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A 3:1 Ratio of Mandible Crossing Direction in White-winged Crossbills

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There are few examples of polymorphisms occurring in simple Mendelian ratios in wild populations of birds (Cooke and Cooch 1968, Smith 1987). Most studies of morphological variation in bird species show continuous variation (e.g. Grant 1986). The direction the lower mandible curves in crossbills (*Loxia*) is an example of a discrete dimorphism. The lower mandible in Red Crossbills (*L. curvirostra*) crosses in equal frequency to the right and to the left (e.g. Ticehurst 1910, Knox 1983, James et al. 1987). In White-winged Crossbills (*L. leucoptera*) the mandibles do not cross in equal frequencies to the left and right (Ticehurst 1910, James et al. 1987). I found that the ratio of mandible crossings in White-winged Crossbills differed from 1:1, however, and that the lower mandible crosses to the right approximately 3 times more often than to the left.

A 3:1 ratio in the frequency of the lower mandible crossings was found in wild-caught White-winged Crossbills (*L. l. leucoptera*) in 1987 in northern Ontario (43 of 145 birds, 29.7%) and in Riding Mountain National Park, Manitoba (11 of 49 birds, 22.4%). Similar frequencies occurred in the collections of White-winged Crossbills accumulated since the late 1800's in the National Museum of Canada (88 of 309 birds, 28.5%), American Museum of Natural History (39 of 141 birds, 27.7%), and Museum of Vertebrate Zoology (37 of 140 birds, 26.4%). None of these alone or in sum (218 of 784 birds, 27.8%) differs from that expected if the ratio of lower mandible crossings of right to left occurs in a 3:1 ratio (Chi-square tests, $P > 0.10$). The frequency of females with lower mandibles crossing to the left (0.312, 90 of 288 females) was significantly greater than expected if the ratio is 3:1 ($\chi^2 = 4.50$, $df = 1$, $P < 0.05$), but not for males (0.243, 100 of 411 males). The biological significance of this difference for females is not known; it may be a statistical artifact because there is nearly a 50% chance that 1 in 8 comparisons would be significant at the 0.05 level. James et al. (1987) also examined White-winged Crossbill specimens from the National Museum of Canada and from three other Canadian museums and found similar ratios overall and between sexes.

These data support the hypothesis that the direction of crossing is determined by a single autosomal diallelic locus, with lower mandible crossing to the right dominant over crossing to the left. The frequencies of the two alleles equal 0.5. This interpretation is consistent with observations of two families of White-winged Crossbills I observed in 1987 where all 4 adults and 7 offspring had lower mandibles that crossed to the right. Convincing support for this hypothesis, or any other genetic hypothesis, requires breeding experiments.

A nongenetic hypothesis for different ratios of mandible crossings has been suggested (James et al. 1987). James et al. (1987) pointed out that the cone scales spiral in two directions about the axis of the cone and that there are two types of cones. They argued that the direction the lower mandible crosses may be influenced by the structure of the cones on which juvenile crossbills forage before their mandibles cross and that the differences in the ratios of bill crossings are related to variation in the spiraling of scales on the cones (phyllotaxy). Whether the different cone types influence foraging behavior and feeding rates is unknown, although such an effect is central to their argument.

Several comments about their hypothesis are in order. First, crossbills foraging on closed cones begin at the base of the cone and progress toward the tip, sequentially prying apart the scales. Consequently, the scale they next separate is usually free of most of the scales that overlap it from below. If this is true, it is difficult to see how such slight differences in cone scale spirals (see James et al. 1987: fig. 1) could influence foraging efficiency. Second, juvenile crossbills forage infrequently and awkwardly before the mandibles begin crossing (pers. obs.). Furthermore, juvenile crossbills often do not orient in the "proper" direction to the cone (see below), and before the mandibles cross juveniles cannot separate closed cone scales (Benkman 1988). Thus, whether slight differences in scale spiraling cause consistent differences in mandible crossing ratios is doubtful. Third, while watching captive crossbills of both species foraging for more

than 30,000 seeds from within 2 m, and often less than 0.5 m away, I have never seen any tendency for crossbills to consistently forage along one of the spirals for the whole cone length. When I started my research I had a similar idea, although in terms of cone defenses against seed predators, but soon realized that such a subtle difference had no consistent effect on foraging behavior. Finally, James et al. suggested that the ratio of mandible crossing direction may match the ratio of cone morphs. James et al. presented data on the frequencies of the two cone morphs for white spruce (*Picea glauca*) and black spruce (*P. mariana*). These are two of the most important seed trees for White-winged Crossbills (Benkman 1987b), yet the ratio of cone morphs did not differ significantly from 1:1. They suggest that the ratio of cone morphs may differ from 1:1 farther north. White-winged Crossbills wander widely over the spruce-fir forests of North America from Alaska to the northeastern United States (Benkman 1987b), and it is not clear why spruce farther north should be more important than those to the south. Because the distribution of the different conifers on which each crossbill species forages is more important than latitude in governing crossbill distributions (Benkman 1987b), the ratio of mandible crossing directions should differ between Red and White-winged crossbills only if the ratio of morphs differ between the *conifer species* selected.

An alternative explanation is that the difference in mandible crossing ratios between White-winged and Red crossbills arose from differential natural selection in foraging differences. The precise orientation of the bill to conifer cones, with the lower mandible directed toward the cone axis, is critical for efficient foraging (Benkman 1987a). White-winged Crossbills forage on the small cones of spruce (*Picea*) and tamarack (*Larix*), whereas Red Crossbills most often forage on pine (*Pinus*) cones. In summer both crossbill species often forage on small thin-scaled spruce cones (Benkman 1987b). The bills appear to be most adapted for harvesting seed in late winter when seed is most limiting (Benkman 1987a, b). At this time, White-winged Crossbills either remove cones from the branch and easily twist the cone before removing seeds, or the cone scales are spread apart (pers. obs.). In all cases White-winged Crossbills can easily orient properly to all parts of the cone or, when cones are open, bill orientation is not critical (see Benkman 1987a, 1988). Although Red Crossbills remove spruce cones from the branches in summer, they leave pine cones attached to the branches and are often limited in the number of feasible positions available for proper orientation to the cone. Perch sites and needles surrounding parts of the cone limit cone access. The part of the cone most accessible would differ for crossbills depending on the direction their lower mandible curves. If Red Crossbills forage on cones previously

visited by crossbills, then the less common bill type would more frequently encounter cones used by the other bill type and would be able to forage efficiently on parts of the cone the previous bird did not use. The stable ratio of mandible crossings, or evolutionary stable strategy (Maynard Smith and Price 1973), would be 1:1. Because crossbills forage in flocks and revisit trees (pers. obs.), an equal frequency of left-to-right mandible crossings may minimize overlap in use of cones. In Europe Red Crossbills do remove pine cones from branches (Stokoe and Stokoe 1960). Whether these crossbills remove cones throughout the year or during periods of relative seed scarcity is unknown.

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