



RESEARCH ARTICLE

Vocal distinctiveness of the Red Crossbill (*Loxia curvirostra*) on the island of Newfoundland, Canada

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ABSTRACT

Ten vocal types of Red Crossbill (*Loxia curvirostra*) are recognized in North America. Little is known about this species' vocalizations on the island of Newfoundland, where the subspecies *L. c. percna* (Bent 1912) was described on the basis of study skins collected in a single year from one area; subsequently a distinctive vocal type was proposed on the basis of one sound recording. We made field recordings (~1000 min) of Red Crossbill vocalizations in Newfoundland to describe vocalizations and compare them with vocal types recognized elsewhere in North America. One class of call ("flight call"; class I call hereafter) was distinctive, and discriminant analysis distinguished 98% of Newfoundland class I calls from mainland North American and European samples. Class I calls of 5 (out of 83) Newfoundland birds resembled recognized vocal types from mainland North America. Other call classes ("excitement/alarm" and "chitter") of Newfoundland birds also differed from mainland North American samples. We conclude that several vocal types of Red Crossbill, one of which may represent *L. c. percna*, occur in Newfoundland. Samples from other areas are needed to determine whether the distinctive vocal type in insular Newfoundland (a) represents *L. c. percna* and (b) is restricted to Newfoundland or also occurs in other areas such as Cape Breton Island.

Keywords: crossbill, *Loxia curvirostra*, Newfoundland, Red Crossbill, taxonomy, vocalization, vocal type

Tipos vocales distintivos de *Loxia curvirostra* en la isla de Newfoundland, Canadá

RESUMEN

Se reconocen diez tipos vocales de *Loxia curvirostra* en América del Norte. Poco se sabe sobre las vocalizaciones de esta especie en la isla de Newfoundland, donde la subespecie *L. c. percna* (Bent 1912) fue descubierta en base al estudio de pieles colectadas en un área en un único año; subsecuentemente se propuso un tipo vocal distintivo en base a un registro de sonidos. Realizamos grabaciones en el campo (~1000 min) de vocalizaciones de *Loxia curvirostra* en Newfoundland para describir las vocalizaciones y compararlas con los tipos vocales reconocidos en el resto de América del Norte. Un tipo de llamada ("llamada de vuelo"; llamada clase I) fue distintiva, y los análisis discriminantes distinguieron al 98% de las llamadas clase I de Newfoundland de las muestras del área continental de América del Norte y Europa. Las llamadas clase I de 5 aves (de un total de 83) de Newfoundland se parecieron a tipos vocales reconocidos del área continental de América del Norte. Las otras clases de llamada ("excitación/alarma" y "chitter") de las aves de Newfoundland también difirieron de las muestras del área continental de América del Norte. Concluimos que varios tipos vocales de *L. curvirostra*, uno de los cuales puede representar a *L. c. percna*, se encuentran en Newfoundland. Se necesitan muestras de otras áreas para determinar si el tipo vocal distintivo de la isla de Newfoundland (a) representa a *L. c. percna* y (b) está restringido a Newfoundland o también se encuentra en otras áreas como la isla de Cabo Breton.

Palabras clave: *Loxia curvirostra*, Newfoundland, taxonomía, tipo vocal, vocalización

INTRODUCTION

Morphological and ecological variation in the Red Crossbill in North America has long interested and confused systematists, and various subspecies schemes have been proposed over the years based on museum specimens (Griscom 1937, Monson and Phillips 1981, Dickerman 1987, Payne 1987). The situation has been greatly clarified through vocal analysis. In the first analysis of both morphology and vocalizations, Groth (1988) revealed two

types of Red Crossbill in Virginia and North Carolina that differ vocally from one another (we follow Groth [1993a] in using the term *vocal type* [or *type*] to refer to vocally distinct Red Crossbill forms). Subsequently he revealed a continent-wide pattern of vocal differentiation in which different vocal types could be recognized and used as a basis for describing parallel differentiation in body measurements and plumage (Groth 1993a). Those findings triggered much research on Red Crossbill differentiation throughout the species' Holarctic range. Other vocal types of North American Red

Crossbill have since been described (Benkman et al. 2009, Irwin 2010), and multiple vocal types have also been recognized in Europe (Robb 2000, Summers et al. 2002, Alonso et al. 2006, Constantine and The Sound Approach 2006, Borrás et al. 2008, Förschler and Kalko 2009, Lindholm 2011, Edelaar et al. 2012).

Vocal types of Red Crossbill recognized by Groth (1993a) differ in ecology (e.g., habitat, conifer-species feeding preference) and ecologically important morphological traits (e.g., body and bill size, palate anatomy; Benkman 1993, Groth 1993a, Benkman et al. 2009, Irwin 2010). Phenotypic divergence is thought to be recent (principally within the last 12,000 years) because vocal types exhibit weak genetic differentiation (Parchman et al. 2006). Nomadism in the Red Crossbill, an adaptation to ephemeral and irregularly distributed cone crops (Benkman 1993, Groth 1993a, Marquiss et al. 2012), presumably contributes to weak genetic differentiation.

Vocalizations can be important in enabling intraspecific ecological divergence (Slabbekoorn and Smith 2002, Price 2008, Wilkins et al. 2013); an example is the “flight call” of the Red Crossbill (we refer to this kind of call as class I; see below). Young birds learn these calls from their parents and the calls are structurally stable across generations (Sewall 2011). Class I calls serve for cohesion of families and flocks (Snowberg and Benkman 2007, Smith et al. 2012). Association of ecomorphologically similar birds is important because their traits (e.g., bill size) are correlated with cone-type preference (Lack 1944) and feeding performance is optimized when crossbills specialize on cones of different conifer species (Benkman 1993, 2010). Furthermore, bill size is heritable (Summers et al. 2007) and hybrids between ecologically differentiated forms likely are selected against (Benkman 1993, 2003). In summary, vocalizations enable and promote differentiation because they contribute to reproductive isolation among different ecomorphological groups (Podos 2010, Servedio et al. 2011, Podos et al. 2013, Seddon et al. 2013). Red Crossbills exhibit mate preferences and mate assortatively on the basis of acoustic cues (Snowberg and Benkman 2007), which helps to explain how phenotypic differences can be maintained across multiple vocal types in sympatry (Knox 1990, Groth 1993b, Smith and Benkman 2007, Summers et al. 2007).

It has long been assumed that the island of Newfoundland (“Newfoundland” hereafter) is home to a single well-marked subspecies of Red Crossbill, *L. c. percna*. Bent (1912) described this subspecies on the basis of 11 specimens that were collected in southwestern Newfoundland in 1912. He noted differences in body and bill size from other North American subspecies recognized at the time, and remarked especially on the much darker plumage of *L. c. percna*. Other workers have supported the distinctiveness of *L. c. percna*, and it has generally been assumed that this taxon is restricted to Newfoundland (“in

the breeding season at least” [Bent 1912:1]; Griscom 1937, Burleigh and Peters 1948, Payne 1987, COSEWIC 2004; but see Bent 1920, Dickerman 1987). Groth (1993a) proposed a unique vocal type for Newfoundland (“type 8”) based on a sound recording from a single individual.

Red Crossbills were considered to be common in Newfoundland through the first three-quarters of the twentieth century (Peters and Burleigh 1951, Erskine 1977). However, Christmas Bird Count data suggest that Red Crossbill numbers on the island declined precipitously in the 1970s, possibly due to habitat reduction and seed competition with, or nest predation by, the Red Squirrel (*Tamiasciurus hudsonicus*; Benkman 1989, COSEWIC 2004). Squirrels were introduced to the Northern Peninsula in 1963 and 1964, and subsequently spread throughout the island through natural and deliberate human-aided dispersal (Northcott 1974, Payne 1976, Goudie 1978). Because of the population decline and assumption that the subspecies *L. c. percna* represents a biological entity and is restricted to Newfoundland, the subspecies is currently listed as Endangered at both Provincial (Newfoundland and Labrador) and Federal (Canada) levels. We studied vocalizations to determine how many and which vocal types of Red Crossbill are present in Newfoundland.

Young et al. (2012) reported a form of class I call from the Red Crossbill in Newfoundland that may not occur elsewhere in North America and on that basis reasoned that *L. c. percna* persists in Newfoundland. Here we confirm and extend that report through acoustic and statistical analyses of Newfoundland sound recordings, and compare Newfoundland calls with samples from continental North America and Europe.

METHODS

Definition of Terms

Call class. We use the term *call class* to refer to a set of structurally similar calls; together these sets constitute a species’ vocal repertoire (Marler 2004). Names used for Red Crossbill call classes sometimes have been onomatopoeic (e.g., *chip* or *dyip*) or given in vague, functional or interpretive terms (e.g., “social” or “threat” calls). Other names suggest specific contexts of use (e.g., “flight” and “traveling” calls). We avoid the use of such names because (a) onomatopoeic names differ across observer languages and cultures, (b) functional or interpretive names usually suggest single functions that have not been rigorously established, and (c) most context-based names imply only single contexts of use. An example of the latter is the call class analyzed in this paper, widely referred to as “flight call.” This type of call class is given by Red Crossbills in varied circumstances, only some of which include flight: in perched flocks prior to or in flight; in flocks that are taking flight after being flushed by a large bird; by males flying to the nest to

TABLE 1. Summary of metadata for Red Crossbills seen or recorded in Newfoundland, February 4, 2010–August 2, 2011.

Location	Number of birds:		Recording dates
	Seen ^a	Recorded ^b	
Howley 49.18°N, 57.09°W	18 (0)	9	2011: April 30, May 1–2
West Brook Ecological Reserve 49.25°N, 56.34°W	7 (5)	2	2011: June 30
Glovertown 48.68°N, 54.03°W	18 (0)	7	2011: January 28–29
Clarenville 48.17°N, 53.96°W	23 (0)	7	2011: February 18, June 26–27
Whitbourne 47.42°N, 53.52°W	24 (8)	13	2010: May 17 & 23–24, July 16 2011: March 9 & 11, April 13, June 8, July 30
South River 47.51°N, 53.29°W	16 (0)	8	2011: June 1, 8, & 10
Upper Gullies 47.49°N, 53.05°W	14 (0)	9	2011: June 21–22
Conception Bay South 47.51°N, 52.93°W	20 (8)	17	2010: February 4, March 31, April 28 2011: June 11, 17, 21
Goulds 47.45°N, 52.74°W	10 (0)	10	2011: July 18, August 1–2
La Manche 47.17°N, 52.92° W	2 (0)	1	2011: July 8
Totals	130	83	33 recording days

^a Number of birds seen: number of adults (number of juveniles); crossbills with brownish heavily streaked plumage were identified as juveniles (Pyle 1997).

^b Number of birds recorded: number of individual adults from which we recorded class I calls.

provision the incubating female and then flying away from the nest to join a foraging flock; during interactions between mates; while foraging or perching in trees; or during pauses between song bouts (Groth 1988, 1993a, Robb 2000, Irwin 2010, Smith et al. 2012, Hynes 2013). In this paper we refer to the “flight call” (“contact call” of Sewall 2008, 2009, Sewall and Hahn 2009, Smith et al. 2012) simply as class I. We also describe call classes II and III (“excitement” and “chitter” calls, respectively, of Groth 1993a) below; they are analyzed in more detail by Hynes (2013).

Study Sites and Subjects

We recorded class I calls from 83 adults across 10 sites in Newfoundland, from February 4, 2010–August 2, 2011 (Table 1). Seven sites were in urban areas: Clarenville and Glovertown in central Newfoundland; and Conception Bay South, Goulds, South River, Upper Gullies, and Whitbourne on the Avalon Peninsula in eastern Newfoundland. Many recordings at these sites were made near bird feeders on private property or in nearby forest. Forest habitat was mainly mature boreal forest; black spruce (*Picea mariana*) and balsam fir (*Abies balsamea*) were the dominant conifers. White spruce (*Picea glauca*) and American larch (*Larix laricina*) were also common, and crossbills were observed feeding in both of these species. In Clarenville, Glovertown, and Whitbourne, cultivated pine (*Pinus* spp.) was present and crossbills also foraged there. The three remaining sites were in or near wilderness areas: La Manche (Avalon Peninsula; dominated by black spruce and balsam fir), West Brook Ecological Reserve, and Howley. At the latter two sites, we recorded crossbills in forests dominated by red pine (*Pinus resinosa*).

We recorded calls with a Fostex FR-LE2 field recorder, a Telinga Pro Series microphone and a 570 mm Telinga

parabola. Vocalizations were sampled at 44.1 Hz and digitized at 16 bits. To augment our Newfoundland sample and extend geographic and species coverage, we obtained >25 hr of archived recordings from other sources: Avian Vocalizations Center, Michigan State University (<http://avocet.zoology.msu.edu/>); Bergmann et al. (2008); Borror Laboratory of Bioacoustics, Ohio State University; Constantine and The Sound Approach (2006); Macaulay Library, Cornell University; Museum of Vertebrate Zoology, University of California, Berkeley; Robb (2000); and xeno-canto (<http://www.xeno-canto.org/>).

We classified call classes from our Newfoundland sample jointly on the basis of context (e.g., whether the bird was in flight or foraging), audile qualities (e.g., soft versus loud) and appearance as spectrograms, as is usual in descriptive studies. For archived recordings, vocal types and call classes were identified and labeled based on published records (e.g., Groth 1993a) or corresponding track metadata. To verify the classifications of vocal types, we also compared class I calls across Newfoundland, mainland North America, and Europe with discriminant analysis (see below). We selected and measured a subset of 245 class I calls from 31 individuals from the archived recordings made outside Newfoundland. Our original Newfoundland field recordings comprised 890 calls from 83 individual birds. Recordings will be deposited in the Macaulay Library, Cornell University.

Acoustic Analyses

We analyzed samples with Praat version 5.3.04 software (Boersma and Weenink 2011). We measured acoustic variables directly from fundamental frequencies using Praat’s autocorrelation algorithm. This technique improves measurement accuracy by obviating the need to measure

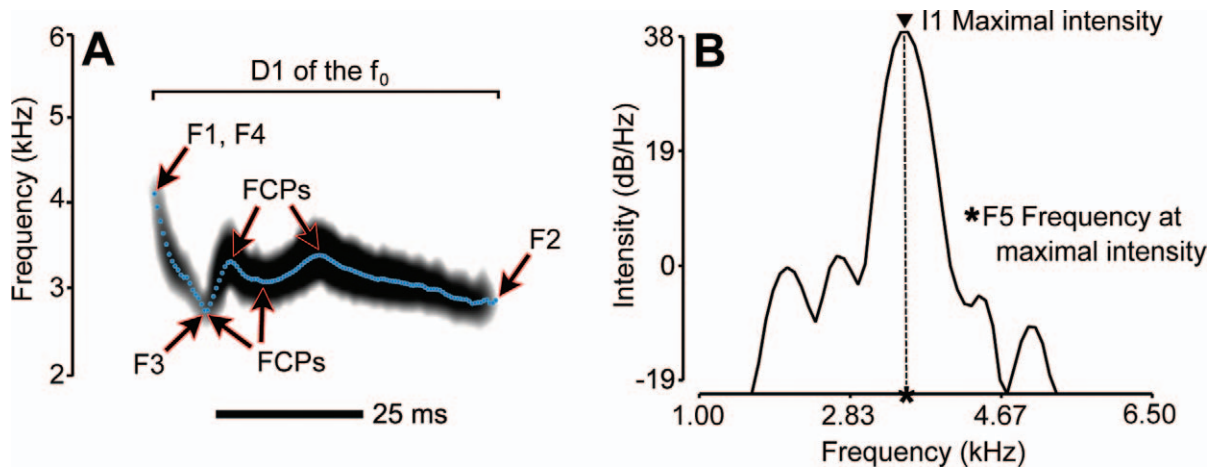


Figure 1. Examples of acoustic variables used in the study for Red Crossbill call classes I–III. **(A)** The fundamental frequency (f_0) of a class I call is shown. Variables were taken from frequency contours (in blue) that were computed with Praat 5.3.04 (Boersma and Weenink 2011). The time interval between successive samples (shown as blue points) along the contour was set at 0.0005 s. Frequency change points (FCPs) were quantified by counting the number of directional frequency changes along the call’s frequency contour (see Methods). The variable *Mean frequency* was computed as the sum of frequency points divided by the total number of sample points. **(B)** Graphical illustration of how *Maximal intensity* (I1) and *Frequency at maximal intensity* (F5) were measured via spectral slice analysis in Praat. F1: *Frequency at start*; F2: *Frequency at end*; F3: *Minimal frequency*; F4: *Maximal frequency*; F6: *Mean frequency*; D1: *Duration*; and I2: *Intensity at maximal frequency*.

variables manually on spectrograms, which vary due to signal amplitude and analysis settings (Zollinger et al. 2012). We measured fundamental frequency (f_0 ; this was the dominant frequency component of class I–III calls) with pitch tracking and measurement tools in Praat’s SoundEditor window (Figure 1). We measured 9 variables on each call: *Frequency at start*, *Frequency at end*, *Minimal frequency*, *Maximal frequency*, *Frequency at maximal intensity*, *Mean frequency*, *Duration*, *Maximal intensity*, and *Intensity at maximal frequency*.

We extracted time-normalized frequency contours to further explore call variation. Time normalization was performed by sampling the extracted contours for a fixed number (64) of frequency points at equal time intervals within each call (McCowan 1995). To quantify frequency modulation (FM), we counted the number of directional frequency changes >50 Hz in magnitude (frequency change points, FCPs) along the frequency contour (Figure 1A).

To determine temporal patterning of calls from Newfoundland birds, we manually measured 556 inter-call intervals on spectrograms from 36 individuals.

Statistical Analyses

To test for microgeographic trends in class I calls, we used nested random-effects models to estimate variance components attributable to variation among Newfoundland recording sites ($n = 10$), individuals ($n = 83$), and calls of individuals ($n = 890$). Individuals were not banded in this study but crossbills at all sites appeared to consist of single cohesive groups; individual and site were assumed to be nested random effects. Variance components were esti-

mated with the “varcomp” function from a fitted “lme” object using the packages “ape” (Paradis et al. 2004) and “nlme” (Pinheiro et al. 2011) in R (version 2.14.0; R Development Core Team 2011). Variables were not independent so we used scores from principal components analysis (PCA; package MASS; Venables and Ripley 2002) as dependent variables. Principal components (PCs) with eigenvalues >1 (Kaiser-Guttman criterion; Jackson 1991) were used in the nested random effects models and provided new uncorrelated variables that contained most of the variation in the original dataset.

We compared class I calls across Newfoundland, mainland North America, and Europe with discriminant analysis (DA; package MASS). PCs from a PCA on calls were used as synthetic uncorrelated variables for the DA (Jombart et al. 2010), using the selection criteria described above. Individual means of call variables were used to test whether individuals could be correctly classified to vocal type. A leave-one-out cross-validation (LOOCV, within DA) technique was used for constructing and validating the classification model. LOOCV is an iterative process that creates jackknifed estimates, where a sample of $n-1$ attempts to predict the class of the remaining sample.

RESULTS

Class I Calls

Structure of class I calls. The basic structure of class I calls from Newfoundland (Figure 2A) was similar to that of calls in Europe and elsewhere in North America (Figure 2B, 2C). Newfoundland calls were brief (~ 50 ms) tones

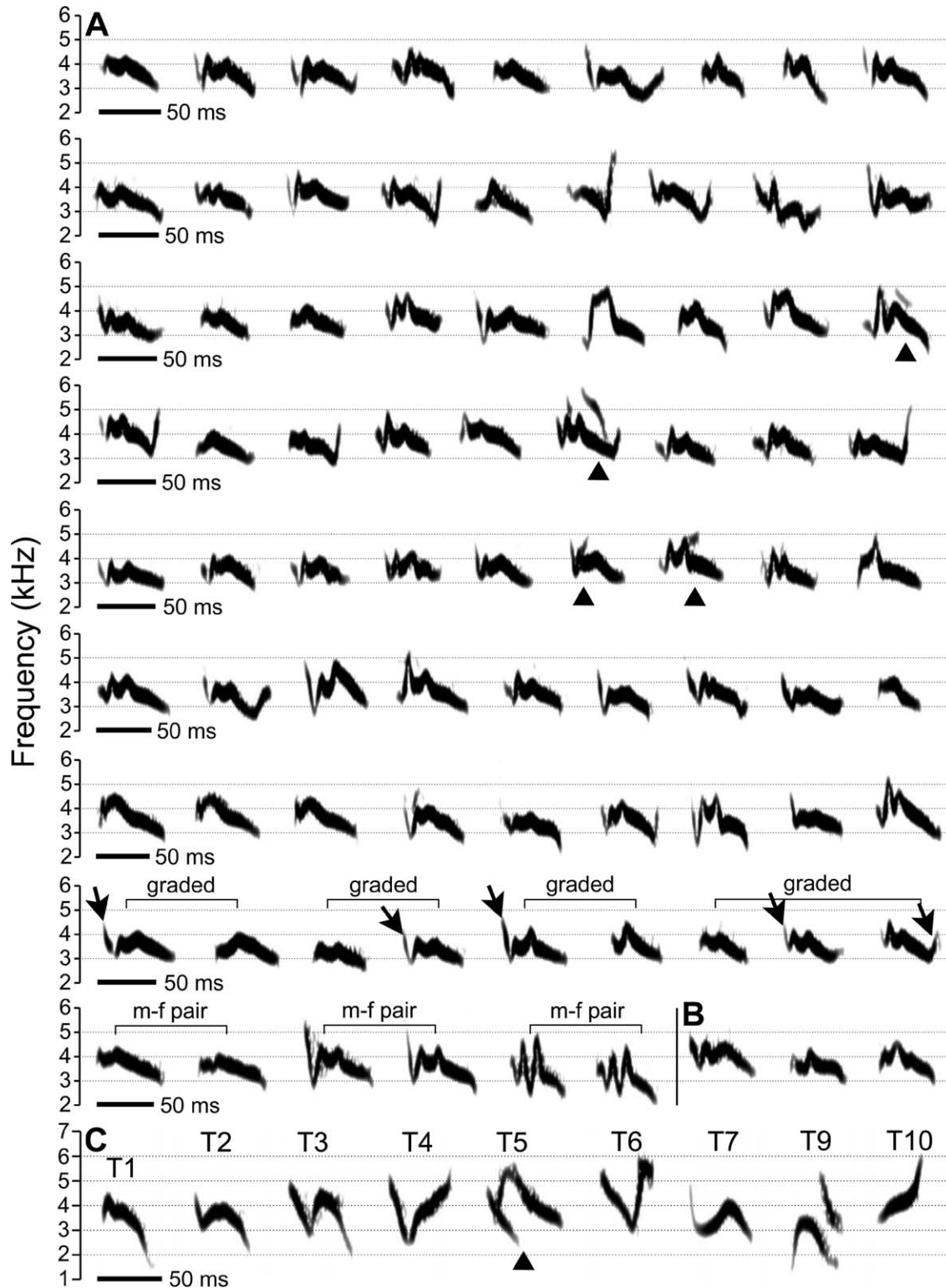


Figure 2. (A) Class I calls of 78 individual adult Red Crossbills (one spectrogram per individual; fundamental frequencies are shown; harmonics, where present, are not displayed because they were at frequencies >6 kHz) recorded in Newfoundland February 4, 2010–August 2, 2011, have a common structural plan but vary considerably in frequency modulation. The sample is similar to some European samples (B; 3 individuals shown) but was acoustically distinct from 9 other North American vocal types (C: T1–T7, T9 and T10). Spectrograms in (A) may represent calls of *L. c. percna*. Examples of three presumed male–female (“m–f”) pairs are labeled; some examples differ across individuals at the beginning or end of the call and may represent grading (marked with arrows). Triangles mark examples of non-linear phenomena.

TABLE 2. Descriptive statistics (grand mean \pm SD, range in parentheses) for variables measured on 1,135 Red Crossbill calls recorded in Newfoundland, February 4, 2010–August 2, 2011. The calls may represent *L. c. percna*.

Acoustic variable	Call class (no. of individuals, no. of calls):		
	I (78, 839)	II (12, 122)	III (30, 174)
Frequency variables (Hz):			
Frequency at start	3,927 \pm 484 (2,988–5,159)	2,407 \pm 260 (1,696–2,687)	3,458 \pm 420 (2,665–4,388)
Frequency at end	3,127 \pm 534 (2,063–5,220)	2,306 \pm 104 (2,180–2,465)	4,088 \pm 797 (2,740–5,838)
Minimal frequency	2,901 \pm 239 (2,063–3,493)	1,878 \pm 227 (1,435–2,156)	3,227 \pm 336 (2,665–4,177)
Maximal frequency	4,292 \pm 367 (3,540–5,220)	2,572 \pm 171 (2,271–2,907)	4,590 \pm 517 (3,661–5,844)
Frequency at maximal intensity	3,624 \pm 180 (2,955–4,138)	2,375 \pm 129 (2,094–2,554)	4,020 \pm 486 (3,366–5,425)
Mean frequency	3,526 \pm 179 (2,885–4,058)	2,303 \pm 112 (2,054–2,452)	3,903 \pm 405 (3,391–5,202)
Temporal variable (ms):			
Duration	50 \pm 6 (34–63)	48 \pm 4 (43–53)	27 \pm 6 (15–41)
Intensity variables (dB/Hz):			
Maximal intensity	75 \pm 5 (58–86)	71 \pm 7 (59–80)	68 \pm 6 (52–77)
Intensity at maximal frequency	59 \pm 9 (36–78)	60 \pm 7 (48–70)	61 \pm 9 (42–76)

with a dominant frequency of \sim 2–5 kHz (Table 2); were typically uttered in series (median inter-call interval \sim 164 msec); often had 3–4 harmonics (Figure 3A); and sometimes exhibited biphonation (Tyson et al. 2007; Figures 2A and 3A). Amplitude commonly peaked \sim midway through the call (Figure 3A) but varied across calls, presumably in part because of orientation of the calling bird to the microphone. Class I calls varied little within individuals and only one bird showed substantial variation (Figure 3B). At least three adult male–female pairs produced pair-specific calls (i.e. call matching [Mundinger 1970]; Figure 2A).

The presence of marked FCPs in class I calls set most Newfoundland birds apart from mainland North American and European samples. Of 890 Newfoundland calls, 556 (62%) had 4–5 FCPs, which appeared M-shaped as spectrograms (Figure 3C; Young et al. 2012). Calls with fewer or more FCPs often showed graded variation, e.g., parts at the beginning or end of calls were added or omitted (Figure 2A); a few of these individuals probably represented other vocal types (see below).

PCA on class I calls. A PCA on the individual means of Newfoundland birds identified the first 3 PCs with eigenvalues >1 , accounting for 73% of the variance (Table 3). Salient variables (i.e. those with loadings >0.40 ; Guadagnoli and Velicer 1988) for the first PC were *Maximal frequency*, *Frequency at maximal intensity*, and *Mean frequency*; salient variables for the second PC were *Frequency at start* and *Duration*.

Variance components. Most of the variance (52–71%) in nested random-effects models on the 3 PCs was explained by variation among individuals (Table 4). Variation among calls accounted for the second-largest amount (23–29%) and variation among sites explained the least (6–19%).

Evidence for other vocal types on the island of Newfoundland. We identified 5 Newfoundland birds

whose calls resembled those of vocal types 2, 4, and 10 from mainland North America (Figure 4; Irwin 2010, Young 2010, Groth 1993a). Hence, 78 of 83 individuals (94%) in our Newfoundland sample may represent *L. c. percna*. For the pooled sample from all locations, DA based on individual means of acoustic variables correctly classified 89% of individuals to vocal type (Figure 5). Most (98%) Newfoundland birds were correctly classified but 5 of 6 European individuals were classified as Newfoundland birds. Vocal types from mainland North America were discriminated well by DA: 86% of individuals were classified correctly.

Other Call Classes

Class II calls. We recorded these calls at 9 of 10 recording sites (Figure 6A). These calls seemed to be elicited by the sudden appearance of different hetero-specific animals including Osprey (*Pandion haliaetus*), Blue Jay (*Cyanocitta cristata*), American Crow (*Corvus brachyrhynchos*), European Starling (*Sturnus vulgaris*), and dog (*Canis familiaris*). In one case, Red Crossbills appeared to use the call as a mobbing signal (Robb 2000), apparently in response to a low-flying Herring Gull (*Larus argentatus*). Calls of this class also were also given by one male just before and following an attempt to copulate with a female; were only recorded from perched birds, sometimes by individuals near bird feeders; and were sometimes inserted into song. Class II calls were stereotyped and varied little across individuals or contexts of use. The calls were relatively low in frequency (Table 2) and showed a distinctive frequency pattern: calls began with an accelerating decline in frequency to a minimum, followed by a decelerating rise in frequency to the end of the call; harmonic stacking typically was present at the frequency minimum (Figure 6A). The median inter-call interval was \sim 179 ms. Newfoundland calls differed greatly from mainland North American samples (Figure 6B) and

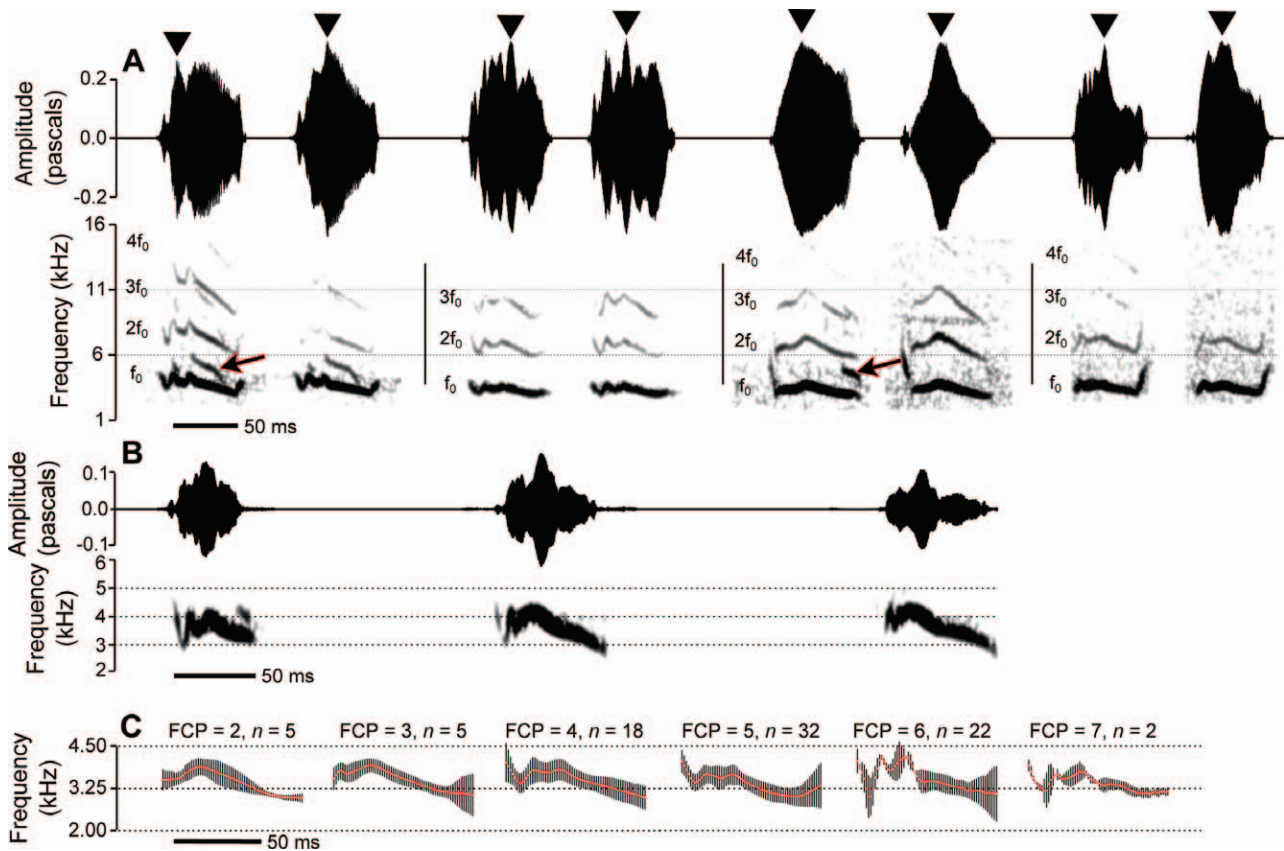


Figure 3. (A) Waveforms and spectrograms of class I calls from four individual Red Crossbills recorded in Newfoundland (from left to right: Goulds, August 2, 2011; West Brook Ecological Reserve, June 30, 2011; South River, June 1, 2011; Howley, May 2, 2011). Triangles (waveforms) and arrows (spectrograms) mark intensity peaks and biphonations, respectively; vertical bars separate individuals. (B) One bird recorded in Clarendville (June 27, 2011) expressed call variation across successive calls (natural call sequence is shown; harmonics are not displayed because they were >6 kHz in frequency). (C) Frequency contours were similar across birds (recorded in Newfoundland, February 4, 2010–August 2, 2011) with the same number of frequency-change points (FCPs) within class I calls. Time-normalized frequency contours for FCP classes are based on grand means of individual birds (*n* adults is indicated). Red lines connect mean FCP values; black vertical bars represent ± 1 SD.

TABLE 3. Results of principal components (PCs) analysis based on individual means (*n* = 83) of class I call variables for Red Crossbills recorded in Newfoundland, mainland North America, and Europe.

Acoustic variable	Variable loadings (explained variance, eigenvalue):		
	PC 1 (36%, 1.8)	PC 2 (20%, 1.3)	PC 3 (17%, 1.3)
Mean frequency	-0.49	0.03	0.24
Maximal frequency	-0.46	0.26	-0.01
Frequency at maximal intensity	-0.43	0.06	0.15
Frequency at end	-0.39	-0.36	0.08
Intensity at maximal frequency	-0.27	-0.13	0.60
Frequency at start	-0.23	0.57	-0.08
Minimal frequency	0.23	-0.37	0.36
Maximal intensity	0.15	0.29	0.62
Duration	0.12	0.49	0.19

resembled calls of the Scottish Crossbill (*L. scotica*; Figure 6C) in the pattern of accelerating/decelerating frequency changes (Figure 6C; patterns of harmonic richness differed however). Calls of this class are widely referred to as “excitement” or “alarm” calls (e.g., Groth 1993a, Robb 2000, Summers et al. 2002, Benkman et al. 2009, Irwin 2010; “toop” of Nethersole-Thompson 1975).

Class III calls. These calls were recorded from at least 30 individuals across 9 recording sites. Some individuals gave these calls in rapid series while pivoting or lifting into flight. They often were accompanied by “soft whirring of wings” (Robb 2000:65) as birds fed and moved within conifers or repositioned themselves at bird feeders; they were never given by birds in full flight. Class III calls had weak or no harmonics and most had simple patterns of FM, such as rises and falls in frequency with one to several FCPs (Figure 7), and they were generally briefer and softer than calls of classes I and II (Table 2). Class III calls were

TABLE 4. Individual differences accounted for most variation (52–71%) in class I calls of Red Crossbills recorded in Newfoundland, February 4, 2010–August 2, 2011. Variance components attributable to recording sites, individuals, and within individuals are shown using the first 3 PCs (Table 3). Variance components were estimated using nested random effects models (calls within adults within recording site; see text).

	Estimated variance component	95% confidence interval	Percent of total variance
PC1			
Site	0.46	0.15–1.44	7
Individuals within recording sites	1.47	1.24–1.74	70
Error	0.84	0.81–0.88	23
PC2			
Site	0.60	0.29–1.25	19
Individuals within recording sites	0.99	0.82–1.19	52
Error	0.75	0.71–0.78	29
PC3			
Site	0.30	0.09–0.97	6
Individuals within recording sites	1.02	0.86–1.21	71
Error	0.59	0.56–0.61	23

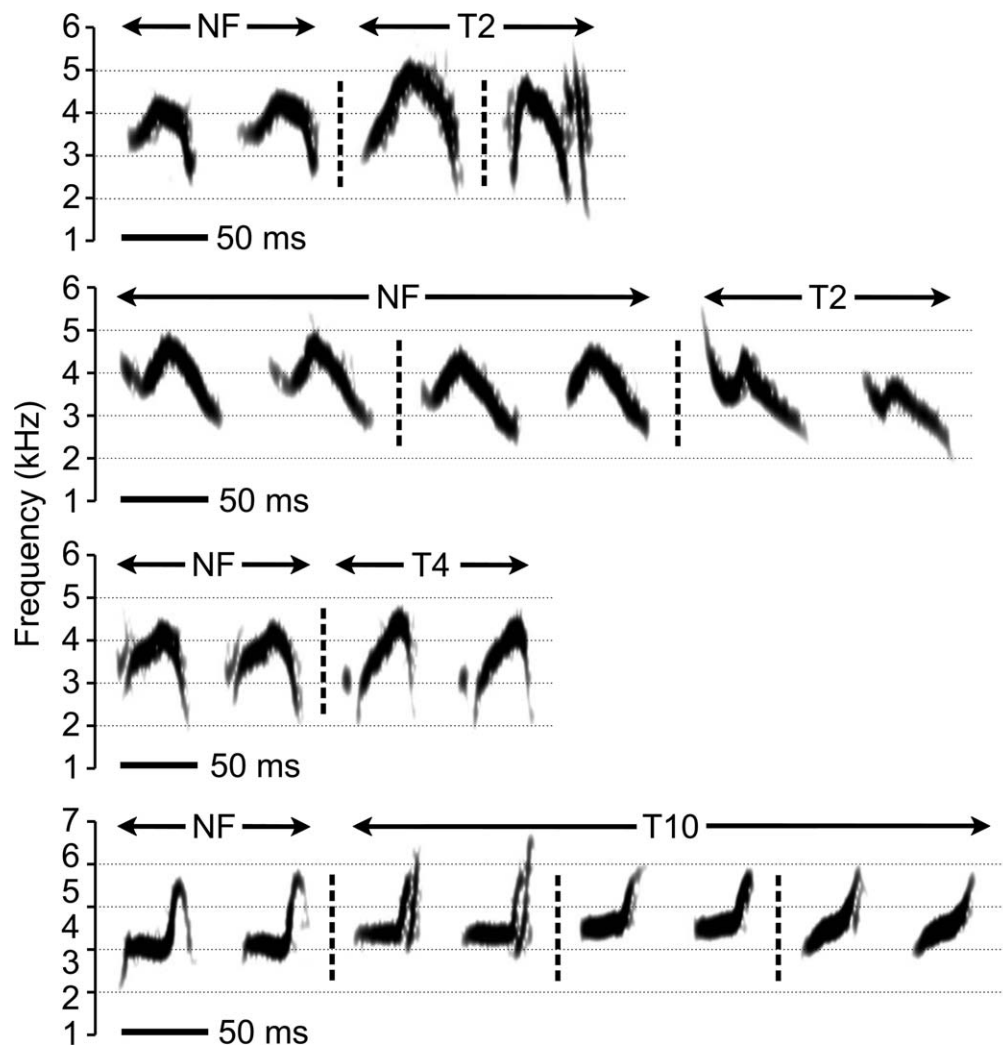


Figure 4. Multiple kinds of class I calls of Red Crossbill occur in Newfoundland (NF = Newfoundland samples) suggesting the presence of several Red Crossbill vocal types on the island. Examples of similar calls from other individuals from mainland North American localities are included for comparison: vocal type 2 (T2), top two panels; vocal type 4 (T4), third panel from the top; vocal type 10 (T10), bottom panel (for variation in vocal types see Groth 1993a). Broken vertical bars separate calls from different individuals. Fundamental frequencies are shown; harmonics are not displayed because they were >6 kHz in frequency.

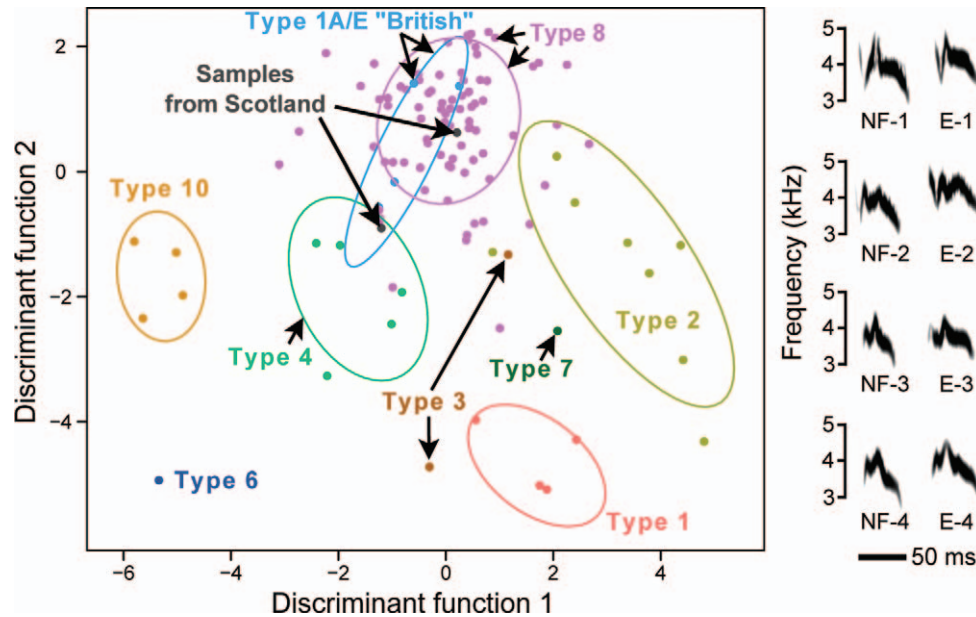


Figure 5. Class I calls of Red Crossbills recorded in Newfoundland differ acoustically from calls recorded elsewhere in North America. This scatterplot shows the first 2 functions of a discriminant analysis on individual means of acoustic variables taken from class I calls from Newfoundland, mainland North America, and Europe. Vocal types are shown in different colors; dots represent individual birds; ellipses represent 95% confidence intervals for vocal types. Spectrograms show some similarities between calls from Newfoundland and Europe (right side; individuals NF-1 to NF-4 and E-1 to E-4, respectively). Fundamental frequencies are shown; harmonics are not displayed because they were >5 kHz in frequency.

uttered singly or in series of up to 6; the median inter-call interval was ~ 154 ms. Most workers refer to these as “chitter” calls (e.g., Groth 1993a, Robb 2000, Irwin 2010).

DISCUSSION

We determined that a distinct kind of call is the most common form of class I call (“flight call”) of Red Crossbills on the island of Newfoundland. These calls signify the presence of a vocal type that is different from those in mainland North America and may represent the morphologically recognized subspecies *L. c. percna*.

Class I and II calls of Red Crossbills have been used as markers for different vocal types (or even different species; Groth 1993a, Robb 2000, Summers et al. 2002, Förschler and Kalko 2009, Irwin 2010). Class I and II calls in our Newfoundland sample of Red Crossbill differ from other described vocal types in having a marked quasi-rhythmic FM (quantified by the number of FCPs) and a distinct declining–rising pattern of FM, respectively. Further, quantitative features of the class I and II samples from Newfoundland birds differ little across contexts (Hynes 2013). Therefore we suggest that most Newfoundland birds represent a different vocal type than occurs elsewhere in North America. Following Groth (1993a), vocal type 8 may be the appropriate name to apply, but his 1981 sample from Newfoundland may represent a class II

call. If the calls do not represent *L. c. percna*, they must represent a previously undescribed Atlantic Canadian vocal type of Red Crossbill, although recent body measurements of Newfoundland birds fall within the known range for *L. c. percna* (Young et al. 2012). Several birds also uttered song motifs that differ from those of Red Crossbills in mainland North America (Hynes 2013).

Our sample of Newfoundland Red Crossbill vocalizations may represent only a part of a widely distributed vocal type of Red Crossbill in Canada’s Atlantic provinces (e.g., Cape Breton Island), and hence *L. c. percna* (assuming that this taxon represents a biological entity) may not be endemic to the island of Newfoundland. To explore this possibility, further sound recordings are needed from western and southwestern Newfoundland, eastern Canada, and the Maritime Provinces, and should be coupled with assessment of morphological characters.

Our Newfoundland sample included some individuals whose class I calls resembled known mainland vocal types (Figure 4), suggesting that other North American vocal types occur on the island. A few other calls from the Newfoundland sample also appeared similar to vocal type 2 (see the first 3 individuals of the seventh row in Figure 2A), but uttered class II calls that were acoustically similar to other Newfoundland samples. Class II calls may be more sensitive indicators of differentiation than class I

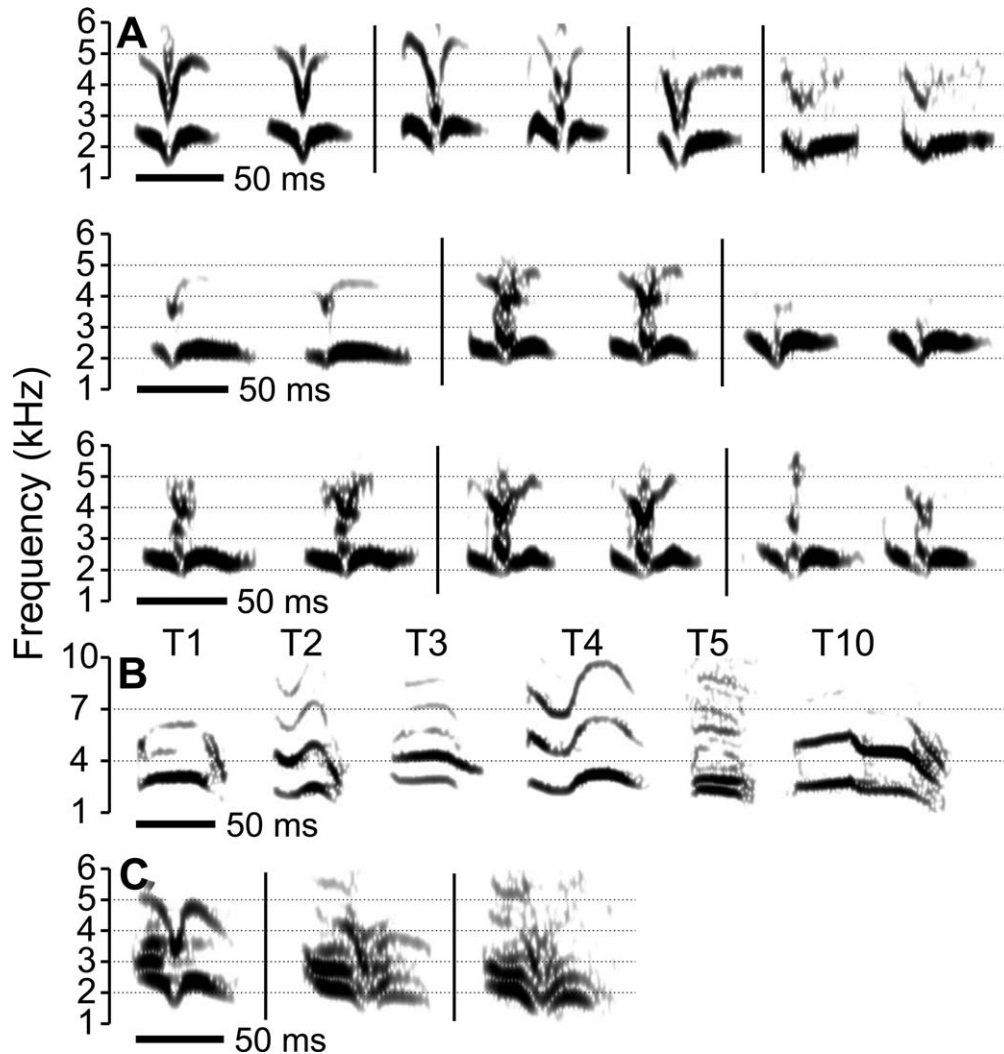


Figure 6. (A) Class II calls of 10 adult Red Crossbills recorded in Newfoundland, May 23, 2010–August 1, 2011 (spectrograms from different individuals are separated by vertical bars). These individuals resembled some European samples (C; 3 individuals depicted) but were acoustically distinct from other North American vocal types (B; T1–T5, T10). Like class I calls depicted in Figure 2A, we suggest that class II calls in (A) suggest the presence of *L. c. percna* in Newfoundland.

calls (Summers et al. 2002), and deserve attention in future studies.

Crossbills appear to exhibit assortative flocking with shared vocalizations (Smith et al. 2012). Therefore, variation among flocks (approximated by recording sites) should exceed among-individual variation if our Newfoundland samples contain more than one vocal type. Our analyses disclosed only minor variation among recording sites and most variation among individuals, suggesting that one vocal type dominated Newfoundland samples. Vocalizations of some Newfoundland birds were extremely similar even over hundreds of kilometers. Many class I calls that we recorded are similar to those that have been recorded from Newfoundland Red Crossbills dating back to 2005 (this study; Young et al. 2012).

Calls from European and Newfoundland birds generally differ from one another (e.g., vocal types A–D, E, and X as described by Constantine and The Sound Approach 2006), although some class I and II calls of Common Crossbills (from mainland Europe) and crossbills from Scotland resemble some Newfoundland samples (Figures 2 and 6). Other acoustic similarities occur between Old World and New World crossbills (e.g., North American vocal type 1 and Parrot Crossbill, *Loxia pytyopsittacus*). The systematic significance of such similarities cannot be appraised in isolation from genetic information, in our opinion. Genetic analysis suggests that Newfoundland Red Crossbills differ from European but not from other North American birds (based on analysis of part of the mtDNA control region from study skin samples; E. A. Perry, personal communi-

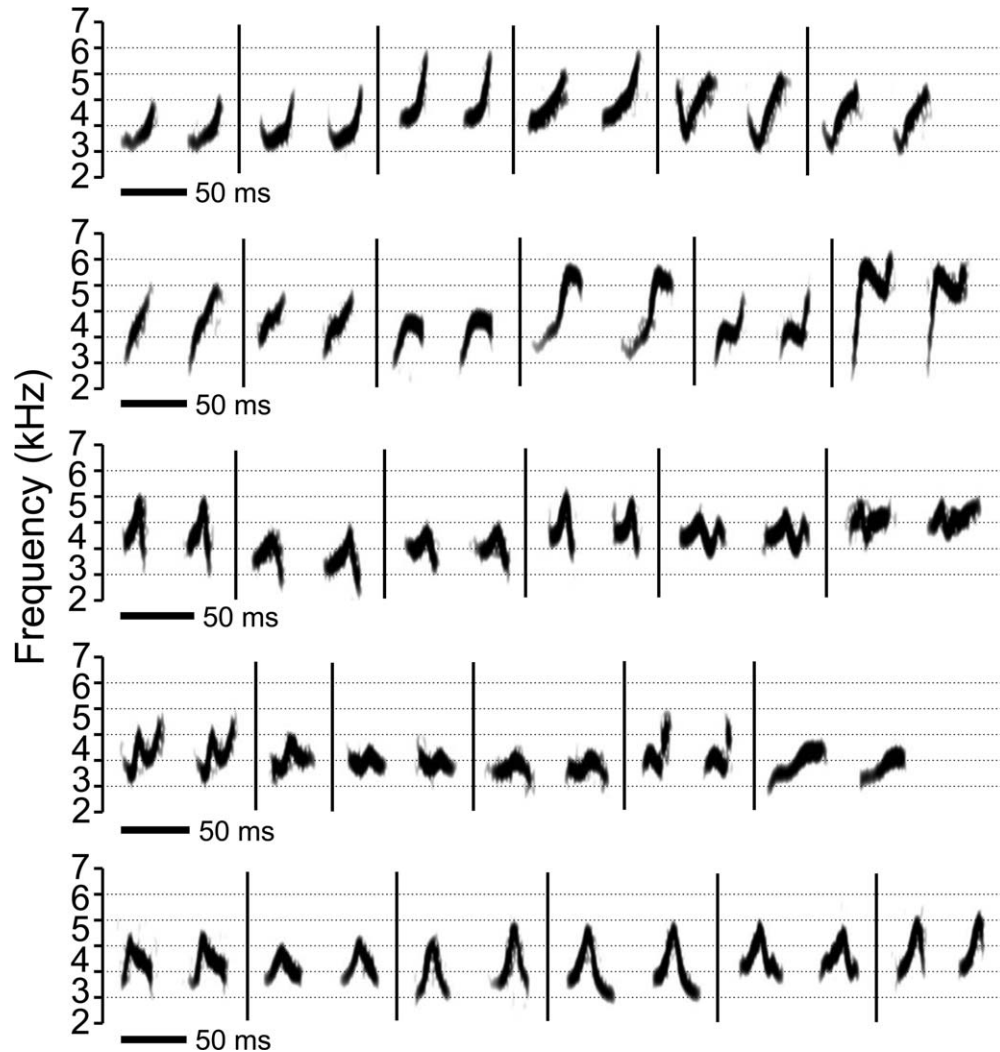


Figure 7. Examples of class III calls from 30 adult Red Crossbills recorded in Newfoundland, May 24, 2010–August 1, 2011 (spectrograms from different individuals separated by vertical bars). Fundamental frequencies are shown; harmonics are not displayed because they were >7 kHz in frequency.

cation). These findings are consistent with limited genetic differentiation among North American vocal types (Parchman et al. 2006) and monophyly within the Old World and New World groups (Questiau et al. 1999), and suggests that vocal similarities between Newfoundland and European Red Crossbills are not of systematic significance. The similarities may represent convergence as a byproduct of morphological adaptation (e.g., bill size) or as an adaptive response to similar habitat acoustics (Slabbekoorn and Smith 2002).

Class III calls have not been well studied in the Red Crossbill; Irwin (2010) suggested that they might be useful in systematics. Class III calls in our Newfoundland recordings varied greatly, which suggests they may not be useful in systematic studies in all cases. Such high variation may represent grading, which is common in

short-range signaling (Green and Marler 1979, Bradbury and Vehrencamp 2011). Further studies would be informative about the communicative significance and systematic value of this call class in the Red Crossbill.

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