Are the ratios of bill crossing morphs in crossbills the result of frequency-dependent selection?

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Summary

The direction the lower mandible curves in crossbills (*Loxia*) is an example of a discrete polymorphism. The lower mandible crosses with equal frequency to the left and to the right in several crossbill populations. I hypothesize that the 1:1 ratio results from negative frequency-dependent selection favouring the rarer morph. A crossbill always orients toward closed conifer cones so that its lower mandible is directed towards the cone axis. Thus, only part of the cone can be reached easily when crossbills have few perch sites and the cone cannot be removed from the branch or otherwise turned round. Since crossbills may visit cones which have previously been foraged on by other individuals, an equal frequency of left-to-right mandible crossings may minimize overlap in the use of cones and enhance foraging efficiency. Experimental data support this hypothesis. Moreover, the variation in the ratio of mandible crossing directions among crossbill populations is consistent with this hypothesis.

Keywords: conifer cones; crossbills; frequency-dependent selection; foraging behaviour; *Loxia*; polymorphism

Introduction

The success of an individual often depends on the frequency in the population of other like individuals (Maynard Smith, 1982; Milinski and Parker, 1991). Frequency-dependent selection is thought to be responsible for maintaining polymorphisms in many natural populations (e.g. Schuster and Wade, 1991; Hori, 1993). For example, a recent and elegant study of a scale-eating cichlid fish (*Perissodus microlepis*) demonstrates that frequency-dependent selection is responsible for maintaining the ratio of left- to right-mouthed fish near a 1:1 ratio (Hori, 1993; Takahashi and Hori, 1994). Another example of a 1:1 ratio in 'handedness,' that concerning the direction the lower mandible crosses in crossbills (*Loxia*; Fig 1), has also been hypothesized to be the result of frequency-dependent selection (Benkman, 1988a). I report here an experimental test of a possible mechanism for generating frequency-dependent selection in crossbills.

Mandible crossing is an adaptation for foraging on partly closed or closed conifer cones (Benkman, 1988b; Benkman and Lindholm, 1991). Crossbills use the tips of their crossed mandibles to bite between cone scales and then the lower mandible is laterally abducted to the side to which it crosses (Tordoff, 1954; Newton, 1972; Benkman, 1987b, 1992). This separates the cone scales and exposes the seeds at the base of the scales, which are then lifted out by the tongue. Crossbills always orient so that their lower mandible is towards the cone axis (Tordoff, 1954; Newton, 1972; Benkman, 1987b). The result is that a crossbill forages on the side of the cone that is opposite to the side to which its lower mandible crosses. If perch sites are limited and the cone cannot be twisted or removed, the portion of the cone on which foraging is most efficient should differ depending on the direction the lower mandible crosses.

Much of crossbill foraging behaviour is consistent with maximizing seed kernel intake rates (Benkman, 1987a, 1989a). For example, crossbills leave seeds in cones when it is more profitable
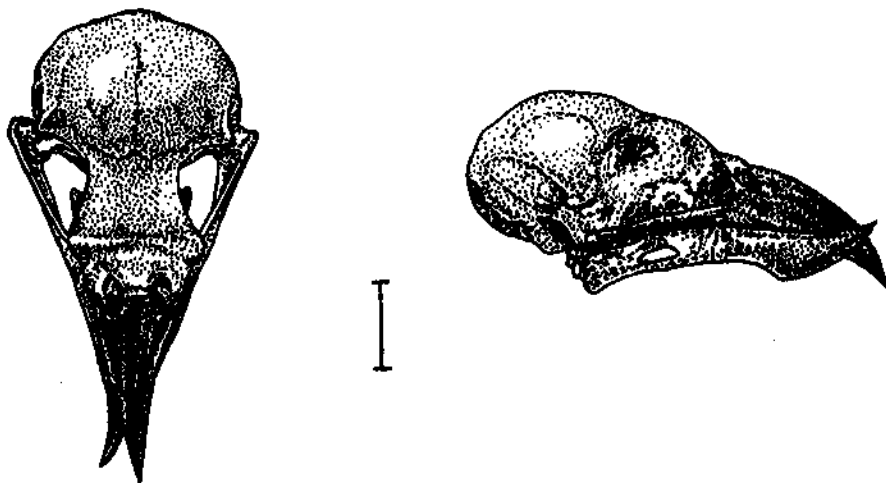
Figure 1. Dorsal and lateral views of the bill and skull of a Red Crossbill (*L. curvirostra*). The lower mandible crosses to the right in this example, but in all crossbill populations some individuals have lower mandibles that cross to the right and some cross to the left. Bar represents 1 cm.

to move on to another cone (Benkman 1989a). The seeds a crossbill leaves in the cone are, therefore, likely to be influenced by the direction to which the lower mandible crosses. Crossbills whose lower mandibles cross to the left are likely to leave different seeds than crossbills whose lower mandibles cross to the right. Consequently, crossbills visiting cones previously foraged on by the same morph should have a lower feeding rate than when foraging on cones previously visited by the opposite morph (Benkman, 1988a). If crossbills can easily twist the cone or remove it from the branch or if perch sites are unlimited, then there is no necessary reason for a consistent depression in the feeding rate in relation to the mandible crossing direction.

Crossbill populations that forage on fixed cones will experience negative frequency-dependent selection, because the rarer morph is less likely to visit a cone foraged on by a crossbill of the same morph type. A 1 : 1 ratio of mandible crossing is predicted (Benkman, 1988a). Such a prediction is not made for populations of crossbills that rely on cones that are twisted or removed from the branch. Because there is no inherent benefit of left or right crossing, deviation from a 1 : 1 ratio is possible in these crossbill populations.

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, personal communication) 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, 1983), 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.

Here I experimentally test the hypothesis that crossbills foraging on cones previously foraged on by the same morph will have a greater reduction in their feeding rate than when foraging on cones previously visited by the opposite morph. I also compare the mandible crossing ratios in various crossbill populations in relation to whether cones are twisted or removed from the branch.

Methods

Seven captive Red Crossbills (type 5 of Groth, 1993) were captured on 18 and 19 September 1993 in a lodgepole pine (*Pinus contorta* var. *latifolia*)-Engelmann spruce (*Picea engelmannii*) forest near Aspen, Colorado. Four of the crossbills (two males and two females) had lower mandibles that crossed to the right and three had lower mandibles that crossed to the left (two males and one female). They were housed in an indoor room partitioned with a 1.2 cm mesh screen into two 1.55 × 2.74 × 2.24 m aviaries. The type 5 crossbills were kept in one aviary and nine other Red Crossbills (types 2 and 5) were in the adjacent aviary. The crossbills remained in excellent condition. They were provided with grit and water containing vitamins and calcium supplement. Fresh cones, usually lodgepole pine, were provided daily over 2 months before and during the experiments, supplemented with sunflower seeds. Fresh pine branches were provided weekly.

Cones were first placed in boiling water for approximately 30 s to separate the resin bond holding the scales closed. The cones were then placed in a sealed plastic bag to keep them closed so that the seeds would not fall out. These cones were gathered from red squirrel (*Tamiasciurus hudsonicus*) middens in the Cypress Hills, Alberta, Canada. The cone lengths averaged 50.7 mm (sd = 3.84, n = 169 cones).

Crossbill feeding rates on lodgepole pine cones were measured between 8 and 16 December 1994. During each experiment a single moisture-closed lodgepole pine cone was secured with a screw to the underside of a branch mounted on the side of the aviary. A ponderosa pine (*Pinus ponderosa* var. *scopulorum*) cone was mounted above the lodgepole pine cone to mimic a cluster of several cones.

To eliminate interference between birds, only one bird occupied an aviary during foraging experiments; the other experimental birds were held in wooden boxes. The crossbills in the adjacent aviary were left alone during the experiments. One crossbill was released into the aviary, then timed from when it first probed between cone scales until it removed and consumed ten seeds. It was then captured and a crossbill with either the same or opposite lower mandible crossing direction was released into the aviary. It was then timed from when it first probed between cone scales until it removed and consumed ten seeds. All foraging bouts were timed to the nearest 0.1 s with a stopwatch. The 20 seeds removed by the birds represent, on average, approximately half the seeds in the cone (C.W. Benkman, unpublished data). Each bird was followed at least once by every other bird. On a given day each bird usually foraged on two or three cones (20-30 seeds) during a series of experiments, which is a small fraction of the number of seeds an individual crossbill consumes during a day.

All analyses were based on the mean number of seconds required by an individual bird to remove and consume ten seeds. Each mean for each bird was based on data from three or four cones and, in three cases, two cones (three of the four birds when individuals followed individuals of the same mandible crossing direction). I used one-tailed paired *t*-tests to test the hypothesis that the mean time per seed of each bird when it first foraged on a cone was less than when it followed a bird of either the same or opposite morph.

Results

The mean time taken by a crossbill to remove and eat a seed from a lodgepole pine cone did not differ between when it was the first bird and when it followed a bird of the opposite morph (Fig. 2, Table 1). In contrast, when a crossbill followed a bird of the same morph it took significantly longer to remove and consume a seed than it did when it was the first bird (Fig. 2, Table 1).
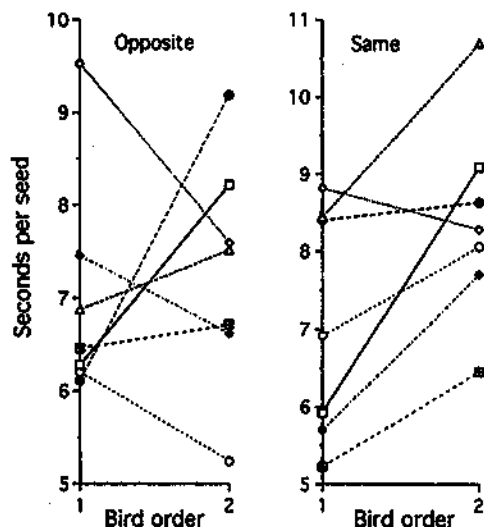

Figure 2. The mean number of seconds per seed for individual crossbills foraging on lodgepole pine cones. Opposite represents trials when the direction the lower mandible crosses differed between the first and second bird to forage on a cone. Same represents when the direction the lower mandible crosses was the same for the first and second bird. The symbols represent individual crossbills.

Table 1. The overall mean (±SEM) number of seconds per seed of seven Red Crossbills foraging on lodgepole pine cones

	Opposite	Same
First bird	7.0 ± 0.46	7.1 ± 0.56
Second bird	7.3 ± 0.48	8.4 ± 0.49
p value[a]	0.68	0.014

[a]One-tailed paired *t*-test (df = 6).
Opposite refers to when the direction the lower mandible crossed in the first bird to forage on a cone was opposite that of the second bird. Likewise, the same refers to when both the first and second bird had lower mandibles that crossed in the same direction.

Table 2. The number of individual crossbills whose lower mandibles cross to the left and right

Species	Direction of lower mandible		
	Left	Right	*p*
(A) Rely on cones that are twisted or removed from branches			
L. l. leucoptera[a]	218	566	< 0.001
L. l. bifasciata[b]	27	51	< 0.01
L. c. minor[c]	248	217	> 0.1
L. c. percna[d]	18	19	> 0.5
L. c. curvirostra[e]	879	748	< 0.001
L. pytyopsittacus[f]	65	58	> 0.5
(B) Rely on cones that are not twisted or removed from branches			
L. l. megaplaga[g]	15	12	> 0.5
L. c. (type 2)[h]	148	137	> 0.5
L. c. (type 5)[i]	46	33	> 0.1

[a]Benkman (1988a).
[b]Ticehurst (1910) and study skins in the American Museum of Natural History (AMNH, New York City) and the Museum of Vertebrate Zoology (MVZ, Berkeley).
[c]Study skins in the MVZ and crossbills caught by T. Hahn (personal communication) and C.W. Benkman.
[d]Study skins in the AMNH, the Museum of Comparative Zoology (Cambridge), the University of Michigan Museum of Zoology and the National Museum of Canada (Ottawa).
[e]J.C. Senar (personal communication).
[f]Ticehurst (1910), study skins in the AMNH and MVZ, and crossbills photographed by A.G. Knox (personal communication).
[g]Study skins in the AMNH, the MVZ, the Natural History Museum (Tring) and the National Museum of the Dominican Republic.
[h]Study skins in the MVZ and crossbills caught by C.W. Benkman.
[i]Study skins in the MVZ and crossbills caught by C.W. Benkman.

Discussion

This experiment confirms the hypothesis that the increase in time per seed when a crossbill forages on a cone previously used by a crossbill of the same morph is greater than when a crossbill follows a crossbill of the opposite morph (Benkman, 1988a). This provides a mechanism by which frequency-dependent selection could act to favour the rare morph and therefore lead to a 1 : 1 ratio of mandible crossings in a population of crossbills. The evolutionarily stable strategy (Maynard Smith, 1982) is a 0.5 frequency of each morph.

A prediction of this hypothesis is that crossbill populations that forage on cones that are not twisted or removed from the branch should have 1 : 1 ratios (Benkman, 1988a). However, crossbills relying on cones that are often twisted or removed may not necessarily have a 1 : 1 ratio. The strongest support of this prediction occurs in the three subspecies of White-winged Crossbills (*Loxia leucoptera*) (see Newton, 1972; Benkman, 1992).

Two subspecies of White-winged Crossbills (*Loxia leucoptera leucoptera and Loxia leucoptera bifasciata*) occur in the northern boreal forests of North America and Eurasia, respectively (Newton, 1972) and both forage on cones that are easily twisted and removed from branches (Benkman, 1988a; C.W. Benkman personal observation; see also Moreton, 1936). *Leucoptera* has a mandible crossing ratio that differs from 1 : 1 (Table 2A), but does not differ from 3 : 1 (chi-squared = 3.29, $p > 0.05$). *Bifasciata* has a mandible crossing ratio that also differs from 1 : 1 (Table 2A), but does not differ from 2 : 1 (Chi-squared = 0.058, $p > 0.5$). The third White-

winged Crossbill, *Loxia leucoptera megaplaga*, resides in the pine (*Pinus occidentalis*) forests on Hispaniola (Benkman, 1994). *Megaplaga* does not twist or remove the cones it forages on (C.W. Benkman, personal observation), nor, as predicted, does its mandible crossing ratio differ from 1 : 1 (Table 2B). This is a particularly strong test of the hypothesis, because the Hispaniolan crossbill is thought to be derived from *L. l. leucoptera* and presumably colonized Hispaniola when spruce (*Picea*) forests extended across the eastern United States in the Pleistocene (see Webb, 1988). Thus, in apparent response to frequency-dependent selection the 1 : 1 ratio has evolved from a ratio that differed significantly from 1 : 1.

Several other crossbills usually twist or remove cones from branches, including *Loxia curvirosta minor* (which specializes on western hemlock (*Tsuga heterophylla*) cones; Benkman, 1993; C.W. Benkman, personal communication), *Loxia curvirosta percna* (assuming *percna* was a specialist on black spruce (*Picea mariana*) cones; see Benkman, 1989b), most populations of *Loxia curvirostra curvirostra* (A.G. Knox, personal communication), including the resident population in the Pyrenees (J.C. Senar and A. Borras, personal communication; see Génard and Lescourret, 1987; Senar *et al.*, 1993) and *Loxia pytyopsittacus* (A.G. Knox, personal communication). The ratio of mandible crossings differs significantly from 1 : 1 in *curvirostra* captured in the Pyrenees by J.C. Senar, but does not differ from 1 : 1 in the other populations (Table 2A). It is unclear why the mandible crossing ratios in some of these crossbill populations have not diverged by chance from 1 : 1, if there is no selection. In at least *percna*, the Newfoundland crossbill, divergence from 1 : 1 may not have occurred because this crossbill probably evolved in the last several thousand years (Benkman, 1989b).

A more important test concerns type 2 and 5 Red Crossbills (see Groth, 1993), both of which specialize on cones that are not twisted or removed from branches (C.W. Benkman, personal observation). Type 2 Red Crossbills are specialized for foraging on ponderosa pine (*P. p.* var. *scopulorum*) cones (Benkman, 1993; C.W. Benkman, unpublished data) and their mandible crossing ratio, as predicted, does not differ from 1 : 1 (Table 2A). Similarly, type 5 Red Crossbills, which are specialized for foraging on lodgepole pine (*P. c.* var. *latifolia*) cones (Benkman, 1993; C.W. Benkman and R.E. Miller, submitted), have a mandible crossing ratio that does not differ from 1 : 1 (Table 2A).

In summary, all three predictions of the hypothesis are supported. First, foraging on a cone that was previously foraged on by the same morph results in a larger increase in foraging time per seed than if the opposite morph is followed (Table 1). This should lead to negative frequency-dependent selection and a 1 : 1 ratio of morphs in populations that rely on cones that are not twisted or removed from branches. Second, crossbill populations that rely on cones that are not twisted or removed from branches have mandible crossing ratios that do not differ from 1 : 1. Third, crossbill populations relying on cones that are twisted or removed from branches do not necessarily have 1 : 1 mandible crossing ratios. In three of six such populations the ratios differed significantly from 1 : 1. Overall, these results provide strong support of the hypothesis that the rare morph can gain an advantage from a reduction in the overlap between the portions of cones used by other crossbills.

Acknowledgements

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