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# On the advantages of crossed mandibles: an experimental approach

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The importance of the crossed mandibles to crossbills for foraging on conifer cones was studied by removing most of the crossed portion of the mandibles of two Red Crossbills *L. curvirostra*. The foraging rate of these two bill-altered crossbills on the cones of three species of conifers was compared to their rates prior to bill alteration and to two controls. The mandible crossing proved essential for extracting seeds from closed cones. However, as cones open the bill crossing becomes less critical. The mandible crossing appears to be one of several adaptations of crossbills that have extended the period during which conifer seeds can be exploited effectively.

The functions of morphological structures can often be understood by detailed observations of organisms. However, a difficulty with ascribing a function to a structure by observation alone is that different observers often come to different conclusions. Experimental investigations of function are desirable but are often either difficult or trivial. For example, removing a bird's leg would make perching or terrestrial locomotion impossible or awkward. In some cases, however, slight modification of structures may provide a means for studying a structure's utility.

One striking example of the difficulty of attributing a function to a structure by observation alone is the crossed mandibles of crossbills *Loxia*. There have been many opinions as to the function of the mandible crossing ranging from those suggesting no adaptive value to those suggesting a specific adaptive function. For example, Buffon (quoted in Yarrell 1829) stated that the mandible crossing was 'an error and defect of Nature, and useless deformity'. Malzer (1937) posited that the mandible crossing allows crossbills to husk seeds with closed bills. Robbins (1932) suggested that the bill crossing was critical in providing access to seeds in conifer cones. He argued that the mandible crossing acted as a lever as the bill was twisted between adjacent cone scales causing the scales to separate. Most recently, the precise function of the mandible crossing has not been addressed (e.g. Tordoff 1954, Newton 1972, Knox 1983), although its importance for foraging on cones has been assumed (Tordoff, pers. comm.).

The crossed part of the mandibles is mostly rhamphotheca and can be removed without altering a crossbill's behaviour (pers. obs.) and thus provides a system where the foraging rate of crossbills with normal mandible crossing and with reduced mandible crossing can be examined. Below I describe an experiment where I compare the foraging rates of captive Red Crossbills *L. curvirostra* with crossed (normal) mandibles to those whose crossed tips had been removed (Fig. 1). Crossbills are excellent study subjects because they are very tame, and their whole foraging substrate can be brought into the laboratory where timed and controlled

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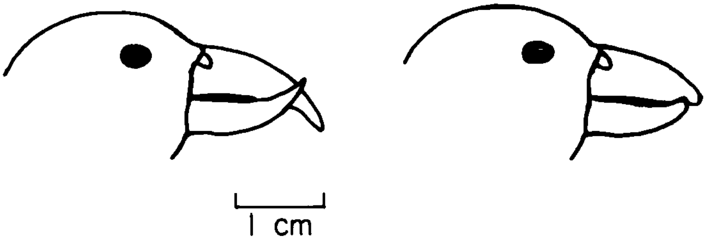

Figure 1. A schematic diagram of the heads of Red Crossbills. On the left is a representation of a bird with crossed mandibles and the bird on the right represents a crossbill with most of its mandible crossing removed as in the experiment.

measurements can be made; crossbills forage nearly exclusively for seeds in conifer cones throughout the year (Newton 1972, Benkman 1987a). I describe both the use and importance of the mandible crossing for crossbills while extracting seeds from conifer cones and suggest several steps in the evolution of the crossbill foraging apparatus.

## Methods

Captive Red Crossbills were housed in a 4 × 3 × 2·5 m indoor aviary and provided with fresh conifer branches, water with vitamins, grit, salt, limited quantities of commercial sunflower and thistle seeds, and conifer cones. During and prior to the experiments, most of the crossbill's diet consisted of seeds which the crossbills had to extract from closed conifer cones.

Foraging trials were conducted in a 1·3 × 0·65 × 0·65 m wooden box that had a partition dividing the box into two equal chambers. A conifer branch with its naturally attached cone was suspended from a clamp approximately 0·3 m above the floor of one of the chambers while a crossbill was in the adjacent chamber. A door was then slid open allowing the crossbill to forage. Prior to the foraging trials crossbills were deprived of access to seed for 14 h or more. Data were recorded with an Apple II+ computer programmed to time and record events for which I pressed keys on a keyboard while observing foraging crossbills. Time spent prying cone scales apart to extract seeds and time spent husking each seed were recorded to 0·1 s. Seed husking included the time from when the seed was first held in the tip of the bill until the kernel was swallowed.

Four Red Crossbills were timed while foraging on green, closed cones of European larch *Larix decidua* (hereafter larch), eastern hemlock *Tsuga canadensis* (hereafter hemlock), and white pine *Pinus strobus* (Fig. 2) between 16 August and 12 October 1983. The cone-bearing branches were all gathered from single trees of each species in Albany County, New York, over one and two day periods in August and September 1983. These conifers were chosen because they represent a wide range of conifer cone structures and because the captive crossbills readily foraged on them. White pine and hemlock seeds are both important to the diet of Red Crossbills in northeastern North America (Benkman 1987a), and larch seed is an important crossbill food in Eurasia (Newton 1972). I kept cones from drying and opening by storing them in plastic bags at approximately 2°C. Prior to each series of foraging trials, each bird was allowed to forage on at least five cones of each conifer species in the aviary.

After recording the foraging data for all four crossbills on the closed cones of each of the three conifer species, I removed nearly all of the crossed portion of the mandibles from two of the four crossbills (Fig. 1). One male and one female had their mandibles altered, while one male and one female served as unaltered controls. Most of the crossed portion of the mandibles was removed by clipping the tips of the mandibles with nail clippers. The experimental birds were then placed in the foraging chambers for a total of several hours with sandpaper covered perches and pitch covered white pine cones. Birds treated in this manner frequently wiped their bills on the perch to remove the pitch, and the wiping served both to shorten the mandibles and to round the cut edges. The control birds were not held in chambers at this time; however, they too were given white pine cones to forage on and removed pitch from their bills by wiping them on conifer branches in the aviary. Other than the bill clipping and being exposed to sandpaper covered perches, all four birds were handled nearly daily, all had pine pitch on their bills from

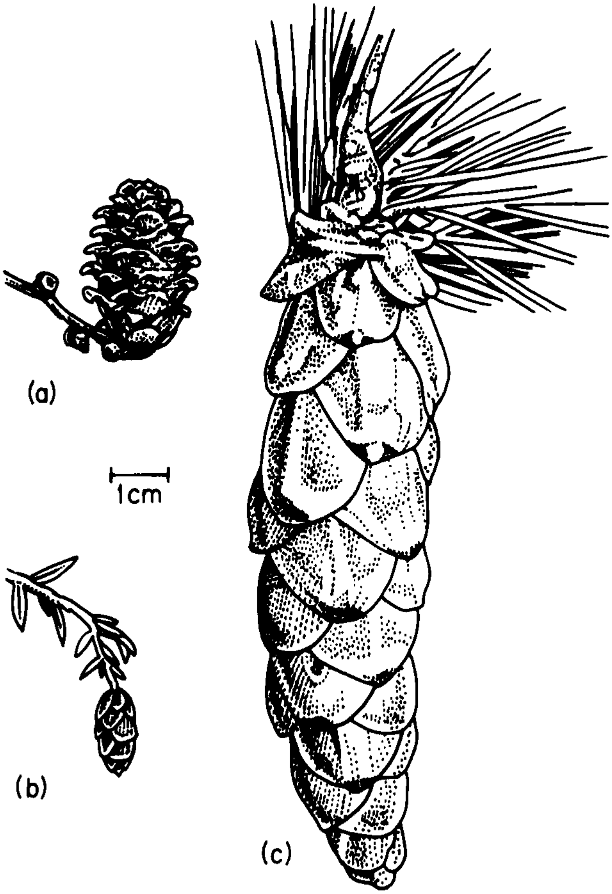

Figure 2. An illustration of the closed cones of the three conifer species used in the experiments: European larch (A), eastern hemlock (B), and white pine (C).

foraging on white pine cones, and all were held in the foraging chambers. There was no indication during the experiments that the experimental birds were injured or stressed by the above procedure and the mandibles grew back to normal lengths within a month. During the experiments, the experimental birds may have been housed in the foraging chambers slightly longer than the controls. However, prior to the experiments each bird had been held in the chambers > 200 h.

In contrast to the field, crossbills in the laboratory, when given only a single cone, will at times forage on the cone even when few seeds remain, causing short-term intake rates to decline substantially. I therefore analysed only the average prying times for a maximum of the first 15 seeds consumed per cone. The prying time per seed for some trials, particularly for hemlock cones, was based on fewer than 15 seeds consumed.

Husking time is the mean from one foraging trial with a white pine cone, based on a minimum of ten seeds in all cases except one. Husking time was not analysed for larch and hemlock, because after bill alteration the experimental birds were unable to extract seeds from cones of these species. Sample sizes refer to the number of foraging trials (cones). All statistical tests were two-tailed Kruskal-Wallis tests.

## Results

The average prying time per seed prior to the bill treatment did not differ significantly between the two experimental and two control crossbills foraging on either of the three conifer species ($P > 0·30$). After I altered the bills of the two experimental crossbills, either they could not extract seeds from the cones of either larch or hemlock or the bill-altered crossbills required significantly more time to obtain a seed as compared to the controls ($\chi^2 = 11·3$, $P < 0·001$) (Table 1). The bill-altered crossbills spent between 22 and 65 s attempting to pry apart the cone scales of larch and hemlock without obtaining any seeds; about ten times longer than the crossbills required to obtain and consume larch and hemlock seeds prior to bill alteration (Table 1). Two days after the experiments on larch, I placed > 50 closed larch cones in the aviary and allowed all the crossbills to forage on the cones. For 20 minutes the two experimental birds were unable to remove seeds from the cones, whereas five other captive crossbills, including the two controls, rapidly removed seeds from the cones.

After bill alteration the two control crossbills (non-altered) removed seeds at faster rates than they did prior to the treatment from closed white pine cones ($\chi^2 = 14·2$, $P < 0·001$). This decline in prying time per seed probably resulted from the cones drying and the scales separating slightly between the two treatments; prying time per seed decreases as cones dry and open (Benkman 1987b).

Prying time per seed did not differ between the bill-altered crossbills and the controls when foraging on open cones that were full of seeds. One dry open white pine cone (these cones were chosen to be as similar as possible) was given to each of the four crossbills. All four birds had very similar average prying times per seed (control birds: $\bar{x} = 1·2$ and $2·7$ s/seed; bill-altered birds: $\bar{x} = 2·5$ and $3·3$ s/seed)

Table 1. *Combined prying times per seed for four Red Crossbills foraging on green, closed cones of three species of conifer. Husking times are also presented for crossbills husking white pine seeds. Symbols between data indicate the statistical significance of the differences between the means*

| | Prying times | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | European Larch | | | | | | Eastern Hemlock | | | | | |
| | Pre-treatment | | | Post-treatment | | | Pre-treatment | | | Post-treatment | | |
| Crossbills | $\bar{x}$ | s.d. | $n$ | $\bar{x}$ | s.d. | $n$ | $\bar{x}$ | s.d. | $n$ | $\bar{x}$ | s.d. | $n$ |
| Bill-altered | 7·2 | 2·6 | 15 | Cannot obtain seeds | | | 3·2 | 1·4 | 13 | Cannot obtain seeds | | |
| Controls | 8·4 | 3·6 | 17 | 5·8 | 2·4 | 6 | 2·8 | 0·5 | 8 | No data | | |

| | Prying times | | | | | | Husking times | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | White Pine | | | | | | White Pine | | | | | |
| | Pre-treatment | | | Post-treatment | | | Pre-treatment | | | Post-treatment | | |
| Crossbills | $\bar{x}$ | s.d. | $n$ | $\bar{x}$ | s.d. | $n$ | $\bar{x}$ | s.d. | $n$ | $\bar{x}$ | s.d. | $n$ |
| Bill-altered | 22·7 | 3·9 | 13 | 33·0 | 15·4 | 8 | 2·9 | 0·5 | 13 | 3·3 | 0·5 | 8 |
| | | | | ** | | | | | | * | | |
| Controls | 24·0 | 5·9 | 13 ** | 7·1 | 2·8 | 8 | 3·1 | 0·4 | 14 * | 2·3 | 0·4 | 8 |

* $P < 0·01$, ** $P < 0·001$.

indicating that the full bill crossing is not critical in extracting seeds from cones whose scales do not enclose the seeds and that the bill-alteration did not impede all foraging abilities.

There was a significant effect caused by the bill-alteration on the average husking time. The bill-altered crossbills (following treatment) had significantly greater husking times than the controls ($\chi^2 = 9{\cdot}7$, $P = 0{\cdot}002$). Prior to the treatment, there was no difference between the average husking times for the experimental crossbills and the controls ($P > 0{\cdot}4$). The difference between the controls and the bill-altered crossbills after bill alteration was caused, in large part, by the decline in husking time for the controls ($\chi^2 = 10{\cdot}8$, $P = 0{\cdot}001$). The relative decline in husking time for the bill-altered crossbills may have been an artifact of my definition of husking time; timing of husking was initiated when the crossbills first held the seeds in the tip of the bill, yet the seed is actually husked (seed coat removed) near the base of the bill away from the portion of the bill that was removed. Nevertheless, bill-altered crossbills required on average only about 1 s more than the controls to husk a seed, whereas they required nearly 26 s more prying time to obtain a seed than did the controls (Table 1).

## Discussion

The experiments described suggest that the mandible crossing in Red Crossbills is essential for efficient seed extraction from the closed cones of at least three species of conifer. Yet the importance of the mandible crossing for obtaining seeds from cones declined as cones ripened and the scales spread apart. The removal of the mandible crossing did affect seed husking time, although the effect was negligible compared to that on prying time. Thus, contrary to Malzer (1937), the mandible crossing is not critical for husking seeds efficiently. In sum, the lack of the mandible crossing hindered some aspects of crossbill foraging, but other aspects were impaired only slightly, if at all.

Cone scales must be separated to expose seeds at the base of the scales so that crossbills can extract seeds with their tongue. Separating adjacent cone scales requires a crossbill to place its bill between the scales. This is simple on cones for which there are gaps between the scales given that sufficient lateral abducting forces can be exerted by the mandibles to spread apart the scales, or that the scales are already wide apart. On closed cones, however, crossbills must create gaps between the scales. This is done by the crossbills biting between the scales with their crossed and pointed mandibles. As can be seen in Figure 1, not only was the mandible crossing partially removed, but the bill tips also became more blunted. The combination of being crossed and pointed is essential in enabling the mandibles to bite between the cone scales effectively. Without the crossed and pointed mandibles crossbills are unable to create the necessary gaps.

The pointed bill tips, *per se*, are doubtfully sufficient for enabling crossbills to create gaps between closed cone scales. Pine Siskins *Carduelis pinus*, Siskins *C. spinus*, and European Goldfinches *C. carduelis* all have pointed bills and anatomical features that should enable lateral forces to be exerted (Tallman & Zusi 1984), yet these species are not known to forage for seed in closed conifer cones (Newton 1972, Benkman, pers. obs.). The pointed mandible tips of crossbills, particularly of the upper mandible, that are oriented in the direction of the biting forces, are probably necessary to create gaps efficiently between closed cone scales.

Lateral mobility of the lower mandible probably evolved because it increased the rate with which seeds could be extracted from partly open cones. Lateral abduction, rather than mandible crossing, would have been selected first because lateral abduction can provide increased access to seeds in cones whose scales are spread apart, and mandible crossing would not be beneficial without the ability to abduct the mandibles laterally. Later, crossed mandibles would have been advantageous since they would have further expanded the time during which conifer seeds could have been used, especially from closed cones. Slightly crossed mandibles are likely to be more effective than no crossing, thus a gradual increase in mandible crossing is plausible. Given that there was an advantage to exploiting seeds in less ripe cones, there was undoubtedly selection for crossbills being able to exert more powerful lateral abducting and biting forces. This would have also enabled exploitation of progressively heavier cones. This sequence of selection responses probably explains the general peculiarities of the foraging apparatus of crossbills. Tallman & Zusi (1984), based in part on a study of a hybrid Pine Siskin-Red Crossbill, also suggest that 'lateral prying' evolved prior to the mandible crossing in the *Carduelis–Loxia* lineage and that there was an increase in bill and body sizes in crossbills as progressively larger cones were exploited.

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