The advantages and evolution of a morphological novelty

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THE role of selective agents in the origin of evolutionary novelties has been controversial[1-3] and has remained outside the realm of experiments. Here we experimentally determine both the benefits of a single trait and the advantages accrued during the presumed sequence of evolutionary steps leading to the fully specialized structure. By comparison of red crossbills (*Loxia curvirostra*, L.), in which the mandibular crossing has been removed, with controls and with the related but less specialized pine siskin (*Carduelis pinus* Wilson), we show the advantage of the mandibular crossing in the extraction of seeds from partially closed conifer cones. We use the natural regrowth of the mandibles to mimic the evolution of mandibular crossing from an unspecialized ancestor, and use the relationship of foraging efficiency to mandibular regrowth to determine a scheme for its (gradual) evolution.

Crossed mandibles characterize crossbills (*Loxia*) (Fig. 1) and have been pivotal in their radiation into about 25 species and subspecies[4,5]. The pointed and decurved upper mandibles are inserted between overlapping conifer cone scales to create gaps which are then widened by lateral abduction of the lower mandibles. Once exposed, the seed is lifted out with the tongue and husked[6,7]. An earlier experiment[8] showed that mandibular crossing was essential for extracting seeds from closed cones. Here we further quantify this relationship for closed and open cones. We also determine the relationship between foraging efficiency and mandibular (rhamphothecae) regrowth to mimic the possible steps in the evolution of mandibular crossing. The regrowth is similar to natural bill growth of young crossbills after fledging (C.W.B., unpublished observations).

Measures of performance provide an index to the degree of adaptation of features[9-11] such as crossed mandibles. The rate of seed (food) intake is an excellent measure of performance[12]. Bill structure influences rates of seed intake by crossbills[7] which, in turn, has been shown to affect crossbill movements, diet selection[13], patch use[14], timing of reproduction[15] and presumably fitness. We measured the seed intake rates of seven captive red crossbills (*L. c. minor*) and five captive pine siskins (Fig. 1) foraging on seeds in the cones of western hemlock (*Tsuga heterophylla* [Raf.] Sarg.). This subspecies of crossbill, mostly confined to the coastal forests from Alaska to California[16], has

TABLE 1 Mean (±s.e.m.) seed extraction times

| | Seed extraction times (s)† | | |
	Experimental	Control	t‡,
Pre-alteration			
Open cones	1.49 ± 0.15	1.13 ± 0.13	1.70
Reclosed cones	1.34 ± 0.08	1.25 ± 0.11	0.70
Closed cones	1.61 ± 0.32	1.84 ± 0.10	0.62
Post-alteration			
Open cones			
Day§ 1	1.92 ± 0.30	1.20 ± 0.14	1.93
6	1.66 ± 0.29	1.43 ± 0.10	0.66
Reclosed cones			
Day 1	‖		
3	5.28 ± 0.11¶	1.33 ± 0.07	30.33***
6	5.57 ± 1.12	1.61 ± 0.32	2.92*
12	3.51 ± 0.26	1.59 ± 0.13⁕	5.85*
17	2.42 ± 0.21	1.59 ± 0.13⁕	3.13*
22	2.72 ± 0.16	1.78 ± 0.21	3.65*
29	1.96 ± 0.07	1.54 ± 0.10	2.86*
36	1.68 ± 0.21	1.24 ± 0.05	1.73
Closed cones			
Day 1	‖		
3	‖	3.06 ± 0.12	
6	‖		
8	‖	2.88 ± 0.19	
12	‖		
17	5.21 ± 0.29¶	2.89 ± 0.09	7.73**
22	4.64 ± 0.35¶	3.30 ± 0.37	2.66*
29††	4.03 ± 0.36	2.81 ± 0.04	2.86*

Data are for four experimental and three control red crossbills foraging on western hemlock cones.

† Seed extraction time is mean total time per seed minus mean seed husking time (see refs 7, 8). After the first seed removed from the cone was swallowed, we (A.K.L.) timed the interval of the extraction and consumption of the following five seeds (10 seeds before bill alteration) to the nearest 0.1 s. Data are based on the means of 9.6 ± 0.1 cones per bird and represent a total of 991 cones. Mean seed husking time (the interval required to remove the seed wing and seed coat and swallow the kernel) was determined each day for each individual on the basis of 16.4 ± 0.7 seeds per sample, for a total of 1,717 seeds.

‡ Two-tailed t-tests: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

§ Days after final bill trimming. We were often unable to obtain foraging data on both experimental and control groups on one day. Thus controls were measured as close in time as possible to bill-altered crossbills (0–3-day difference). Days refer to day of foraging trial of the experimental group, except for closed cones on days 3 and 8.

‖ Unable to remove five seeds from five cones.

¶ Based on data from three birds.

⁕ Represent data gathered on day 15.

†† Closed cones were depleted before seed extraction time for bill-altered crossbills converged to those of controls.
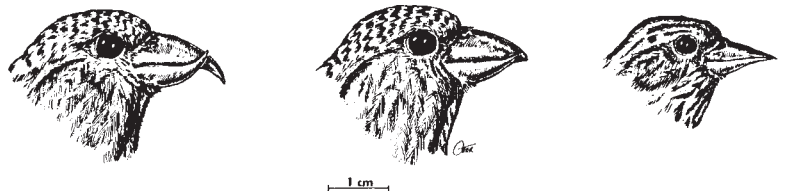
mandible length (mm) = 8.446 + 0.094 (day) − 0.001 (day)^2, $r^2 = 0.99$, $F_{2,5} = 288.40$, $P < 0.0001$), whereas the mandible lengths of controls grew slightly (upper mandible: mm per day = 0.004 ± 0.001, $r^2 = 0.84$, $F_{1,6} = 30.80$, $P < 0.005$) or not at all (lower mandible: mm per day = −0.0003 ± 0.005, $r^2 = 0.001$, $F_{1,6} = 0.005$, $P > 0.90$). Thirty-three days after bill clipping and three days before the last experiments the upper and lower mandibles were 96.9 and 101.2% of their original lengths, respectively. We did not determine repeatability of bill measurements during the study, but mean re-measurement error on 42 study siskins after one week was 0.04 mm for the upper mandible and 0.08 mm for the lower mandible. The upper mandible was measured from the anterior edge of the right nares to the tip of the mandible. The lower mandible was measured from the base where the rami meet to the tip of the mandible.
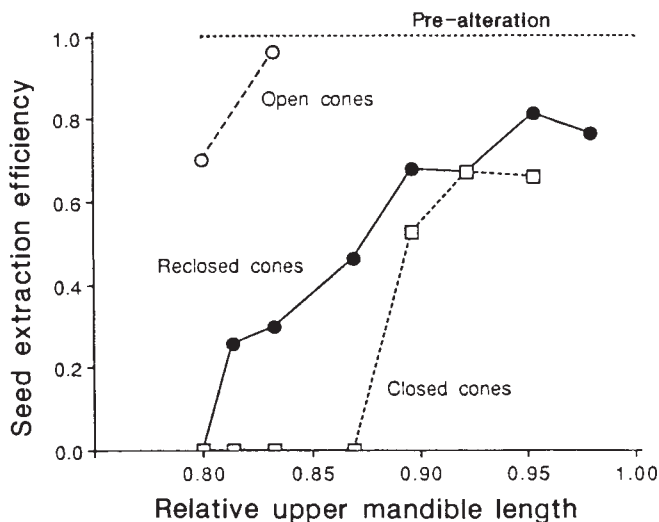
FIG. 2 Seed extraction efficiency of bill-altered crossbills relative to controls during mandible regrowth. The abscissa represents the ratio of the upper mandible length as estimated from the regression for regrowth (see Fig. 1 legend) to that measured before clipping. Measurements of the upper mandible were used because they are more accurate than those of the lower mandible (see Fig. 1 legend). The ordinate represents the reciprocal of mean seed extraction time for bill-altered crossbills divided by the same for controls, standardized to the same ratio before bill ablation. Foraging trials were conducted on birds that had fasted for $\geqslant 16$ h. Open cones: scales had separated, thus exposing seeds (common during dry periods from autumn to spring). Reclosed cones: scales had separated, but were closed from moisture due to rain or humidity (autumn to spring). Closed cones: scales had yet to separate (summer). All cones (19.5–22.5-mm long) were gathered from two trees.

a bill that is adapted for foraging specifically on western hemlock seeds (C.W.B., in preparation). Siskins also forage on hemlock seeds but have a more generalized diet[17,18]. We used cones representing summer foods (closed green cones) and winter foods (dry open cones and cones reclosed from moisture).

Mandibular crossing is essential for extracting seeds from between closed cone scales and increases in mandibular crossing enhance foraging efficiency on reclosed cones (Fig. 2, Table 1). The bill-altered crossbills could consistently remove seeds from closed cones, whose scales are difficult to separate, only after the upper mandibles had regrown to 90% of their original length. As the experimentally altered mandibles regrew to their original lengths, times to extract seeds from closed and reclosed cones converged on extraction times of controls (Fig. 2). Siskins could not consistently extract seeds from closed or reclosed cones during foraging trials. Thus, slightly crossed mandibles are advantageous for foraging for seeds in reclosed cones. As mandibular crossing increases, foraging efficiency increases on reclosed cones and seeds between tightly closed scales of closed cones become accessible.

Crossbills with and without mandibular crossings do not differ in their efficiency of seed extraction from open cones (Table 1). The rapid increase in efficiency on open and reclosed cones between the first and second post-alteration trials (Fig. 2) may reflect crossbills learning to use their shortened bills. Seed husking times of bill-altered crossbills do not differ from controls at any time on any cone (t-tests, $P > 0.20$). The absence of significant differences in these comparisons indicates that bill alteration did not injure the birds.

Siskins extract seeds from open cones at similar rates (1.02 ± 0.11 s per seed (mean $\pm$s.e.m.); sample size, $N = 5$ birds) to crossbills before bill alteration (1.33 ± 0.12 s per seed, $N = 7$ birds: $t = 1.88$, d.f. 10, $P > 0.05$) and may out-compete crossbills for these seeds. On the basis of measured foraging rates, average number of seeds consumed per cone (mean $= 15$ and 9 seeds

per cone for crossbills and siskins, respectively), and assuming equal travel time between cones (3.4 ± 0.87 s, $N = 9$, for crossbills in field (C.W.B., unpublished data)), identical assimilation efficiencies, estimated daily energy expenditures[19] and mean lean body mass (26.7 g for 7 crossbills, 12.5 g for 5 siskins), we estimate that siskins require only 74% as much time as crossbills to meet their daily energy demands when foraging exclusively on seeds in open hemlock cones. These results indicate that access to seeds in open cones has not been critical in the evolution of the mandible crossing.

We conclude that directional selection for increases in mandibular crossing enhances foraging efficiency on reclosed or incompletely opened conifer cones and is responsible for the origin of crossbills from an unspecialized ancestor. The subsequent diversification of crossbills reflects adaptations for harvesting seeds from various conifers. The ancestral crossbill may have been a pine siskin-like finch (Carduelis)[20,21] which laterally abducted its lower mandible[22] to improve access to seeds such as those between separated conifer cone scales[8]. Isolated occurrences of slight mandibular crossings are found occasionally in many species (C.W.B., unpublished observations). Our results indicate that such an occurrence in an unspecialized crossbill ancestor would lead to selection for progressively greater mandibular crossing to improve foraging efficiency on moisture-closed winter cones. Selection would have ensued for increased mandibular crossing to exploit a resource unavailable to less specialized finches, especially in winter which is the time when food is most limiting[5,13]. The shape or curvature of the mandibles also affects foraging efficiency[7,8,23]. Curvature of the mandibles could be altered presumably by differential growth within the rhamphotheca. As mandibular crossing increased, seeds in progressively more closed cones, such as those of maturing cones of summer, would be harvested. Hence, the mandibular crossing secondarily enabled specialization on seeds in conifer cones throughout the year. □

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