RED CROSSBILL (Loxia curvisrotra) CALL-TYPES OF NEW YORK: THEIR TAXONOMY, FLIGHT CALL VOCALIZATIONS, AND ECOLOGY

Matthew A. Young

Cornell Lab of Ornithology 159 Sapsucker Woods Road, Ithaca, NY 13820 may6@cornell.edu

Red Crossbill (Loxia curvirostra) populations around the world vary greatly in traits ranging from overall size and bill morphology to flight call vocalizations. Their taxonomy has a confused history, but it is now known that differences in flight call vocalizations are critical to differentiating as many as 25 distinct groups known as call-types (Groth 1993, Benkman 1999, Irwin 2010a), and that many of these may represent incipient species (Parchmen et al. 2006). These call-types correspond with small differences in bill depth morphology, which correlate with differing ecological specializations (Benkman 1993, Benkman 1999, Irwin 2010a). For example, the average bill depth for large-billed call-type 2, which is most efficient feeding on ponderosa pine (Pinus ponderosa) (Benkman 1993), is 9.67mm (Groth 1993a), whereas the small-billed call-type 3, which is most efficient feeding on Western Hemlock (Tsuga heterophylla) (Benkman 1993), is 8.19mm (Groth 1993a). Bill depth is thought to be most heritable, since it's resistant to wear, unlike bill length (Benkman 1993). Most call-types have a key conifer or conifers (Benkman 1993) on which they feed most efficiently, and these key conifers exist in a core zone of occurrence (Dickermen 1987, Knox 1992, Kelsey 2008, Young 2010), which is an area where the corresponding call-type is most abundant. Often when key conifers fail in this core zone of occurrence, crossbills will switch to alternate conifers that provide the highest energy yields (Benkman 1987). This is why call-types can be seen foraging on several different species of conifers.

Bill depth differences aside, it's still nearly impossible to identify crossbills definitively in the field based on morphology, and therefore it's essential to record crossbill flight calls for analysis. Extremely large or small specimens of a given call-type can overlap morphologically with several other call-types (Groth 1993a). As many as ten call-types of Red Crossbill can be found across North America (Groth 1993a, Benkman 1999, Ken Irwin 2010a), and as already stated, each may represent a different species, or more likely, an incipient species (Parchman et al. 2006). Types 2, 3, 4, 5, 6, 7, 9, and 10 find their home, or core zone of occurrence, in regions of the West where call-types appear to be adaptively radiating (Benkman 1993, Benkman 1999, Irwin 2010a). The most widespread call-types in North America are Types 1, 2, 3, 4 (Groth 1993a), and 10 (Irwin 2010a), with Type 1 most common in the East (Young 2010, Blankenship et al. 2010). Records of a quasi-resident Appalachian Red Crossbill call-type date back to before Griscom (1937), and Groth's studies in the 1980s

revealed Type 1 to be common in North Carolina and Virginia (Groth 1988, 1993a).

Evidence presented by Sewall (2010) supports the idea that Red Crossbill flight calls are an example of reliable signaling because identification of appropriate companions and mates is essential to species integrity through prezygotic isolation. Sewall (2009) has also presented evidence that adults show limited vocal learning, likely facilitating distinctive flight calls in Red Crossbill types. It can certainly be challenging to differentiate flight calls of the various Red Crossbill call-types and some on-line sites offer help (Groth 1993b, Young 2008b, Irwin 2010b). Flight calls are the sound typically described as "jip-jip" or "whit-whit". To be able to find and identify crossbills, it's essential to develop a familiarity with these flight calls, which occasionally are also given by perched birds. Birds that are singing can give flight-like calls, but it is highly recommended that birds singing not be identified to call-type until more work is done on crossbill song vocalizations.

Knowing when and where to look for crossbills is very important. Birds flying overhead are often the most vocal, and believe it or not, birds feeding atop a conifer just 15 meters away can be very quiet and easily missed. When feeding, the sound most often heard is the very subtle crackling of the birds extracting the seed from the seedcoat. Sometimes this is the only sound they make as the seedcoats drop to the ground. With much practice, however, many of the call-types (hereafter Type or Types) can be identified in the field. Nearly all flight call recordings can be identified with certainty via audiospectrographic analysis (once in a while you need to let one go as unidentified). The audiospectrographic analysis gives a computer printout of the bird's voice. To analyze them I used Raven Pro 1.3 (Charif et al. 2008). In this paper I will discuss New York State's Red Crossbills, focusing on their flight call vocalizations and also their ecology and taxonomy.

TAXONOMY

In previous work on New York State taxonomy of Red Crossbills, four geographical subspecies were identified as occurring within the state (Bull 1974, p. 566):

L. curvirostra minor – from south-central Canada to north-central US.

L. c. pusilla – Newfoundland, winters in northeast US.

L. c. sitkensis – Alaska to northwest California, winters to northeast US.

L. c. benti – southern Montana to southwest US.

As noted above, contemporary crossbill researchers prefer to describe Red Crossbill taxa in terms of call-types. By definition, crossbill call-types don't correspond neatly with geographical subspecies, because several crossbill call-types can at least occasionally nest sympatrically. The distribution and ranges listed below for each call-type are defined from the analysis of several hundreds

of crossbill recordings obtained via The Macaulay Library of Sounds at The Cornell Lab of Ornithology, Florida Museum of Natural History, The Museum of Vertebrate Zoology at Berkeley (aka Jeff Groth's collection), Borror Laboratory of Bioacoustics, xeno-canto, and several other crossbill enthusiasts across the country. For distribution, I also referenced Ken Irwin (2010a) and Evans and O'Brien (2002). Based on the work of flight calls (Groth 1993a, Benkman 1999, Irwin 2010a), I have identified these forms from smallest to largest occurring in New York State (NYS).

Type 3—Smallest-billed Form

First Type Specimen: Craig W. Benkman, 25 miles south of Albany, New York, 4 February, 1985 (Groth 1993a).

History, Distribution and Status: Its core zone of occurrence is estimated to be from Pacific Northwest to Alaska; it also occasionally wanders across the southern boreal zone to the northeastern United States, sometimes even occurring here in numbers. Type 3 rarely occurs in Intermountain West to Arizona. Based on the analysis of recordings, it has invaded NYS in 1984-85, 1994-95, 1997-98, 2006-07, 2008-09 and other years dating back to 1887-88. This Type corresponds most closely to L. c. minor, but the latter also includes other specimens of similar morphology such as Type 10. Type 3 breeds rarely to occasionally in NYS, mostly across the northern part of the state. During major irruptions, Type 3 can be common in the Adirondacks and locally common south of the Adirondacks. It appears to be rare on the coast of New York.

Flight Call Vocalization: The flight call of the Type 3 is weaker and squeakier sounding than the other call-types. The spectrogram (see Figure 1) looks a bit like a lightning bolt with its zig-zag appearance—it starts out with a downward component, followed by a short upward component connected to a second downward component. Occasionally, there can be tails at both the beginning (less common) and end of the typical zig-zag appearance. During the second downward-modulated component, the call can level out just slightly as it continues downward. Type 3 can sound a bit like a weaker version of a Type 1 or 2, but Type 1 is sharper and louder and Type 2 is huskier and more powerful. The spectrograms of Type 3, however, cannot be confused with any other call-type unless too small of a scale is used. If too small a scale is used, Type 3 can look a little like Type 5 or even a kinked Type 2—this is a prime example of why a large enough scale is essential and why I suggest a scale similar to what Groth used. Type 3 can sound a bit similar to Type 5, but Type 5 often gives a twangy sound instead of a squeaky sound.

Ecology: This call-type uses hemlock (*Tsuga sp.*) more readily than any of the other call-types found in North America and is most common in Pacific Northwest coastal hemlock forests. This is where it finds its core range and is

most regularly abundant. Type 3, and less so Type 10, are the most highly irruptive call-types in the Northeast during most invasions. When it irrupts eastward, it often irrupts with Type 10. Unlike Type 10 though, all birds seem to depart the area once cone crops start developing out west. Type 3 regularly uses Eastern Hemlock (*Tsuga candensis*) but also uses various spruces (*Picea sp.*) readily when irrupting into the Northeast. Because of its small bill, it uses pines much less so than the other types. Despite this, I have seen it feeding on Eastern White Pine (*Pinus strobus*) at least a few times and Red Pine (*Pinus resinosa*) at least once.

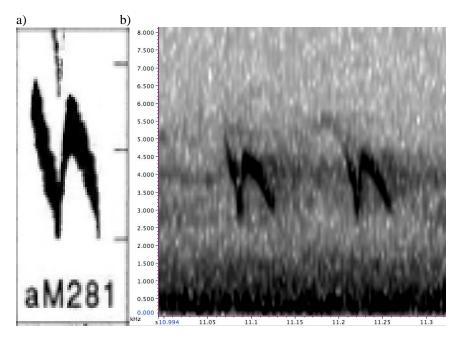


Figure 1. Spectrograms of Type 3 Red Crossbill flight calls. a) Spectrogram of Type 3 used and adapted with approval from Groth 1993a. b) Type 3 recorded Matthew A. Young, Summerhill, New York, 4 April 2009 (Macaulay Library of Sounds #161296). The dark lines on the sides of the Groth's spectrographs are for kHz lines 3, 5, 7.

Type 10—Medium-billed

First Type Specimen: Gregory F. Budney and Matthew A. Young, Dryden, New York, 17 May 1998 (Macaulay Library of Sounds # 130478). Craig W. Benkman recorded either a Type 4 or 10 Hamilton County, New York 14 February 1985 (Groth 1993a), but Benkman (pers. comm.) could not confirm which call-type was present.

History, Distribution and Status: Type 10 occurs in a core zone of occurrence from northern California to southern British Columbia (BC); it also occasionally occurs across the southern boreal zone in numbers to the Northeast. It has not been reported in the Intermountain West. Appears to be quasi-resident in small widely scattered numbers in the Northeast from the Adirondacks (Matt Young unpublished data) northward to the Maritimes. Occasionally occurs in southern NY and rarely south of NY to Maryland. Can occur along coast south to NY and NJ (Michael O'Brien, pers. comm.), as in the winters of 2001-02 and 2007-08. Appears to be the most common Type at NY coastal locations, but breeding along coast of NY uncertain at this time. Based on the analysis of recordings Type 10 has been documented in the Northeast in nearly 40% of the years dating back to 1959 and also likely occurred in the 1887-88 invasion. L. c. sitkensis is the subspecies to which it could be assigned, but it is hard to be certain, given similarities between L. c. sitkensis and L. c. minor. In recent years it has been recorded in NY 1984-85, 1994-95, 1997-98, 2006-07, 2007-08, 2008-09, and 2011. The 1997-98 invasion involved 1000s of Type 10 and several Type 3. Type 10 breeds occasionally in NYS, but most commonly in the Adirondacks.

Flight Call Vocalization: It wasn't until Ken Irwin recently described Type 10 (Irwin 2010a) that it became widely known. However, the idea that there was a crossbill call-type that gave a flight call similar to Type 4 but lacking in a strong downward component had existed for several years. Irwin has found large flocks of Type 10 regularly in the Sitka Spruce (Picea sitchensis) forests of coastal northern California to central Oregon. The flight call of Type 10 is perhaps one of the easiest call types to recognize. It's a very thin, slightly weak, non-musical whit-whit. The whit-whit sounds much like the "whit" call of an Empidonax flycatcher (e.g., Least or Dusky Flycatcher). The spectrogram (see Figure 2) is dominated by an upward component. There are distinct differences between Type 4 and 10 spectrograms, and the two are best looked at as a gradation with Type 4 containing a downward and upward component and Type 10 usually just giving the upward component. However, Type 10 spectrograms do appear to be more variable than most of the other call-types (Irwin 2010a). The spectrogram for Type 10 can look like a checkmark, uptick, or the letter "u". The Type 10 flight call can sound similar to the White-winged Crossbill weet-weet call.

Ecology: Despite being most efficient at feeding on Sitka Spruce of western coastal forests, Type 10 appears to be one of, if not the most frequently occurring call-types in the Northeast. They seem to ecologically associate with various spruces first and foremost, but will also snack on Eastern White Pine and to a lesser extent Eastern Hemlock in the Northeast. Given that it is most closely associated with Sitka Spruce, it is not surprising this call-type is perhaps the most frequently occurring call-type from the Adirondacks northward to the Maritimes where several species of spruce occur.

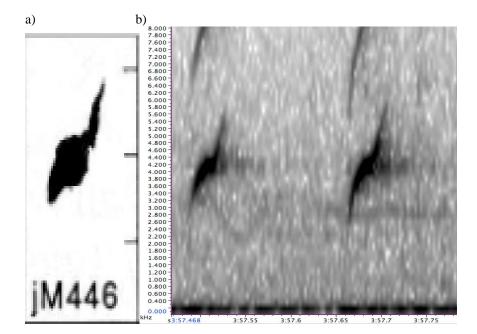


Figure 2. Spectrograms of Type 10 Red Crossbill flight calls. a) Spectrogram of Type 10 used and adapted with approval from Groth 1993a. b) Type specimen of Type 10 recorded Gregory F. Budney and Matthew A. Young, Dryden, New York, 17 May 1998 (Macaulay Library of Sounds #130478).

Type 1—Medium-billed

First Type Specimen: Gregory F. Budney and Matthew A. Young, Georgetown, New York, 5 August 2006 (Macaulay Library of Sounds #137497).

History, Distribution and Status: Core zone of occurrence is from southern NY to northern Georgia in the mountains; also appears to wander rarely to occasionally to northern NY and southern Maritimes, and rarely across southern boreal to Pacific Northwest and southern Alaska. Only found at inland mountainous sites. Corresponds most closely with L. c. pusilla (Dickerman 1987) but likely includes some specimens classified as Type 10 or Type 4. It has also been historically assigned to L. c. neogaea. It has been recorded in NYS every year since at least 2004 and bred here in numbers in 2004-05, 2007, and 2008-09. It is quasi-resident and breeds fairly commonly across many of the state lands in the southern half of NYS. It has not been reported at coastal locations in New York.

Flight Call Vocalization: The Type 1 or "Appalachian" Red Crossbill flight call sounds much like a Type 2 Red Crossbill. In both call-types the spectrograms

are dominated by a downward component. To be able to identify these two call-types with certainty, audiospectrographic analysis is essential. The Type 1 spectrogram will start with an initial upward component the vast majority of the time, and the downward part descends more quickly than that found in the Type 2 (see Figure 3). Overall, the Type 1 flight call is a quicker, dryer and sharper flight call than the Type 2 and it sounds like a chewt-chewt-chewt. Like the Type 5, Type 1 can produce sound polyphonically, meaning they use separate parts of their syrinx simultaneously like a *Catharus* thrush. Occasionally a very rare variant of Type 1 can produce calls that slightly overlap and therefore look slightly similar to a Type 5 spectrogram. This Variant Type 1, however, does not sound much like Type 5.

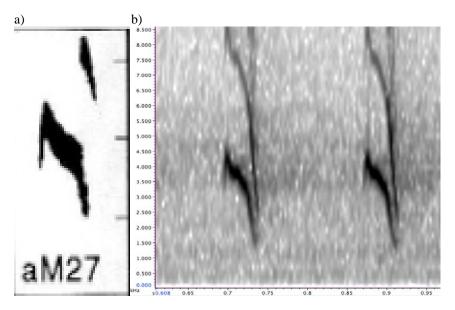


Figure 3. Spectrograms of Type 1 Red Crossbill flight calls. a) Spectrogram of Type 1 used and adapted with approval from Groth 1993a. b) Type specimen of Type 1 recorded Greg Budney and Matt Young, 2006 Georgetown, New York, 5 August 2006 (Macaulay Library of Sounds #137497).

Ecology: Unlike the other call-types discussed thus far, Type 1 occurs primarily in the East, particularly in the central and southern Appalachians (Young et al. in review), but it does not appear to be the most common type in the northern parts of the Northeast. The main ecological associations for Type 1 here in the East are Red Spruce (Picea rubens), White Spruce (Picea glauca) (in the Northeast only), Eastern White Pine, and Eastern Hemlock. During the late winter months, when these conifers have dropped most of their seed, it appears to switch to harder-coned pines such as Red Pine, Pitch Pine (Pinus rigida), and Virginia Pine (Pinus virginiana) (pers. obs. Groth 1993). It appears as if it could be more of a generalist, which would make sense given there's little competition

with other call-types here in the East. In areas of central NY, this type can be seen feeding and nesting in Norway Spruce (*Picea abies*) almost every year in at least small numbers from February to September. It has also used several other conifer species when nesting, such as Red Pine and European Larch (*Larix decidua*). In some years it can be quite common in state forests in southern NY. It appears to be rare to occasional north of southern NY, but more study is needed to be certain.

Type 4—Medium-billed

First Type Specimen: Matthew A. Young, Summerhill, New York, 4 April 2009 (Macaulay Library of Sounds #161298). Craig W. Benkman recorded either a Type 4 or 10 Hamilton County, New York, 14 February 1985 (Groth 1993a). Benkman (pers. comm.) could not confirm which type was present.

History, Distribution and Status: Core zone of occurrence is from Washington to British Columbia; occasionally wanders to Intermountain West to Arizona. Appears to be relatively rare across southern boreal into Northeast south to Ohio. Type 4 perhaps breeds very rarely in NYS. There is no subspecies that can be accurately associated with Type 4. Subspecies L.c. neogaea was once incorrectly assigned to the "old northeastern subspecies" (Dickermen 1987) despite it likely representing a call-type that commonly occurs in the West.

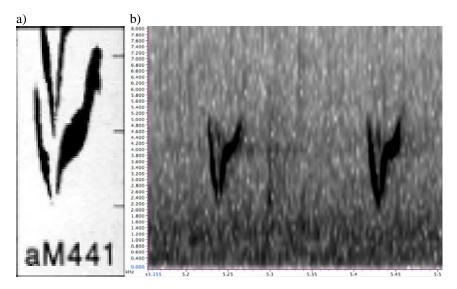


Figure 4. Spectrograms of Type 4 Red Crossbill flight calls. a) Spectrogram of Type 4 used and adapted with approval from Groth 1993a. b) Type specimen of Type 4 recorded by Matt Young, Summerhill, New York 4, April 2009 (Macaulay Library of Sounds #161298).

Flight Call Vocalization: The flight call of the Type 4 is one the easiest to recognize even when compared to Type 10 (it was recently split from Type 10; see Type 10 above). It's a very bouncy, almost musical down up jeyip-jeyip-jeyip. The spectrogram (see Figure 4) is dominated by a down up component with the ending section looking very similar to the Type 10 flight call. Overall the flight call resembles the letter "v".

Ecology: This call-type is most abundance in the Douglas Fir (*Pseudotsuga menziesii*) forests of the Pacific Northwest, but it is also widespread in North America, like Types 1, 2, 3, and 10, and therefore is at least rarely found here in the East. In the Northeast, it associates with spruce and white pine (and other pines). With a little practice, this flight call is very recognizable from Type 10 and other call-types.

Type 5—Large-billed

First Type Specimen: Only one record in all of the East and New York. Recorded by Gregory F. Budney and Matthew A. Young (Macaulay Library of Sounds #138299) in Pharsalia, New York, 5 August 2006 (Young 2010).

History, Distribution and Status: Core zone of occurrence is Intermountain West from BC and the Cascades south to at least Colorado. Is occasional in Arizona and New Mexico and rare to western coastal states. Only one record in Northeast and NY, as described above. Would be most appropriately assigned to subspecies *L. c. benderei*, but, in part, has also been assigned to *L. c. benti*. Breeding uncertain in NYS, and would be, at best, accidental or very rare.

Flight Call Vocalization: Type 5 Red Crossbills have two elements that drop in frequency, but the two elements are given in very slightly different frequency domains (see Figure 5). The lower elements are generally simpler and show less variation individually, whereas the upper elements usually rise sharply before modulating downward (Groth 1993). The second element starts a fraction of a second after the first element. On the spectrograph this second element often connects or hints at connecting to the first element, thus forming the letter "n" or "h". Occasionally the two elements don't connect at all. Generally speaking, both elements are given nearly simultaneously. The idea that both elements modulate differently, basically over the same time span, is likely evidence that the Type 5 uses different halves of its syrinx, thus producing sound polyphonically not unlike a Catharus thrush (Groth 1993a, Pieplow 2007). The human ear often doesn't pick up the time lag between the two elements, and therefore the overlapping quality of the elements is heard as a single note, almost like the striking of two keys on a typewriter at nearly the same time. Occasionally the human ear can discern the two elements. To the human ear, Type 5 sounds very "twangy".

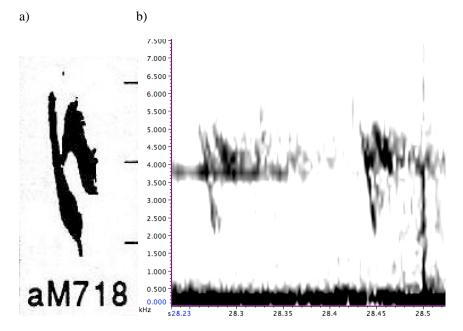


Figure 5. Spectrograms of Type 5 Red Crossbill flight call. a) Spectrogram of Type 5 used and adapted with approval from Groth 1993a. b) Type specimen of Type 5 recorded by Gregory F. Budney and Matthew A. Young (Library of Sounds #138299) in Pharsalia, New York, 5 August 2006.

Ecology: Type 5 most commonly occurs in Lodgepole Pine (*Pinus contorta*) forests of the West, but also will snack on various spruces and western pines. Given that Lodgepole Pine is a fire-driven species, it appears likely that the absence/presence of fire plays a significant role in the distribution and evolution of Type 5 in the West. Status in the East is very uncertain, but could increase with the massive dieoff of Lodgepole Pine from mountain pine beetle. The birds in Pharsalia were in areas of spruce and Red Pine.

Type 2—Large-billed

First Type Specimen: Craig W. Benkman, Albany, New York, 30 March 1982 (Groth 1993a).

History, Distribution and Status: The core zone of occurrence for Type 2 is in Intermountain West north to southern BC and the Cascades and Sierras, and south into at least northern Mexico; occasional to the western coastal states. Occurs somewhat regularly most years in very small widely scattered numbers somewhere in the East from Ontario to Georgia. Call-types occurring in Mississippi, Texas and Plains states are very likely Type 2. This is the most

commonly occurring large-billed type in NY and has occurred in the Northeast in 1969-70, 1982, 1984-85, 1997-98, 2009, 2010, and 2011. Would be most appropriately assigned to subspecies *L. c. benti*, but, in part, has also been assigned to *L. c. benderei*. Type 2 breeds occasionally across NYS in small numbers, and based on distribution of various species of conifers in the state, is most likely type to breed on Long Island or in areas away from the mountains.

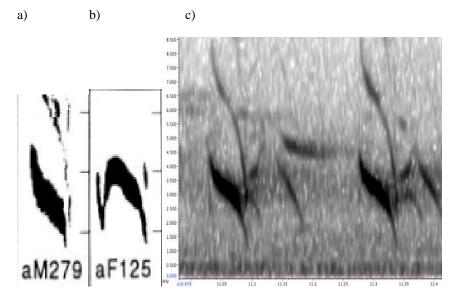


Figure 6. Spectrograms of Type 2 Red Crossbill flight calls. a) Spectrogram of a typical Type 2 used and adapted with approval from Groth 1993a. b) Spectrogram of a "kinked" Type 2 used and adapted with approval of Groth 1993. c) Type 2 recorded Matthew A. Young, Fabius, New York, 28 March 2009 (Macaulay Library of Sounds #161299).

Flight Call Vocalization: Type 2 flight calls are a bit more powerful and husky sounding than those of the Type 1. The downward component of the spectrogram is more gradual, and the initial upward component found in the Type 1 is absent (see Figure 6). Additionally, the call (as it appears on the spectrogram) will often level out a bit before continuing its downward trend. The call sounds like cheewp-cheewp-cheewp. Both call-types often have secondary ending components, but they're stronger and consistently present in Type 1. Additionally, the Type 2 flight call is given near or below 4.5 kHz whereas the highest point of the initial upward component of the Type 1 flight call is usually between 4.5-5 kHz (Figure 3). Often, Type 2 will produce what is called a "kinked" spectrogram, however, birds producing this call-type of spectrogram seem to be rare in the East. This "kinked" call-type appears to be the most common call-type given by Type 2 in the West, and as Benkman suggested (1994), might be evidence of a very recent divergence between Type 2 in the East and West. This "kinked" flight call first goes down and then up

before going back down. This spectrogram can look a bit like a Type 3, but the difference in sound is quite evident with Type 2 sounding much stronger and huskier. The flight calls of the Type 1 and Type 2 Red Crossbill are probably the least likely to be confused with the veet-veet of the White-winged Crossbill.

Ecology: Type 2 is most abundant in ponderosa pine forests of the West. More than any other call-type, Type 2 will readily feed on hard pines like Red Pine, Pitch Pine and non-native Scotch (*Pinus sylvestris*) and Austrian Pine (*P. nigra*) in the Northeast. It once nested using Austrian Pine on SUNY-Albany campus in 1982 (Craig Benkman, pers. comm.). This call-type also readily feeds on white pine and various spruces. This call-type has perhaps the most varied diet and is the most widespread Red Crossbill call-type in North America (Groth 1993), even occurring in areas of the Plains where ornamental conifers have been planted. It has been seen using perhaps more than a dozen species of conifers while nesting.

Type 8—not definitely known from New York State

L. c. percna (large-billed) corresponds to the Newfoundland Type 8 and was at one time incorrectly assigned to *ssp. pusilla*. There is no definitive evidence that it wanders to the Northeast. It appears to be an island endemic that does not wander any farther than to small offshore islands, but not to mainland Canada.

IRRUPTIONS

With the exceptions of Type 1 (quasi-resident across the southern part of the state) and Type 10 (small numbers possibly resident in the Adirondacks), Red Crossbills occur in New York primarily as irruptives. Given the diversity and predominance of soft-coned conifers (spruces, larches, hemlocks, white pine), dietary overlap could be great across call-types most years. Therefore, it would not be unexpected some years to find several Types feeding on the same conifer species in the same area. It is very likely that at least a few Type 1 Red Crossbills were present during the invasions described below. It also appears that in great irruptions, western invading Types (3 and 10) (pers. obs.) can swamp the modest numbers of regularly occurring Type 1 found here in southern NY. Below I outline some of the more significant invasions from the past 25 years.

1984-85: The 1984-85 irruption was one of the largest on record, and when Types 2, 3 and 4, and/or 10 (Groth 1993a) arrived here in New York they found one of the best bumper conifer cone crops on record (Messineo 1985). The spruces and Eastern Hemlock produced great cone crops and as a result several call-types were suspected of successfully nesting (Messineo 1985). The irruption *The Kingbird* 2011 June; 61 (2)

started in late fall of 1984 and went through May-June 1985 (Messineo 1985, Crumb 1985). The irruption coincided with very large Pine Siskin and White-winged Crossbill invasions, which also resulted in widespread breeding. Crossbills were mostly present in higher elevation areas with abundant conifers. Most of the individuals of invading call-types, particularly Type 3, appeared to move out of the Northeast (pers. obs.) in June, likely migrating back into their core range where new cone crops were forming on their key conifers.

1997-98: Like most crossbill irruptions, this one also started in the late fall, but unlike the 1984-85 invasion, birds did not find a widespread bumper cone crop. Many Christmas Bird Counts from the Adirondacks to Long Island reported good numbers of Red Crossbills. This invasion was made up of thousands of Type 10s with numbers of Type 3s. A suspected Type 2 was also recorded in central NY during the spring of 1998 (Macaulay Library of Sounds # 113520). Several northeastern recordings of Type 10 from this invasion exist in Cornell's Macualay Library of Sounds. Many of these recordings also contain a few Type 3. Evans and O'Brien's Night Flight Call Guide (2002) also has northeastern recordings of Types 2, 3, and 10 from this invasion. Unlike the 1984-85 invasion, breeding was thought to be rare. The largest concentration of both crossbill species (White-winged and Red) was found at Cook's State Forest in northwestern Pennsylvania (Hess at al. 1998). At Cook's State Forest birds were reported to be mostly feeding on Eastern Hemlock (Hess et al. 1998).

2006-07: In addition to White-winged Crossbills and to a lesser extent Pine Siskins, much of New York experienced a modest widespread invasion of Red Crossbill call-types. During July of 2006, at least one pair of Type 5 (the first ever for the state) and many Type 1 Red Crossbills were recorded in central New York (Young 2010). In July 2006 Type 1 could be heard singing at many state forests, and juveniles were seen at Muller Hill State Forest in September 2006. Type 1 continued to increase across the southern part of state with several dozens of adults with juveniles seen through June 2007—at least one group of Type 3 with juveniles was also seen in April 2007 (Young 2010).

As 2007 began, numbers of Types 3 and 10 invaded northern parts of the state, and on a trip to the Adirondacks with Greg Budney in March we recorded several Type 3s. During that same period Sean O' Brien recorded Type 10s (pers. obs.) near Paul Smith's. Birds could be seen feeding and heard singing in areas of spruce and hemlock in the Adirondacks throughout that spring. Almost all of the birds departed the Adirondacks by May 2007, and at least small numbers of both Types were strongly suspected of successfully nesting. During December of 2007 and into 2008 several Red Crossbills started to show up in coastal areas from Connecticut to Long Island and New Jersey. Analysis of recordings from Connecticut, given to me by Nick Bonono, yielded mostly Type 10 and a few Type 3. I strongly suspect the birds on Long Island were also mostly Type 10. Some of the birds present in late 2007 and into 2008 were likely holdovers from the larger 2006-07 invasion.

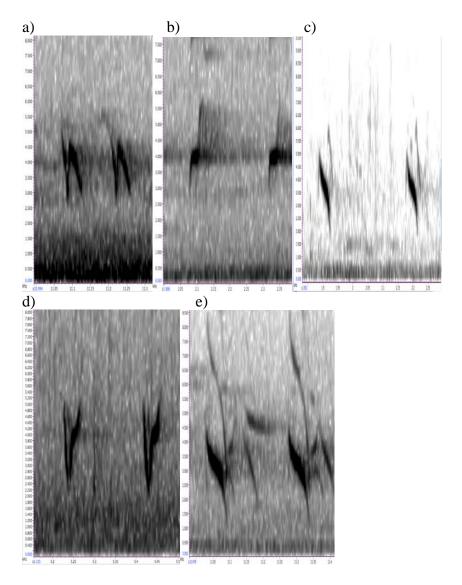


Figure 7. Types 2, 3, and 4 (a, d, e) are the same used above. Types 1 and 10 (b, c) recorded Summerhill, New York, 18 April 2009 (Type 1 Macaulay Library of Sounds #165189 and Type 10 Macaulay Library of Sounds #165188). This illustrates for the first time five different call-types were present in central New York 28 March-18 April 2009.

March-April 2009: New York and the Northeast experienced a massive invasion of Pine Siskins and White-winged Crossbills. An invasion this size had not been seen since 1989. Later in the invasion, fairly localized and modest numbers of five different call-types of Red Crossbills appeared (see Figure 7). This was the first time five different call-types were documented in NY at the *The Kingbird* 2011 June; 61 (2)

same time. As the spectrograms in this paper show, Types 1, 2, 3, 4, and 10 were present during this brief irruption. All five types were recorded at Summerhill State Forest on 18 April 2009. Only a couple each of Types 2 and 4 were present, with Type 1 being the most common and evenly distributed. Many birds were heard singing at several locations and perhaps a few nested. I suspected a very low incidence of nesting because no juveniles were seen. The sheer numbers of White-winged Crossbills, Pine Siskins and Red Crossbill call-types probably were higher than the resources needed for widespread nesting, and the behavioral environment present likely prohibited effective pair bonding (Groth, pers. comm.). A Red Crossbill pair was seen copulating at Summerhill State Forest, Cayuga County in April 2009 (Tom Johnson, pers. comm.). During this invasion, call-types were seen feeding on Norway spruce and Red Pine. Nearly all of the invading call-types departed by early May (one Type 4 was recorded Pharsalia July 2009) while many Type 1s remained. Type 1 has nested every year since 2004.

RESEARCH AND THE FUTURE

Studies have shown that some call-types in the United States and Europe pair with their own call-types, suggesting there may be fairly distinct populations to consider for any conservation efforts. Thus far, documentation of hybridization between different call-types has been very rare: 1-5% of pairs (Benkman et al. 2009, Summers et al. 2007, Groth 1993c). In the South Hills of Idaho, where a resident population of Type 9 occurs sympatrically with Types 2 and 5, interbreeding was found to be less than 1% in a large sample size of 1,704 paired crossbills (Benkman et al. 2009). The Type 9 South Hills crossbill was proposed for species status during the last AOU revisions, but the proposition was very narrowly rejected. Whether crossbill call-types assortively pair under differing environmental conditions is an area in need of further study.

Historical declines of Red Crossbill in the Northeast in the early 1900s were likely related to logging of mature coniferous forests according to Dickerman (1987). Dickerman specifically mentioned the decline of a medium-billed bird, but it's obvious today that medium-billed crossbills are still the most frequently occurring (pers. obs.). Three different medium-billed call-types occur in the state, which would be expected given that most conifers (i.e., hemlock, spruces) in the Northeast best match the bill depth morphologies of medium-billed crossbills. The vast majority of crossbills recorded in the East are of medium-billed call-types 1, 4, and 10, especially call-types 1 and 10.

The preservation of diverse conifer forests will ensure the Red Crossbill's future in New York and the northeastern United States. While forest maturation in New York will increase available habitat for crossbills, stressors such as the hemlock wooly adelgid, logging, global warming, and acid rain will compromise habitat, particularly for Type 1, which finds its home in the Appalachians. It's also clear that the state forest plantations have led to an

increase in appropriate habitat. A certain percentage and diversity of conifers should be maintained in these state lands across New York.

As previously mentioned, there is a need for much additional fieldwork focusing on Red Crossbills across their range. This is particularly true across eastern North America where they occur erratically and can be quite difficult to locate, let alone study in detail. The potential for some call-types to be recognized as distinct species warrants additional efforts to record crossbill vocalizations. One thing is certain: birders in New York and elsewhere should have their "crossbill radar" on any time they are encountered. With much practice, many of the call-types can be identified in the field, but audiospectrographic analysis is always recommended. When Red Crossbill call-types are observed, an attempt to record their flight calls using any available means (including video recorders, camcorders with audio or even some cell phones) may lead to a better understanding of the their ecology. Any recordings can be sent to me at the address above.

ACKNOWLEDGEMENTS

I'd like to thank Craig Benkman, Jeffrey Groth, Tom Hahn, Ken Irwin, and Nathan Pieplow for continued discussion about the Red Crossbill complex. Jeffrey Groth was instrumental in helping me go through dozens of recordings so I could fine-tune my ability to audiospectrographically analyze the various flight calls of the Red Crossbill call-types. Craig Benkman is always great with giving details about the natural history of the various call-types. I would like to thank the Macaulay Library of Sounds at The Cornell Lab of Ornithology, Florida Museum of Natural History, The Museum of Vertebrate Zoology at Berkeley (aka Jeff Groth's collection), Borror Laboratory of Bioacoustics, and xeno-canto for the use of recordings. I'd like to especially thank Curator Greg Budney at the Macaulay Library of Sounds as he was instrumental in helping me fine-tune my recording abilities—as one can see, Greg Budney recorded a number of the tracks cited. Lastly I'd like to thank Julie Siler for editing help, and for listening to me go on and on about crossbills!

LITERATURE CITED

- Benkman, C. W. 1987. Food profitability and the foraging ecology of crossbills. Ecological Monographs 57: 251-267.
- Benkman, C. W. 1993. Adaptation to single resources and the evolution of crossbill (*Loxia*) diversity. Ecological Monographs 63: 305-325.
- Benkman, C. W. 1999. The selection mosaic and diversifying coevolution between crossbills and lodgepole pine. American Naturalist 154: S75-S91.
- Benkman, C. W., J. W. Smith, P. C. Keenan, T. L. Parchman, and L. Santisteban. 2009. A new species of Red Crossbill (Fringillidae: *Loxia*) from Idaho. Condor 111: 169-176.

- Blankenship K., M. A. Young, and S. Holtzman 2010. Red Crossbills: Breeding Records and Call Types in Georgia and the Southeastern United States. The Oriole 74: 1-14.
- Charif, R. A, A. M. Waack, and L. M. Strickman. 2008. Raven Pro1.3 User's Manual. Cornell Laboratory of Ornithology, Ithaca, NY.
- Dickerman, R. W. 1987. The "old northeastern" subspecies of Red Crossbill. American Birds 41: 188-194.
- Evans, W. R., and M. O'Brien. 2002. Flight Calls of Migratory Birds Eastern North American Landbirds. Old Bird, Inc., Trumansburg, New York.
- Griscom, L. 1937. A monographic study of the Red Crossbill. Proceedings of the Boston Society of Natural History 41: 77-210.
- Groth, J. G. 1988. Resolution of cryptic species in Appalachian Red Crossbills. Condor 90: 745-760.
- Groth, J. G. 1993a. Evolutionary differentiation in morphology, vocalizations, and allozymes among nomadic sibling species in the North American Red Crossbill (*Loxia curvirostra*) complex. University of California Publications in Zoology 127: 1–143.
- Groth, J. G. 1993c. Call matching and positive assortative mating in red crossbills. Auk 110: 398–401.
- Hess, P., M. R. Leahy, and R. M. Ross. 1998. Pennsylvania's Crossbill Winter of 1997-98. Pennylvania Birds 12: 2-6.
- Irwin, K. 2010. A new and cryptic Call Type of the Red Crossbill. Western Birds 41: 10-25.
- Irwin. K. 2010. Red Crossbill Research: http://www.madriverbio.com/wildlife/redcrossbill/. Accessed 3 Jun 2011.
- Kelsey, T. R. 2008. Biogeography, foraging ecology and population dynamics of red crossbills in North America. Doctoral Dissertation, University California, Davis, December 2008.
- Knox, A. G. 1992. Species and pseudospecies: the structure of crossbill populations. Biological Journal of the Linnean Society 47: 325-335.
- Parchman, T. L., C.W. Benkman, and S.C. Britch. 2006. Patterns of genetic variation in the adaptive radiation of New World crossbills (Aves: *Loxia*). Molecular Ecology 15: 1873–1887.
- Pieplow, N. 2007. Colorado Crossbill Types: 2, 4 and 5. Colorado Birds: 41: 202-206.
- Sewall K. B. 2009. Limited adult vocal learning maintains call dialects but permits pair-distinctive calls in Red Crossbills. Animal Behavior 77: 1303–1311.
- Sewall K. B. 2010. Early learning of discrete call variants in red crossbills: implications for reliable signaling. Behavioral Ecology and Socibiology 65: 157-16.

- Summers, R. W., D. C. Jardine, M. Marquiss, and R. Rae 2002. The distribution and habitats of crossbills *Loxia* spp. in Britain, with special reference to the Scottish crossbill *Loxia scotica*. Ibis 144: 393-410.
- Young, M. A. 2008a. Red Crossbill (*Loxia curvirostra*). Pp. 612-613 in The Second Atlas of Breeding Birds New York State, K. J. McGowan and K. J. Corwin, eds. Cornell University Press, Ithaca, NY.
- Young, M. A. 2008b. Introduction to Differences in Crossbill Vocalizations: http://ebird.org/content/ebird/news/introduction-to%20crossbill-vocalizations. Accessed 3 June 2011.
- Young, M. A. 2010. Type 5 Red Crossbill in New York: first confirmation east of the Rocky Mountains. North American Birds 64: 343-346.
- Young, M. A., K. Blankenship, M. Westphal, and S. Holtzman. In review. The "Appalachian" Type 1 Red Crossbill (*Loxia curvirostra*). North American Birds.

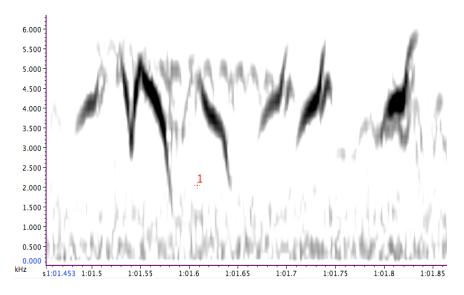


Figure 8. Spectrogram above illustrates a flock of call-types 3, 10, and 1. As it reads from left to right: Type 10, Type 3, Type 1, Type 10, Type 10, Type 10. Recorded by Matthew A. Young in Pitcher, New York, 15 March 2009 (Macaulay Library of Sounds #163231).