Red Crossbill Types in Colorado: Their Ecology, Evolution, and Distribution

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Introduction

Colorado is blessed with conifer-clad mountains and with them come crossbills (*Loxia* spp.). They are specialized for foraging on seeds in conifer cones. Thus, when conifers produce large cone crops, crossbills often move in to feed and breed. Although the more northerly boreal White-winged Crossbill (*Loxia leucoptera leucoptera*) can at times be found in the high-elevation forests of Engelmann spruce (*Picea engelmannii*) south to the San Juan Mountains and into northern New Mexico, Red Crossbills (*L. curvirostra* complex) are more common and widespread in Colorado. Red Crossbills are a morphologically diverse group. Initially, the size variation among crossbills caused taxonomists to split it into many subspecies (Griscom 1937). However, research by Jeff Groth (1993a) showed that it was more accurate and informative to categorize Red Crossbills by their flight calls rather than as geographic subspecies.

Red Crossbill Call Types and Foraging Methods

Nine 'call types' are recognized in North America (Table 1). Several are indistinguishable by bill and body size (e.g., call types 1 and 4), but most of them do differ morphologically from other call types (Groth 1993a). Each of the call types we have studied (call types 2, 3, 4, 5, 8, and 9) is specialized for feeding on a single species of conifer (Benkman 1993, 2003, Parchman and Benkman 2002). This does not mean these types will not forage opportunistically on other conifers; rather, each call type has evolved to exploit a single species or subspecies of conifer. Such specialization requires that crossbills can reliably find a particular type of conifer seed, because crossbills are less efficient than other finches at foraging on non-conifer seeds (Benkman 1988). The most important characteristic of a conifer for all crossbill types is that it must reliably hold its seeds in closed or partially closed cones through late winter and into spring. If cones are not closed or partially closed, less specialized species will deplete the seeds.

The decurved upper and lower mandibles of crossbills enable them to exert and withstand the strong biting forces at the tips of their mandibles necessary for forming gaps between cone scales (Fig. 1). If the mandibles were straight like a Pine Siskin's, crossbills would be unable to exert much force at the mandible tips before shearing forces would break them off. Once crossbills form gaps between the scales, the lower mandible is abducted to the side, exposing the seeds at the base of the scales (Fig. 2). Crossbills then use their extendable tongue (as in hummingbirds and woodpeckers, the hyoid apparatus of a crossbill's tongue extends around the back of its skull) to lift the seed out, and they then husk the seed and swallow the kernel.

Bill size, especially bill depth, determines how fast crossbills can remove seeds from between closed cone scales, whereas the structure of the horny palate of the upper mandible is critical for husking seeds (Benkman 1993). Crossbills have evolved bill and body sizes that are about two to three times larger than their redpoll-like ancestors. The large bill and associated musculature are critical for providing the necessary forces for spreading apart cone scales and extracting seeds from closed or partly closed cones. However, the conifer seeds that crossbills regularly eat are on average rather small. Thus, crossbills have evolved a horny palate structure that enables them to handle small seeds quickly (Benkman 1988). In particular, the lateral grooves in the palate of the upper mandible are narrower than in other cardueline finches, allowing crossbills to secure small seeds with their tongue while they crack and remove the seed coat with their lower mandible.

Because bill size and palate groove width influence how rapidly seeds can be removed from cones and husked, respectively, conifer species with seeds of different sizes favor the evolution of crossbills of different sizes. For example, the smallest New World Red Crossbill, call type 3, which is found most commonly in the Pacific Northwest, is adapted to and more efficient than any other call type at foraging on the small thin-scaled cones

Figure 1. This shows a male type 9 or South Hills crossbill biting between lodgepole pine cone scales so that he can then laterally abduct (spread) his lower mandible to the side (see fig. 2). Crossbills generally forage near the distal end of the cones where most of the seeds are located.

of western hemlock (*Tsuga heterophylla*) (Benkman 1993). On the other hand, these type 3 or hemlock crossbills are very inefficient at foraging on seeds and cones larger and harder than those of Douglas-fir (*Pseudotsuga menziesii*). Hemlock crossbills should be rare in Colorado, and when found are likely to be associated with Engelmann spruce. I do not know of records from Colorado, but specimens have been collected in both New Mexico (New Mexico State University Vertebrate Museum) and Arizona (Monson and Phillips 1981).

Figure 2. This shows a female type 9 or South Hills crossbill laterally abducting her lower mandible to spread apart the scales of a lodgepole pine cone. Her asymmetric jaw musculature enables her to exert strong abduction forces to spread apart cone scales, exposing seeds at the base of the scales.

The next largest crossbill commonly found in the West is call type 4, the Douglas-fir crossbill (Benkman 1993). Although Douglas-fir is widespread in Colorado, the Rocky Mountain subspecies of Douglas-fir, unlike the one in the Pacific Northwest, does not hold seeds in its cones consistently through winter. Thus, although Douglas-fir crossbills are common in the Pacific Northwest, they are much less common in the Rocky Mountains. When found, they are likely to be foraging on seeds of either Douglas-fir or Engelmann spruce, because they have difficulty removing seeds from the hard woody cones of Rocky Mountain lodgepole pine (*Pinus contorta latifolia*) and are unable to remove the hard woody seed coats of Rocky Mountain ponderosa pine (*Pinus ponderosa scopulorum*) (Benkman 1993).

The largest-billed crossbill in the New World is call type 6 (Groth 1993a), which has been found in the United States mostly in southwestern New Mexico and southeastern Arizona. It may have occurred occasionally in Colorado. However, because it is associated with pines in Mexico, and given the decline of its habitat, one should not hold out hope for seeing it in Colorado.

Only two conifer species in Colorado produce seeds reliably enough to support crossbills from year to year. They are Rocky Mountain lodgepole pine and Rocky Mountain ponderosa pine, and not surprisingly, each of these two species supports a crossbill call type. These two call types are roughly intermediate in size between the small-billed hemlock crossbill and the massive-billed Mexican crossbill (Groth 1993a). The lodgepole pine crossbill, or call type 5, has a slightly smaller bill than the ponderosa pine crossbill, or call type 2; it also has disproportionately narrow palate grooves because lodgepole pine seeds are only about one-tenth the size of ponderosa pine seeds (Benkman 1993). These two call types are by far the most common crossbills in Colorado, and with effort, one should be able to locate both of them somewhere in Colorado in any given month, although with the extensive mortality of lodgepole pine in some parts of the state, finding lodgepole pine crossbills will become increasingly difficult. During good cone crop years where ponderosa pine and lodgepole pine co-occur, or if Engelmann spruce is having a large cone crop, both call types can often be heard at the same time.

Table 1. Geographic distribution of Red Crossbill types. Three types occur regularly in Colorado: Types 2, 4, and 5.

Type 1	Red Spruce Crossbill	Occurs in spruce forests of southern Appalachians and Pacific Northwest
Type 2	Ponderosa Pine Crossbill	**Widespread and present all year in Colorado; the most common call type in Colorado**
Type 3	Western Hemlock Crossbill	Presumed rare in Colorado
Type 4	Douglas-fir Crossbill	**Uncommon in Colorado and central Rocky Mountains**
Type 5	Lodgepole Pine Crossbill	**Widespread and present all year in Colorado, but less common than Type 2**
Type 6	Sierra Madre Crossbill	Occurs from Mexico north to southern Arizona and New Mexico; unlikely in Colorado
Type 7		Uncommon, scattered in and between Cascades and Northern Rockies
Type 8	Newfoundland Crossbill	Newfoundland; possibly extinct
Type 9	South Hills Crossbill	Restricted to South Hills and Albion Mountains in southern Idaho where red squirrels are absent

Conifer Seed Availability

Understanding and predicting patterns of abundance of a given crossbill call type requires knowledge of the cone ripening and seed shedding patterns of the conifers. Once these patterns are understood, crossbills become more predictable.

All Colorado cone-bearing conifers vary in seed production from year to year and may produce few if any seeds in a given area in a given year. When they do produce seeds, their seeds and cones ripen over the summer, so that by early autumn, seeds are mature and cones are fully formed.

Crossbills begin moving in search of large developing cone crops in late May (Benkman 1987). Large cone crops are favored by crossbills not only because they contain more cones but also because they contain more seeds per cone, since pollen production and therefore pollination rates are correlated with seed cone production. This benefits crossbills because the more seeds per cone, the more rapidly crossbills can extract seeds from cones and the longer seeds are held in the cones (Benkman 1987).

Once crossbills locate a large developing cone crop, they begin nesting as early as the first weeks of July or August (Benkman 1990). For example, I have seen them building nests in ponderosa pine forests as early as 28 June (1983) in the Jemez Mountains, New Mexico, and as late as 25 August (1990) in Round Mountain Campground, Pike National Forest. Crossbills also begin nesting as early as the first week of July while foraging on white spruce (*P. glauca*) in the Northeast (Benkman 1990), and I suspect they will do the same if there is a large Engelmann spruce cone crop. Some crossbills remain paired between years (P. C. Keenan, personal communication), which presumably enables them to initiate nesting quickly.

Conifer cones usually begin to open and shed their seeds in early autumn. When cones initially begin to open, seeds become readily accessible to crossbills as well as to other seed-eaters such as Mountain Chickadee and Red-breasted Nuthatch. But as seeds are shed, crossbill feeding rates decline (Benkman 1987). How long crossbills remain in an area depends on the size of the cone crop and on weather conditions. Large cone crops and cool moist conditions tend to result in more seeds being held longer. Seed retention in the cones may often be sufficient for ponderosa pine crossbills to breed while foraging on ponderosa pine seeds in spring. Bailey and colleagues (1953) describe what were undoubtedly ponderosa pine crossbills nesting in ponderosa pine from January to April, and this call type may begin building nests as late in the spring as 9 April (in 2006 along Cherokee Park Road near the Colorado-Wyoming border) while feeding on the seeds in cones produced the previous autumn. The same is probably true for crossbills foraging on other conifers such as lodgepole pine and Engelmann spruce, although Engelmann spruce is more likely to shed most if not all of its seeds earlier in the year. Indeed, all conifers with thin-scaled cones tend to shed their seeds early, which explains why crossbills only specialize on thin-scaled cones like western hemlock in humid areas such as the coast of the Pacific Northwest (Benkman 1993).

Lodgepole pine in the Rocky Mountains differs from other conifers in Colorado because it frequently produces serotinous cones. Serotinous cones remain closed until, for example, crown fires heat the cones, releasing the seeds. Serotiny is favored where stand-replacing disturbances such as fire are likely to occur during the lifetime of the plant (Enright et al. 1998). Seed predators, however, can select against serotiny by stealing the seeds from the cones before fire can open them, preventing trees from reaping the benefits of storing this canopy seed bank (Enright et al. 1998). Red squirrels (*Tamiasciurus hudsonicus*) are such a seed predator. Because of their extensive cone harvesting, red squirrels have favored trees that do not produce serotinous cones, so that in most areas fewer than half of the trees produce serotinous cones (Benkman and Siepielski 2004). In addition, selection by red squirrels has resulted in the evolution of fewer seeds per cone and a higher proportion of woody cone to seed, so that only about one percent of the cone is seed (Smith 1970, Benkman et al. 2001, 2003).

Because red squirrels remove much of the cone crop, lodgepole pine crossbills tend to be rather uncommon in Rocky Mountain lodgepole pine forests (Benkman 1999, Siepielski and Benkman 2005). Indeed, if you see large numbers of crossbills in Colorado, they are more likely to be ponderosa pine crossbills than lodgepole pine crossbills. Furthermore, crossbills are unable to access seeds in serotinous cones until the cones have aged and weathered for several years, allowing a few or more cone scales to separate (Benkman et al. 2003). Many of the older cones remaining on serotinous-coned trees are open, presumably because crossbills and perhaps other seed predators have shredded their scales. However, because the canopy seed bank accumulates and weathers gradually, lodgepole pine seeds are more likely than seeds of other conifers to remain available in a given area from season to season and from year to year. This undoubtedly explains why lodgepole pine crossbills can be found consistently in lodgepole pine forests in the Rocky Mountains, albeit at low densities. For example, in the mountain ranges east and west of Laramie, Wyoming, lodgepole pine crossbills seem to be present year-round, year after year.

Systematics

Because the breeding distributions of the various call types overlap and two or more call types can breed in a given forest, call types are not geographic races or subspecies. However, definitive evidence that crossbills represent "good" species has been difficult to gather. Recent genetic evidence (Parchman et al. 2006) indicates that call types do not interbreed freely and that gene flow between call types is restricted. But these data are inadequate for determining whether hybridization is rare. Direct evidence on the mating behavior of crossbills while breeding is required. Unfortunately, the nomadic behavior of crossbills and their irregular timing of breeding have made it difficult to observe large numbers of breeding crossbills. Jeff Groth recorded about 30 "pairs" of male and female crossbills in the southern Appalachians (Groth 1993b). Although I suspect that they were likely "paired," they do not represent a random sample of breeding crossbills. For example, most of these crossbills were not breeding when they were captured; therefore we cannot eliminate the possibility that hybrid pairs are simply less likely to remain paired after breeding.

Fortunately, in 1997 I found a common and resident call type (call type 9) in two isolated mountain ranges in southern Idaho, the South Hills and Albion Mountains, where other call types also occasionally breed. Call type 9 is abundant in these two ranges because lodgepole pine is plentiful and red squirrels are absent (Benkman 1999). Moreover, in the absence of red squirrels the frequency of serotiny is nearly 100 percent (Benkman and Siepielski 2004), so the trees store a huge canopy seed bank on which this South Hills crossbill relies. In these ranges, call type 9 is coevolving in an evolutionary arms race with lodgepole pine (Benkman 1999, Benkman et al. 2001, 2003). As the lodgepole pine has evolved increased seed defenses against crossbills, the crossbills in turn have evolved a larger bill. Two graduate students of mine, first Julie Smith and then Lenny Santisteban, have recorded over 1,500 breeding crossbills during the past six years and they have found that fewer than one percent of the breeding South Hills crossbills pair with a non-South Hills call type. This is much less frequent than the rate of hybridization found in, for example, sapsuckers or Darwin's finches. Our estimate of reproductive isolation for South Hills crossbills is also stronger than that found for "good" plant species (Smith and Benkman 2007). We have not found hybrid pairs between lodgepole pine and ponderosa pine crossbills, which are the two other call types that breed in the South Hills, but our sample sizes for these two call types are inadequate to argue that these two call types also represent species. However, our behavioral studies indicate that they are likely reproductively isolated from each other and we suspect that, with perhaps the exception of call type 7 (see Parchman et al. 2006), all call types may appropriately be recognized as species if one employs the biological species concept allowing occasional hybridization.

What is possibly most remarkable is that we strongly suspect that both ponderosa pine and South Hills crossbills have diverged from lodgepole pine crossbills within the past 7,000 years. Ponderosa pine in the Rocky Mountains has expanded its distribution from a rather restricted area in southern New Mexico and Arizona since the last glaciation; it reached northern Colorado only 7,000 years ago. As recently as 5,000 years ago, lodgepole pine in the South Hills was expanding from a much smaller distribution following a warm period

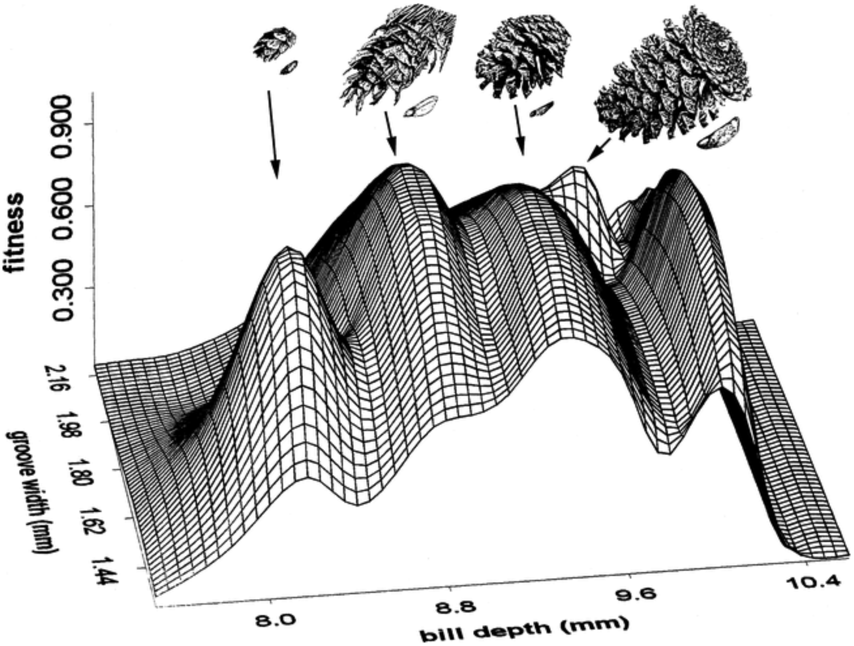

Figure 3: The estimated fitness (survival) for Red Crossbills in relation to variation in bill depth and palate groove width while foraging on four species of conifers in the West. The adaptive peaks correspond to the following conifers from left to right: Douglas-fir, Rocky Mountain lodgepole pine, Rocky Mountain ponderosa pine, and South Hills lodgepole pine. From Benkman (2003).

when lodgepole pine had shifted considerably upwards in elevation (Smith and Benkman 2007). It is difficult to envision ponderosa pine crossbills evolving much before 7,000 years ago or South Hills crossbills evolving before 5,000 years ago. This represents extremely rapid speciation.

How has reproductive isolation evolved so quickly between call types adapting to alternative conifers? We have found that natural selection for foraging on alternative conifers is strongly divergent, favoring the evolution of different bill structures, which is the ultimate reason there are so many call types (Benkman 1993, 2003; see Fig. 3). But how does reproductive isolation evolve so quickly? Strongly divergent ecological selection should favor assortative mating because hybrids will tend to be intermediate in size and less likely to survive (Benkman 1993, 2003, Snowberg and Benkman 2007). As expected, female crossbills in captivity strongly prefer to associate with male crossbills of their own call type (Snowberg and Benkman 2007). Perhaps even more important, especially during the early stages in the evolution of a call type, is strong selection favoring assortative flocking by similar morphologies.

Years ago, when I used to spend much time in the field measuring feeding rates of crossbills, I noticed that flocks of crossbills appear to assess tree quality as a group. When crossbills land in a tree and begin foraging, they are generally quiet. However, sometimes one or two crossbills may begin to call, as if saying, “I’m doing poorly, how are you doing?” If the rest of the flock remains quiet and continues foraging, then the callers cease calling and forage. Maybe they had found a poor cone or branch and the others were more successful. In other cases, if one or two crossbills begin calling and others join in, creating a crescendo, they all fly off. In some cases in which I had already measured feeding rates, it was obvious that crossbills flew off because there were few seeds in the cones. Since then, we have shown experimentally that crossbills can more rapidly assess tree quality by watching foraging flock mates (Smith et al. 1999). Such group assessment only works well if flock members have similar feeding abilities (Smith et al. 1999). A small-billed crossbill in many cases would not benefit from observing a large-billed crossbill. This should favor assortative flocking by like morphologies. We believe that distinct “call types” evolved because they allowed crossbills to readily flock with crossbills having like morphologies, since it would be easier for them to recognize similar crossbills by call type than by subtle differences in palate structure and bill size and shape. Because crossbills flock year-round and chose mates within flocks, assortative flocking may have been key to the rapid radiation of crossbills.

Conclusion

I suspect that we will be studying crossbills for years to come. The other day one of my graduate students recommended that I read a paper by Dr. William L. Brown, Jr. (1922-1997), the great naturalist and ant biologist who was a professor at first Harvard and then Cornell University. Brown wrote in *The Quarterly Review of Biology* in 1957: "Were I an ornithologist, I think that the finches of the genus *Loxia* would take up most of my research time. No group of birds seems to offer more tantalizing problems in that area of biology where systematics, ecology, zoogeography, population dynamics, and ethology overlap." I began studying crossbills 25 years ago. I just wish I could have shown this quote to my dissertation committee members when I embarked on my research. Maybe then their jaws would not have dropped so far when I first mentioned studying crossbills.

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