

A NEW AND CRYPTIC CALL TYPE OF THE RED CROSSBILL

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ABSTRACT: I describe a new call type (type 10) of the Red Crossbill (*Loxia curvirostra* complex) associated with Sitka Spruce (*Picea sitchensis*) in Humboldt County, California. As with other types of the crossbill's flight calls, the birds using this type of call apparently constitute a subset of the species that is cohesive socially, behaviorally, and morphologically. The patterns of frequency and amplitude modulation of flight calls of type 10 are similar to those of the second half of type 4 but change in frequency more slowly and are given at a higher pitch. The flight calls of type 10 vary among individuals and within an individual's repertoire, perhaps to a greater extent than in other call types. Most type 10 birds gave *toop* calls distinctly different from those of all other call types, but a few were similar to those of types 2 and 4. Likewise, the *chitter* calls of type 10 differed from those of the three call types (2, 3, and 4) found most commonly near type 10. The song repertoires of types 10 and 4 differed as well. Type 10 crossbills are intermediate in size between types 3 and 1. Large numbers of type 10 were resident in Sitka Spruce forests from 2001 to 2010, whereas the few type 4 birds recorded in spruce stands remained only briefly. Morphological and behavioral evidence indicates that type 10 is specialized for foraging on seeds in Sitka Spruce cones.

Groth (1993a) categorized the extensive variation within the Red Crossbill (*Loxia curvirostra*) in North America into eight call types on the basis of differences in vocalizations and morphology. Each call type differs in its flight, excitement ("toop"), and alarm calls, but each call type is best recognized from the flight call because it is the most commonly given and most diagnostic vocalization (Groth 1993a). Benkman (1999) subsequently identified a ninth call type. Moreover, evidence is increasing that at least some of these call types represent biological species (Groth 1993a,b, Smith and Benkman 2007, Benkman et al. 2009). Indeed, Benkman et al. (2009) have argued that call type 9 represents a biological species on the basis of high levels of reproductive isolation and morphological and genetic divergence from other sympatric call types.

Two or more types of Red Crossbills often nest in the same area and mate assortatively by flight-call type (Groth 1993b, Edelaar et al. 2004, Smith and Benkman 2007, Summers et al. 2007). In one investigation <1% of the pairs identified consisted of two flight-call types (Smith and Benkman 2007). Flight calls play a role in assortative mating. In trials of mate choice, Snowberg and Benkman (2007) found that females preferred males that had the same type of flight call as their own. Although there often were many type 3 birds nearby during the formation of pair bonds, in my study I detected no pairing of birds using different call types.

Red Crossbills usually learn the flight call of one parent, both parents, or a sibling, imitate it, and continue to use that type of flight call (Groth 1993a, Sewall 2008). Although individuals may, over time, modify the structure of their flight call to a slight extent, the new forms that they produce remain within the range of variation of that type of flight call (Sewall 2008, Keenan

A NEW AND CRYPTIC CALL TYPE OF THE RED CROSSBILL

and Benkman 2008). Crossbills normally do not change the type of flight call that they use and do not use two or more types of flight calls. There is strong evidence that the type of flight call that an individual uses remains stable over its lifetime (Adkisson 1996, Sewall 2009).

Even though most crossbills eat seeds from the cones of two or more species of conifers, Benkman and colleagues (Benkman 1993, 1999, Benkman and Miller 1996, Parchman and Benkman 2002) found that in North America most call types have evolved a different bill morphology adapted to optimize efficiency of feeding on the cones of a specific “key” conifer species that provides a reliable food source when other conifers have few seeds. Benkman (1993) thought that the Sitka Spruce (*Picea sitchensis*) could represent a key conifer species and predicted that there may be a small form of the Red Crossbill adapted to Sitka Spruce. Here, I present my observations of the vocalizations, morphology, and behavior of Red Crossbills and their occurrence in and use of Sitka Spruce in northwestern California. I describe a new call type, type 10. It appears that Groth (1993a) recorded a few type 10 birds but lumped them with type 4. This new call type differs in morphology and habitat association from other Red Crossbills and may represent a form adapted to Sitka Spruce.

STUDY AREA AND METHODS

I studied Red Crossbills in Sitka Spruce forests in Humboldt and Del Norte counties, California, from 40.56° to 41.70° N and from 124.08° to 124.35° W. Sitka Spruce, the only species of spruce in the study area, occurs on the coastal slope from sea level to an elevation of 400 m in small pure stands fragmented by logging, small mixed stands where it is the dominant species, and as a rather minor component of mixed-conifer forests dominated by Coast Redwood (*Sequoia sempervirens*). As elsewhere, the number of trees is declining with logging and home building, and here it is being replaced with redwood planted in timber holdings. In late November 2001, Red Crossbills invaded Humboldt County, and I found crossbills with a distinctive flight call foraging almost exclusively on Sitka Spruce seed. Red Crossbills with these unusual vocalizations have remained in these Sitka Spruce forests through February 2010. Most of my observations were made at Patrick’s Point and Big Lagoon state parks, Humboldt County. Additional observations were made at scattered sites in interior Humboldt County, along the coast of Humboldt County between Ferndale and Big Lagoon, within 8 km south from the mouth of the Klamath River in Del Norte County, along the northern coast of Del Norte County, along the Oregon coast as far north as Coos Bay, in central Oregon around Crater Lake, in northwestern Washington, and in southeastern Arizona. I observed crossbills through 10 × 40 binoculars and a 15–40 × 60 spotting scope from dawn through early afternoon on 1917 days from 1999 to 2009.

I recorded crossbill vocalizations with a Super unidirectional microphone and a Sony TCM-20DV tape recorder and used Cool Edit 2000 to produce and analyze audio spectrograms from the recordings. I recorded songs from numerous individuals that used type 10 calls and catalogued their song repertoire as well as a small sample of different songs from type 4 crossbills.

A NEW AND CRYPTIC CALL TYPE OF THE RED CROSSBILL

I also examined a recording of type 4 song on the Cornell Laboratory of Ornithology website at www.animalbehaviorarchive.org (Macaulay Library: catalog number 87926) and spectrograms of a few type 4 songs published by Adkisson (1996).

Over most of its range, Sitka Spruce produces cone crops that can vary greatly from year to year (Harris 1990). I estimated Sitka Spruce cone crops by arbitrarily selecting sample plots of 40 trees that appeared to be representative of the surrounding tract. I then categorized each tree as producing a poor, moderate, or abundant cone crop so that I could make a rough estimate of cone crops to characterize yearly and regional differences.

In June and July 2005, professional banders with more than 10 years of experience at Redwood Sciences Laboratory (U. S. Forest Service) established a banding station in McKinleyville, California, to capture and measure crossbills that used type 10 flight calls. They measured bill length (from the anterior edge of the nares to the tip of the maxilla) bill depth (along a plane perpendicular to the tomia at the anterior edge of the nares), tarsus, wing chord, and body mass of each crossbill captured. Following the method of Benkman (1993), I also made molds of the horny palate of two type 10 crossbills to determine the width of the bill's husking groove. I used a dissecting microscope with a scale in the eyepiece to measure the distances to the nearest 0.01 mm; I rounded off dimensions to the nearest 0.05 mm as did Benkman (1993). I recorded the flight calls of each bird as it was released, but a few did not call and so were not included in the analyses. From their flight calls, I identified 89 measured crossbills as type 10. Two of type 3 and one of type 4 were also captured, but I did not include them in the analyses.

RESULTS AND DISCUSSION

Vocalizations

I recorded calls from more than 1400 crossbills in Humboldt County. Of these only 5 were type 1, ~185 were type 2, ~450 were type 3, ~165 were type 4, and 21 were type 5 (Figure 1). Types 1–5 were recorded mostly during irruption years (1999, 2004, 2006, and 2008). Additionally, I recorded crossbills of types 2–5 at other sites in the region, two of type 7 crossbills near Crater Lake, Oregon, and one of type 6 in southeastern Arizona. Of the nine crossbill call types previously described in North America (Groth 1993a, Benkman 1999, Benkman et al. 2009), type 8 apparently occurred only on Newfoundland but may now be extinct (Parchman and Benkman 2002), and type 9 is restricted to two small mountain ranges in southern Idaho (Benkman et al. 2009). I have no recordings of these last two call types (see Groth 1993a, Smith and Benkman 2007, Keenan and Benkman 2008, and Benkman et al. 2009 for spectrograms). Groth (1993a) found types 2–5 to be widespread in western North America, although type 3 has a more northern distribution and type 5 occurs more inland. He found type 1 mostly in eastern North America but also in the Pacific Northwest, type 6 in southeastern Arizona (from which it presumably ranges south into Mexico), and type 7 on the east side of the Cascade Mountains and in the northern Rocky Mountains. Beginning in late November 2001, I identified

A NEW AND CRYPTIC CALL TYPE OF THE RED CROSSBILL

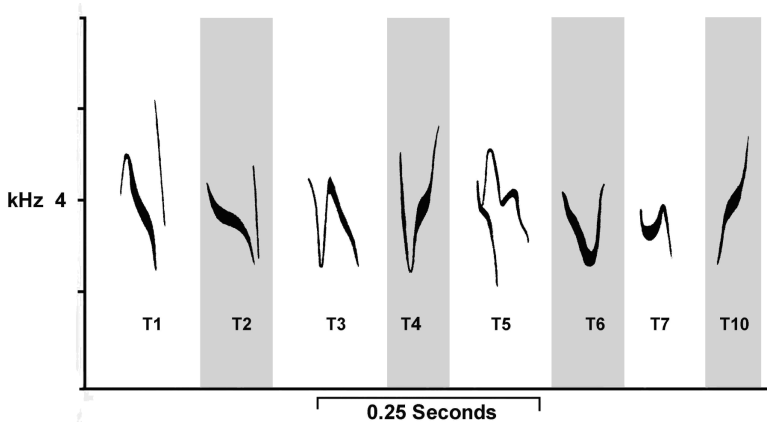


Figure 1. Spectrograms of representative flight calls of eight of the ten types known from North American Red Crossbills. For types 8 and 9, see Groth (1993a) and Keenan and Benkman (2008), respectively.

a new call type from northwestern California (type 10) as crossbills using this call invaded Humboldt County. During observations of flocks at 48 sites from 2002 to 2010 I recorded ~630 type 10 crossbills.

Flight calls. Inspection of Figure 1 reveals that only two known call types resemble type 10: type 6 and type 4 both have components rising in pitch at the end. Type 6 actually sounds nothing like type 10. Most of the energy (amplitude) is imparted in the falling component of the call, and generally there is very little modulation of the final rising portion of the call. Crossbills that use type 6 calls are extremely large and rarely found north of southeastern Arizona. Crossbills that use type 4 calls, however, are abundant and widespread in the western United States, and their calls are closely similar to type 10. Previously, if other observers have detected type 10, they have categorized it as type 4 (Groth 1993a, Thomas P. Hahn pers. comm.), perhaps supposing that the bird had omitted the initial falling component. Figure 2 shows the range of individual variation in the flight calls of type 4 and provides a comparison of the flight calls of type 4 with a representative sample of type 10 flight calls. The most typical flight calls of type 10 are simple in structure (Figure 2: 6–8) and resemble the last half or the rising portion of type 4 flight calls (Figure 2: 1–5). In the field, I often failed to detect the first half of a type 4 flight call unless I recorded and analyzed it. Some type 4 flight calls sounded very similar to some of those of type 10, hence my use of the term “cryptic” to describe the new type of crossbill; refer to the recordings comparing these two flight call types on the website at www.westernfieldornithologists.org/kirwin/ and <http://madriverbio.com/wildlife/redcrossbill>.

Within type 10, the structure of the flight call varies greatly from individual to individual (Figure 3). The male and female of a mated pair often match the structure of each other’s call. This matching usually develops by one bird imitating its mate’s call or each bird adjusting its call so that they both con-

A NEW AND CRYPTIC CALL TYPE OF THE RED CROSSBILL

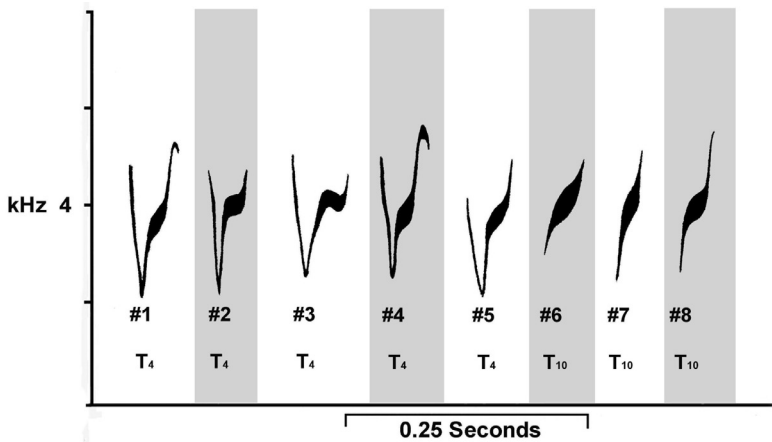


Figure 2. Comparison of the Red Crossbill's flight calls of type 4 and type 10, showing the range in variation of type 4 in western North America. All calls of type 4 begin with a fall in frequency. Most typical of type 4 is trace 5, the most extreme deviation from typical is trace 3. In type 10, the frequency rises at a rate slightly less than that of the rising portion of western Type 4 calls. Type 10 calls are shorter than type 4 and usually given at a slightly higher frequency.

verge on a variant intermediate between the two original forms. (Mundinger 1970, 1979, Groth 1993b, Keenan and Benkman 2008, Sewall 2008). I recorded many mated pairs that were "call matching," and some of these calls are the most complexly modulated calls in Figure 3, indicating that even the calls that differed greatly from the typical form were recognized as flight calls by other birds using type 10.

Some type 10 crossbills used two different forms or variants of type 10 flight calls, but this apparent dimorphism was difficult to quantify or even document conclusively. I had many observations where I thought a bird had changed from one flight call to another, but because other type 10 birds were nearby, I could not always rule out the possibility that I may have recorded two birds sequentially. I recorded only six birds using two variants of the type 10 flight call (Figure 4) when, to my knowledge, they were at least 60 m from any other crossbills. I recorded over 45 individuals that changed from one flight call to a different variant when they were giving a series of calls when I was reasonably certain that only one bird was calling (28 of these can be found in the section on alternate flight calls used by type 10 birds at <http://madriverbio.com/wildlife/redcrossbill>). This determination was supported by the observation that all of the calls came from the same location and were given at a constant rate. During a bout of calling, an individual usually gives a series of calls with intervals of ~180 msec between calls with only minor variation. This interval can vary by bout of calling or individual. In the recordings, during a series, each bird changed from one flight call to a different variant of type 10 without any deviation in the interval between calls, as would be expected if only one bird was calling. I heard other birds as

A NEW AND CRYPTIC CALL TYPE OF THE RED CROSSBILL

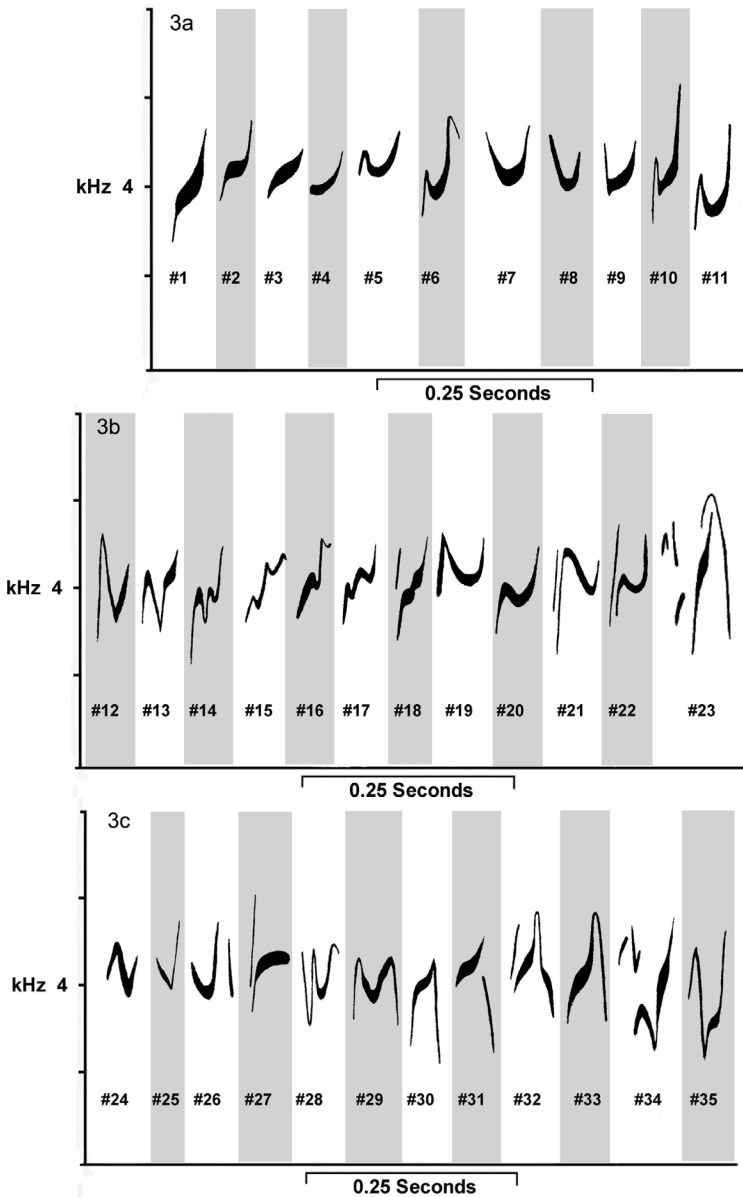


Figure 3. Range of variation in the Red Crossbill's flight calls of type 10. Most individuals' calls are like those represented in traces 1-3, fewer are like those represented in traces 4-6, and fewest are like those represented in traces 7-35. The range of individual variation in crossbills using type 10 calls is greater than in any other type.

A NEW AND CRYPTIC CALL TYPE OF THE RED CROSSBILL

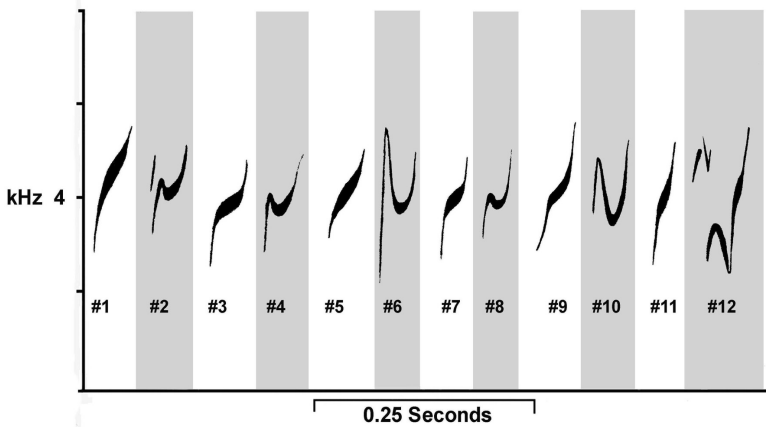


Figure 4. Red Crossbills that used two flight calls of six variants of Type 10 flight calls. In each pair of calls, one (left) has a simple modulation pattern and one (right) has a complexly modulated pattern.

they changed from using one variant of the type 10 flight call to another but did not record them. It seems that many of the crossbills that gave type 10 calls used two variants of the type 10 flight call. In contrast, Groth (1993a) reported that fewer than 10 of 700 crossbills he recorded used two variants of their type of flight call. In type 10, use of a complex call probably enhances recognition of individuals and mates because complex calls differ from individual to individual more than simple calls do.

Use of two variants of the type 10 flight call also varied within and among individuals. Complexly modulated flight calls seemed to be linked to reproductive behavior. Their use declined following molt in autumn and increased from midwinter through summer with singing and other activities associated with breeding. In the following, the values are for the total number of calls and do not reflect the number of birds calling. In winter (October–March), 83.6% of all flight calls recorded were simple and 16.4% were complex ($n = 1939$), whereas in the spring and summer breeding season (April–September) 58.3% were simple and 41.7% were complex ($n = 4722$). Many anecdotal observations led me to infer that type 10 crossbills tend to use a simple flight call (Figure 3: 1–3) for communicating with other flock members and a more complex flight call (Figure 3: 5–35) for communicating with their mates. Birds engaging in maintenance activities such as foraging tended to use a simple call. On many occasions throughout this study I observed flocks in which several individuals were using complex calls during breaks between bouts of singing or when they were interacting with their mate, but when these flocks were startled, usually by the sudden appearance of a large bird nearby, the entire flock flushed and most, if not all, members of the flock gave simple flight calls (Figure 3: 1–3) or, at most, a slight variation of the simple call (Figure 3: 4). I observed a male on 11 consecutive days as he tended a female on the nest. During this period I recorded 76 flights by the

A NEW AND CRYPTIC CALL TYPE OF THE RED CROSSBILL

male toward a group of crossbills foraging 70–100 m away and 73 return flights to the nest. He used a simple flight call (Figure 4: 1) on every flight away from the nest, but he used a more complex call (Figure 4: 2) on every return flight to the nest and his mate. Another male, also provisioning a nest, usually used a complex call when flying both to and away from the nest (and mate) and used a simple call only occasionally when moving from the nest to a foraging flock.

To determine if type 10 has been recorded elsewhere, I examined various sources including Groth (1990, 1993a). In figure 15a,b of Groth (1993a), calls of crossbills recorded on the central Oregon coast in Sitka Spruce and Douglas-fir (*Pseudotsuga menziesii*; Groth 1990) appear to be more characteristic of type 10 (no falling component, slope and frequency band similar) than of type 4. There also appear to be type 10 calls in Groth's (1993a) figure 21 from the south shore of Lake Superior. These were included in Groth's range of type 4 calls (compare with the range in Figure 2 above). Because of the similarity of these spectrograms to those of type 10, it seems possible that Groth may have included measurements from some type 10 birds in his set of type 4, which could have affected his morphological characterization of crossbills that used type 4 calls (possibly deflating mean values; see below). I also examined the Red Crossbill flight calls on the compact disc *Flight Calls of Migratory Birds, Eastern North American Landbirds* (www.oldbird.org). In the recordings from Minnesota, there are flight calls of 14 type 4 crossbills in the same frequency band as those that were recorded in western North America, but in all of these the frequency falls more rapidly then rises more slowly than in type 4 in the West. Therefore type 10 rises more slowly than type 4 in the West but more rapidly than those in the small sample from the East. This CD also has recordings of many flight calls given by 17 crossbills (reported as type 4) that have all of the characteristics of type 10 flight calls I recorded in northwestern California. These were recorded in New Jersey, Maryland, and Minnesota. I also examined a recording of one type 10 recorded in northwestern Wisconsin on the *Bird Song Ear Training Guide* CD (www.caculo.com). On the Cornell Laboratory of Ornithology website (www.animalbehaviorarchive.org) there are recordings from Maine of at least nine crossbills giving type 10 calls (catalog number 12985).

Excitement or toop calls. Nethersole-Thompson (1975) described *toop* calls given by the Scottish Crossbill (*L. scotica*) associated with anger, alarm, or excitement. Although Groth (1993a) called them "excitement calls," Adkisson (1996) used the terms *toop* and *tooping* to describe these calls. For each call type, it appears that the alarm call and the *toop* call are related because *toops* can be used for alarm and the two calls are similar in structure (see Groth 1993a). Alarm calls are given at a slightly lower frequency. I heard alarm calls seldom and briefly at low amplitude, and I recorded only a few of them. The *toops* of types 2, 4, and 10 differ from each other slightly (Figure 5). *Toops* of types 2 and 4 often have harmonics and rarely include a high-frequency element. I seldom recorded harmonics with type 10 *toops*, and most of these consisted of a low-frequency element given simultaneously with a high-frequency element that overlapped the last portion of the low-frequency element. The structure of the high-frequency element was usually reminiscent of a first harmonic. The low-frequency ele-

A NEW AND CRYPTIC CALL TYPE OF THE RED CROSSBILL

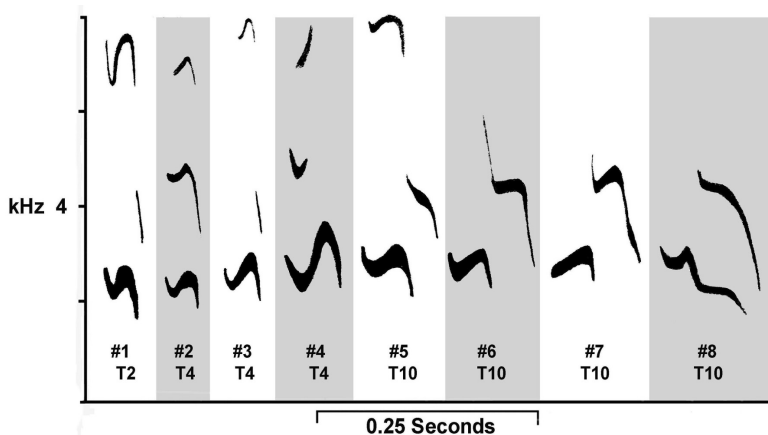


Figure 5. The *toop* or “excitement call” of Red Crossbills that used call types 2, 4, and 10. Type 2 is represented by trace 1, type 4 by traces 2–4, and type 10 by traces 5–8. A few *toops* were so similar that identifying them to one of these three types was difficult. Type 10 crossbills have a strong tendency to include a high-frequency signal that overlies a lower-frequency element (produced simultaneously by the other “voice”) and continues long after the low-frequency element has terminated (traces 5–7). Prolonged *toops* (trace 4) are occasionally given by type 4 crossbills. Type 10 birds also use an alternative form of *toop* that is prolonged (trace 8) but is unlike type 4 *toops*.

ment of individual 5 in Figure 5 produced a second harmonic, and the bird added a high-frequency element similar to a type 2 flight call. After the low-frequency element had terminated, type 10 crossbills tended to continue this high-frequency element longer than did birds of any other call type (Figure 5: 5–7). Some type 4 *toops* were unique in structure. They were longer in duration, more modulated, and the bandwidth of their frequency was greater than in the others (Figure 5: 4). I never heard this call from any other type of crossbill. Type 10 crossbills sometimes used a prolonged *toop* that was different in form (Figure 5: 8). It was given occasionally by one or two birds that were in groups *tooping* at Northern Pygmy Owls (*Glaucidium gnoma*) and was also used in the context of reproductive behavior. I recorded it once from a female whose mate immediately responded and copulated with her. Marler (1956) described four “social calls” (analogous to *toop* calls) that Chaffinches (*Fringilla coelebs*) apparently modified from an alarm call. These differ slightly in structure and are used in different contexts. Many Pine Grosbeaks (*Pinicola enucleator*) use two forms of their “location call” (Adkisson 1981), which is analogous to the crossbill’s *toop* call.

Chitter calls. I recorded *chitter* calls (see Groth 1993a, Robb 2000) from types 2, 3, 4, and 10 (Figure 6). Most *chitter* calls were given by birds as they moved from the tops of trees to bushes next to ponds where they drank. Because their field of view was usually obscured by vegetation, crossbills gave these calls when they seemed to be apprehensive of potential danger. They

A NEW AND CRYPTIC CALL TYPE OF THE RED CROSSBILL

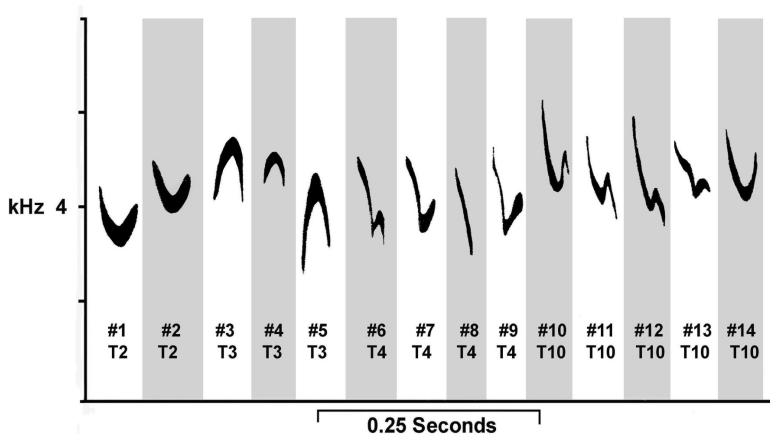


Figure 6. *Chitter* calls of Red Crossbills of type 2 (traces 1–2), type 3 (traces 3–5), type 4 (traces 6–9), and type 10 (traces 10–14). Note in type 4 that the initial long falling portion appears concave, whereas in Type 10 it appears convex. Then type 10 calls rise more rapidly than the corresponding portion of type 4 calls.

scanned rapidly and were skittish or nervous, and they often abandoned the attempt to drink and flew to the top of a tree. I once recorded *chitters* from a bird that was threatened then attacked by another crossbill, and once from a bird that was close to a bird being attacked by a third crossbill. The *chitter* calls of type 10 differ clearly from those of types 2 and 3 (Figure 6). Although the *chitter* calls of types 4 and 10 appear similar, there are consistent differences (Figure 6). In the initial long falling portion of type 4 calls the rate of frequency change slowly increases, whereas in type 10 calls the rate decreases. The type 4 call rises at a constant rate that is lower than the rate in the rising portion of the type 10 *chitter* call. The differences among these four call types suggest that each type may have a *chitter* call that is unique. Robb (2000) identified differences in the *chitter* calls among several types of crossbills in Europe. Flight calls and possibly *toops* that have been modified to varying degrees can be used like *chitters*, as noted also by Groth (1993a) and Robb (2000).

Songs. Most of the elements I examined in the small samples I obtained of type 4 song are very different from anything I recorded from type 10 (not shown). In moderately large samples, these differences are similar to those between the songs of type 2 and type 3 or between either of those and type 10, suggesting (but far from demonstrating) a level of differentiation comparable to that seen between other types. Each type of crossbill may have a large song repertoire. It is not known if any repertoire varies regionally. Almost nothing is known regarding the rate of change (evolution) of a repertoire or the magnitude of the modifications made over time.

I have established a website with recordings of Red Crossbills at <http://madriverrbio.com/wildlife/redcrossbill>. This site has various calls from many call types and useful clues for distinguishing between the calls of these types

A NEW AND CRYPTIC CALL TYPE OF THE RED CROSSBILL

of crossbills, as well as songs. A subset featuring calls of eight call types and variation within type 10 is at www.westernfieldornithologists.org/kirwin/. These recordings have also been submitted to the Cornell Laboratory of Ornithology for archiving in its Library of Natural Sounds.

Cone Crops and Occurrence of Call Type 10

Along the coast from Ferndale, California, to Coos Bay, Oregon, I identified two patterns of cone production to the north and south of Endert's Beach, 3 km south of Crescent City, Del Norte County. From Endert's Beach south, Sitka Spruce trees produced cones abundantly every year from 1998 through 2009. From Crescent City to Coos Bay (north of Endert's Beach), I estimated the cone crop from 2003 to 2006 to be only ~70% of that south of Endert's Beach. Consequently, Sitka Spruce seed was especially abundant in Humboldt and southern Del Norte counties (south of Endert's Beach), and the high relative humidity near the coast enhanced seed retention in the cones (and see references in Benkman 1993).

The geographic break in cone-production patterns also coincided with an even greater difference in crossbill occurrence. North of Endert's Beach, I did not detect crossbills during surveys along the southern Oregon coast from 2003 to 2006 and near Crescent City from 2001 to 2007. However, I regularly found 48 flocks containing at least 600 type 10 crossbills from Endert's Beach south to Ferndale; most occurred north of Trinidad. Since most spruce trees were on private land, which I did not survey, I suspect that the total population was much greater.

I searched for Sitka Spruce and crossbills in northwestern Washington in August 2005. In the area from Oak Harbor to the Canadian border and inland to the Cascade Mountains I found only a few Sitka Spruce near Puget Sound, 5 km south of the Canadian border at Birch Bay, Washington, and recorded six type 10 crossbills there.

I encountered Red Crossbills regularly in at least fair numbers in Sitka Spruce forests in Humboldt County from 1971 to 1999, suggesting that these spruce trees had produced a good crop in many of the years prior to this study, suggesting that type 10 may have been here in the past.

Flock Sizes and Site Fidelity

I recorded distinctive flight calls at specific sites repeatedly for periods as long as 2 years. At these sites, I did not find much variation in the sizes of the flocks that might indicate movements of flocks or individuals between sites. Only on rare occasions did I see one to three birds venture into the home range of an adjacent flock, but they always returned within 12 minutes. These observations suggest that many individuals (and perhaps major portions of flocks) remained in a limited area for extended periods. From 2002 to 2009, I monitored four flocks almost daily, four others weekly, and 40 less often. I found no evidence of any site being abandoned, even briefly. Each flock apparently resided in its own relatively small discrete home range throughout this period. Here, I give only the counts of the number of birds in each flock during the winter outside of the breeding season of June to August. By focusing on the period outside of breeding I was able to exclude

A NEW AND CRYPTIC CALL TYPE OF THE RED CROSSBILL

recruitment of fledglings and dispersal of juveniles. In winter, flock sizes of type 10 crossbills averaged 17.7 individuals. Three of the 48 winter flocks held 9–11 birds each, and 45 had 14–21 birds. I surveyed only four areas where there was continuous spruce forest extensive enough to contain two or more flocks. Together these four areas held 11 flocks. Ten of the groups used sites (home ranges) that were roughly circular with diameters that ranged from ~640 to 750 m. The eleventh group, the eastern flock at Patrick's Point, used a site ~350 by ~920 m. For all 11 flocks, the distance between the centers of adjacent home ranges varied from ~780 to 860 m.

Morphological Characteristics

The various call types of North American Red Crossbills differ morphologically. Ranked by size in order from the smallest (type 3) to the largest (type 6) they are 3, 10, 1, 4, 7, 5, 2, 9, 8, and 6. Benkman (1993, 1999, 2003) and Benkman and Miller (1996) found a positive relationship between the mean depth of the bill of the various call types and the pliability of the scales on the cones of each call type's "key" species of conifer. Crossbills with deep bills are more efficient than smaller-billed crossbills at opening the cones of conifers with thick and/or stiff scales. Conversely, smaller-billed crossbills are more efficient on smaller, thinner-scaled cones. Type 3 ($\sigma\sigma$ = 8.19 mm; ♀♀ = 8.10 mm; mean bill depths from Groth 1993a unless noted otherwise) is well adapted for opening the cones of the Western Hemlock (*Tsuga heterophylla*) (Benkman 1993), which has papery scales that are slightly more flexible and smaller than those of Sitka Spruce. Type 1 ($\sigma\sigma$ = 8.80 mm; ♀♀ = 8.72 mm) has been hypothesized to be adapted to the Red Spruce (*P. rubens*) in eastern North America (Parchman et al. 2006; see also Groth 1993a). Type 4 ($\sigma\sigma$ = 9.00 mm; ♀♀ = 8.52 mm) is adapted to Douglas-fir (Benkman 1993). Sitka Spruce cone scales are much more flexible than those of Douglas-fir. By comparison, type 10 crossbills measured in this study (Table 1) are smaller than type 4, and their mean bill depth ($\sigma\sigma$ = 8.55 mm; ♀♀ = 8.37 mm) is intermediate between that of types 1 and 3. The mean values of bill length, tarsal length, and mass for type 10 (Table 1) are also intermediate between those of types 1 and 3 (Tables 2 and 3). The mean wing chord of males and females of type 10 is slightly shorter than that reported for type 3 (Table 3).

Crossbills of type 10 are small, although the male in Figure 7 has a bill that looks proportionately deep. Sean McAllister took this photograph on 9 March 2009, 3 km south of Crescent City. He also recorded the bird's flight call, and I identified it after examining spectrograms.

The groove on the sides of the upper mandible's horny palate is where the bird holds seeds while husking them (Newton 1972, Benkman 1993). The width of this husking groove is adapted to the size of the seeds of each call type's "key species" (Benkman 1993). Like the other morphological characteristics, the widths of the husking grooves of types 1, 3, 4, and 10 overlap. The samples of type 1 ($n = 1$) and type 10 ($n = 2$) are too small to allow for a detailed comparison of the overlap. Benkman predicted that a crossbill adapted to Sitka Spruce should have a husking groove ~1.55 mm wide. The widths of the husking grooves of the two type 10 birds for which I made palate

A NEW AND CRYPTIC CALL TYPE OF THE RED CROSSBILL

Table 1 Measurements of Red Crossbills of Call Type 10

	Bill depth at nares (mm)	Bill length from nostril (mm)	Tarsus	Wing chord	Mass
Males					
<i>n</i>	54	54	45	49	53
Minimum	8.0	12.2	14.3	78.0	22.1
Maximum	9.5	15.4	19.8	86.0	34.4
Mean	8.55	14.02	16.72	82.69	27.99
Standard deviation	0.33	0.87	1.09	1.84	2.03
Standard error	0.05	0.12	0.16	0.26	0.28
Females					
<i>n</i>	35	35	29	32	35
Minimum	7.9	10.9	14.6	76.0	23.5
Maximum	9.0	15.2	17.5	86.0	37.2
Mean	8.37	13.45	16.20	81.09	27.44
Standard deviation	0.33	1.14	0.62	2.26	2.34
Standard error	0.06	0.19	0.11	0.40	0.40

molds were 1.50 and 1.55 mm, narrower than the mean value of 1.75 mm for type 4 birds and conforming to Benkman's (1993) prediction.

In addition to bill size and palate structure, the foraging behavior of the type 10 crossbills I observed suggests that they have evolved to exploit Sitka Spruce seeds. Crossbills using type 10 calls spent most of their time in Sitka Spruce, and almost all seeds I saw them eating were of that species. The birds flew only rarely and briefly to conifers other than Sitka Spruce and seldom foraged on them. For example, Shore Pine (*Pinus contorta contorta*) was common at most of my study sites, yet during >10,000 hours of observing type 10 crossbills, I saw only three Shore Pine seeds eaten by them. Red Alder (*Alnus rubra*) was common at all sites, but I saw fewer than 30 Red Alder seeds consumed. After irruptions, type 4 birds spent far less time (<2

Table 2 Measurements of Red Crossbills of Call Type 1^a

	Bill depth at nares (mm)	Bill length from nostril (mm)	Tarsus	Wing chord	Mass
Males					
<i>n</i>	39	39	39	39	39
Minimum	8.3	13.3	18.0	83.8	25.8
Maximum	9.4	15.7	20.4	95.4	34.5
Mean	8.80	14.49	19.16	89.41	30.49
Standard error	0.041	0.101	0.090	0.374	0.284
Females					
<i>n</i>	33	33	33	33	33
Minimum	8.3	12.9	17.3	82.1	24.5
Maximum	9.2	15.0	20.3	90.3	35.1
Mean	8.72	14.19	18.19	86.50	29.09
Standard error	0.040	0.099	0.103	0.395	0.389

^aSource: Groth (1993a).

A NEW AND CRYPTIC CALL TYPE OF THE RED CROSSBILL

Table 3 Measurements of Red Crossbills of Call Type 3^a

	Bill depth at nares (mm)	Bill length from nostril (mm)	Tarsus	Wing chord	Mass
Males					
<i>n</i>	28	28	28	28	28
Minimum	7.8	11.7	17.2	81.8	23.8
Maximum	8.7	14.3	19.9	88.5	32.2
Mean	8.19	12.74	18.80	85.88	27.32
Standard error	0.046	0.117	0.127	0.343	0.443
Females					
<i>n</i>	33	33	33	33	33
Minimum	7.7	11.8	17.5	78.0	23.7
Maximum	8.5	13.7	19.4	85.5	29.4
Mean	8.10	12.81	18.47	82.37	26.54
Standard error	0.055	1.127	0.109	0.518	0.469

^aSource: Groth (1993a).

weeks) at sites with spruce than did any other call type, and many flocks of type 4 crossbills spent the winter and spring at inland sites having Douglas-fir. Conversely, I never heard type 10 in Douglas-fir. The smaller bills of type 3 birds should better enable them to forage in Sitka Spruce. The preference of type 3 crossbills for Sitka Spruce was apparently greater than that of type 4 but less than that of type 10. During four invasions, large numbers of type 3 birds arrived in October, foraged in the spruce, but left in early June the



Figure 7. Male Red Crossbill that used call type 10, 3 km south of Crescent City, California, 9 March 2007. This individual's bill appears deeper than average for its call type.

Photo by Sean McAllister

A NEW AND CRYPTIC CALL TYPE OF THE RED CROSSBILL

following year. The relationship between type 10 and species of conifers in the eastern United States is not known.

CONCLUSION

The combination of distinct vocalizations, the difference in average bill depth from other call types with which it occurs (a minimum difference of about 0.2 mm from other call types, similar to the differences between other call types occurring together, e.g., Groth 1993a, Benkman et al. 2009), and the use and apparent specialization of these crossbills on Sitka Spruce, the one conifer in the Northwest that had been predicted to have a call type associated with it (Benkman 1993), all indicate that the crossbills I describe here should be recognized as the tenth North American call type, type 10.

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