How Crossbills Make Their Bill Tips Cross

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OBSERVATIONAL EVIDENCE SUGGESTS A POSSIBLE MECHANISM FOR INITIATING THE DEVELOPMENT OF THE CROSSED-BILL MORPHOLOGY IN RED CROSSBILLS

All adult crossbills in the genus, Loxia, in the finch family (Fringillidae) have permanently crossed bill tips to enable them to efficiently pry cone scales apart to remove seeds from evergreen cones with their dexterous tongue. There appears to be no consensus or direct observations reported in the scientific literature as to how or when the bill tips on young crossbills become crossed. It is believed by some workers that young crossbills are not in any way actively involved in causing their bills tips to cross. In this document, I provide observational, photographic and anecdotal evidence to the contrary that lends support to the alternate hypothesis that it is the behavioral actions of each individual bird that sets into motion the eventual configuration of its crossed bill as having either a left or right projecting lower bill.

For photographic evidence the last three young Red Crossbill (Loxia curvirostra) I received for rehabilitation were documented with photos until the tips of their bills were successfully crossed and the young birds were able to remove evergreen seeds from cones. Photos were taken of two uninjured siblings received in 2017, at intervals from the time of the late hatchling stage when they arrived for care, to after the tips of their bills were crossed. One post-fledgling, received in 2008 was injured with a broken leg and was lying in a nest of soft rags that afforded it no firm object to grasp and twist with the tips of its bills. As a result of being unable to exert any twisting action on its mandibles, the tip of the lower bill grew upward directly into the bottom of the upper bill, forcing the mouth to be open and remain that way. That bird

APRIL 13 Dark RECR. A hatchling Red Crossbill that was estimated to have hatched sometime around April 3 or 4 is shown in a photo taken on April 13, 2017, showing its finch like bill with the tip of the upper bill slightly lengthened and beginning to turn down.

served as a control to show that the bill-twisting behavior is necessary for the tips of the mandibles of post-fledglings of crossbill species to be successfully crossed.

Over the 50 plus years that I rehabilitated birds, I received over 20 hatchling Red Crossbills and cared for them until their bills were crossed and they were ready for release. My many observations per day of over 20 post-fledgling crossbills, which were in my care after being orphaned or in two cases injured, consistently showed that these young birds actively engaged in behaviors, which appeared to apply a bill-twisting type of force at a certain period in their development. During that period, all healthy crossbill post-fledglings raised by other rehabbers and I, had been observed to grasp with the tips of their bills small broken branches, knobs or other protrusions they found on the branches on which they perched. After taking the protrusion in its bill tips, all of the post-fledgling crossbills that were healthy and able to stand quickly twisted the upper bill one way and the lower bill the other way. They did this twisting behavior over and over, hundreds of times a day. Those young crossbills began the bill-twisting movements at approximately 29 to 30 days of age, which is well over a week after fledging.

It can be hypothesized that those numerous bill-twisting movements per day over several days would likely change the tips of the mandibles in a manner that caused the birds to develop a cross-billed morphology.

The fingernail like covering, made of keratin, on the bills of most birds is called the rhamphotheca. Their bill-twisting behavior appears to be stimulated by the accelerated growth of the specific portion of the rhamphotheca at the tips of both the upper and lower bills, which will be henceforth referred to as "the fast bill tip growth period" because that is what Dr. Craig Benkman called it (per. comm.). The bill of a young crossbill, after hatching and prior to the sudden fast bill tip growth period, looks similar in shape to the bills of other hatchlings in the finch family. This is shown on the Red Crossbill hatchling that was assumed to be about 10 to 11 days old in the photo on page 1.

Approximately 9 days after fledging and begin flying around with their parents, one might postulate that certain growth hormones produced by the pituitary gland of the young crossbills are genetically programmed to activate. This hypothetical hormone surge, if it were growth hormone produced by the pituitary gland, would likely cause the observed accelerated growth of the specific portion of the rhamphotheca at the tips of the upper and lower bills. And similar triggers of gene expression likely prompt the birds to begin the observed twisting movements of the bills, which has to completely coincide with the sudden fast growth of the bill tips. However, I could not determine by close observation or photos why one bird twisted the lower bill to the left and the upper bill to the right and another bird, a sibling in the case of the last two hatchlings I raised, would twist its bills the opposite. Dr. Jamie M. Cornelius, Department of Integrative Biology, Oregon State University, Corvallis, Oregon hypothesized that the twisting direction by each individual bird may be directed by lateralization of their brain (per. comm.).

On April 13, 2017, I received two healthy crossbill hatchlings. Photos I took at various times during the ensuing period in the young crossbills' development show how the bill tips appeared from above, below and from both sides prior to and during the period of bill-twisting, and immediately after the bill tips were permanently crossed.

What was observed was that as soon as the bill tips go into the period of fast growth, a young crossbill begins to bite on something, like a knot or a small branch, quickly twisting its head sideways, which produces a force that appears to cause the tip of the upper bill to be pushed slightly toward one side and the tip of the lower bill be pushed toward the other side. Whichever way the bird twists the lower bill determines whether it will go to the left or to the right of the upper bill, if ones point of reference is focused on the lower bill, as some ornithologist's focus seems to be. Or whether the upper bill will go to the left or to the right of the lower bill, if one's focus is on the upper bill, as it seems to be for most regular bird watchers. I have assumed that bird watchers referring to "righties" and "lefties" were talking about the direction that the upper bill projected.

One of the young crossbills was observed to twist its upper bill to the right and the lower bill to the left. The other was observed to twist its upper bill to the left and the lower bill to the right. It has been stated to me that the upper mandible does not cross in the horizontal plane. However, I observed that when the young crossbills exhibited the bill-twisting behavior, they twisted both bill tips simultaneously, resulting in

the upper bill having a slight curve toward the side it was twisted and the lower bill having a slight curve in the other direction (see the photos from straight below on pages 12 and 13). It appears that the pressure created by the biting and then twisting motions of the bird actually bends the still somewhat malleable rhamphotheca at the tips of the mandible in the direction the bird twists. This slight curve in the bills is clearly shown in the photos taken after the bill tips had finished the fast growth period and had been permanently crossed.

When the fast bill tip growth period began on the injured bird, the tip of the lower bill grew directly up into the bottom of the anterior of the upper bill forcing the bills apart**.** As it couldn't stand and perform the twisting action on its bill tips, I had to decide which way to make the upper bill go and taped the tip of the upper bill to the left of the lower bill. The bill tips were held in that crossed position between feedings and at night, until the fast bill tip growth period had finished and the tips were permanently crossed. The photos of the injured bird shows that if a young crossbill is not able to twist its own bill tips to make them cross, the bird's mouth will be forced open further and further by the fast growing lower bill tip pushing into the bottom of the upper bill. After three to five days of bill tip growth, the bird would not be able to pick up seeds or preen its feathers and so would likely not survive.

It can be hypothesized that without the twisting behavior the young birds do themselves, the rhamphotheca of the bill tips would likely remain straight as shown on the injured bird and would eventually cause mortality.

It has been suggested that perhaps the biting and twisting by the post fledgling crossbill youngsters is simply displaced desire to be foraging on cones and the crossing would have occurred without any behavior on the bird's part contributing to their crossed-bill morphology. When I raised the hatchling crossbills, I put ponderosa pine cones filled with seeds in the flight box with the fledged crossbills while I was still feeding them many times a day. Since they were not able to fly around with their parents and the other members of the flock to observe how to remove evergreen seeds, I wanted them to see and become use to cones. I never observed any of the youngsters trying to remove seeds from the cones or saw any evidence that they paid any attention to the cones prior to the bill tips being crossed.

The bill tips had been observed to be twisted over and over many times per minute, possibly over a 1000 times a day and were permanently crossed when the tips of the mandibles were long enough to keep them projecting past one another permanently in the crossed position. At around 39 days of age, the birds stopped twisting on protuberances on branches and with the mandible tips permanently crossed the process appeared to be finished. It usually took at least several hours, and sometimes a day or two for one of the youngsters to figure out how to remove the seeds from the Ponderosa Pine cones, after which the others quickly joined in removing and eating pine seeds. Apparently by watching the first bird's actions, they determined how to use their bill tips to pry open the cone scales and remove the pine seeds with their tongues. The crossbill post fledgling with the broken leg had flown around with its parents and other flock members prior to being injured. Even though it was alone in the flight box, it immediately seemed to know how to pry the scales open and remove the pine seeds as soon as it could stand and walk on its healed leg and was put into the flight box with pine cones. This suggests a learning process may take place for the young crossbills, after fledging and prior to the fast bill tip growth period of their development.

From the inferred day of hatching on April 3 or 4, to the end of the bill crossing process on May 11, would make the birds approximately 39 to 40 days old when the bills were permanently crossed and the birds could extract seeds from pine cones. However, the age of the birds when the bills are permanently crossed may vary by a day or two in the wild, because of inclement weather, food availability or other factors that might affect the nourishment and growth of hatchling birds. This could result in the total developmental period being nearly 6 weeks from hatching to permanently crossed bills, depending on the nutrition they received.

There is no way to determine whether the direction of a fledgling's twisting movement as it grasps a projection is genetically preprogrammed or if it is caused by some other kind of individual preference, but researchers have shown that the lower bills on approximately half of Red Crossbills cross to the right and approximately half to the left. Since the two healthy young crossbills were siblings, they likely had the same genetic makeup. Females of some bird species mate with more than one male but I could find no research on this issue in crossbills. One of the two healthy crossbill youngsters in my care twisted its lower

bill to the left and the other twisted its lower bill to the right. Thus what determines "why" a specific bird twists so the lower bill goes to the left and the upper to the right, or twists the opposite way was not determined.

HYPOTHESES ON HOW IMMATURE CROSSBILLS PHYSICALLY PARTICIPATE IN CAUSING THE CROSSING OF THEIR BILLS AND WHEN IN DEVELOPMENT THIS BEHAVIOR OCCURS.

It is hypothesized that when the documented fast growth period of the mandible tips begins at approximately 30 days after hatching, it is the observed behavioral actions of each individual bird consisting of hundreds of bill-twisting motions per day for approximately 8 days that results in changing the mandible tips in a such a manner that causes the birds to have a cross-billed morphology with either a left or a right projecting lower bill when the fast growth period ends, and at approximately 39 days of age give or take a couple of days, the bills are successfully crossed.

It is hypothesized that without the observed bill-twisting motions by the post fledgling bird, the rhamphotheca of the bill tips would likely remain straight resulting in eventual mortality.

PHOTOGRAPHIC DOCUMENTATION OF BILL DEVELOPMENT SUPPORTS THESE HYPOTHESES

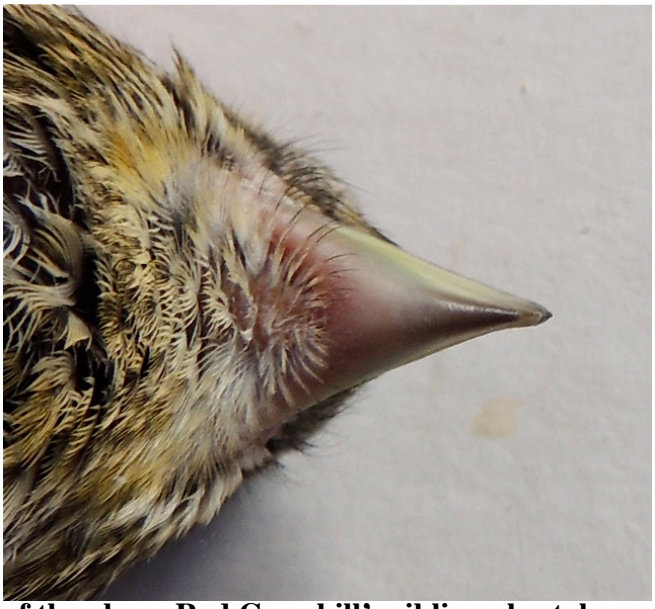
The photos in this document are photographic evidence for how and at what age young crossbills engage in bill-twisting movements that appear to contribute significantly to their crossed-bill morphology, as well as the observed changes in length of the bills in that time period. Included are important photos that show the detrimental consequences to an individual and its mandible tips when it is incapable of performing the bill-twisting behavior.

APRIL 26 AT APPROXIMATELY 23 DAYS OF AGE.

APRIL 26 Dark RECR. The bills of the same dark Red Crossbill shown on Page 1, photographed again on April 26, 2017, 13 days after the photo as a hatchling was taken.

The dark Red Crossbill and its sibling were able to fly and were eating by themselves when the April 26 photos were taken. They were about 23 days old, depending on the exact day of hatching, which I calculated to be around April 3 or 4. These photos show the bills from the right side and from a bottom view. The tip of the upper bill had grown somewhat longer than it was in the photo on page 1, but there is no evidence of crossing or of which way the tip of the upper or the tip of the lower bill will go. Both bills

appear to be aligned in a perfectly straight position and the bills have not yet begun the period of fast growth of the tips. This bird can be told from its sibling by the darker facial feathers, so it is referred to as the dark RECR fledgling.



APRIL 26 Light RECR. These are the same views of the above Red Crossbill's sibling also taken on April 26, 2017. This bird has lighter feathers around the eyes and on the face. It will be referred to as the light RECR fledgling. As on the dark RECR fledgling, the upper bill tip has grown somewhat longer than when it arrived for rehab, and is beginning to turn downward, but there is no evidence to indicate which direction the mandibles will be crossed.
MAY 1 AT APPROXIMATELY 30 DAYS OF AGE.

MAY 1 Dark RECR. The photos on this page show four different views of the bills of the dark RECR fledgling on May 1, 2017, one week after the photos on page 5 were taken. The photos above show both sides of the bills. The bills tips remain in a straight position, with no indication as to which side the lower and upper bills will go. The upper bill tip is observably longer than it was on April 26. On both bills, the length of the entire bill had visibly increased.

MAY 1 Dark RECR. These photos show the bills of the dark RECR fledgling in a top view on the left and a bottom view on the right on May 1. The bills remained in a straightforward position and there is no evidence of crossing or of which way the bills will cross in the photos.

MAY 1 Light RECR. The photos on this page show the bills of the light RECR fledgling Red Crossbill, taken on May 1, 2017. The above photos show both sides of the bills. The bills tips remain in a straightforward position, with no indication as to which side the lower and upper bill will go. Similar to its sibling, the length of the upper bill had increased slightly.

MAY 1 Light RECR. These photos show a top view on the left and a bottom view on the right. As on its sibling, there is still no evidence of crossing or of which way the lower and upper bill will go. Both bills appear to be perfectly straight, although the upper bill tip is slightly longer than it was on April 26.

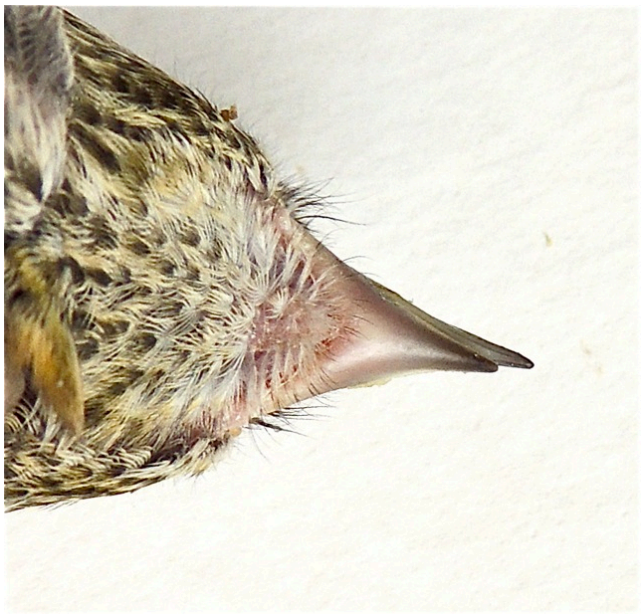
Both birds began biting and making a twisting movement with their bills using small branches and raised areas of bark on May 3, 2017, three days after the photos were taken of their bills on May 1. The following photos were taken of the light RECR fledgling on May 8, reaching for and biting on the bark or short broken off branches on the main branch used for a perch. After taking hold of the protrusion on the main branch, the bird would make the twisting movement to make the upper bill go to the left of the lower bill.

The light RECR just before hopping to its left to twist on a piece of bark that stuck up on the branch. Then it reached down, grasped the bark and twisted. I shot the photo slightly too soon, just before it took hold of the bark. Since I was using flash, it took quite a while for the camera to process a photo and get ready to take the next photo.

When the bird reached down and grasped the bark as shown in the photo on page 9, I took the photo just before the bird twisted and let go. The birds do this reaching and twisting very quickly. I didn't realize that it would be so difficult to get a photo. Unfortunately, it was too dark in the box for the camera to take video. I took a lot of photos like the two above over the next three days that showed the light RECR just prior to or just after twisting on the bark or short branch before I finally was able to get a photo with the branch actually in the bill. After many more tries like the ones above and lots of blurry photos, I finally succeeded in getting the photo on page 9 of the light RECR twisting on one of the small broken branches. That photo and the photos on this page were taken on May 8, 2017. The dark RECR fledgling wouldn't twist its bill tips when I was watching it. It would just look at me as if it expected to be fed. However, I could peek into the box and watch it without it seeing me. It twisted its bills on the bark or short branch stubs when it couldn't see me, just like its sibling did. After I succeeded getting the photo of the light RECR holding the short branch in its bills, I had to leave for the rest of the afternoon. The next day, I didn't have time to take photos, but I saw them both twisting their bills prior to feeding them, and when I looked in at them several times to check on them. After May 10, I didn't see either of them twisting their bills. As both bird's bills were permanently crossed, they were apparently not stimulated to twist them any longer. After photographing both birds' bills from both sides and top and bottom on May 11 (shown on page 11, 12 and 13), I put them in a large flight room. In the next week, they built up their flight muscles, their bill tips grew somewhat longer and they removed many pine seeds from pinecones. When they could fly well and had sufficient experience at removing the seeds from pinecones on pine branches placed in their room, they were released where they could join the mixed flock of finches that were coming to our bird feeders. Our land has a large number of old Ponderosa Pine trees with many cones with seeds in them, so the two birds had plenty of food.

After getting many photos of the light RECR reaching for a protuberance as in the photo above or just after it let go, I finally succeeded in getting the photo below on page 10, of the bird actually biting on one of the branches to twist its bills. These photos were taken on May 8.

This is the photo of the light RECR fledgling biting on a broken branch on May 8. Right after I took the photo, I observed it make a quick twisting motion that forced its upper bill to the left and the lower bill to the right. It then released its hold on the branch. It reached down and repeated the motion while the camera was getting ready to take another photo. This was the best photo I was able to take of the bird grasping a protuberance right before twisting its bill tips.



MAY 8 The dark RECR fledgling had developed a crossed bill configuration with its lower bill projecting to the left and the upper bill projecting to the right, which became more pronounced as the bill tips grew. These photos were taken on May 8, 2017, the same day as I finally succeeded in taking my best photo of the light fledgling actually biting on the branch shown in the photo on page 10. On this bird, the bills can be observed to be long enough to remain crossed.

MAY 8 The light RECR fledgling developed a crossed bill configuration with its lower bill projecting to the right and the upper bill projecting to the left, which became more pronounced as the tips grew as shown by these photos. These photos were taken on May 8, 2017 the same day as the photo on page 10, showing this bird grasping projections on the branch. This bird's bill tips were not yet crossed quite as much as those of the dark RECR but were long enough to remain crossed.

MAY 11 The photos on this page are of the bills of the dark RECR fledgling on May 11, 2017. As can be observed, on that day the upper and lower bill tips had grown visibly longer and were in their permanently crossed position. This bird had a crossed bill configuration with the lower bill projecting to the left and the upper bill projecting to the right.

MAY 11 The top and bottom views of the dark RECR on May 11 clearly show the observably longer bill tips in their permanently crossed position. In the bottom view on the right, it can be observed that the lower mandible has been bent slightly to the left and the upper mandible has clearly been bent to the right. The curve in the upper mandible can easily be observed in the above photo taken of the bottom of the bills.

MAY 11 This page shows the same four views of the bills of the light RECR on May 11, 2017 after its bills were completely and permanently crossed.

MAY 11 In top and bottom views of the bills, the bird had its lower mandible projecting to the right and the upper mandible projecting to the left. The bills are in their permanently crossed position. The curve in the upper mandible is not as obvious on this bird as on its sibling's bills shown in its photos on page 12.

THE CONTROL POST-FLEDLING RED CROSSBILL THAT WAS UNABLE TO TWIST ITS BILLS BECAUSE OF A BROKEN LEG

Several years ago, I was asked by Craig Benkman what would happen if a young crossbill was not able to twist its bills while the tips were in the period of fast growth. He used the terminology, "fast growth period of the bill tips" when talking to me.

In spring of 2008, I received a fledging Red Crossbill with a broken leg who answered that question. It was brought to me right at the beginning of the period of fast bill tip growth, but the bird's mouth was still able to close. I splinted the leg and propped the bird upright with rags. In the middle of a nest of soft fabric and unable to stand, the bird was not able to exert any twisting action on its bill while the bill tips grew. The question of what would happen was soon answered. The upturned tip of the lower bill began pushing upward against the underside of the anterior of the upper mandible. The upper bill tip was also growing rapidly, but in a downward curve. The fast growing upturned lower bill forced the bird's the mandibles apart and the mouth to remain open. That condition is clearly shown in the photos of that injured young Red Crossbill on page 15. Note that in the last photo on page 16 after the tips were crossed, the bill tips were observably much longer than in the first two photos.

Not wanting the bills to hold the bird's mouth open permanently, I had to tape the bird's bills in a crossed position between feedings to cause it to develop a cross-billed morphology so the bird would be able to close its bills, drink, eat and remove seeds from pine cones. I had to remove and then replace the tape each time I fed the bird, about every 20 to 30 minutes except at night when the bird and I were sleeping. At night, the tips were taped in a crossed position.

The leg was healed and the bird was walking normally 9 days after I received it. By then the bill tips were fully-grown, crossed and the fast growth of the tips had stopped. Consequently it did not bite and twist after it was able to use its legs. My taping the bill in a crossed position appeared to be completely successful. The bird was able to extract pine seeds from the pinecones I provided for it. It put its crossed bills between the scale and the cone shaft in the normal way for crossbills, opened its bill to expose the seed, and removed the seed with its tongue. Because it had obviously been flying around with its parents and siblings before being injured, it knew how to remove pine seeds from the cones and began doing so immediately after it could walk on its healed leg. After it had built up its flight muscles, I released it in our yard near our bird feeders. It joined the other finches in the mixed flock of finches coming to our feeder.

The first two photos below show the injured crossbill's bills prior to taping them crossed, showing the tip of the lower bill tip growing upward directly into the bottom of the upper mandible and forcing the bird's mouth to remain permanently open. As the lower bill tip grew longer, the bills were forced to remain further apart. The bird would not have been able to eat or drink if I had allowed this to continue.

This photo shows the straightforward configuration of both bills on the young crossbill with the broken leg before I taped the upper mandible tip to the left of the lower mandible tip.

This is a side view showing the straight bills before I taped the upper bill to the left of the lower bill. There was no indication at all which direction I should make the upper bill go, but as can be seen in the next photo, the taping worked.

This photo shows the same post-fledgling after the bill tips had finished their fast growth. I determined which way the lower bill crossed on this bird since I taped them in this position. The bird didn't decide and possibly its genes weren't involved. However, there was a 50% chance I taped the upper bill in the direction the bird would likely have twisted it. Its bill tips permanently remained in the crossed position in which I taped them and worked perfectly to remove seeds from pinecones.

PHOTOGRAPHIC PROOF THAT YOUNG CROSSBILLS IN THE WILD FLEDGE PRIOR TO THEM HAVING A CROSS-BILLED MORPHOLOGY

These are two links to websites with photos of fledgling and post-fledgling Red Crossbills showing that the bill tips are not crossed. The first link shows an adult male feeding a post-fledgling youngster whose bill tips are just beginning their fast growth period.

https://ncmountainwoman.blogspot.com/2009/05/fledgling-is-red-crossbill-one-for.html

https://julielue.com/2018/05/09/red-crossbill-baby-pictures/

This is a May 2021 photo of a female Red Crossbill with two fledglings before their bill tips began the fast growth period and prior to doing the twisting motion of their mandibles to make their bills cross. This photo provided by Jim and Lark Greaves is also strong evidence that the bill tips on young crossbills do not cross prior to fledging as some sources state they do.

DISCUSSION OF WHAT CROSSBILL RESEARCHERS AND CROSSBILL STUDIES STATE CONCERNING HOW AND WHEN THE BILLS OF CROSSBILL SPECIES ARE CROSSED.

I could not by observation determine "why" one bird twisted so the lower bill went to the left and the upper to the right, or twisted the opposite way. In his study Knox, 1972, concluded that the direction the lower mandible crosses is determined early in development. He hypothesized that the asymmetry of the jaw could be the stimulus or genetic trigger for the direction the birds twist their bills. Another crossbill researcher, Dr. Craig Benkman, told me he had not observed young crossbills during the fast growth period of the bills so had not observed the birds twisting their bills to make them cross. He said he believed what previous researchers had said in their studies concerning this aspect of a crossbill species' development, but he found my photos intriguing. He suggested that I would have to do a large study with many young crossbills, saying a group of birds that were free to make their bills cross and a group of controls to show what would happen if the young birds were prevented from making their bills cross would be needed. I had already sent him the photos of the post-fledgling crossbill with a broken leg. I asked Dr. Benkman how I would be able to "control" a

group of healthy, uninjured crossbill fledglings, but he had no answer for that. I told him that the controls would all have to be euthanized because they wouldn't be able to eat or drink with the bills permanently held apart by the long upturned lower bill growing into the bottom of the upper bill. I said a rehabber would never do that to a healthy bird and neither would an ethical researcher. Having served on an Animal Control and Use Committee for six years, I am certain that such a study would not or at least should not ever be approved.

The following paragraph is what Benkman said in his study about the direction of crossing (Benkmam, 1996). http://www.uwyo.edu/benkman/pdfs%20of%20papers/benkman_1996.pdf

"Whether the direction of crossing is environmentally (James et al., 1987; Groth, 1992) or genetically based (Benkman, 1988a; Groth, 1992) has been the focus of much speculation but few studies. However earlier unpublished observations of nestling Red Crossbills (Loxia curvirostra) (H.B Tordoff, per. comm.) show that there is likely to be little environmental influence on the mandible crossing direction. Tordoff had a captive breeding colony of Red Crossbills and he found that nestling crossbills consistently abducted their lower mandible to the side to which it later crossed. The asymmetric jaw apparatus and possibly even the asymmetric jaw musculature (Knox, 1972), apparently begins to develop early in the nestling stage and possibly even while in the egg. Thus, even though the mandibles begin crossing several weeks after fledging (Newton, 1972) the direction the lower mandible crosses is determined much earlier in development. Although this does not eliminate environmental effects on the mandible crossing direction, it makes it extremely difficult to envision phenotypic variation as an adaptive response to environmental variation since parents feed nestlings regurgitated seed kernels." Note that Benkman says that what Newton states in his study "does not eliminate environmental effects on the mandible crossing direction." Thus, an environmental effect, such as the birds themselves twisting the mandible tips to make them cross is entirely possible.

Interestingly, Groth (Groth, JG, 1992. Further information on the genetics of bill crossing in crossbills. The Auk 109(2):383-385) stated the following concerning the hypothesis that the directionality of the bill crossing could possibly be modified during the period of fast bill tip growth. "No current data disprove the hypothesis that directionality has the potential for environmental modification during the critical stage when the mandible tips grow enough to cross. Asymmetrical muscle development on the sides of the head and behavioral "handedness" (see Knox 1983) for example, potentially could develop only after crossing direction has been determined."

If as Knox observed, the direction the lower mandible crosses is determined early in development, his observed asymmetry of the jaw could have been the stimulus or genetic trigger for what I and other rehabbers observed concerning the way the birds constantly twisted their bills, appearing to cause the fast growing lower bill tip to go to the right or left of the fast growing upper bill. However, the statement "the mandibles begin crossing several weeks after fledging" Benkman attributed to Newton (Newton, 1972) is not consistent with what I documented on the young crossbills. For example, it was almost 2 weeks between the photo on page 1 taken on April 13 of the hatchling dark RECR and the next photos on page 4 of the same bird as a fledgling on April 26. On April 26, both birds could fly and eat sunflower seeds and other bird food by themselves, thus I would assume that would have been 2 or 3 days after their date of fledging if they had been raised by their parents. A week after April 26, on May 3, the two siblings began twisting their bills on protuberances on the branches in their flight box. That was right at the beginning of the fast bill tip growth period. They had stopped all twisting by May 11, when their bills were permanently crossed and their bill tip growth returned to replacement bill tip growth. Thus, on the 2 post-fledgling crossbills that I

documented with photos, the mandibles began to be twisted the same direction many times a day, apparently to cause them to cross since that is what occurred, approximately 9 days after fledging, not several weeks. Other rehabbers and I observed close to the same timing on all of the crossbill young that we raised and released.

I received the 2 birds whose multiple photos are in this document for care when they were older hatchlings, with their feathers still growing. Thus, I assumed the birds were between 9 and 11 days old when I received them on April 13. They would have been approximately 38 to 40 days old when the bills were permanently crossed and the birds could begin removing seeds from cones. If the birds fledged at approximately 18 to 20 days old, plus or minus a day or two, it took approximately 20 to 21 days or three weeks after fledging until the bills were permanently crossed. That could be called "several weeks after fledging," but why not say approximately three weeks rather than "several weeks," which could be any where from 3 to 6 or 7 weeks. Apparently, this time period had not been well documented.

In their study, Edelaar et al. (2005) stated the following in their abstract. "Unusual among birds, the bill tips in crossbills (Loxia spp.) overlap in the vertical plane, with the tip of the lower mandible to either the left or right of the tip of the upper mandible when viewed from above. Patterns observed in wild populations and experimental foraging data suggest that a 1:1 ratio of left- to right-crossing individuals is maintained by frequency-dependent natural selection in some populations, and that genetic drift causes deviation from a 1:1 ratio in other populations. Both processes require a genetic basis for this remarkable polymorphism, yet few data are available that address whether, and how, mandible crossing direction is heritable. To test for a genetic basis of this trait (single or quantitative, autosomal or sex-linked), we analyzed resemblance in mandible crossing direction between related captive-bred individuals of several crossbill taxa with standard statistical techniques as well as modern animal model methodology. Surprisingly, we did not find statistically significant support for a genetic basis of mandible crossing direction. Comparisons of the ratio of left- to right-crossing males and females in wild populations also did not support a sex-linked quantitative genetic basis. We conclude that mandible crossing direction may have uncharacteristically low heritability, but we cannot rule out that it is nongenetically determined." (Pim Edelaar, Erik Postma, Peter Knops, and Ron Phillips. "No Support for a Genetic Basis of Mandible Crossing Direction in Crossbills (Loxia Spp.) *The Auk* 122, no. 4 (2005): 1123-129.) https://www.jstor.org/stable/4090517

The findings in that study by Edelaar et al. does not preclude the birds themselves manifesting a behavior conducive to making their bills cross by doing a twisting with their mandible tips as other rehabbers and I observed. Phenotypic variation occurs when the expression of the genes is changed in response to the environment. It could be assumed that the birds twisting their own mandibles on protuberances to make them cross would be considered an environmental effect. Any asymmetry of the jaw, if there is such, likely occurs during development in the egg. Thus the asymmetry might be the genetic stimulus that dictates the direction the bill tips are caused to go by the twisting behavior of the birds themselves. However, nothing I observed on the birds, indicated asymmetry of the jaw exists prior to the birds doing the twisting of the bill tips.

Obviously, such factors as the fast growth of the bill tips on the fledglings when it is time for them to begin procuring their own food, as well as the downward curve of the upper bill as it grows and the upward curve of the lower bill as it grows are triggered by the genes of the crossbills. However, the young birds in the photos shown herein strongly indicates that the bird itself, twisting its own mandible tips on bark and branches, determine which direction the bills cross. Neither photos nor close observation showed whether the direction is choice or is genetically triggered. However, the

drawings of jaw muscles from Wikipedia, shown below on page 19, drawn by William Yarrell for his 1843 paper on crossbills, may be a clue as to how the direction is genetically triggered.

What was definitely observed and documented by rehabbers is that the birds twisted their mandible tips over and over for several days, using bark or short branches, which appeared to force the upper bill and the lower bill to cross in the direction the birds twisted.

DISCUSSION REGARDING OUR HYPOTHESIS THAT CROSSBILLS PHYSICALLY CAUSE THEIR BILLS TO CROSS AND SUGGESTIONS FOR FURTHER STUDIES

The null hypothesis as stated to me by researchers who studied crossbills is as follows:
"The bills on young crossbill species cross with the lower bill tip going to the left or to the right of the upper bill tip at some point during development because of genetics, with the birds themselves having no part in the process. "

From observations by myself and other rehabbers and the photos in this document, this null hypothesis was not proven and in fact was shown to be mostly false. Also, I could find no observations, documentation, data, photos or other information in published crossbill studies that provides evidence or actual verification for the null hypothesis.

Based on the photos of the two 2017 Red Crossbill fledglings, until the birds begin to pry their bills, there is no visible evidence in the shape of the bills or the behavior of the birds to indicate which direction the fast growing bills will eventually be twisted. This does not imply that the direction each bird twists is not genetically programmed as there was no evidence to show whether it was or not.

When I taped the bills crossed on the 2008 injured Red Crossbill fledgling, I made the decision to make the upper bill go to the left and the lower to the right. The bird's bills were still successfully crossed. What happened on that bird regarding the lower bill growing into the bottom of the upper bill and forcing the mouth to remain open prior to the bills being taped in a crossed position likely do not disprove the hypothesis that genetics dictate which way the bills have to be crossed. I had a 50-50 chance of making the bills cross the way the bird would have twisted its mandibles, if it had been able to stand and twist. What occurred with this bird proved nothing about that particular genetic factor.

Hopefully, this document is evidence for indicating that fledging crossbills do twist their bills to make their mandible tips cross, thus disproving the null hypothesis. If the bills "genetically" grow into a crossed position, with the bird having no part, the bill tips should have done so on the crossbill fledgling with the broken leg. Obviously there is no monetary gain or any other reason for crossbill researchers and other ornithologists to insist the hypothesis, "the bills just suddenly cross with no action on the bird's part," is true. One has to wonder why there is so much resistance against giving the young birds credit for what they do themselves with regard to making their mandible tips cross by their own actions.

After reading what it says about crossbills in Wikipedia, it appears that some of the information on young crossbills posted there appears to be incorrect. Here are two such paragraphs about crossbill youngsters that contain misinformation.

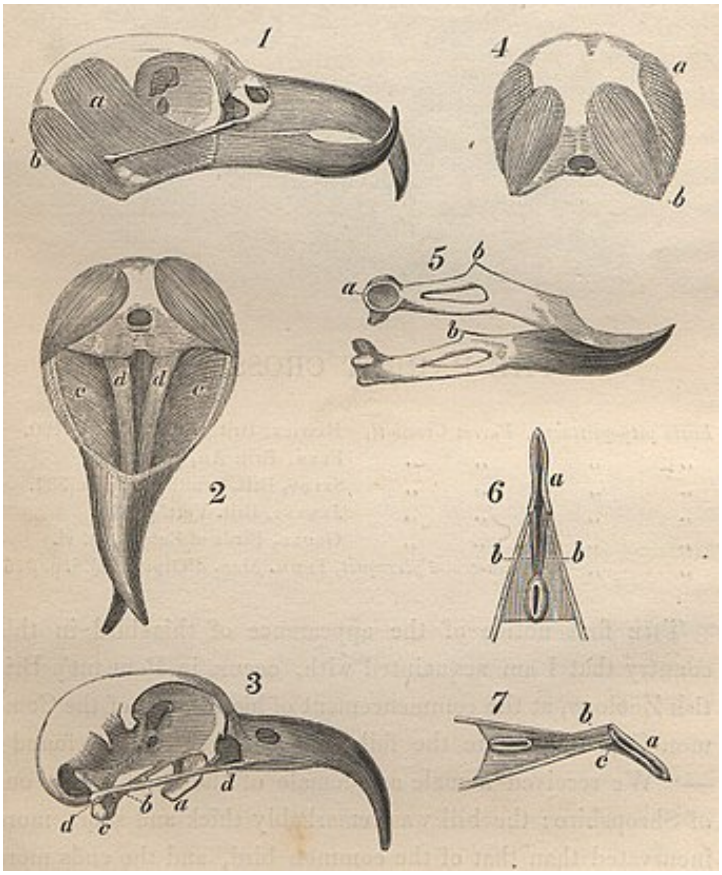
"The mechanism by which the bill-crossing (which usually, but not always, occurs in a 1:1 frequency of left-crossing or right-crossing morphs) is developed, and what determines the direction has hitherto withstood all attempts to resolve it." As shown in this document, this statement is actually not correct concerning the mechanism, since the mechanism is the bird itself making its own bills cross by twisting the tips of the mandibles during the fast growth period. I reported this observed mechanism to crossbill researchers, including Dr. Craig Benkman over 10 years ago. It would seem that crossbill researchers who have captive crossbills in aviaries could have put up cameras by now, to record what the crossbill youngsters do when the researchers are not directly observing them. The researchers could then see that the birds themselves determine the direction the bills cross by each bird twisting its fast growing mandible tips to make the bills cross in the direction the bird itself twists them.

The other Wikipedia paragraph is as follows, "It is very probable that there is a genetic basis underlying the phenomenon (young birds whose bills are still straight will give a cone-opening behavior if their bills are gently pressed, and **the crossing develops before the birds are fledged and feeding independently),** but at least in the red crossbill (the only species which has been somewhat thoroughly researched regarding this question) there is no straightforward mechanism of heritability."

This statement – **"the crossing develops before the birds are fledged and feeding independently"** appears to be completely incorrect based on personal observations and the photograph on page 17. The young crossbills other rehabbers and I raised **could fly and eat sunflower seeds and baby bird food by themselves for over a week before the fast bill tip growth began, thus the bill crossing behavior took place several days after fledging. Young crossbills normally fledge at between 15 and 20 days and the crossbills I raised were between 38 and 40 days old by the time the bills were permanently crossed.** Between 38 and 40 days old is approximately twice as old as they were when they fledged, thus not even close to prior to fledging. In the wild, the parents continue to feed pine seeds to the fledgling birds until their bills have successfully crossed, at which time the young crossbills are able to remove seeds for themselves.

Regarding the direction the individual bird twists its bills, obviously something stimulates the individual crossbill post-fledgling to twist its lower bill either to the left or to the right and of course the upper bill the opposite way when the fast bill tip growth period begins. It is easy to understand how the rush of growth hormones that stimulate the mandible tips to grow much faster for several days would likely also genetically stimulate the bird to twist them to make them cross. However, close observation did not indicate what stimulates the birds to twist their mandibles in the direction they do. Several studies have shown that about half of Red Crossbill youngsters are "lefties" and half are "righties." So about half twist the lower bill to the right and the upper bill to the left and about half twist the bills the opposite way, but no study shows what might stimulate each individual bird to do what it does.

This May, 2022 photo of an adult Red Crossbill by Eugene Beckes clearly shows the curve in both the upper and lower bills.



From Wikipedia https://en.wikipedia.org/wiki/Crossbill, this is a drawing from an 1843 paper by William Yarrell that shows the skull and jaw anatomy on an adult crossbill.

In the above drawing of the muscles of the jaws by William Yarrell, the muscles on the left side are shown to be somewhat larger than those on the right of the bird's head in drawing (Number 4). I have no idea if a drawing of a crossbill with the lower bill going to the left of the upper bill would have larger muscling shown on the right side of the bird's head. The tip of the upper bill is drawn curved to the left in a top view (Number 2) and the lower bill is drawn curved to the right. I observed such curves on the bills of birds I raised after the bills had crossed. Those curves in the bills are visible in my photos.

I don't like birds to be deliberately killed even for science. However, it should be possible on dead birds that have accidentally been killed to x-ray the skull and jaw bones and then closely examine the muscles on the sides of the head of hatchling crossbills to determine if the muscling is different for each side as this drawing suggests. However, Yarrell's drawing depicts the jaw muscles on an adult bird. Thus, the muscles on the side of the jaw that had to work the hardest during its life, the left side on the specimen drawn by Yarrell, would most likely be larger than the muscles on the right. Such a difference would likely not be evident for the muscles of a hatchling or a fledgling prior to it making its mandibles cross. It seems that in the 178 years after Yarrell published his drawing, someone would have thought of examining and comparing the muscles on dead hatchlings, fledglings and adults. Depending on what is found, such examinations possibly might help explain how and if there is a "straightforward mechanism of heritability."

In this age of high technology, it should be simple to x-ray the jaws of dead nestling crossbills to determine if they actually have the asymmetric jaw apparatus and the asymmetric jaw musculature that Knox reported (Knox, 1972) and that Yarrell's drawing suggests on an adult. It should be easy to

prove with x-rays and/or dissection of birds of various ages whether this asymmetry actually develops early in the egg, in the nestling stage, or if it only occurs on adults after the birds have successfully caused their own bill tips to cross and the use of their bill tips results in the jaw muscle being larger. Best of all, this type of research would not be inhumane if the heads of accident-killed nestlings, fledglings, post-fledglings and adults were used.

Finally and most importantly, in this age of cameras everywhere, if crossbill researchers still have crossbills in aviaries and want to observe how the young crossbills make their own bills cross, it should not be difficult to put cameras where fledglings can be constantly viewed and videoed. This would allow researchers to actually see how the young crossbills bite and twist hundreds of times per day on various protuberances on the branches on which they are perched to cause the tips of their mandibles to cross and after several days, remain permanently crossed. Such videos would show whether the live post-fledgling crossbills are involved in the crossing of their own mandible tips and how many times a day they twist their mandibles until the bills are permanently crossed. Such photographic evidence would also prove our hypothesis that post-fledgling crossbills physically contribute to making their own bills cross by twisting the bill tips continuously in the daytime during the period of fast bill tip growth, and at the same time the videos would provide a more precise age for the birds when they make their bills cross, than is currently in the scientific literature. Both of these factors seem to lack agreement, or any actual substantiation in the current published crossbill studies or on most websites on the Internet where many people obtain information on wildlife.

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INTERESTING PHOTOS SHOWING HOW CROSSBILLS PICK UP GRAVEL AND SALT FROM ROADWAYS

The following photos on page 24 were taken on February 2022 by Mike Daniels, Hamilton, MT. His interesting photos show very clearly how crossbills pick up the salt covered gravel with their tongues. This behavior has been known for decades (see Tozer, 1994), but good photos of it seem to be somewhat lacking.