type A. Several birds uttered a flight call which we named vocal type L. However, this flight call might be also derived from vocal type A (Fig. 4). In contrast to the "slash form" of type B it is best characterized by a "backslash" starting at

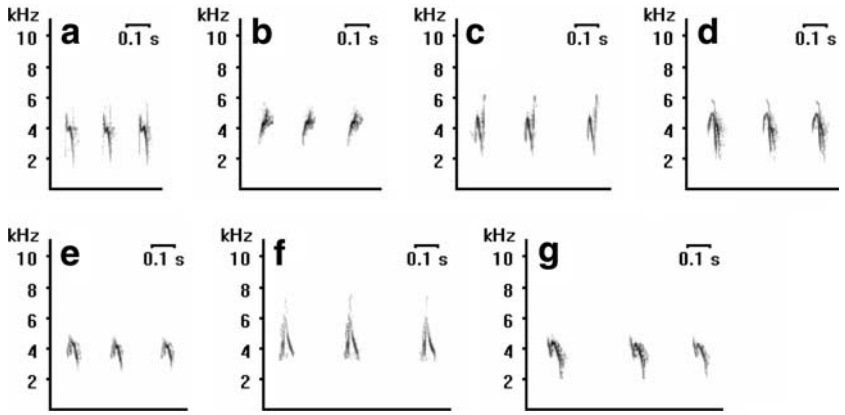

Fig. 2a–g Vocal types of flight calls in crossbills recorded during our study and classified by Robb (2000) and Constantine and The Sound Approach (2006): **a** vocal type A "Wandering Crossbill", Causse Méjean/France; **b** vocal type B "Bohemian Crossbill" Sierra de Cazorla/Spain; **c** vocal type C "Glip Crossbill"; **d** vocal type D "Phantom Crossbill" Black Forest/Germany; **e** vocal type E "British Crossbill"; **f** vocal type F "Scarce Crossbill", Causse Méjean/France; **g** vocal type X "Parakeet Crossbill", Sardinia

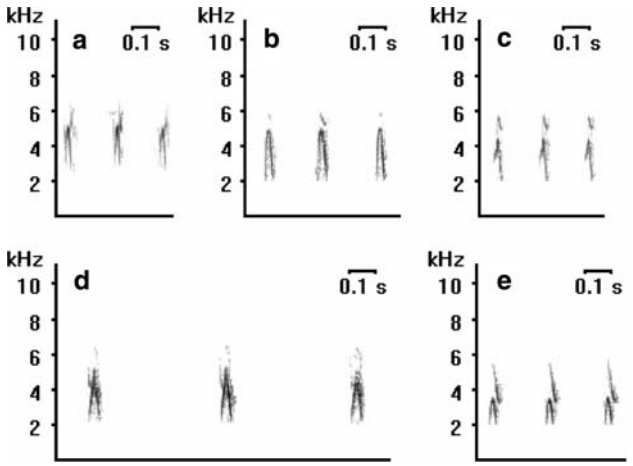

Fig. 3a–e Vocal types of flight calls in crossbills recorded during our study in the Catalonian Pre-Pyrenees: vocal type G "Pyrenean Crossbill", Port del Comte/Spain (**a–e**). Note the high variability of this call in this study area. However, all of the calls have the "reversed V structure" in common

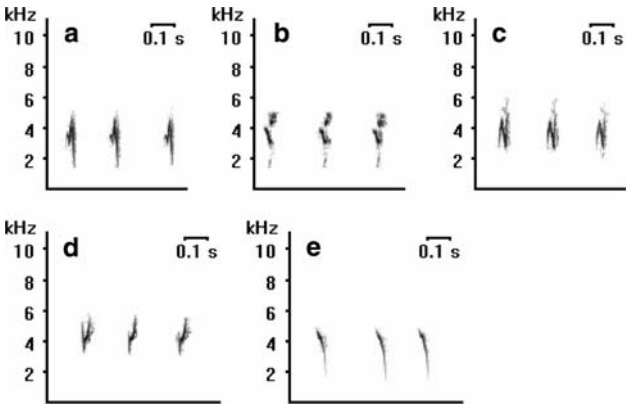

Fig. 4a–e Other vocal types of flight calls in crossbills recorded during our study: **a** vocal type H "Corsican Crossbill", Col d' Illerata/France; **b** vocal type I, Sierra de Javalambre/Spain; **c** vocal type J, Sierra de Javalambre/Spain; **d** vocal type K, Sierra de Cazorla/Spain; **e** vocal type L, Causse Méjean/France

about 4.5–4.7 kHz with a mean frequency of around 4–4.1 kHz and an ending frequency of about 2.8–3.0 kHz.

Catalonian Pre-Pyrenees

None of the flight call recordings from the Catalonian Pre-Pyrenees closely resembled any of the crossbill vocal types presented by Robb (2000) and Constantine and The Sound Approach (2006). Despite a high number of recordings in the area, we found only one vocal type that we named "Pyrenean crossbill" (vocal type G). The basic call structure was composed of a reverse "V" with low starting and high ending frequencies. This vocal type showed a rather high degree of variation (Fig. 3), with the lowest frequencies at 1.9–2.1 kHz and the highest frequencies at 4.4–5.5 kHz. Mean frequency was about 3.7–4.3 kHz. The crossbills were either recorded in Scots Pines *Pinus sylvestris* or in Mountain Pines *Pinus mugo uncinata*.

Central Spain

In the Sistema Central of Spain (Central System of Spain), crossbills were recorded in the Sierra de Gúdar and the Sierra de Javalambre. The flight call recordings from both areas were similar and consistently showed three vocal types. Some of these were most similar to the "Glip Crossbill" (vocal type C). Others looked like a mixture of this vocal type with the vocal type G recorded in the Pyrenees. Since they did not fully fit into the schemes of these two types, we classified them as vocal type J (Fig. 4). The flight calls were shaped like a flash, with an "up-down-up" frequency modulation (low starting and ending

frequencies). The lowest frequencies were 2.5–2.6 kHz and the highest 5.1–5.2 kHz. Mean frequency was about 3.9–4.0 kHz. Another vocal type that we registered only for one individual in the Sierra de Javalambre (vocal type I) was shaped like a "semicolon" (Fig. 4). The lowest frequency was about 2.8 kHz and the highest frequency about 4.9 kHz. Mean frequency was about 3.6–3.7 kHz. Finally, we registered a few flight calls that were most similar to the "Parakeet Crossbills" (vocal type X). Scots Pines (*Pinus sylvestris*) predominated at both study sites with a few Mountain Pines (*Pinus mugo uncinata*) in the higher elevations of Sierra de Gudar.

Southern Spain

We found three flight call types in the Sierra de Cazorla. Birds predominantly uttered calls of "Bohemian Crossbills" (vocal type B), while a few called like "Phantom Crossbills" (vocal type D). One flight call type was found exclusively in Cazorla (vocal type K). It was structured like a "V" with high starting and ending frequencies (Fig. 4), showing some similarities to the vocal type B. The lowest frequencies were 3.0–3.1 kHz and the highest 5.0–5.1 kHz. Mean frequency was about 4.0–4.1 kHz. In the Sierra de Cazorla, crossbills live mainly in forests composed of Black Pine (*Pinus nigra*).

Corsica

The thick-billed crossbills from Corsica are treated as the subspecies *corsicana* (Clouet and Joachim 1996). The flight calls of this form (vocal type H) differed from all other crossbill flight calls by their flash-shaped structure with average starting frequencies and low ending frequencies (Fig. 4). The lowest frequencies were 2.4–2.7 kHz and the highest were 4.4–4.6 kHz. Mean frequency was about 3.4–3.8 kHz. Additionally, we recorded some flight calls of "Phantom Crossbills" (vocal type D) in the same group of crossbills. Birds on Corsica live mainly in forests consisting of Laricio Pines (*Pinus laricio*) and Maritime Pines (*Pinus pinaster*).

Sardinia and Capraia

On both islands, crossbills occur irregularly during invasions. There are only three breeding records from Sardinia (Grussu and Asuni 2003) The acoustic recordings we obtained from both islands during an invasion in April 2002 revealed flight calls with the structure of "Parakeet Crossbills" (vocal type X). The birds at Monte Limbara on Sardinia were feeding on Black Pine (*Pinus nigra*) seeds, while the birds on Capraia were observed in Aleppo Pines (*Pinus halepensis*).

Discussion

Solving the riddle of the distinct vocal types of flight calls and apparently related cryptic species in the Common Crossbill complex is one of the most challenging tasks in the evolutionary ecology of birds. The groundbreaking work of Groth (1988, 1993) and Benkman (1993) on the North American Red Crossbill complex opened up new avenues for research into crossbill speciation in North America as well as in Europe. However, the functional background and the maintenance of these distinct crossbill forms with their characteristic vocal types over time and space remain unknown.

Distribution of vocal types in Europe

Besides the seven known vocal types described by Robb (2000) and Constantine and The Sound Approach (2006), we found at least six new vocal types in crossbill populations of Southwest Europe. Although some of these vocal types might be merged in the future with others, when we know more about their variation, six distinct vocal types are dominant in Northern and Central Europe, which we will henceforth call "Northern Crossbills".

Vocal type A—"Wandering Crossbill"

Following Constantine and The Sound Approach (2006), this is one of the most widespread vocal types in Europe. Robb (2000) indicates its occurrence in the Netherlands, Belgium, Estonia, France, Germany, and Sweden. Bergmann (personal communication) recorded it in the Bregenzerwald (NW Austria). We found this vocal type in Central France and Southwest Germany, but we also report it for the first time in Spain. Most recordings of this vocal type originate from Scots Pine and Norway Spruce forest, but Fouarge (2005) also found them in Belgium in larch *Larix spec.* and Douglas Fir *Pseudotsuga spec*. Apparently crossbills with this vocal type appear in all kinds of conifer forests of Europe when they produce seeds. This might be linked to a high degree of nomadism.

Vocal type C—"Glip Crossbill"

Flight calls of this vocal type have a similar distribution range to vocal type A. They have been recorded so far in the Netherlands, Belgium, Britain, Denmark and Fenno-Scandinavia (Robb 2000; Fouarge 2005; Constantine and The Sound Approach 2006) as well as in the Alps (Clouet and Joachim 1996). We found flight calls of this vocal type in South Germany, Central France, and Central Spain. Apparently, crossbills with this vocal type are mostly drawn to Norway Spruce forest (Robb 2000). However, it

also occurs in birds feeding in larch and Douglas Fir (Fouarge 2005) as well as in Scots Pine and Mountain Pine, as we have found in our study.

Vocal type D—"Phantom Crossbill"

This vocal type has so far been only recorded in the Benelux and Southern England (Robb 2000; Fouarge 2005; Constantine and The Sound Approach 2006). We found the flight calls of this vocal type to be very abundant in Norway Spruce and Mountain Pine forest of the Black Forest in Southern Germany. Additionally, crossbills with this vocal type appeared in small numbers in Southern Spain (Black Pine) and, more surprisingly, in some instances on Corsica (Laricio Black Pine).

Vocal type E—"British Crossbill"

This vocal type was supposed to be the counterpart of the well-known Scottish Crossbill, so far found only in Britain and the Netherlands according to Robb (2000) and Constantine and The Sound Approach (2006). However, our results revealed that this vocal type also occurs in Scots Pine forest in the Cevennes (Central France).

Vocal type F—"Scarce Crossbill"

The flight calls of this vocal type have only been recorded in the Benelux previously (Constantine and The Sound Approach 2006). We found a crossbill with such flight calls in Scots Pine forest in the Cevennes (Central France) as well.

Vocal type X—"Parakeet Crossbill"

Constantine and The Sound Approach (2006) described that birds with this vocal type were highly nomadic. The flight calls of this vocal type have been recorded from Finland to Spain and in the UK. It appears to be the dominant vocal type in Norway Spruce forests of the Alps and Scandinavia. Fouarge (2005) observed it mainly in forest stands with larch *Larix spec.* and pines *Pinus spec.* We recorded flight calls of this vocal type in the Black Forest of Germany (Norway Spruce and Mountain Pine) and the Sistema Central of Central Spain (Scots Pine). Furthermore, all of the crossbills observed during an invasion in Sardinia (Black Pine) and the island of Capraia (Aleppo Pine) uttered flight calls of this vocal type.

The following seven vocal types seem to be more abundant or exclusively found in populations from southern breeding areas. We therefore call them "Mediterranean Crossbills".

Vocal type B—"Bohemian Crossbill"

According to Robb (2000), this vocal type is found in the Netherlands, in the Bayrischer Wald of Germany and in Greece. It was furthermore recorded in the Almtal of East Austria (Bergmann, personal communication) and Corsica (Clouet and Joachim 1996). The crossbills associated with this vocal type are thought to be mainly drawn to Black Pine forest. Confirming these expectations, we found flight calls of this vocal type only in Black Pines of South Spain in the Sierra de Cazorla, but we could not confirm this vocal type in Corsica which is covered, in part, with Black Pine forest.

Vocal type G—"Pyrenean Crossbill"

The crossbills of Port del Comte mountain in the Catalonian Pyrenees predominantly used a flight call which we did not record anywhere else (Fig. 3). A similar call type for the Pyrenees has been previously documented by Clouet and Joachim (1996) and Summers and Jardine (2005). In our study, this vocal type was the only one found in this area despite extensive recordings. This might be associated with the observation that the crossbill population of the Pyrenees is highly sedentary (Génard and Lescourret 1987, Senar et al. 1993). Crossbills in this area use as a food resource three pine species at different elevations, thus taking advantage of subsequent fruiting periods: Black Pines produce seeds first at low elevation, followed by Scots Pines at medium elevation and finally Mountain Pines at high elevation. Hence, the crossbills in this area do not migrate long distances but conduct localized altitudinal movements due to food resources. Furthermore, the records presented by Summers and Jardine (2005) for the sedentary populations of Majorca, Cyprus and Morocco also show similarities in terms of the shapes of the calls.

Vocal type H—"Corsican Crossbill"

The flight calls of the Corsican Crossbills are distinct from any other Mediterranean crossbills. As occurs with Pyrenean Crossbills and with Balearic Crossbills, Corsican Crossbills are highly sedentary and live mainly in Laricio Black Pine and Maritime Pine forest. Similar to the Balearic Crossbills (Alonso et al. 2006), this island form is characterized by a stronger bill and shorter wings. It is therefore treated as a distinct subspecies. The flight call shown by Clouet and Joachim (1996) for Corsica differs from our recordings and is more like vocal type C.

Vocal type I—"Javalambre I Crossbill"

We found this flight call in only one individual crossbill in the Scots Pine forests of the Sierra de Javalambre.

Vocal type J—"Javalambre II Crossbill"

This flight call is similar to that of the "Glip crossbills" (Robb 2000) and might be a variation on this call type. The birds with these calls were recorded in Scots Pine forest.

Vocal type K—"Cazorla Crossbill"

This V-shaped flight call type only occurred in the Black Pine forests of the Sierra de Cazorla in South Spain. As in the Pyrenees, the crossbill populations in this mountain range are very sedentary. The calls differ from all other Mediterranean Crossbills that we recorded and also from the flight calls presented by Summers and Jardine (2005) for Majorca, Cyprus and Morocco.

Vocal type L—"Cevennes Crossbill"

These calls from crossbills were recorded frequently in Scots Pines of the Causse Méjean in the French Cevennes. They have some similarities with the calls of vocal type A crossbills and might be a variation on this call type.

Evolution of different crossbill forms

There is evidence from North America of an ongoing evolution leading to ecological speciation of distinct crossbill forms in conjunction with specific vocal types. This speciation seems to be based on an increasing divergence in the use of food resources, specifically the cones of various species of conifers (Benkman 1993, 2003, Smith and Benkman 2007). In this context, it is also well recognized that differences in bill shapes of European crossbill species are associated with their respective feeding habits and cone types (Newton 1972; Summers et al. 2007). In line with this observation, Massa (1987) and Alonso et al. (2006) also found a correlation between bill size and the size of pine cones in Mediterranean crossbills. Bill size seems to be further linked to the vocal types of the birds. Summers et al. (2007) investigated mating behaviour and patterns of inheritance of bill size and vocal type of flight calls within three crossbill taxa in Scotland (*scotica*, *pytyopsittacus*, *curvirostra*). They found crossbills to mate predominantly with birds with similar bill sizes and vocal types (assortative mating). Bill size, in this case bill depth, was a highly heritable trait. It appears that, on the one hand, the three crossbill taxa did not interbreed freely, and on the other hand, they are not yet fully reproductively isolated from each other. This might explain the lack of genetic differentiation in neutral DNA (Questiau et al. 1999; Piertney et al. 2001), besides the possibility that the speciation is very recent and therefore only visible in sensitive, fast-evolving markers.

It is reasonable to assume that in the Mediterranean areas the highly sedentary lifestyle due to stable food resources is the main driving force for the development of local crossbill forms (Senar et al. 1993). Sedentary crossbills are mostly associated with pine species, which generally offer, in contrast to spruces, more stable food resources. Additionally, several pine species often fructify subsequently in the same area at different elevations, e.g. Black Pines, Scots Pines and Mountain Pines in the Catalonian Pre-Pyrenees. All of the sedentary crossbill forms that we recorded in our study have vocal types that do not match the ones described by Robb (2000) and Constantine and The Sound Approach (2006) for Common Crossbills of North and Central Europe and may therefore reflect an independent taxonomic status of the Mediterranean crossbill forms.

For a better understanding of the crossbill evolution in Europe, it seems worth checking the fossil evidence. Eck (1981) was the first to propose that historically crossbills from Central Europe might have spread centrifugally northwards and southwards, leading to sedentary forms in areas with suitable resources, e.g. pine forests in the Mediterranean (Massa 1987). Murray (1978) and Tyrberg (1991) proposed a more comprehensive scenario for the evolution of crossbills in Europe, where in the Pleistocene Mediterranean crossbills are likely to have followed the advancing pine forests northwards. They might have subsequently become isolated in the Scots Pine forests of Fennoscandia (*pytyopsittacus*) and in the Caledonian Scots Pine forests of Scotland (*scotica*) due to post-glacial warming and the related extension of deciduous woodland. Later, the Spruce Crossbill (*curvirostra*) is thought to have expanded westwards along with the westwards expansion of its main food plant and may have caused *pytyopsittacus* to diverge through character displacement, while all crossbills feeding on pine that remained in Central Europe are likely to have been displaced by crossbills feeding on spruce. The Scottish and the Mediterranean crossbills are likely to have persisted due to their isolation. In addition to variations in morphology and genetics, divergence in vocalisation is to be expected over time and space between these different crossbills. Hence the recently found differences in vocal types might contain phylogenetic information about the origin of the different forms.

This scenario would fit somewhat with the pattern of different vocal types with discontinuous variation, as it is currently known. The wide distributions of some flight call

types suggest several highly mobile North and Central European crossbill forms (vocal types A, C, D, E, F, X) with extensive nomadism (*curvirostra* group) in contrast to more sedentary forms in the Mediterranean (e.g. vocal types G, H, K of this study), Scotland (*scotica*) and Scandinavia (*pytyopsittacus*). Interestingly, the call structures of the latter more closely resemble the calls of Scottish and Parrot Crossbills than the calls of North and Central European *curvirostra* crossbills (see also Summers and Jardine 2005). They might therefore reflect a common phylogenetic origin and at the same time different food preferences (pines vs. spruces).

If this hypothesis is true, the sympatric occurrence of "Spruce Crossbills" in the native areas of Scottish Crossbills and Mediterranean Crossbills could represent a relatively recent development caused by the large-scale cultivation of spruce forest in Central Europe over the last two centuries and the associated westward expansion of nomadic crossbill forms from the Taiga. Accordingly, it is important to note that vocal types of the "northern crossbill forms" also occur in the Mediterranean, although only in very low numbers (e.g. in Spain, Corsica, Capraia, Sardinia). This shows, nevertheless, that the nomadic populations regularly reach the Mediterranean areas. In contrast, none of the Mediterranean vocal types have so far been recorded in Central Europe (Robb 2000; Constantine and The Sound Approach 2006, this study). This unidirectional movement is confirmed by ringing recoveries as well (Zink and Bairlein 1995; Newton 2006). It seems probable that the different vocal types that we documented in our study represent more or less independent populations which have not had enough time to diverge in morphology and genetics yet and/or may continue to interbreed to an unknown extent. Alternatively, assortative mating may act as an isolating mechanism that prevents the forms from merging into one gene pool (Summers et al. 2007, Smith and Benkman 2007). In this scenario, the distinct vocal types could play a decisive role in fostering "species integrity".

Outlook

Our data provide some preliminary and new insights into variations in crossbill vocalisation, in particular about the distribution of different flight call types across Europe. The findings raise important questions about crossbill evolution. (1) Is the European crossbill complex at the beginning of a sympatric speciation process where differences in food selection play a major role? (2) Can we find adaptive responses in bill morphology to different cone types of different conifer species? (3) Do the different vocal types of crossbills found in this study reveal different adaptations to food resources, e.g. in terms of bill morphology? (4) Are different crossbill populations really characterized by one specific vocal type? (5) To what extent is vocal matching of calls between social partners of different origin possible? (6) To what extent are flight calls learnt or inherited? (7) If they are learnt, are the distinct crossbill forms able to use several of the vocal types?

Because of the continuous increase in the number of discovered vocal types, which is likely to rise even further when studying East European and Asian crossbill populations, care needs to be taken in the current discussion over labelling all crossbill forms prematurely as "species". This is especially important since recent evidence from genetic analyses suggests that there is a much lower genetic differentiation between crossbill forms than expected, even between the morphologically and behaviourally rather distinct Parrot Crossbills and Common Crossbills (Questiau et al. 1999; Piertney et al. 2001). It is debatable whether full species status should be given to the different crossbill forms on the basis of only vocal types (Summers et al. 2007; Edelaar 2008). Interestingly, in a study on partially isolated Citril Finches *Carduelis citrinella* with a similar distribution to the crossbills described in this study, vocalisation patterns also differed considerably (Förschler and Kalko 2007). However, genetic evidence to support the species status of the localised populations is lacking (Pasquet and Thibault 1997). A promising approach has come from North America, where restricted gene flow based on inferred allele frequency variation has been observed for some forms of the North American Red Crossbill complex (Parchmann et al. 2006). However, in contrast, tree-based analyses using 440 AFLP loci did not separate individuals from the eight vocal types properly. Other studies investigating the regional source areas via stable isotope analyses (Marquiss et al. 2008) may also help to elucidate more about the origin of the different crossbill populations and vocal types. To conclude, a lot more work must be done in the future in order to gain a full understanding of the mechanisms and importance of vocalisation in crossbill speciation and its relationship to morphological and genetical traits.

Zusammenfassung

Vokalisationstypen in südwesteuropäischen Kreuzschnabelpopulationen (*Loxia* spp.)

Die Evolution der Kreuzschnäbel gehört zu den faszinierendsten Bereichen der evolutionären Ökologie der Vögel. In Nordamerika konnte gezeigt werden, dass verschiedene Kreuzschnabelpopulationen, die äußerlich morphologisch kaum zu unterscheiden sind, große Unterschiede in ihren Lautäußerungen zeigten. Auch in Europa wurden kürzlich ähnliche Unterschiede in den Rufen nachgewiesen. Dabei

spricht einiges für die Annahme, dass es sich bei den verschiedenen Formen teilweise sogar um bisher unerkannte Kreuzschnabel-Arten handeln könnte, die sich an verschiedene Ressourcen (Koniferenarten) angepaßt haben. Allerdings gibt es auf molekulargenetischer Basis bislang noch keine schlüssigen Beweise für diese Hypothese. Grundlegende Studien zur Verbreitung der Vokalisationstypen („vocal types") und der unterschiedlichen Nutzung von Nahrungsressourcen können daher zum besseren Verständnis der Rolle dieser Vokalisationstypen im Artbildungsprozeß der Kreuzschnäbel beitragen. Wir untersuchten das Auftreten verschiedener Vokalisationstypen in Kreuzschnabel-Vorkommen Südwesteuropas. Neben den bereits bekannten und in Nordeuropa weit verbreiteten Vokalisationstypen fanden wir im südwestlichen Mittelmeerraum mindestens sechs weitere Typen. Einige davon waren auf einzelne Gebiete beschränkt, beispielsweise die Pyrenäen, die Sierra de Cazorla, die Sierra de Javalambre und Corsica, und waren scheinbar direkt an bestimmte Habitattypen und die darin vorkommenden Koniferenarten gebunden. Insgesamt waren die im Mittelmeerraum gefundenen Vokalisationstypen deutlich weniger weit verbreitet. Dies ist wahrscheinlich auf die erhöhte Seßhaftigkeit dieser Populationen aufgrund der größeren Nahrungsstabilität zurückzuführen. Die nord- und zentraleuropäischen Kreuzschnäbel sind im Gegensatz dazu stark nomadisch, da sie im wesentlich von der Fichte abhängig sind und daher immer wieder zum Abwandern gezwungen werden. Die mit ihnen assoziierten Ruftypen waren in unserer Studie folglich auch deutlich weiter verbreitet. Interessanterweise ähnelten die Rufe der sedentären Mittelmeerpopulationen zumindest teilweise den Rufen von Kiefernkreuzschnabel *L. pytyopsittacus* und Schottischem Kreuzschnabel *L. scotica*, die ebenfalls bevorzugt Kiefernsamen fressen und ein geringes Nomadisierungsverhalten zeigen. Möglicherweise spiegelt sich in den Vokalisationstypen die gemeinsame phylogenetische Herkunft der Taxa wieder. Wir formulieren daher die Arbeitshypothese, dass es in Europa zwei Hauptgruppen von Kreuzschnäbeln gibt: Zum einen die eher seßhaften und überwiegend Kiefernsamen fressenden Formen (Kiefernkreuzschnabel, Schottischer Kreuzschnabel und die Kreuzschnäbel des Mittelmeerraumes) und zum anderen die stark nomadischen Kreuzschnäbel Nord-, Zentral- und Osteuropas, die sich vorwiegend von Fichtensamen ernähren. Weitere Studien sind nötig, um die genetische Verwandtschaft zwischen diesen verschiedenen Kreuzschnabelformen und die Rolle der Vokalisationstypen bei der Partnerwahl im Falle sympatrischen Vorkommens aufzuklären.

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