

Fast cultural evolution of Crossbill (*Loxia* spp.) calls in the Palaearctic

RALPH MARTIN,*¹  JULIEN ROCHEFORT,² ROGER MUNDY^{3,4,5,6} & GERNOT SEGELBACHER¹

¹University of Freiburg, Freiburg, Germany

²Savigny-sur-orger, France

³Platform Bioinformatics and Biostatistics, VetMedUni, Vienna, Austria

⁴Cognitive Ethology Laboratory, German Primate Centre, Leibniz Institute for Primate Research, Kellnerweg 4, Göttingen, 37077, Germany

⁵Department for Primate Cognition, Georg-August-University Göttingen, Göttingen, Germany

⁶Leibniz ScienceCampus Primate Cognition, Göttingen, Germany

Learned vocal signals of birds provide one of the most comprehensive sources of evidence for culture in animals. Such vocal signals often vary spatially and temporally. Signal variation can be driven by direct factors such as cultural drift and selection or by indirect factors such as changes in the environment, which may affect morphology and therefore acoustic capability. In this study we analysed flight and excitement calls of several call types of the Red Crossbill *Loxia curvirostra* and other crossbill species. Calls were recorded between 1962 and 2019 across the Palaearctic region. We measured acoustic similarity within flight and excitement calls and modelled the size of the effect attributed to temporal and geographical distance. Geographical distance between different sampling locations explained less call variation compared with temporal distance, and temporal variation within the excitement calls was smaller than in the flight calls. We conclude that calls of most call types of Red, Scottish and Parrot Crossbill are an example of cultural evolution. We suggest that excitement calls are less modifiable because they can serve better in dangerous situations when they are stable in time and space. In addition, we found no clear support for increasing or decreasing flight call similarity of call types while or after being in contact, as found in another study from North America. The reasons for the cultural evolution in calls of Palaearctic crossbills remain unclear.

Keywords: call changes, call types, geographical variation, Parrot Crossbill *Loxia pytyopsittacus*, Red Crossbill *Loxia curvirostra*, Scottish Crossbill *Loxia scotica*, temporal variation, Two-barred Crossbill *Loxia leucoptera bifasciata*.

Animal culture usually refers to ‘those group-typical behaviour patterns shared by members of a community that rely on socially learned and transmitted information’ (Laland & Hoppitt 2003). It can be found in many different animals such as fish (Brown & Laland 2001), whales (Rendell & Whitehead 2001) and primates (Whiten 2017). Within birds, it is known that hummingbirds

(Trochilidae), parrots (Psittaciformes), passerines (Passeriformes) and a few other species learn some of their vocalizations from conspecifics, which are thus culturally transmitted (Catchpole & Slater 2015). Song is particularly well studied in birds and learned songs often vary spatially (Lovell & Lein 2013, Bolus 2014, Hamao *et al.* 2016, Diblíková *et al.* 2019, Lee *et al.* 2019) and temporally (e.g. Common Chaffinch *Fringilla coelebs*, Ince *et al.* 1980; Chestnut-sided Warbler *Setophaga pennsylvanica*, Byers *et al.* 2010; Savannah Sparrow *Passerculus sandwichensis*, Williams *et al.* 2013;

*Corresponding author.

Email: ralph.martin@posteo.de

Twitter ID: @RalphJoMartin

Three-wattled Bellbird *Procnias tricarunculatus*, Kroodsmas *et al.* 2013). It is presumed that any change in the song is driven by the general principles of evolution: drift, mutation, immigration and selection (Mesoudi 2015, Aplin 2019). Therefore, changes in the song of a population of birds are generally referred to as 'cultural evolution'. Birds' calls have been much less studied, as they had been assumed to be predominantly innate (Thorpe 1961, Marler 1963). Nowadays, it is known that several bird species, e.g. Psittaciformes (Rowley 1980, Farabaugh *et al.* 1994) and the Carduelinae (Mundinger 1979), learn some of their calls. Evidence for cultural evolution of calls, however, has so far only been described for the Cassia Crossbill *Loxia sinesciuris* (Porter & Benkman 2019).

The Red Crossbill *Loxia curvirostra* can be separated into distinct vocal groups referred to as 'call types' (or 'vocal types'). Each call type is identified by a unique combination of a distinct flight call (FC) and a distinct excitement call (EC; Groth 1993a, Robb 2000, Summers *et al.* 2002, Martin *et al.* 2019). FCs are learned by juvenile birds from their parents (Groth 1993a, Sewall 2010), while it is unknown whether ECs are learned or innate. The ability or willingness to learn is reduced in adult Red Crossbills (Sewall 2009), but they can match their mates' FCs during mating (Groth 1993b, Keenan & Benkman 2008). In the Palaearctic, call types are linked to a home region, a so-called 'core breeding area' (Martin *et al.* 2020), a region where they are typically found. Core breeding areas of different call types do not overlap. However, in response to food shortages (Lack 1944, Newton 2006), crossbills *Loxia* spp. can move to new areas, resulting in temporally overlapping breeding ranges of different call types. After such invasions, crossbills typically return to their area of natal origin (Newton 2006). Martin *et al.* (2019) identified 21 call types of crossbills in the western Palaearctic. Of these, 17 were attributed to Red Crossbill (designated N01–N15, N17 and S02), two to Parrot Crossbill *Loxia pytyopsittacus* (N21 and N22) and one each to Scottish *Loxia scotica* (N20) and Two-barred Crossbill *Loxia leucoptera bifasciata* (N19). Some ECs of these call types are similar to those found in previous studies conducted in north-western Europe (Robb 2000, Constantine & The Sound Approach 2006) and Scotland (Summers *et al.* 2002). However, the corresponding

FCs differed considerably between these studies, except for Two-barred Crossbill, whose calls were largely identical. One possible explanation for this discrepancy in FCs could be previously undetected geographical or temporal variation. The latter was observed in the Cassia Crossbill in North America (Porter & Benkman 2019). In their study, the authors presented data showing that over the years the FCs of the Cassia Crossbill have become increasingly distinct from the call type of the Red Crossbill, which is the most common in its range.

To investigate the drivers for the differing FCs found by Martin *et al.* (2019) and previous studies (Robb 2000, Summers *et al.* 2002, Constantine & The Sound Approach 2006), we analysed the impact of both temporal and geographical distance on 11 call types across four species of crossbills. Our study is specifically focused on Britain and Ireland and therefore on Red Crossbill call type N06, whose core breeding area is restricted to the northern part of this region (Figs S1 and S2; analysis in Martin *et al.* 2020). Britain and Ireland are ideal study areas for several reasons. Firstly, there have been numerous studies on crossbills conducted in this region over a long period of time (Nethersole-Thompson 1975, Knox 1989, Summers *et al.* 2002, 2007, Summers & Buckland 2011), providing an exceptionally good database. Additionally, the data are spatially well distributed, which is important for studying geographical variation. Secondly, only a few other call types of Red Crossbill cross the English Channel and the North Sea regularly (Martin *et al.* 2020), which reduces the potential impact of other invading call types on local call type N06. Finally, as the Red Crossbill has only been resident in Britain and Ireland since the late 19th century (Holloway 1996), the recent colonization presents a unique opportunity to analyse potential ongoing differentiating systems in calls and identify the potential drivers of call variation.

We here address two hypotheses: first, if geographical distance is the primary factor causing the observed mismatch in FCs in different previous studies, we expect the complete range of FC variation for a given call type to be evident at any given time (hypothesis 1). Alternatively, if temporal distance is the main driver of FC mismatch (hypothesis 2), then we would expect all birds of a call type to produce similar FCs at any given time. As temporal distance increases, we anticipate that the

FCs would become increasingly different, with the role of geographical distance between FCs playing a minor role.

METHODS

For the study, we analysed 11 call types across four species of crossbills (Red Crossbill: N01, N03, N04, N06, N07, N08, N10, N11; Two-barred Crossbill: N19; Scottish Crossbill: N20; Parrot Crossbill: N21), for which we could cover a large temporal and spatial variation of the data. We specifically focused our analysis on Britain and Ireland and therefore on call type N06, which is restricted to the northern part of this region (Martin *et al.* 2020; Figs S1 and S2). This ensured that impacts of invading call types were reduced, as only a few other crossbills with different call types have been recorded in Britain and Ireland (see Introduction for further reasons). In fact, Britain and Ireland were originally unsuited for resident Red Crossbills because the only native conifer species available to crossbills was *Pinus sylvestris* (San-Miguel-Ayanz *et al.* 2016). In these forests, Scottish Crossbills (or alternatively Parrot Crossbills – see the association of Scottish Crossbill with the introduced *Pinus contorta*, Summers & Broome 2012) are considered endemic (Nethersole-Thompson 1975). Red Crossbills reached Britain only during invasions formerly (cf. citation of Matthew Paris 1251 in Nethersole-Thompson 1975 and Roger Twysden 1593 cited in Bewick 1847). The planting of *Picea* spp. and *Larix* spp. started, to a small extent, in Great Britain between the 16th and 19th centuries (*Picea abies* about 1548, *Picea sitchensis* in 1831, *Larix decidua* in the early 17th century; Anderson & Taylor 1967, Davies 1979, Woodland Trust 2020) and increased especially in the 1950s (Warren 2009). Breeding of Red Crossbills is presumed to have been rare in the 19th century (Holloway 1996), but numbers increased at the beginning of the 20th century, especially after the 1909/10 irruption. Holloway (1996) presumes that Red Crossbills have been resident in Britain and Ireland since at least the end of the 19th century.

Our database consisted of the Palaearctic crossbill recordings used in the study of Martin *et al.* (2020) (sources given in Tables S1 and S2, Data S1). Additionally, we digitized analog sound recordings to add historical data especially from

Britain (sets of data were from many different people, mainly from Ron Summers, David Jardine and Simon Elliot). Furthermore, one of us (R.Ma.) visited many forests of Britain and Ireland ($n = 92$, see Fig. S3) in autumn 2016 to collect a recent database with a large spatial coverage. The distribution of the recordings is shown for each call type in Figures S2 and S4–S13. While in some countries in Central Europe such as the Netherlands data are somewhat biased towards years with crossbill invasions (especially during invasions of Parrot Crossbills, e.g. autumn 2013), data from Austria, France, Germany, Great Britain, Scandinavia, Switzerland and the Eastern Palaearctic are much less affected. This is due to ongoing research on the differentiation and distribution of crossbills (Summers *et al.* 2002, 2004, Summers & Buckland 2011, Martin *et al.* 2019, 2020), the fact that many of the current data originate from a large-scale survey of Red Crossbill calls (see above) and that data originate from travelling birders whose itineraries were not linked to crossbill invasions.

We assigned each recording to a ‘crossbill season’ (e.g. Newton 2006, Alonso & Arizaga 2011), which begins with the onset of the coning cycle (Hölzinger 1997). In central and northern Europe this is typically in June or July (Thies 1996) and ends the following spring, typically in May, when the cone scales open and seeds are shed; seeds then become unavailable to Red Crossbills (Summers & Proctor 2005, Summers 2018). During a cone crop failure in an area, Red Crossbills leave and search for new feeding areas in early summer with the beginning of a new cohort of cones.

We searched for calls (FCs and ECs) which we could assign to the call types defined by Martin *et al.* (2019) (the most recent classification of European crossbill calls). If FCs and ECs of the same individual were available (see Table 1 for sample size), we checked whether both FCs and ECs matched the definition of the respective call type. If one of the calls did not, we searched for comparable calls in all recordings to ensure that the full range of call variation associated with the respective call types’ FCs and ECs was included. Despite the similarity of the FCs of N06 and N02 (cf. Martin *et al.* 2019), we excluded the latter from the evaluation because the ECs differed, FCs differed on average as well, and spatial distribution did not overlap (N02 is distributed especially on the Balkan Peninsula and rarely in central Europe; Martin *et al.* 2020). In the New Forest

(Hampshire, UK), we found a population with calls similar but not identical to N06. We included this population in call type N06 but conducted statistical analysis both with and without these birds. As separation of Scottish Crossbill and Scottish Parrot Crossbills is not always straightforward, we only included typical calls of these (cf. Robb 2000, Summers *et al.* 2002, Constantine & The Sound Approach 2006, Martin *et al.* 2019, Summers 2020).

To investigate the geographical and temporal similarity of the calls, we used only one call from each recording, selecting the analysed call randomly. The final sample sizes for the study are provided in Table 1. To avoid including calls from the same individual more than once in the analysis, we only used recordings made at least 2 km apart or more than 100 days apart at the same site. We converted all recordings to 44-kHz wav-files (16 bit) and then visually compared the calls in the spectrograms using the Raven software (Cornell Lab of Ornithology 2019). For statistical analysis, we calculated the pairwise similarities of each combination of calls (and thus individuals) of the same call type separately for the FCs and ECs using the correlation tool in Raven. This tool performs two-dimensional correlations between spectrograms, resulting in a measure of the similarity of both calls (values range from 0 to 1; Charif *et al.* 2010). Correlation analyses are well suited for comparing contact calls (Charif *et al.* 2010, Porter & Benkman 2019) and have the advantage of estimating the overall similarity of audio signals, and therefore might include acoustic variables not accounted for in multivariate analyses of multiple acoustic variables (Cortopassi & Bradbury 2000, Nowicki & Nelson 2010). The correlations were obtained using the 'biased' and 'normalized' options of Raven and were determined for signals that were bandpass filtered from 0.9 to 7.5 kHz. The temporal and geographical distances between all call combinations were calculated using the 'lubridate' (Grolemund & Wickham 2011) and 'geosphere' (Hijmans 2016) packages in R (R Core Team 2019).

To investigate the effects of temporal and geographical distance on the calls, we fitted a Linear Mixed Model (LMM; Baayen 2008) with a Gaussian error distribution for each call type in R, using the function 'lmer' of the R package 'lme4' (Bates *et al.* 2015). The correlation coefficients were used as response variables. The key predictors in these

models were the fixed effects of temporal distance (number of days elapsed between the recording dates of pairs of calls) and spatial distance (distance between the recording sites of pairs of calls in km). We included the identities of the two calls to be compared as random intercept effects. To keep type I error rates at the nominal level of 5%, we included random slopes of temporal and spatial distance within both random effects, but not the correlation parameters between the random intercept and random slope terms (Schielzeth & Forstmeier 2009, Barr *et al.* 2013). We visually assessed the distribution of the predictor and the response variable and transformed them to obtain approximately symmetrical distributions (Table S3). To allow for comparison of the estimated coefficients, we scaled both predictors to a mean of zero and a standard deviation of one. We also checked for homogeneity of residuals (Field 2009). This found no violation of the assumptions of normally distributed and homogeneous residuals. To determine significance, we used a permutation test (Adams & Anthony 1996). To this end, we simultaneously randomized the recordings across recording locations and times. Hence, this was conceptually a Mantle test (Sokal & Rohlf 1995). We conducted 1000 permutations into which we included the original data as one permutation and determined the *P*-value as the proportion of permuted datasets revealing a log-likelihood at least as large as the original data. If this test revealed a significant effect, this meant that recording time and site affected the variability of the calls. We performed one such test for both the FCs and the ECs of all analysed call types. Table 1 shows the sample sizes for all the models used.

To investigate whether co-occurring call types or crossbill species affect each other's flight calls as observed by Porter and Benkman (2019), we tested for temporal changes in FC similarity over time between N06 and invading call types of Red Crossbill as well as the resident Scottish Crossbill. This included those call types commonly found in Britain and Ireland (N03, N04, N08; Summers 2004, R. Martin and J. Rochefort pers. data), as well as the Scottish Crossbill (N20; Summers 2004 and R. Martin and J. Rochefort pers. data). If more than 10 recordings of different individuals of N03, N04, N06, N08 or N20 were available in sufficient quality for a given season, we calculated the average pairwise similarities of each FC (and

Table 1. Summary statistics of the permutation test and the Linear Mixed Models.

Call type	Permutation test			Linear mixed model						n	FCs and ECs of the same individual	Temporal range	Geographical range (km)
	Overall P-value	Temporal distance	Geographical distance	Temporal distance		Geographical distance							
		P-value	P-value	Estimate	se	Estimate	se						
N01	FC	0.004	0.001	0.039	−0.0132	0.0040	−0.0039	0.0034	128	61	1979–2020	2755	
N01	EC	0.001	0.01	0.001	0.0183	0.0121	−0.0427	0.0196	81		1985–2019	2596	
N03	FC	0.001	0.001	0.021	−0.0366	0.0041	−0.0019	0.0014	313	70	1962–2020	7071	
N03	EC	0.101	0.08	0.499	−0.0071	0.0067	−0.0027	0.0058	82		1963–2020	6061	
N04	FC	0.001	0.001	0.001	−0.0121	0.0020	−0.0032	0.0009	628	174	1967–2020	10 237	
N04	EC	0.001	0.001	0.004	−0.0094	0.0039	−0.0055	0.0034	218		1979–2020	8964	
N06	FC	0.001	0.001	0.027	−0.0317	0.0026	−0.0014	0.0014	376	171	1981–2020	2753	
N06	EC	0.001	0.001	0.001	−0.0204	0.0031	−0.0106	0.0038	230		1982–2020	2457	
N06 without New Forest	FC	0.001	0.001	0.329	−0.0298	0.0031	−0.0007	0.0015	335	154	1981–2020	2753	
N06 without New Forest	EC	0.001	0.001	0.236	−0.0085	0.0034	−0.0010	0.0015	227		2000–2020	2753	
N07	FC	0.021	0.001	0.036	−0.0103	0.0025	−0.0016	0.0012	234	89	1997–2020	2121	
N07	EC	0.007	0.001	0.003	−0.0163	0.0097	−0.0113	0.0056	122		1974–2020	918	
N08	FC	0.001	0.001	0.001	−0.0375	0.0032	−0.0030	0.0012	501	109	1974–2020	10 964	
N08	EC	0.001	0.001	0.791	−0.0276	0.0056	−0.0006	0.0032	140		1976–2020	8631	
N10	FC	0.249	0.194	0.913	−0.0062	0.0097	0.0004	0.0056	81	36	2001–2020	1493	
N10	EC	0.001	0.001	0.198	−0.0338	0.0150	−0.0095	0.0152	46		2007–2020	1370	
N11	FC	0.001	0.001	0.249	−0.0040	0.0039	−0.0010	0.0011	258	75	1971–2020	2612	
N11	EC	0.613	0.008	0.001	0.0067	0.0064	−0.0203	0.0043	115		1966–2020	2409	
N19 (TBC)	FC	0.295	0.001	0.648	−0.0288	0.0153	0.0046	0.0122	50	36	1991–2020	8706	
N19 (TBC)	EC	0.067	0.557	0.699	−0.0084	0.0255	0.0061	0.0221	45		1991–2020	8925	
N20 (SC)	FC	0.001	0.001	0.052	−0.026	0.005	−0.009	0.003	284	82	1996–2016	342	
N20 (SC)	EC	0.001	0.001	0.001	−0.007	0.003	−0.021	0.003	254		1996–2016	1140	
N21 (PC)	FC	0.038	0.001	0.173	−0.0120	−0.0047	−0.0027	0.0025	151	45	1979–2020	3027	
N21 (PC)	EC	0.006	0.01	0.429	−0.0170	−0.0156	−0.0050	0.0062	84		1982–2019	2404	

‘Call similarity’ was used as response, ‘temporal distance’ and ‘geographical distance’ as fixed effects, and ‘individual identity’ as random effect. N19 refers to Two-barred Crossbill (TBC), N20 to Scottish Crossbill (SC), N21 to Parrot Crossbill (PC) and the other call types are Red Crossbills. Estimates in the Linear Mixed Model are marked in bold if the respective effect (temporal or geographical distance) was significant and larger than the other. Values in italics indicate that the respective effect size was smaller but still significant, whereas values in bold + italics indicate overlapping effect sizes. The symbol ‘n’ refers to the number of crossbills that were included in the analysis, after applying the filtering criteria of a minimum distance of 2 km or a minimum time interval of 100 days between individuals.

therefore individual) of N06 and the other call type or crossbill species as described above. We checked whether there were clear trends for increasing or decreasing similarity. As the extent of the invasions of N03, N04 and N08 to Britain and Ireland varies between seasons, the impact of these call types on N06 is likely to vary as well. To account for this, we calculated the proportion of the respective call type of all Red Crossbills recorded in Great Britain and Ireland in a given season. Call similarities of N06 and the invading call type (N03, N04, N08) were compared for the season of the invasion as well as in the subsequent season (if the effect was delayed), to determine whether there was a correlation between the call similarity of two call types and their frequency of encounters.

RESULTS

A visual comparison of the spectrograms of the analysed Red Crossbill call types (N01, N03, N04, N06, N07, N08, N10, N11), Scottish Crossbill (N20), Parrot Crossbill (N21) and Two-barred Crossbill (N19) revealed that the FCs obviously changed over time, except for Two-barred Crossbill (Fig. 2a,b, Figs S14–S25). For most call types of Red Crossbill and other crossbill species (except Two-barred Crossbill), the temporal change in FCs varied in a given time period, with some changes being small and others being large. For instance, in N08, FCs remained stable from 1962 until 1999, changed rapidly afterwards, and then were stable again from about 2010 until 2019. The low FC similarity observed within call types and crossbill species did not show any significant correlation with larger distances, with one exception: calls of N06 in the New Forest differed from other localities where N06 was present (Figs 1, 2a, and Fig. S18). In the ECs, none of the call types and crossbill species showed any obvious temporal or spatial variation, with two exceptions: in N06, ECs showed no obvious temporal variation for the period from 2000 to 2019 (Fig. 2a, Fig. S17); however, there was a substantial change of EC structure between 1980 and 2000 and in Scottish Crossbill, ECs changed slightly, especially between 2005 and 2009 (Fig. 2b, Fig. S23).

Table 1 shows the results of our statistical analysis on the similarity of FCs and ECs between different call types, considering both temporal and geographical distances. Overall, we found that FC

similarity decreased with increasing time lag, except for Two-barred Crossbill and N10. Notably, the dataset for N10 covered the shortest period of time in this study. Larger geographical distances did not significantly decrease the similarity of FCs (N10, N11, Two-barred Crossbill N19, Scottish Crossbill N20, Parrot Crossbill N21) or the effect was smaller than that of temporal distance (N01, N03, N04, N06, N07, N08). In the ECs, we observed a decrease in similarity with increasing time lag (N01, N04, N06, N07, N08, N10 as well as Parrot and Scottish Crossbill); in addition, we found that geographical distance decreased EC similarity (N01, N04, N06, N07 and Scottish Crossbill). The effect sizes of temporal distance and geographical distance were more even than in the FCs. To control for potential effects of the deviating population of N06 in the New Forest, we also evaluated the data of N06 without these birds. After removing these birds, geographical distance no longer had a significant effect on call similarity in FCs and ECs of N06. However, the effect of temporal distance remained. To summarize, call similarity decreased over time in most of the analysed Red Crossbill call types as well as in Parrot and Scottish Crossbill in the FCs, but not as much or not significantly in the ECs.

Comparing the similarity of several call types (N03, N04, N08 and N20) with N06 over time, there was no clear trend of FCs to become more or less similar to each other (Fig. 3). N20 appeared to be increasingly different from N06, but the similarity appeared to have increased again in later years. Furthermore, we found no clear trend of increased or decreased FC similarity between the invading call types (N03, N04 and N08) and local call type N06 in relation to the strength of invasions, either in the season of the invasion or in the season after the invasion (Fig. 4, Figs S26–S28). However, we found that during the seasons with the highest abundances of the invading call types as well as in the seasons after, FC similarity mostly decreased (Fig. 4).

Based on our study, we can infer that several names of previous call types are synonyms for each other, denoting the respective temporal variation during the study period. Specifically, N01 is equivalent to type 'B' (Robb 2000), N03 is equivalent to type 'A' (Robb 2000), as well as '2B' (partially, as N03 and N08 were not separated in this study; Summers *et al.* 2002), and the so-called type 'Y'

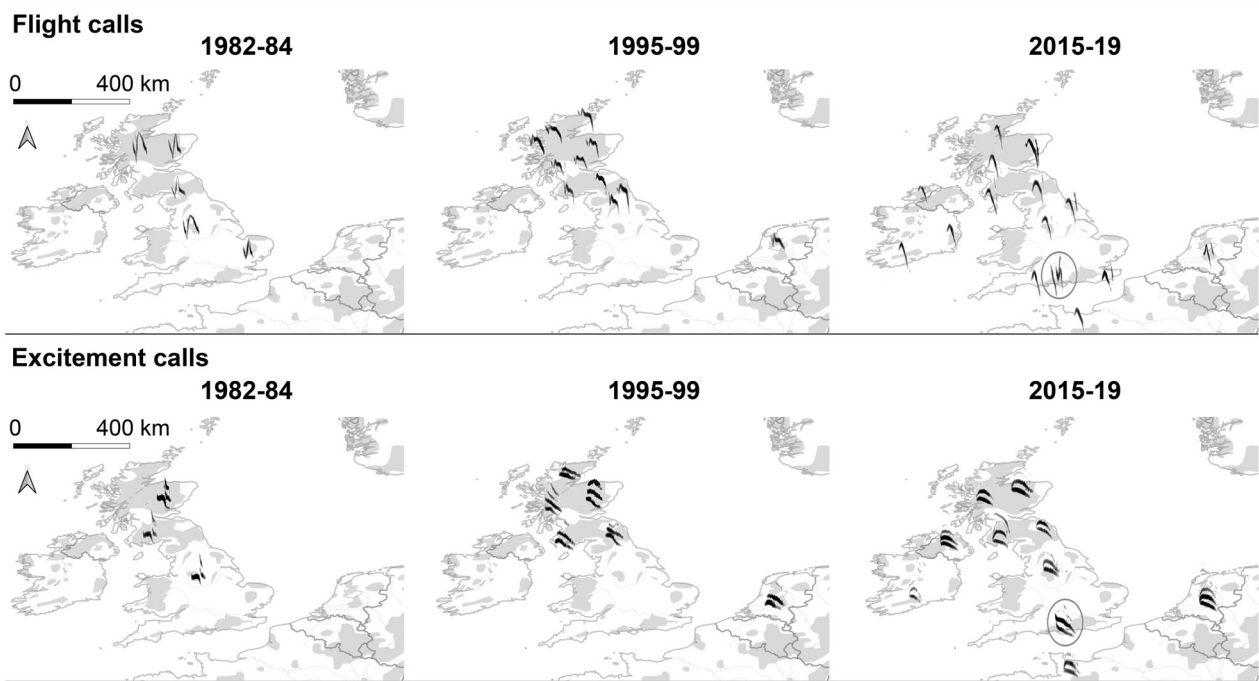


Figure 1. Exemplary temporal and spatial variation of calls in the Red Crossbill call type N06. The circle marks the calls in the New Forest. Distribution data of Red Crossbill are from BirdLife International and Handbook of the Birds of the World (2017), and maps are drawn with Natural Earth (2018).

(Edelaar *et al.* 2004), N04 is equivalent to types 'C' (Robb 2000) and '4E' (Summers *et al.* 2002), N07 is equivalent to type 'D' (Robb 2000), N08 is equivalent to '2B' (partially, see explanation for N03; Summers *et al.* 2002) and type 'X' (Constantine & The Sound Approach 2006), and N20 is equivalent to Scottish Crossbill '3C' (Summers *et al.* 2002, Constantine & The Sound Approach 2006).

DISCUSSION

Due to large differences between FCs found by Martin *et al.* (2019) and earlier studies (Robb 2000, Summers *et al.* 2002, Constantine & The Sound Approach 2006) we tested whether the discrepancy between FCs were due to geographical variation, or calls had changed over time. We analysed 11 call types across four crossbill species in Europe and found that geographical patterns did not explain the variation of calls across the different call types. However, we observed that call similarity decreased over time, particularly in the FCs, whereas geographical distance did not result in a decrease of call similarity (FCs) or only weakly

affected it (ECs). Therefore, we conclude that our results support the hypothesis that temporal distance accounts for the observed variation of FCs in the analysed call types in Red, Parrot and Scottish Crossbills.

Comparison with call evolution in crossbills in North America

Slight cultural evolution of crossbill calls has been described in previous studies in Northern America and there have been indications of similar effects in Europe (cf. Keenan & Benkman 2008, Porter & Benkman 2019, North America; Summers 2020, Europe). Our results support these findings and suggest that cultural evolution seems rather to be the rule than the exception in crossbills, at least from a Palaearctic perspective. Furthermore, our study shows that the pace of cultural evolution of crossbill FCs is high in the Palaearctic region and faster than described for any other group of birds.

The reason for this fast cultural evolution is unclear. In North America, the FCs of the endemic Cassia Crossbill have diverged from those of an abundant call type of the 'Ponderosa Pine

Crossbill' (an American call type of Red Crossbill; Groth 1993a, Keenan & Benkman 2008, Porter & Benkman 2019). The authors presumed this character displacement helps to reduce heterospecific flocking with the Ponderosa Pine Crossbill. Homospecific flocking is beneficial for crossbills, as they use public information from their flock-mates to assess resource quality (Smith *et al.* 1999). The feeding rate of a flock is decreased when flock-mates differ in their ability to exploit a shared resource. It is thought that the sympatry of the Cassia Crossbill and Ponderosa Pine Crossbill has only recently occurred, which is why the FCs of the Cassia Crossbill and Ponderosa Pine Crossbill are thought to still diverge.

The British and Irish Red Crossbills with call type N06 are also likely to be a recently emerged and established population, as there were no resident Red Crossbills before the end of the 19th century (Holloway 1996). However, we did not find clear evidence of increasing divergence between the FCs of N06 and those of the three most commonly invading call types of Red Crossbill (N03, N04 and N08), although we cannot rule out some impact (as the highest abundances all show a more or less decreasing FC similarity). Contrary to the results reported for Cassia Crossbill and Ponderosa Pine Crossbill, these four call types do not use different food resources to our knowledge (Martin *et al.* 2020, own data). All feed especially on seeds from *Picea sitchensis* in Great Britain but also on *Picea abies* as well as different species/hybrids of *Larix* spp. (Marquiss & Rae 2002). Therefore, each individual can provide comparable quality of information on resource availability, which could explain the lack of ongoing FC divergence. Alternatively, the call types may have already diverged. The analysed call types of Red Crossbill live parapatrically (temporally sympatric) in Scotland, but not sympatrically, which could reduce competition. The situation differs between the Scottish Crossbill and Red Crossbill (N06), as both live sympatrically in Scotland. Although both could provide differing quality of information about food resources to a flock (N06

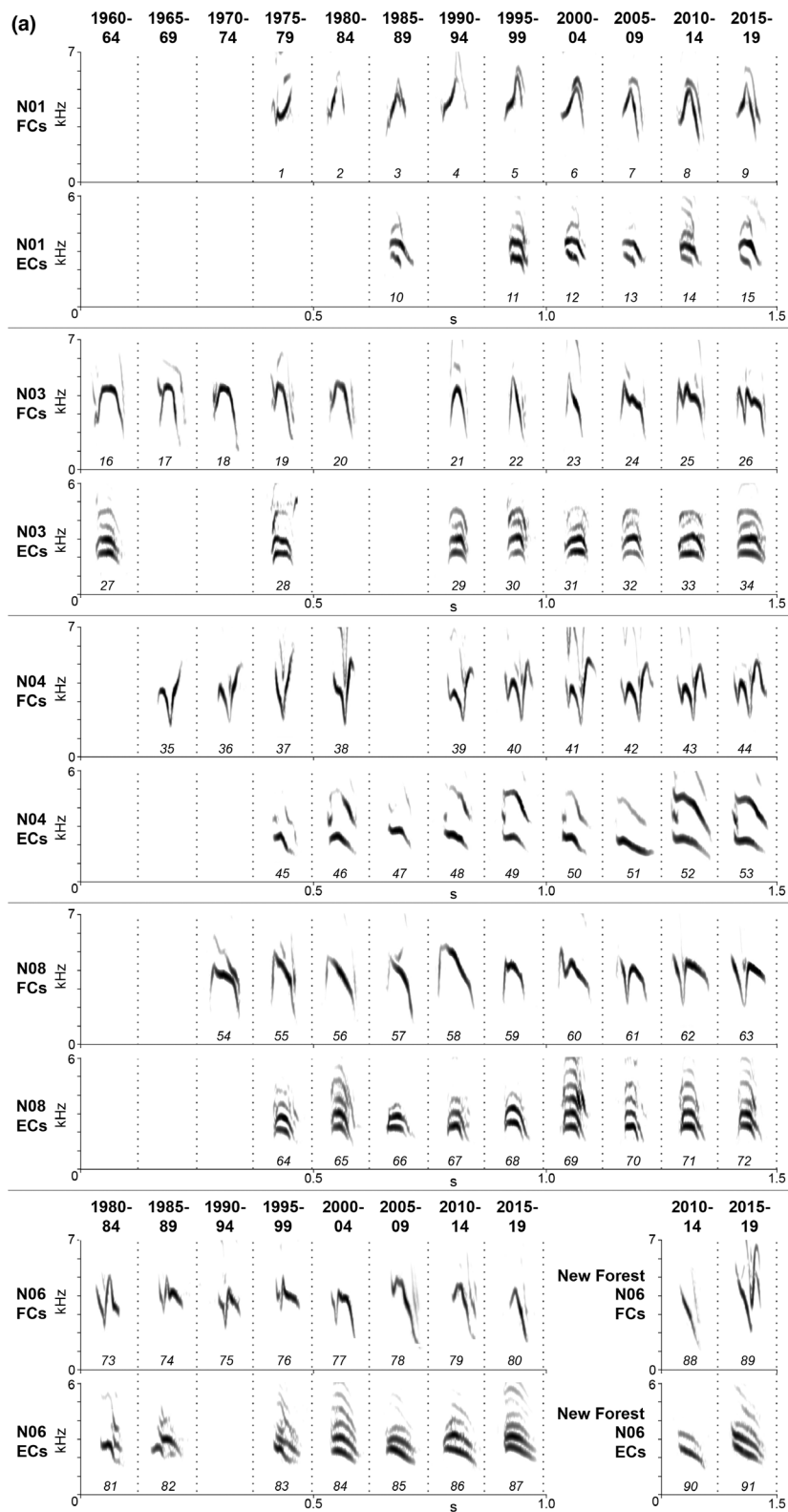
is associated particularly with *Picea sitchensis* and Scottish Crossbill with *Pinus contorta*; Summers & Broome 2012), we found no clear trend here either. Again, Red Crossbill (N06) and Scottish Crossbill have perhaps already separated sufficiently acoustically and hence they hardly affect each other any longer. This assumption is supported by the lack of known hybridization between the two species (Summers *et al.* 2007). In summary, we found no clear relationship between FCs of N06 and invading call types of the Red Crossbill and Scottish Crossbill.

Comparison with results of call evolution in other animals

Cultural evolution occurs in the songs of numerous bird species (Aplin 2019) but is also known in other vocal learning animals such as Humpback Whales *Megaptera novaeangliae* (Rendell & Whitehead 2001, Garland *et al.* 2011), Killer Whales *Orcinus orca* (Filatova *et al.* 2015), elephant seals *Mirounga* sp. (Le Boeuf & Petrionovich 1974) and, of course, humans (Eckardt *et al.* 2008). The reasons for vocal changes are usually not apparent and the details are not well understood. Mostly, however, the drivers for cultural evolution are assumed to be similar to those of 'normal' evolution (e.g. Mesoudi 2015, Aplin 2019), namely: (1) cultural drift (e.g. Common Chaffinch, Baker & Jenkins 1987, Lynch *et al.* 1989); (2) cultural mutation (e.g. Slater *et al.* 1980, Lynch *et al.* 1989); (3) selection (e.g. Yellow-rumped Cacique *Cacicus cela*, Trainer 1989; and Darwin's finches, *Geospizini*, Grant & Grant 2010); and (4) immigration (Mennill *et al.* 2018).

Cultural drift occurs especially in small or fragmented populations (e.g. strong bottleneck effects during colonization of new areas; Price 2008) with limited exchange between populations. Such conditions are found in resident Red Crossbills in fragmented forests in the Mediterranean region. Cultural drift might also explain the differing calls of Red Crossbills in the New Forest (small, temporally isolated population). However, it cannot

Figure 2. (a) Spectrograms of calls of five call types of Red Crossbill recorded between crossbill season 1960 and 2019, with each call originating from a different bird. See Data S3 for details on recording data for each call. (b) Spectrograms of calls of six call types across four crossbill species recorded between crossbill season 1960 and 2019, with each call originating from a different bird. N19 refers to Two-barred Crossbill, N20 refers to Scottish Crossbill, N21 refers to Parrot Crossbill, and the other call types refer to Red Crossbill. See Data S3 for details on recording data for each call.



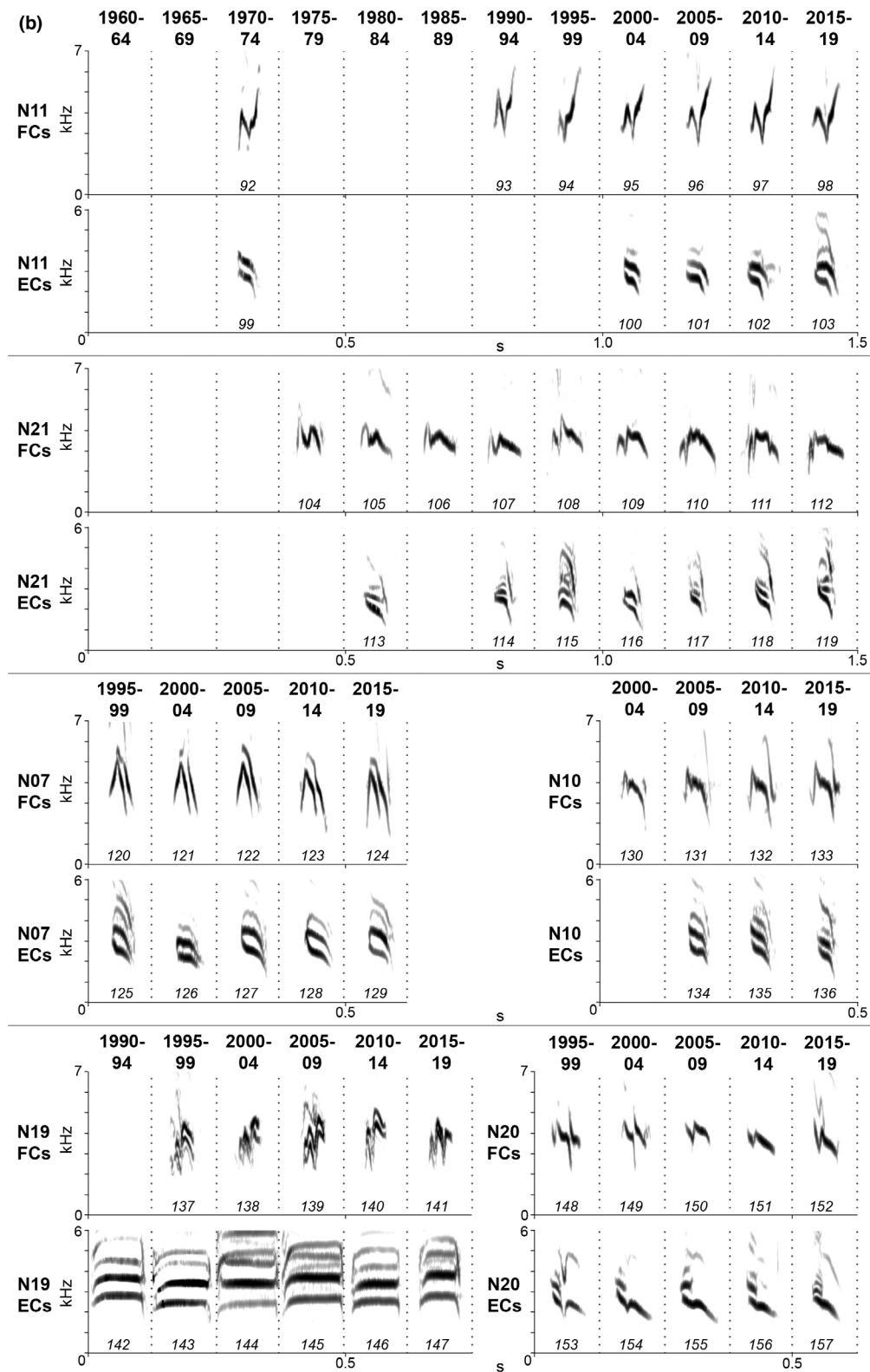


Figure 2. (Continued)

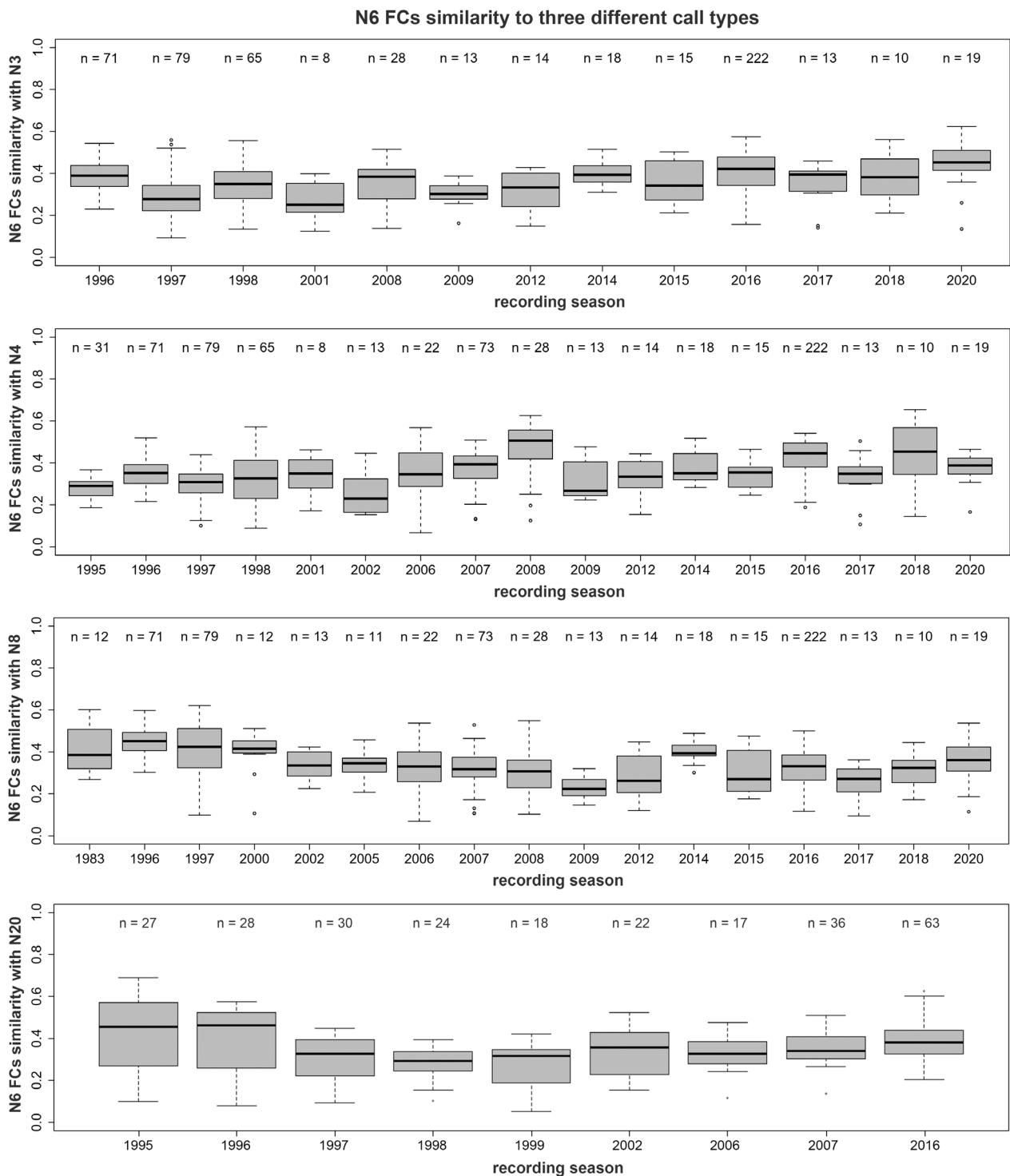


Figure 3. FC similarity (cross-correlation values) of local N06 to the three most commonly invading call types in Great Britain and Ireland (N03, N04, N08) as well as Scottish Crossbill (N20) in different recording seasons.

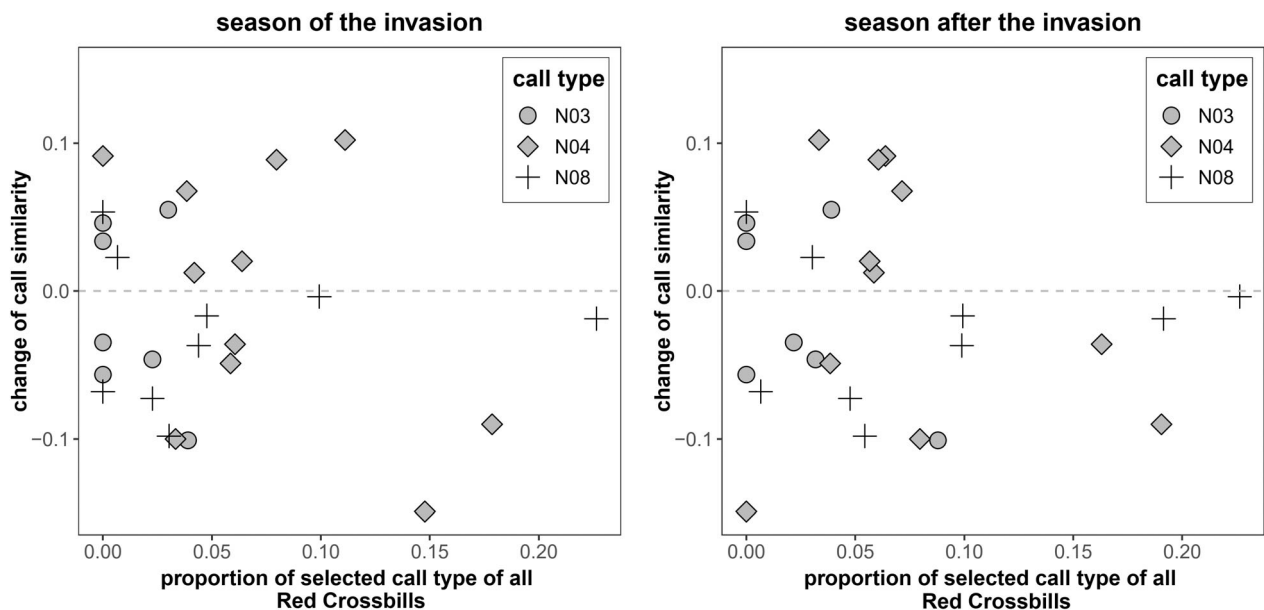


Figure 4. Changes in FC similarity between local call type N06 and invading call types N03, N04 and N08 in relation to strength of an invasion to Great Britain. Left-hand plot shows changes in FCs during invasion season, and right-hand plot shows changes in FC similarity one season after invasion.

explain the overall call evolution shown in this study, as some of the call types studied (N03, N04 and N08) are currently widespread (Martin *et al.* 2020). Although, during invasions, groups of these call types are scattered over almost the entire Palaearctic region, sometimes segregated from other groups (comparable to small fragmented populations), this situation usually lasts for only 1 year or a few years. Afterwards, most or all individuals leave the invasion area and may reunite in the original area (Newton 2006, Martin *et al.* 2020).

The second hypothesis is cultural mutation, which can happen irregularly through rare innovations that are adopted by many other individuals (as observed in Humpback Whales; Noad *et al.* 2000) or continuously. Reasons for the latter could be young birds' erroneous learning or during call-matching processes within pairs (during pair formation, mates develop pair-specific calls whereby some pairs seem to form 'new calls' and some pair mates develop an intermediate call; Groth 1993b, Keenan & Benkman 2008, R. Martin and J. Rochefort pers. data).

The third hypothesis based on cultural evolution is selection. Individual birds may benefit from using certain call variants (Trainer 1989, Payne

1985). One example was observed in crossbills by Porter and Benkman (2019) and has been discussed previously. Another example is given by Trainer (1989), who suggested that females' response to songs wanes over time, and novelty in songs keeps up females' interest. However, we do not have any data to assess the impact of such an effect. Selection can also be driven by habitat, which can have a direct or indirect effect. In the former, sound transmission is strongly dependent on habitat characteristics, particularly the density of vegetation (Slabbekoorn *et al.* 2002, Catchpole & Slater 2015). A changing habitat could thus affect transmission and hence favour calls with certain characteristics. However, although forests change, especially due to human forestry, it is unlikely that habitat parameters will change sufficiently within a few years. Additionally, other forest-dwelling, closely related species living in the same region as the analysed crossbills do not change their calls (e.g. Northern Bullfinch *Pyrrhula*, Fig. S29). The indirect effect implies, for example, a change of food resources and a subsequent adaptation of the morphology. Morphology can affect bird songs, with bigger birds tending to produce lower frequencies and bill size limiting temporal and performance components

(Podos 2001, Christensen *et al.* 2006, Huber & Podos 2006, Derryberry *et al.* 2018, Porter & Smith 2019). However, birds are obviously not always at the limit of their vocal capabilities (e.g. Black-bellied Seedcracker *Pyrenestes ostrinus*; Slabbekoorn & Smith 2000). This is also true for crossbills, with individuals frequently using perfect imitations of FCs from other call types in their song (Fig. S30) and juveniles are capable of learning calls from foster parents of a different call type (Groth 1993b, Sewall 2010). Finally, bill size differs partly more between sexes than between call types in Europe (Edelaar *et al.* 2004). Therefore, morphology is unlikely to be responsible for the change of calls in call types (cf. Smith *et al.* 2012).

The fourth hypothesis, immigration, presupposes a mixture of individuals with different call types. Mixed breeding does occur, albeit rarely (Summers *et al.* 2007, Keenan & Benkman 2008, R. Martin and J. Rochefort pers. data). As pair mates match their calls (Keenan & Benkman 2008), and young crossbills mimic the calls of their parents (Keenan & Benkman 2008, Sewall 2010), pairs of mixed call types can incorporate new call characteristics into the call pool of a call type horizontally and vertically. Immigration can also reduce similarity of calls (Porter & Benkman 2019). However, in our study, we found no clear correlation between the similarity of calls of N06 to other call types and the extent of their invasion in the current or past season.

To summarize, it is likely that various factors have an impact on call evolution in crossbill call types. Drift may have large effects particularly during the establishment of new populations of crossbills or in resident populations. Regular cultural mutation may account for consistent changes in calls. In our view, the irregular speed of cultural evolution can only be explained by randomly occurring, rare innovations for which there is a strong preference, or by irregular invasions of crossbills. As previously discussed, the latter explanation would imply either immigration followed by horizontal and vertical cultural transmission between call types (increasing call similarity), or a decrease in call similarity to commonly invading call types. We have not found any compelling arguments to support one of these explanations over the others.

Regardless of the mechanism underlying cultural evolution in crossbill calls, the combinations of rapidly changing calls with assortative flocking

and assortative mating by calls (Groth 1993a, Snowberg & Benkman 2007, Summers *et al.* 2007, Edelaar 2008, Smith *et al.* 2012) enable populations to differentiate quickly (dialect differentiation; Trainer 1989) and thus simplify adaptation to new habitats within short periods of time. The Red Crossbills in the New Forest, one of the largest, contiguous forests in southern Britain, fit this scenario. The forest is somewhat isolated from the core breeding area of call type N06 (which is found in northern Britain and Ireland; Martin *et al.* 2020), and partly fulfils the presumed requirements for a core breeding area of a new call type (continuous food supply by a broad range of conifers; Martin *et al.* 2020). This has enabled Red Crossbills to remain largely resident and isolated from the rest of N06 there. Consequently, their calls can drift and differentiate slightly from the rest of the call type N06.

Differing pace of cultural evolution in different vocalizations

It is interesting to note the differing pace of cultural evolution in the FCs and ECs (fast in FCs, slow or absent in ECs). Possible explanations are that there is selection for similarity of ECs, or the genetically determined acoustic template specifies the ECs more precisely than the FCs. As a result, the ECs may be less altered by learning, which could explain the similarity of the ECs in many crossbill call types while FCs are dissimilar. In line with these results, Mundinger (1979) assumed that the alarm calls of finches and buntings are evolutionarily informative. In the Red Crossbill, the ECs have a similar function as alarm calls, whereas the FCs serve as contact calls (Robb 2000, Summers *et al.* 2002). It is advantageous for conspecifics to recognize invariable alarm calls quickly but, more importantly, it can increase the fitness of the caller in case of danger for various reasons such as the 'confusion effect' (Charnov & Krebs 1975). Comparable results were found in other species such as Hinde's Babbler *Turdoides hindei*, in which contact calls showed strong differentiation of calls across the species distribution range, whereas alarm calls were more conserved (Habel *et al.* 2018).

In summary, FCs and ECs are probably subject to different selective pressures: FCs have a strong cultural component that can adapt to new flocks and facilitate communication with specific flock

members or mates, while ECs are stable so as to be easily understood by all individuals of the species/call type.

Synchronized vocal change in large populations

Our study suggests that calls can change within 5–10 years in most or all individuals of a crossbill call type, even when separated by distances of up to 10 000 km temporally. As such effects are only known from song studies (most studies of bird vocalizations focus on songs and not on calls) we will compare our results with these. Temporal change of song is known in several species, such as in the Savannah Sparrow *Passerculus sandwichensis* (Williams *et al.* 2013), Hermit Warbler *Setophaga occidentalis* (Janes & Ryker 2013) and Yellow-rumped Cacique *Cacicus cela* (Trainer 1989). However, the synchronized change in such a large population like our study within a comparably short time is remarkable. Otter *et al.* (2020) reported that the typical song in the White-throated Sparrow *Zonotrichia albicollis* was replaced by another variant between 1960 and 2000, and then again by a third variant between 2000 and 2019, across distances of more than 3000 km (perhaps such a transition from one song to another would better be called ‘song revolution’, as in whales; Noad *et al.* 2000). Geolocator tracking confirmed that birds from different parts of the breeding range overwinter together and have the opportunity to learn songs from each other (Otter *et al.* 2020). Crossbill call types frequently meet in their core breeding area if there is a good cone crop (Martin *et al.* 2020). This behaviour is comparable to the meeting events of White-throated Sparrows in their wintering area. Until now, horizontal transmission in crossbills has only been demonstrated in pairs and thus very extensive contact of individuals. However, if crossbills are capable of decreasing their call similarity to other call types without being mates (Porter & Benkman 2019), it should also be possible for them to increase their call similarity to their flock mates (as in the closely related Eurasian Siskins *Spinus*; Mundinger 1970). Further research on this topic would be desirable.

Summing up, we are only beginning to understand cultural evolution and its drivers in animals (Filatova *et al.* 2015, Mesoudi 2015, Whiten 2019, Otter *et al.* 2020). However, it is known that

cultural differences sometimes constrain mating, even without any drawback of interbreeding. Therefore, cultural evolution ‘may play a crucial role in species formation by promoting genetic isolation on secondary contact’ (Grant & Grant 1996) and is thus worthy of further study.

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AUTHOR CONTRIBUTIONS

Ralph Martin: Conceptualization; methodology; investigation; funding acquisition; writing – original draft; writing – review and editing; visualization; validation; project administration; formal analysis; data curation; resources. **Julien Rochefort:** Data curation; resources; conceptualization; visualization; writing – review and editing; validation. **Roger Mundry:** Conceptualization; methodology; supervision; formal analysis; validation; visualization; writing – review and editing. **Gernot Segelbacher:** Conceptualization; supervision; project administration; writing – review and editing; funding acquisition; visualization.

CONFLICT OF INTEREST

None declared.

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ETHICAL NOTE

None.

Data Availability Statement

The data supporting the findings of this study are available on reasonable request from the corresponding author.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Data S1. Recordists.

Data S2. Recording details to Figure 2.

Data S3. Recording details to Figure 3.

Figure S1. Relative proportion of Red Crossbill call type N06 of all Red Crossbills in recordings from Great Britain, Ireland and other countries where it has been detected.

Figure S2. Temporal and spatial distribution of Red Crossbill call type N06 recordings used in this study.

Figure S3. Forests visited during the 2016 search for Red Crossbills, with locations indicated on the map.

Figure S4. Distribution of analysed calls of Red Crossbill call type N01.

Figure S5. Distribution of analysed calls of Red Crossbill call type N03.

Figure S6. Distribution of analysed calls of Red Crossbill call type N04.

Figure S7. Distribution of analysed calls of Red Crossbill call type N07.

Figure S8. Distribution of analysed calls of Red Crossbill call type N08.

Figure S9. Distribution of analysed calls of Red Crossbill call type N10.

Figure S10. Distribution of analysed calls of Red Crossbill call type N11.

Figure S11. Distribution of analysed calls of Two-barred Crossbill call type N19.

Figure S12. Distribution of analysed calls of Scottish Crossbill call type N20.

Figure S13. Distribution of analysed calls of Parrot Crossbill call type N21.

Figure S14. Spectrograms of calls of N01 Red Crossbills from 1980 to 2019.

Figure S15. Spectrograms of calls of N03 Red Crossbills from 1962 to 2019.

Figure S16. Spectrograms of calls of N04 Red Crossbills from 1967 to 2019.

Figure S17. Spectrograms of calls of N06 Red Crossbills from 1982 to 2019.

Figure S18. Spectrograms of calls of presumed call type N06 recorded in the New Forest near Southampton from 2010 to 2015.

Figure S19. Spectrograms of calls of N07 Red Crossbills from 1997 to 2019.

Figure S20. Spectrograms of calls of N08 Red Crossbills from 1974 to 2019. ECs in the left row, FCs in the right row.

Figure S21. Spectrograms of calls of N10 Red Crossbills from 2002 to 2019.

Figure S22. Spectrograms of calls of N11 Red Crossbills from 1967 to 2019.

Figure S23. Spectrograms of calls of N20 Scottish Crossbills from 199 to 2019.

Figure S24. Spectrograms of calls of N21 Parrot Crossbills from 1980 to 2019.

Figure S25. Spectrograms of calls of N19 Two-barred Crossbills from 1991 to 2019.

Figure S26. Similarity of calls of N06 (from Great Britain) with N03 in different seasons and abundance of N03 in Great Britain in the respective season.

Figure S27. Similarity of calls of N06 (from Great Britain) with N04 in different seasons and abundance of N04 in Great Britain in the respective season.

Figure S28. Similarity of calls of N06 (from Great Britain) with N08 in different seasons and abundance of N08 in Great Britain in the respective season.

Figure S29. Spectrograms of calls of Northern Bullfinches in Central Europe from 1969 to 2018.

Figure S30. Red and Parrot Crossbill imitating FCs of other call types in one of their song themes.

Table S1. Sources for crossbill recordings used in this study.

Table S2. Number of recordings per country including analysed call types/crossbill species.

Table S3. Transformations of the predictors and the response for the LMM.