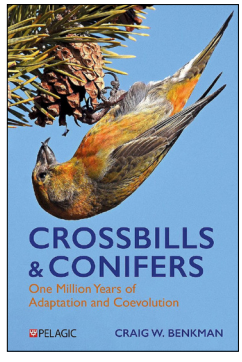
Crossbills & Conifers: One Million Years of Adaptation and Coevolution

By Craig W. Benkman. 2025. Pelagic Publishing. 224 pages, 76 illustrations, 120.00 CAD, Hardcover, 55.00 CAD, Paper. Also available as an E-book.



In *Crossbills & Conifers*, Craig Benkman provides his insights into the amazing coevolutionary arms race between these two organisms. He focusses mostly on the crossbills of North America: Red Crossbill (*Loxia curvirostra*), White-winged Crossbill (*Loxia leucoptera*), and Cassia Crossbill (*Loxia sinesciuris*).

In Chapter 1 (Why Crossbills? Crossbills, Conifers and the Origins of an Interaction), Benkman explains that cardueline finches, such as crossbills, have lower mandibles that can move laterally as well as vertically when husking seeds. This increases the force they can exert on the seeds and the potential angles they can use to reach them, making these birds more efficient at extraction; most seed-eating birds use only vertical force. Crossed mandibles (the upper mandible is straight while the lower mandible twists to either side) enable crossbills to spread the closed scales of cones apart and access the seeds within. There is an equal frequency of right- and left-crossing mandibles in the North American crossbill population, and this trait is not inherited. So, why do the crossings differ? Crossbills do not eat all the seeds in a cone; the law of diminishing returns encourages birds to move on when they are expending more energy than they acquire from their efforts. From a given perch, the most accessible seeds for a foraging crossbill are those on the side of the cone opposite to which its lower mandible crosses towards, and so when a second crossbill arrives to feed it will benefit from having a bill that crosses in the opposite direction. Crossbills use their tongue to secure seeds in lateral grooves in their upper palates, while they crack seed coats with especially sharp points (tomiums) on the same side of their lower mandibles.

Crossbills frequently disperse to locate large conifer seed crops—a large-scale migration that birders know as an irruption. As Benkman notes in Chapter 2, conifer seeds will often fail for multiple years following a bumper crop. Many crossbills are nomadic, wandering up to 4500 km from natal to breeding sites or between breeding sites (which also makes it difficult to estimate population numbers). In March or April, they search for developing seed crops, and then commonly nest in July and August, which coincides with seed ripening. However, after bumper crops crossbills might nest in late winter or spring; cold temperatures aren't a challenge as long as there is a good seed crop. In Chapter 3, Benkman discusses how cone structure influences a crossbill's access to seeds. Crossbills will feed on many species of conifer trees, switching between species when seeds start to run low. In fall, they generally feed on thinner-scaled cones that would not survive winter (such as those of spruce trees), and then they progress to cones with thicker scales that hold their seeds longer, such as those of pines.

In Chapter 4, Benkman discusses the variation in size and rich diversity of vocalisations among Red Crossbills. They have 10 to 12 categories of "call types" (the total number depends on which authority you're using), and Benkman found that each call type is adapted to a particular conifer with seeds that are especially reliable from late winter to spring—the period of greatest food scarcity (p. 57). Crossbills are very tame and readily feed on cones provided to them, so Benkman and colleagues were able to observe crossbills in experimental settings in an aviary to complement the observations they made in the wild.

The coevolution between conifers, Red Squirrels (*Tamiasciurus hudsonicus*), and crossbills is a fascinating story (Chapter 5, Coevolution: Crossbills are More than just Ornaments). Conifers guard against seed predation in two ways: thicker cone scales and serotiny (a trait where cones remained closed for many years until heat, generally from fire, melts the resinous bonds holding the scales closed). Thicker distal scales respond to crossbill predation, making it harder for the birds to access these seeds. For squirrels, non-serotinous cones are only available for a few weeks in the autumn between seed maturation and shedding, whereas serotinous cones remain vulnerable for years. The presence of squirrels greatly suppresses crossbill numbers by exerting selection pressure that reduces the frequency of serotiny, and by precipitously harvesting serotinous cones before crossbills can access the seeds.

Throughout the summer and fall of 2025, as I was reading and reviewing this book, I frequently heard (and sometimes saw) crossbills in forested areas of Alberta and British Columbia feeding on bumper conifer seed crops. Such contact calls, inherited from their parents, serve to coordinate flock movements (Chapter 6). It is advantageous to flock with individuals of the same call type, because they will have similar bill sizes and hence similar foraging abilities.

Many of the numerous crossbill call types may

have evolved following the expansion of conifers in the last 9000 to 10 000 years and may represent sibling subspecies (Chapter 7). Cassia Crossbill is only found in two small mountain ranges in southern Idaho and has speciated due to behavioural isolation, whereby individuals associate with others producing the same contact calls as their own. Cassia Crossbills stay within such a small range because there are no Red Squirrels, and Lodgepole Pine (*Pinus contorta*) there produces prolific serotinous cones that stay on the branches for decades, slowly weathering enough for the crossbills to dig between the scales. This provides reliable year-round food. As explained in Chapter 8, bumper seed crops can lead to multiple call types feeding together and interbreeding. This reduces reproductive isolation, such as that which led to Cassia Crossbill speciation.

In Chapter 9, Benkman discusses the threats to cone production and causes of widespread cone failure that impact crossbill populations: short harvest rotations; increases in size, frequency and severity of wildfires; increases in bark beetles and other insects; and hotter temperatures causing serotinous cones to open and drop seeds before crossbills can harvest them.

Benkman suggests some outstanding research questions in the Epilogue. For example: What delayed the evolution of crossbills? What can crossbills tell us about other birds and ecology, and evolution more generally? Perhaps crossbills fascinate Canadian birdwatchers because they are our winter finches, not migrating south as most other species do.

This book is well organized into a preface and 10 chapters, and it includes a five-page glossary, 25 pages of references, and a five-page index. There are 76 figures and plates, graphs, photo comparisons, and maps. Seven of the chapters have text boxes that explain concepts that may be tangential to the main topic, such as Causes and Consequences of Variation in Frequency of Serotiny (p. 88).

In the Preface, Benkman states that his goal is a book for graduate students and academics as well as passionate naturalists and birders. In distilling nearly 30 years of research into one book (I noted 63 papers written or co-authored by Benkman in the references), he succeeds with the first audience, but I think the second audience will find it dense. It would have helped to include a layperson's summary at the end of each chapter. Or, perhaps he needs to write a second book.

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