Journal of Biogeography (*J. Biogeogr.*) (2007)

ORIGINAL ARTICLE

Geographical differentiation, acoustic adaptation and species boundaries in mainland citril finches and insular Corsican finches, superspecies *Carduelis* [*citrinella*]

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ABSTRACT

Aim In birds, differentiation of acoustic characters is an important mechanism of reproductive isolation that may lead to an ethological–acoustic barrier, resulting in the formation of new species. We examined acoustic variation in mainland citril and insular Corsican finch populations, with the aim of assessing the degree of acoustic differentiation between both members of the superspecies *Carduelis* [*citrinella*] and documenting possible variation between local subpopulations that are geographically isolated.

Location We chose study sites throughout the geographical ranges of citril and Corsican finches. For the citril finch, we obtained samples from the Black Forest (Germany), the Cevennes (France) and the Pyrenees (Spain); for the Corsican finch, we obtained samples from the islands Capraia and Sardinia (Italy) and Corsica (France).

Methods We analysed frequent contact calls and elements of the perch song. Vocalization patterns of the study populations were compared by means of discriminant and hierarchical cluster analyses.

Results There were significant differences in vocalization characteristics of perch songs and contact calls, which permitted unambiguous discrimination of citril and Corsican finch populations. However, we also detected significant differences in contact calls between mainland citril finch subpopulations. There was a pattern of clinal variation in vocalization: short, steeply modulated signals in the northern part of the geographical range (Black Forest) and long, shallowly modulated signals in the southern part (Pyrenees).

Main conclusions Acoustically, mainland citril and insular Corsican finches separate well in their contact calls and perch songs. However, variation in the two vocalization patterns between subpopulations of mainland citril finches indicates that acoustic characteristics can evolve very quickly, not only on islands but also on the mainland. Local habitat differences may play a crucial role in the rapid evolution of these signals under full or partial isolation of small subpopulations. To judge the importance of signal variation as a pre-mating isolating barrier, future studies will have to determine whether members of the distinct subpopulations are able to match their signals to each other if they re-meet, and whether intraspecific species recognition is still possible.

Keywords

Acoustic adaptation, *Carduelis citrinella*, *Carduelis corsicanus*, citril finch, Corsican finch, island population, pre-mating isolation, speciation, species recognition, vocalization.

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www.blackwellpublishing.com/jbi
doi:10.1111/j.1365-2699.2007.01722.x

INTRODUCTION

Reproductive isolation of formerly connected bird populations, either geographically or by means such as mating preference, is considered to be a major cause of avian speciation (Newton, 2003). Populations living in discontinuous or isolated areas inevitably diverge from one another for reasons such as random genetic drift, random mutations, natural selection due to particular environmental conditions, or sexual selection (Slabbekoorn & Smith, 2002a; Newton, 2003). These processes lead to differences in morphological, behavioural, ecological and acoustic characters (Martens, 1996; Martens *et al.*, 2004; Patten *et al.*, 2004).

Divergences in vocal traits may be particularly important in the process of bird speciation (Martens, 1996; Gee, 2005) as a principal isolating mechanism alongside variations in coloration and mate choice via cultural female preference (Boughman, 2002; McKnaught & Owens, 2002). Acoustic differences directly affect intraspecific communication, for example the ability of individuals to recognize each other, and the ability of males to attract females and to establish and maintain territories (Kroodsma & Miller, 1982; Baker & Cunningham, 1985; Slabbekoorn & Smith, 2002a). Vocalization in songbird populations can vary considerably, and this variation can be regarded as dialects of subgroups of a population, and as temporal or spatial variants of the auditory communication system of a species (Wickler, 1986). The variation can be very pronounced, frequently occurring in subpopulations on a macrogeographical level. Such divergence in vocalization may lead to complete isolation through the establishment of an ethological–acoustic barrier in conjunction with behavioural differences (Martens, 1996).

In studies of vocal divergence, it is of special interest to focus on species that live in local populations across disjunct distributional ranges. Montane birds often breed in small areas separated by hundreds of kilometres, with little or no exchange of individuals and genes. Disjunct distributional ranges can arise either by the splitting of a once continuous distribution (vicariance) or by long-distance dispersal and subsequent colonization (Newton, 2003). The citril finch *Carduelis* [*citrinella*] is a good example of a passerine bird species with a once-continuous but nowadays disjunct range (Newton, 2003). The main reason for this range reduction may be linked to the fact that the species' preferred habitat (semi-open pine forest) decreased drastically in abundance and distribution due to changes in vegetation composition favouring deciduous forest, following a period of early warming. Two morphologically distinct forms, citril finch *Carduelis* [*citrinella*] *citrinella* (Pallas, 1764) and Corsican (citril) finch *Carduelis* [*citrinella*] *corsicanus* (Koenig, 1899), inhabit as relict forms higher mountain systems of south-western and Central Europe and some mountainous Mediterranean islands.

The taxonomic status of the two forms remains unclear. Pasquet & Thibault (1997) detected genetic differences in the mitochondrial DNA, but regarded the variation as too low to warrant species status. However, a reinterpretation of the same data by Sangster (2000), in combination with known variations in morphology (Cramp & Perrins, 1994; Pasquet, 1994) and vocalization (Chappuis, 1976; Cramp & Perrins, 1994), prompted the Association of European Rarities Committees to treat the two forms as distinct species with independent evolutionary histories (Sangster *et al.*, 2002). Large areas between the subpopulations of both forms are not settled (Voous, 1960; Cramp & Perrins, 1994). Furthermore, the distinct subpopulations of the two forms often inhabit different habitat types (semi-open pine forest in citril finch vs. tree-heath macchia in Corsican finch; Förschler & Kalko, 2006b), with varying ecological conditions and physical characteristics that affect sound transmission.

We analysed selected parts of the vocalization of citril and Corsican finch subpopulations throughout their range, with the main goal of assessing possible signal variation across subpopulations. We expected to find differences in vocalization between the two forms, reflecting their hypothesized reproductive isolation and independent evolutionary histories. Because of differences in ecological conditions (vegetation cover: conifer forest vs. open scrubland; Förschler & Kalko, 2006b), and larger distances between subpopulations on the mainland, we also analysed differences in vocalization according to the 'acoustic adaptation hypothesis' (Hansen, 1979; Rothstein & Fleischer, 1987; Wiley, 1991; Blumstein & Turner, 2005), which predicts that the structure of bird signals is adapted to the respective transmission conditions of the surrounding habitat.

METHODS

Study species

The citril finch, *C.* [*citrinella*] *citrinella*, is patchily distributed and occurs at higher altitudes in the mountain ranges of Central and south-western mainland Europe (Alps, Black Forest, Vosges, Jura, Massif Central, Cevennes, Pyrenees, Cantabrian Mountains, and several mountainous areas of central Spain), generally above 800 m a.s.l. (Cramp & Perrins, 1994; Baccetti & Märki, 1997; Glutz von Blotzheim & Bauer, 1997). The Corsican (citril) finch, *C.* [*citrinella*] *corsicanus*, lives exclusively on the mountainous islands of Corsica, Sardinia and several Tuscan islands, in particular Capraia, Elba and Gorgona (Cramp & Perrins, 1994; Baccetti & Märki, 1997; Thibault & Bonaccorsi, 1999).

Study sites

The study was conducted in selected areas (Fig. 1) throughout the distributional range of citril and Corsican finches (Cramp & Perrins, 1994). Recordings of citril finches were obtained on the Schliffkopf mountain in the northern Black Forest, Germany (April–July 1999, April–June 2000), at Mont Lozère and Causse Méjean in the French Cevennes (April 2002), and at Port del Comte in the Catalonian pre-Pyrenees (April–July 2002). Recordings of Corsican finch were conducted on Corsica (April–June 2001, May–June 2003), mainly in the high valley

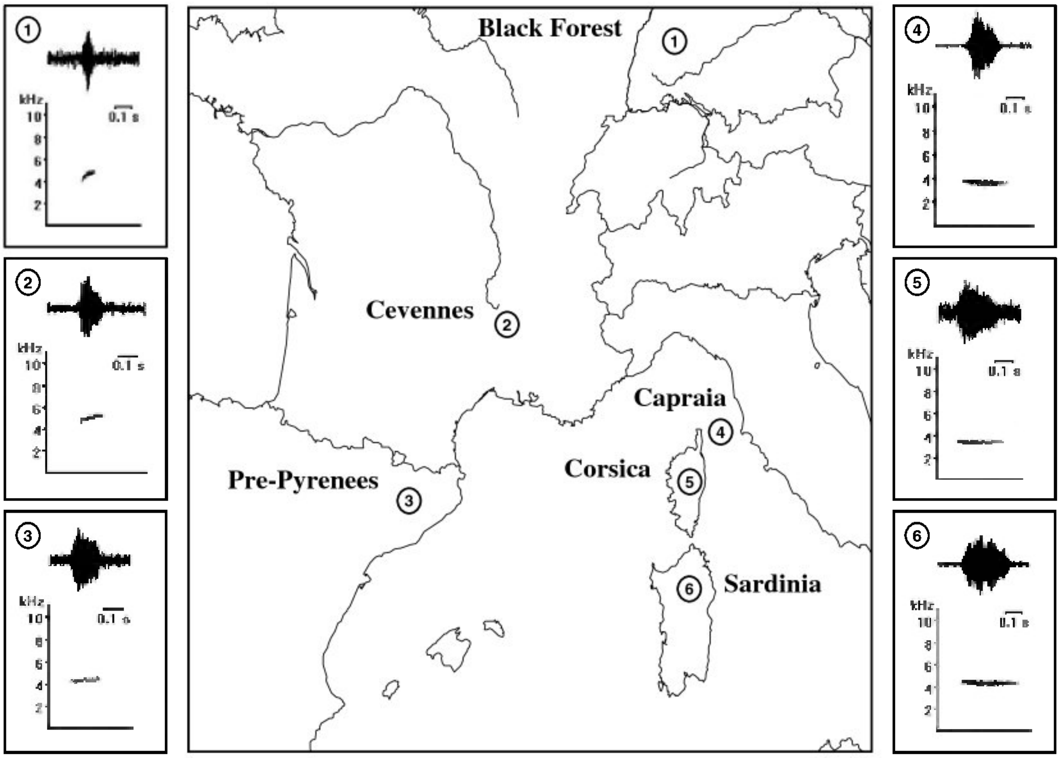

Figure 1 Study areas of mainland citril finches and insular Corsican finches with oscillograms [amplitude (dB) vs. time] and representative sonagrams [frequency (kHz) vs. time] of the contact calls. (a) Citril finch on Schliffkopf mountain, Black Forest, March 2002; (b) citril finch at Causse Méjean, Cevennes, April 2002; (c) citril finch on Port del Comte mountain, pre-Pyrenees, April 2002; (d) Corsican finch on Monte Arpagna, Capraia, April 2003; (e) Corsican finch at Col d'Illarata, Southern Corsica, April 2001; (f) Corsican finch on Monte Limbara, Sardinia, April 2003.

of Niolo (Haute-Corse) and the mountain range of the Massif de l'Ospedale (Corse-du-Sud), in Sardinia on Monte Limbara (Gallura) (April–June 2003), and on the island of Capraia (March–May 2003). All recordings were obtained during the breeding season (main singing and calling period) to allow direct comparison of the vocalizations.

The breeding areas studied varied mainly in the extent of forested and open areas (Förschler & Kalko, 2006a,b). Citril finches in the Black Forest inhabit semi-open breeding areas, mainly with spruce (*Picea abies*) and mountain pine (*Pinus mugo rotundata*) and well developed undergrowth; those in the Cevennes occur in Scots pine (*Pinus sylvestris*)-dominated semi-open woodland with little undergrowth, while the birds in the pre-Pyrenees prefer breeding areas dominated by mountain pine (*Pinus mugo uncinata*) with little undergrowth. In contrast, Corsican finches on Capraia occur in open tree-heath (*Erica arborea*) scrubland without any pine woodland; those on Corsica (Massif de l'Ospedale, Niolo) live mainly in semi-open maritime pine (*Pinus pinaster*), black pine (*Pinus nigra*) and tree-heath-dominated scrubland, while those on northern Sardinia (Monte Limbara) inhabit open to semi-open black pine and tree-heath-dominated scrubland.

Calls and songs of citril and Corsican finches

Current knowledge on vocalizations of citril and Corsican finches is summarized by Chappuis (1976) and Cramp & Perrins (1994). Both finches produce a number of distinct calls in a specific behavioural context (flight calls, alarm calls, contact calls). We concentrated on a contact call that was emitted very frequently by both forms, mostly while sitting on perches (Fig. 1).

Both forms produce three song types: flight songs, perch songs and slow songs (personal observation). For our study, we focused on the most frequently performed perch song. The perch song of the citril finch has a twittering and tinkling or rapid, at times strained, babbling quality, often resembling other finches, especially European goldfinch (*Carduelis carduelis*) and European serin (*Serinus serinus*). It frequently starts with one to several well spaced elements, followed by a series of characteristic elements consisting of short buzzes, rattles, trills, and frequently also flight calls (Chappuis, 1976; Cramp & Perrins, 1994). The song of the Corsican finch differs from that of the citril finch in its more segmented structure. It is also performed at a much slower rhythm, often resembling the song of the common linnet (*Carduelis cannabina*) or winter wren (*Troglodytes troglodytes*) (Chappuis, 1976; Cramp & Perrins, 1994).

Sound recordings

Citril and Corsican finch vocalizations were recorded with a directional microphone (supercardioid Sennheiser [Hannover, Germany] microphone module ME 66 with powering module

K6, including windbreak) on a portable tape recorder (Sony WM-DC6 professional [Sony, Japan]) using chrome dioxide cassettes (Sony UX-S, IEC II/Type II 90 min [Sony, EU]). To obtain good sound recordings, the birds were approached as closely as possible (mainly 5–25 m) without disturbing them, and the microphone was pointed directly towards the calling or singing 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 from the sound source.

Sound analysis

Recordings were analysed in the laboratory with the program Avisoft-saslab pro (ver. 4.2; Raimund Specht, Berlin, Germany). For analysis, signals were processed with a Fast Fourier Transform (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. Measurements were made with cursors on the screen with measurement points set 20–35 dB above background noise (max. 72 dB). Data were transferred to Microsoft Excel 2000 for further calculations. Statistical tests were performed with the programs SigmaStat 2.0 (San Jose, CA, USA) and spss 11.0 (München, Germany) for windows.

In total we analysed 6596 contact calls of 390 individuals, giving an average of about 17 contact calls for each individual (min. 10, max. 20 calls per individual). The analysis comprised contact calls of 206 Corsican finches (Capraia, 44 individuals; northern Corsica, 41; southern Corsica, 54; Sardinia, 67) and 184 citril finches (Black Forest, 66; Cevennes, 55; pre-Pyrenees, 63). For each contact call we quantified four characteristics: starting frequency (kHz), terminal frequency (kHz), bandwidth (kHz) and duration (s). Additionally, the slope of the contact calls (sweep rate) was calculated as bandwidth divided by call duration (kHz s^{-1}). For statistical analyses, the pooled average values of individuals were used for comparison between the study populations.

We also analysed 1045 perch songs of 152 males (average 6.9 songs/male), including 63 Corsican finches (southern Corsica, 30 individuals; Sardinia, 33), although none from northern Corsica and Capraia where sample size was too low, and 89 citril finches (Black Forest, 32 individuals; Cevennes, 26; pre-Pyrenees, 31). To reduce effects of season on song quality and pattern (Leitner *et al.*, 2001), only perch songs from the same reproductive phase (main breeding period) were selected. Songs of citril and Corsican finches are rather complex, containing various phrases, syllables, and elements (Chappuis, 1976; Cramp & Perrins, 1994). Therefore we quantified the following characteristics of the perch songs: starting frequency of introductory notes (kHz), terminal frequency of final notes (kHz), bandwidth (kHz) and duration (s) of the full song.

Statistics

We used anovas and pairwise multiple comparison (PMC) to compare song and call parameters of the study populations, and classified them by means of canonical discriminant analyses and hierarchical cluster analysis. Linear regressions were used to test for significant links between latitude and call parameters. Finally, we conducted Mantel tests to address the relationship of geographical distance and call parameters. We used the statistical programs statistica and SigmaStat for analyses.

RESULTS

Differentiation of contact calls

Contact calls differed significantly between the two forms across their distributional ranges (Fig. 2). There was a distinct north–south gradient across subpopulations, with longer calls in southern areas as opposed to shorter calls in northern areas. These differences were significant between citril and Corsican finches (Kruskal–Wallis anova, $H = 318.323$, d.f. 6, $P = < 0.001$) as well as between nearly all subpopulations studied, with the exception of the four Corsican finch populations (PMC, Dunn's method). Starting and terminal frequency of the contact call varied across subpopulations, with higher frequencies in the northern subpopulations. We found variation in starting frequency (Kruskal–Wallis anova, $H = 130.536$, d.f. 6, $P = < 0.001$), with significant differences between Black Forest birds and all other populations, and between birds from the Cevennes/pre-Pyrenees and Corsican birds (PMC). Terminal frequency also varied (Kruskal–Wallis anova, $H = 275.044$, d.f. 6, $P = < 0.001$), with significant differences between citril and Corsican finch populations, and also between Black Forest birds and those from the Cevennes and pre-Pyrenees (PMC). The slope of the contact call was steepest in the Black Forest, intermediate in the Cevennes, and lowest in the pre-Pyrenees (Fig. 2). Birds from Corsica had shallower-sloped calls that were slightly modulated upward (northern Corsica) or downward (Capraia, Sardinia, southern Corsica) (Fig. 2). Slope variation between the study groups was significant (Kruskal–Wallis anova, $H = 331.631$, d.f. 6, $P = < 0.001$).

A canonical discriminant analysis revealed that 71.4% of original group cases were classified correctly (Table 1). The contact calls of citril and Corsican finches, as well as of Black Forest (98.5%), Cevennes (90.9%) and pre-Pyrenees (85.7%) birds, could be separated with a high percentage of correct classification (Table 1). The separation of Corsican finches from Capraia, northern Corsica, southern Corsica and Sardinia was less obvious, but almost two-thirds (64.2%) of the birds from Sardinia were still classified correctly. Interestingly, Corsican finches from northern Corsica showed a minor overlap with birds from the pre-Pyrenees (Table 1). A hierarchical cluster analysis based on starting frequency, terminal frequency and call duration also separated contact calls of Corsican and citril finches (Fig. 3).

Comparing all contact calls across the study sites, we found a significant correlation between duration of contact call and latitude (linear regression, $R = 0.912$, $P = 0.004$; Fig. 2). Significant correlations were also found between latitude and slope

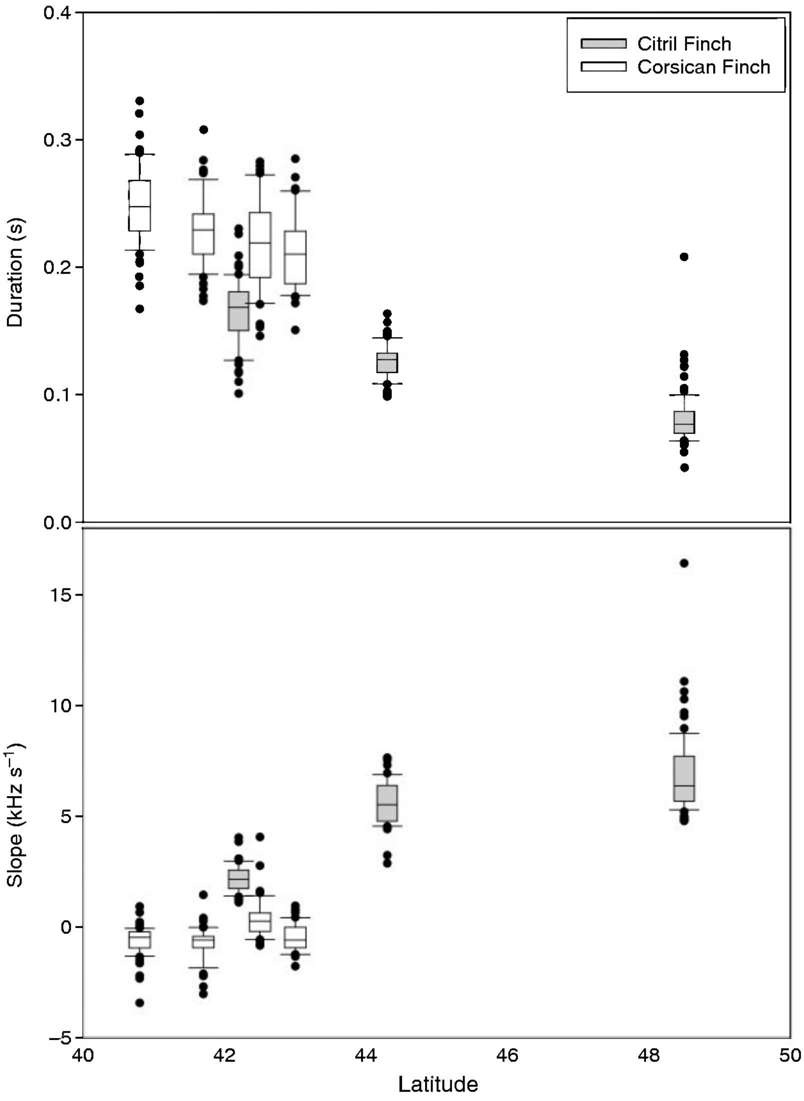

Figure 2 Duration(s) and slope (kHz s^{-1}) of contact calls ($n = 390$ individuals) in citril and Corsican finch populations in seven study areas of differing latitude (from left to right, white box plots: Sardinia $n = 67$ individuals; southern Corsica $n = 54$; northern Corsica $n = 41$; Capraia $n = 44$; grey box plots: pre-Pyrenees $n = 63$; Cevennes, $n = 55$; Black Forest, $n = 66$). A Kruskal–Wallis ANOVA provided significant differences in duration ($H = 318.3$, d.f. $= 6$, $P < 0.001$) and slope ($H = 331.6$, d.f. $= 6$, $P < 0.001$) between the populations.

Table 1 Classification results of a canonical discriminant analysis showing real and predicted group membership of citril and Corsican finches ($n = 390$ individuals) from seven study areas, derived from acoustic variables of the contact call, including starting frequency, terminal frequency and call duration (percentages in brackets).

	Predicted group membership: 71.4% of original group cases classified correctly							
Study sites	Black Forest	Cevennes	pre-Pyrenees	Capraia	Northern Corsica	Southern Corsica	Sardinia	Total
Black Forest	65 (98.5)	1 (1.5)	0	0	0	0	0	66
Cevennes	3 (5.5)	50 (90.9)	2 (3.6)	0	0	0	0	55
pre-Pyrenees	3 (4.8)	0	54 (85.7)	0	6 (9.5)	0	0	63
Capraia	0	0	1 (2.2)	16 (36.4)	11 (25.0)	8 (18.2)	8 (18.2)	44
Northern Corsica	0	1 (2.4)	4 (9.8)	8 ((19.5)	22 (53.7)	0	6 (14.6)	41
Southern Corsica	0	0	1 (1.8)	11 (20.4)	4 (7.4)	28 (51.9)	10 (18.5)	54
Sardinia	0	0	0	11 (16.4)	4 (6.0)	9 (13.4)	43 (64.2)	67

(kHz s^{-1}) of the contact call (linear regression, $R = 0.877$, $P = 0.009$; Fig. 2), as well as its terminal frequency (linear regression, $R = 0.794$, $P = 0.033$; Fig. 2). Contact calls became longer, steeper and lower in frequency with decreasing latitude (Fig. 2). Similarly, the divergence in call length was strongly correlated with geographical distance (Mantel test, $R = 0.912$, $P = 0.008$). This observation was also made for the slope of the calls (Mantel test, $R = 0.861$, $P = 0.013$).

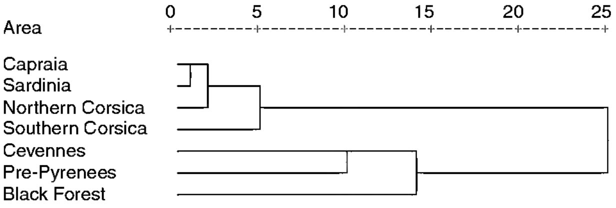

Figure 3 Dendrogram of hierarchical cluster analysis of contact calls ($n = 390$ individuals) in seven study areas depicted as Euclidian distance with average linkage between study groups based on starting frequency, terminal frequency and call length (Black Forest, $n = 66$ individuals; Cevennes, $n = 55$; pre-Pyrenees, $n = 63$; Capraia, $n = 44$; northern Corsica, $n = 41$; southern Corsica, $n = 54$; Sardinia, $n = 67$).

Song variation

Similarly to the contact call, average duration of perch songs showed a clear gradient from northern to southern subpopulations (Fig. 4). Birds on Sardinia sang longest, as opposed to birds in the Black Forest, which had the shortest perch songs. Variations between study groups were significant (Kruskal–Wallis ANOVA, $H = 48.864$, d.f. 4, $P < 0.001$; Table 2). Bandwidth of the perch song differed significantly (ANOVA, $P < 0.001$). On average, bandwidth was lower in the Black Forest and the Cevennes than in the other areas (PMC). The frequency of the initial notes of the song differed significantly (Kruskal–Wallis ANOVA, $H = 95.628$, d.f. 4, $P < 0.001$), with higher frequencies in Corsican finches from Sardinia and Corsica than in citril finches (PMC).

By means of a canonical discriminant analysis, 63.8% of original group cases were classified correctly (Table 2). Correct classification was highest for the Black Forest (71.9%) and the pre-Pyrenees (85.6%). Classification of Corsican finch subpopulations was less clear. However, a hierarchical cluster analysis based on song duration, frequency of the initial note and bandwidth of the song clearly separated Corsican from citril finch song.

DISCUSSION

We studied the variation of contact calls and perch songs in locally isolated allopatric mainland citril and insular Corsican finches (superspecies *Carduelis* [*citrinella*]). As expected, our data revealed clear differences between both forms. However, we also found acoustic divergence between subpopulations of mainland citril finches, which formed a clinal, latitudinal north-to-south pattern. Birds in the southern areas of their distributional range (pre-Pyrenees, Corsica, Sardinia, Capraia) produced longer, more shallowly modulated, lower contact calls than birds in the northern areas (Black Forest and Cevennes), which produced shorter, more steeply frequency-modulated, higher-pitched contact calls. Similar results were obtained for perch song, where populations in the south produced longer songs of greater bandwidth compared with birds from the north. The further the subpopulations were separated from each other, the larger was their divergence in vocalization, an effect that is also known from other studies on birdsong (Slabbekoorn & Smith, 2002b).

To explain the observed acoustic differentiation between the subpopulations, we assume that local habitat conditions are highly likely to play an important role, as physical characteristics of vocalization, such as its spectrum and time structure, are known to be shaped by environmental conditions (Wiley & Richards, 1982; Endler, 1992; Dabelsteen *et al.*, 1993; Forrest, 1994; Slabbekoorn & Smith, 2002b). Modifications of sound transmission by microclimate and vegetation structure can be important selection pressures on birds living in different habitats (Wiley & Richards, 1982; Brown & Handford, 2000; Irwin, 2000; Nemeth *et al.*, 2001; Slabbekoorn *et al.*, 2002; Naguib, 2003). If such selection pressures are present over larger geographical ranges and longer periods, they may lead to divergences in the spectrum and time characteristics of bird songs and calls (Doutrelant *et al.*, 2000; Slabbekoorn & Smith, 2002b) and consequently may influence the evolution of bird vocalizations and ultimately result in speciation.

Mainland citril finches generally live in more wooded habitats, such as conifer forests, while insular Corsican finches inhabit more open areas, such as tree-heath scrub (Förschler & Kalko, 2006b), which may have influenced the divergence of vocalization of the two forms. We postulate that the rather long and low signals of constant frequency in Corsican finches may be better suited for sound transmission through dense scrubland. However, to adequately judge possible effects of habitat structure on vocalization patterns, further studies have to be conducted that concentrate on a detailed analysis of vegetation structures and their influences on sound propagation. This may help to answer the question of how the vocalizations in the subpopulations of citril and Corsican finches have developed, which elements of the vocalizations travel best through distinct environments, and how significant the habitat-induced selection pressures on the vocalization patterns of the two finches are.

In addition to habitat-induced factors, body size, vocal tract and bill shape may also play important roles with regard to acoustic divergence (Laiolo & Rolando, 2003; Podos & Nowicki, 2004). However, according to the available data on the morphometry of citril and Corsican finches, both forms do not show large variations in body size (Märki & Biber, 1975; Brandl & Bezzel, 1989; Cramp & Perrins, 1994; Borras *et al.*, 1998), with the exception that Corsican finches have slightly shorter wings (Cramp & Perrins, 1994). Therefore we conclude that body size plays a minor role, which is supported by the fact that Corsican finches (average body mass 11.5 g) are slightly smaller than citril finches (average body mass 12.5 g), yet have lower contact calls.

If we look at the scattered distributional range of citril and Corsican finches, we find a heterogeneous pattern of larger and smaller 'regio-populations'. These are affected by specific local environmental conditions, such as the more-or-less

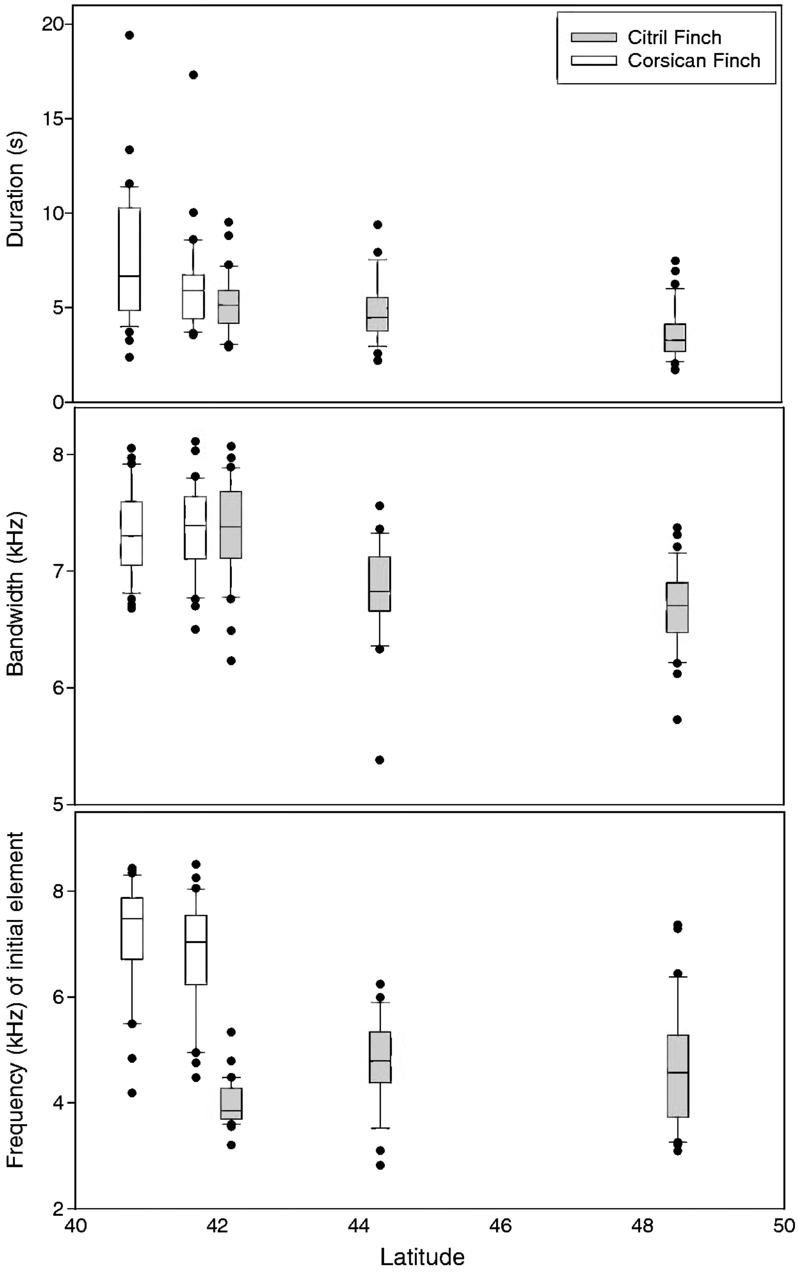

Figure 4 Song duration(s), bandwidth (kHz) and frequency (kHz) of initial song elements in citril and Corsican finch populations ($n = 152$ individuals) in five study areas of differing latitude (from left to right, white box plots: Sardinia $n = 33$ individuals; Corsica $n = 30$; grey box plots: pre-Pyrenees $n = 31$; Cevennes, $n = 30$; Black Forest, $n = 32$). A Kruskal–Wallis ANOVA provided significant differences in duration ($H = 48.9$, d.f. = 4, $P < 0.001$) and frequency of the initial element ($H = 95.6$, d.f. = 4, $P < 0.001$), an ANOVA for parametric distributed data a significant difference in bandwidth ($P < 0.001$) between the populations.

isolated geographical position of Corsican finches on Mediterranean islands, or of citril finches on isolated mountain systems. Divergences in vocalization, such as distinct call and song duration, call slope, starting frequency and terminal frequency – such as we found in our study – can be regarded as a result of this isolation and regional adaptation in the form of so-called 'regiolects' (Martens, 1996). These regiolects may contain phylogenetic information on the settlement history and former population exchange of the subpopulations. In studies on crests and kinglets (Regulidae), such an association has been found between molecular divergence and parallel acoustic differentiation between island and continental populations (Päckert *et al.*, 2003; Päckert & Martens, 2004).

Isolation-induced variations such as we observed in our study could act as pre-mating isolating barriers if birds are separated over a longer time and mate recognition is interrupted, unless the populations re-meet again in time (Martens, 1996; Newton, 2003; Gee, 2005). One of the main questions is therefore to judge the extent of isolation between insular and mainland populations. It remains unclear whether the subpopulations of citril and Corsican finches are indeed reproductively isolated, as proposed by Sangster (2000); Sangster *et al.* (2002). Some breeding areas of both taxa (the mainland population of citril finches in the southern Alps and the Cevennes) are even within sight of the island populations of Corsican finches in northern Corsica and Capraia during high-pressure weather periods.

Table 2 Classification results of a canonical discriminant analysis showing real and predicted group membership of citril and Corsican finch (n = 152 individuals) from five study areas, derived from perch song variables, including starting frequency and duration (percentages in brackets).

	Predicted group membership: 63.8% of original group cases classified correctly					
Study sites	Black Forest	Cevennes	pre-Pyrenees	Corsica	Sardinia	Total
Black Forest	23 (71.9)	3 (9.4)	3 (9.4)	2 (6.2)	1 (3.1)	32 (100)
Cevennes	7 (26.9)	14 (53.8)	4 (15.4)	1 (3.9)	0	26 (100)
pre-Pyrenees	3 (9.7)	3 (9.7)	25 (85.6)	0	0	31 (100)
Corsica	2 (6.7)	1 (3.3)	0	17 (56.7)	10 (33.3)	30 (100)
Sardinia	0	3 (9.2)	1 (3.0)	11 (33.3)	18 (54.5)	33 (100)

Mainland citril finches are known to migrate considerable distances (Yeatman-Berthelot, 1991; Cramp & Perrins, 1994; Zink & Bairlein, 1995; Fornasari *et al.*, 1998). Birds from Garmisch-Partenkirchen (German Alps) have been recovered in the Cevennes and Mont Ventoux areas, about 600 km south-west of their breeding areas (Bezzel & Brandl, 1988). Recent observations of wintering birds in southern Spain (Benoit & Märki, 2004), and the capture of citril finches in the Spanish exclave of Ceuta in North Africa (Navarrete *et al.*, 1991), confirm that they are able to migrate longer distances. Occasional records in the Balearic Islands (Cramp & Perrins, 1994) show that these movements can also include to Mediterranean islands. The establishment of a small population of the sedentary white-winged snowfinch (*Montifringilla nivalis*) of the Alps in the Corsican mountains (Thibault & Bonaccorsi, 1999) also demonstrates that settlement by montane birds with only slight migrational tendencies may occur from time to time over longer distances. Consequently, we cannot exclude a more-or-less regular exchange between citril and Corsican finches, which would also mean that reproductive isolation may not yet be complete. Probably this exchange is mostly unidirectional, as it is more likely that dispersing citril finches from the Alps reach Corsica than the reverse, given the lack of long-distance migration behaviour in Corsican finches (Cramp & Perrins, 1994; Thibault & Bonaccorsi, 1999).

If such a low-level but regular exchange of individuals occurs, how does this affect vocal communication (Gee, 2005) and species recognition (Mathevon & Aubin, 2001) between the two (sub)populations? In this context, coding–decoding processes, which determine the intraspecific recognition of signals, are important factors in aiding the establishment process in other subpopulations. Although differences in vocalization are generally considered important mechanisms promoting species integrity and preventing hybridization and introgression, it remains unclear at what level acoustic differences relate to differences in population genetics, particularly in allopatric taxa (Martens *et al.*, 2004). Furthermore, several studies have shown that some species can adjust their vocalization pattern after dispersal to new breeding grounds (Payne & Payne, 1997). Mathevon & Aubin (2001) point out that some bird species exhibit a high tolerance to signal modifications, which suggests that they might be less sensitive concerning modifications between subpopulations (see also Gee, 2005). Therefore if citril and Corsican finches re-meet, we assume that species recognition by signal matching between the two forms cannot be excluded with certainty.

To conclude, citril and Corsican finches are clearly separated by several acoustic parameters, as shown by the results of cluster analyses. This matches the taxonomic diagnosis based on morphological and molecular markers (Pasquet & Thibault, 1997; Sangster, 2000; Sangster *et al.*, 2002). However, we also found clear differences between subpopulations of mainland citril finches in the Black Forest, the Cevennes and the pre-Pyrenees, where vocal divergence has obviously changed rather quickly in mountain ranges with little or no connectivity, probably due to the small population sizes. To judge the significance of the observed signal differentiation for the taxonomic status of the Corsican finch, more evidence is needed, ideally via detailed genetic studies confirming or rejecting the supposed reproductive isolation of allopatric citril and Corsican finches. Moreover, behavioural experiments would be desirable to demonstrate that these differences truly comprise a pre-mating isolating barrier that prevents effective acoustic communication and ultimately hybridization between the two forms.

ACKNOWLEDGEMENTS

This work was undertaken in cooperation with the Max Planck Research Centre for Ornithology, Vogelwarte Radolfzell, Germany. Field work was kindly supported by Jacques Blondel and Philippe Perret (Centre d'Ecologie Fonctionelle et Evolutive, Montpellier, France), Nicola Baccetti and Fernando Spina (Istituto nazionale per la Fauna Selvatica, Bologna, Italy), Sergio Nissardi (Cagliari, Italy), Antonio Borras, Toni Cabrera, Josep Cabrera and Juan Carlos Senar (Museu Ciències Naturals, Barcelona, Spain), Ulrich Dorka (Tübingen, Germany) and Jürgen Kläger (Baiersbronn, Germany). Peter Berthold (MPI Vogelwarte Radolfzell, Germany), Timothy Coppack (Institute of Avian Research, Wilhelmshaven, Germany), Liesbeth de Neve (Granada, Spain), Alexander Tahory, Brian Hillcoat and two anonymous referees provided helpful comments on the manuscript. The study was conducted with financial support from the Max Planck Research Centre for Ornithology and the Landesgraduiertenförderung Baden-Württemberg, University of Ulm, to M.I.F. It was also supported by a fellowship within the Postdoc-Programme of the German Academic Exchange Service (DAAD).

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Editor: Nicholas J. Gotelli