



Short Communications and Commentaries

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Further Information on the Genetics of Bill Crossing in Crossbills

JEFFREY G. GROTH¹

Museum of Vertebrate Zoology, University of California, Berkeley, California 94720, USA

Ticehurst (1910) was among the first to note that White-winged Crossbills (*Loxia leucoptera*) with right-crossing lower mandibles substantially outnumber left-billed birds, while in the Red Crossbill (*L. curvirostra*) the ratio is nearly 1:1. James et al. (1987) found that in *L. leucoptera* the ratio of right- to left-billed birds is approximately 3:1. In a large sample, Benkman (1988) found a 3:1 ratio in *L. leucoptera* and suggested that this ratio reflects simple Mendelian inheritance.

The 3:1 Mendelian ratio is well-known in genetic systems of one locus with two alleles and complete dominance. This ratio is expected in the special case of the phenotypes of F_1 progeny in matings between two heterozygotes. Benkman (1988) proposed that the gene for right-crossing is dominant, therefore giving rise to three times as many right-billed birds. He further proposed that the frequencies of the two alleles must be 0.5 and 0.5 in order for the species as a whole to show the 3:1 Mendelian ratio.

An obvious flaw in this proposition is that there is no particular reason to expect entire populations or species to show a 3:1 Mendelian ratio, even if the genetic mechanisms for morphism are inherited in a Mendelian fashion. In addition to the "Mendelian" ratio in *L. leucoptera*, Benkman (1988:578) cited two other examples from the literature of polymorphisms occurring in "simple Mendelian ratios in wild populations of birds." In one of the examples cited, Cooke and Cooch (1968) did not discuss morph frequencies in populations, but rather frequencies in progeny from crosses between morphs. In a second study, Smith (1987) measured frequencies of morphs in 10 geographic regions. Each region had a different morph frequency and had close to "Mendelian" 3:1 ratios in only one or two regions.

Benkman's (1988) calculations of chi-square values for morph frequencies in *L. leucoptera* were in error (apparently only one of the two compartments in each contingency table was counted), leading to his acceptance of the 3:1 ratio as true. I reexamined his data and recalculated the chi-square statistics. Of 784 *L.*

leucoptera (sexes combined), 218 were left-billed, while under a 3:1 ratio only 196 would be expected. These data gave $X^2 = 3.29$ ($df = 1$, with $P < 0.10$; not $P > 0.10$ as indicated by Benkman 1988:578), which indicates a substantial deviation from 3:1. Benkman divided his sample by sex and found 90 left-billed females out of 288, which is not only significantly different from 3:1 (72 expected, $X^2 = 6.0$, $df = 1$, $P < 0.02$), but actually closer to 2:1 (96 expected).

In support of his hypothesis of right-crossing dominance, Benkman (1988) observed seven right-billed juvenile *L. leucoptera* fed by four right-billed adults (presumably the parents) in the field. This observation is consistent with a right-dominant system, but it does not falsify other interpretations. Verification of the right-dominant mechanism would have been more conclusive if offspring of two left-billed birds were examined, because these matings would theoretically produce only left-billed offspring.

I observed matings between two left-billed *L. curvirostra* in captivity, which produced seven offspring (in three broods), two of which were right-billed (one each in the first and last broods). This should not have occurred under a right-dominant model, because left-billed birds would be homozygous recessive and all resulting progeny would be left-billed. However, an alternative, left-dominant system would not be falsified by this result. If both parents were heterozygous, an average of one right-billed offspring should occur out of every four.

The left-dominant model is the reverse of Benkman's, yet it also is consistent with his observation of right-billed adults with right-billed juveniles. In the left-dominant model, right-billed birds would be homozygous recessive and, therefore, would produce only right-billed offspring. Of course, it is conceivable that the two species have different genetic mechanisms for bill crossing. However, without further information, it is most parsimonious to hypothesize that such a mechanism evolved only once in *Loxia*.

Based on Benkman's (1988) morph frequencies and assuming Hardy-Weinberg equilibrium in the species, a left-dominant model predicts gene frequencies in *L. leucoptera* to be 0.150 (left) and 0.850 (right). There is no reason these frequencies should be less likely than 0.5 and 0.5. It is clear that the (roughly approximate) 3:1 phenotypic ratio produced in nature

¹ Present address: Department of Ornithology, American Museum of Natural History, New York, New York 10024, USA.

has nothing to do with "Mendelian" 3:1 ratios and is only coincidentally similar.

I recorded bill-crossing direction in 3,647 specimens of North American *L. curvirostra*. Sexes combined, 1,895 were left-billed and 1,752 were right-billed, which is significantly different from a 1:1 ratio ($X^2 = 5.61$, $df = 1$, $P < 0.02$). I found that 1,182 of 2,256 males (52.4%, $X^2 = 5.17$, $df = 1$, $P < 0.05$) were left-billed, and 713 of 1,391 females (51.3%, $X^2 = 0.88$, $df = 1$, $P > 0.3$) were left-billed, showing a slight excess of this morph in both sexes. Using the original phenotypic frequencies in *L. curvirostra* (and Hardy-Weinberg assumptions), under the as yet unfalsified left-dominant model, the frequencies of the two alleles would be 0.693 (right) and 0.307 (left). Therefore, it would be likely that two left-billed *L. curvirostra* chosen at random (such as in the first mating of captives discussed above) would be heterozygous, because heterozygotes would comprise about 78% of all left-billed birds. Further breeding experiments should be performed to assess other unfalsified genetic or nongenetic hypotheses.

Several other genetic mechanisms for bill crossing can be evaluated with the existing data. Although sexes differed slightly in morph frequencies in both species, neither right- nor left-dominant models of sex-linked inheritance would be consistent with available evidence. For birds in which a sex-linked mode of inheritance is known (e.g. the Gouldian Finch, *Chloebia gouldiae* [Southern 1945] and nestlings of the Mute Swan, *Cygnus olar* [Munro et al. 1968]), the sexes differ markedly in their phenotypic frequencies. In the four possible one-locus/two-allele/sex-linked systems for crossbills (left and right dominant in each species), the phenotypic frequencies in the females (the heterogametic sex) would need to equal the hypothetical gene frequencies for the entire population (the males would have Hardy-Weinberg proportions). Yet, in none of the four cases for *Loxia* do calculations using these models fit the data.

Even if the two species of crossbill have different genetic mechanisms and right dominance holds for *L. leucoptera*, Benkman (1988) did not explain why two alleles should exist at frequencies of precisely 0.5. One hypothesis is that these frequencies are maintained because the polymorphism is balanced by selection, or there is selection favoring heterozygotes (Ford 1945). Instead, Benkman (1988:579) implied that selection on bill-crossing direction is not operative in *L. leucoptera*. Without selection, and only chance and genetic drift operating, there is no reason to predict that gene frequencies should approach 0.5; instead, because of finite population size, the chances of any population remaining at a 50:50 gene frequency become less each generation (Wallace 1981).

On the other hand, Benkman (1988:579) did suggest that *L. curvirostra* experiences frequency-dependent selection because birds revisit cones, therefore mak-

ing it less profitable for individuals to forage on cones previously visited by the same morph. He postulated that revisitation is common when birds forage on cones of *Pinus*, while it is not common or unimportant for other cones (used by *L. leucoptera*), such as those on spruce (*Picea*) and larch (*Larix*), which are removed from branches or not revisited. This hypothesis is testable, because populations of crossbills vary in conifer usage. For example, one would expect a 1:1 morph ratio in pine-dependent *L. leucoptera megaplaga* of Hispaniola.

If frequency-dependent selection is important, a second expectation is that populations of *L. curvirostra* not associated with *Pinus* cones, such as small-billed forms, would have fluctuations away from 1:1, as in *L. leucoptera*. To test this, I estimated bill-crossing frequencies using a subset consisting of all *L. curvirostra* specimens (fully-grown birds only) with lower-mandible widths of 9.0 mm or less ($n = 814$; most of these specimens were labeled *L. c. minor* or *L. c. sitkensis*). In this sample, 411 were left-billed and 403 were right-billed. These frequencies are very similar to those found in the total sample of *L. curvirostra*.

The developmental mechanism responsible for bill-crossing direction in *Loxia* remains incompletely understood. Several types of abnormal bill crossing in domestic fowl have genetic bases (Landauer 1938), but none of these appear related to crossing mechanisms in *Loxia*. James et al. (1987) speculated that nongenetic developmental responses by juvenile birds to cone-scale spiraling direction (phyllotaxy) is the cause of crossbill bill-crossing ratios in the wild. Their hypothesis predicted that cone-morph frequencies in food trees of *L. leucoptera* should match those of bird bills; however, they admitted that available data did not support their hypothesis. This contradiction does not prove that crossing direction in crossbills has a genetic basis. No current data disprove the hypothesis that directionality has the potential for environmental modification during the critical stage when the mandible tips of juveniles grow enough to cross. Asymmetrical muscle development on the sides of the head and behavioral "handedness" (see Knox 1983) for example, potentially could develop only after crossing direction has been determined. It would be worthwhile to study these auxiliary changes in pre-crossing juveniles. Onset of these changes before the development of bill crossing would favor the hypothesis of genetic determinism in crossing direction. Nongenetic (sensu James et al. 1987) or random factors might explain the 1:1 phenotypic frequency seen in *L. curvirostra*, but this would leave the skewed distribution in *L. leucoptera* unexplained. Another question is whether there may be similarities between crossbill "handedness" and handedness in human populations, which consistently show a great predominance of right-handers. Human handedness is not inherited in a simple Mendelian fashion, and is

thought to be related to functional asymmetry in hemispheres of the brain (Annett 1985).

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Estimating Absolute Densities of Flying Seabirds Using Analyses of Relative Movement

LARRY SPEAR, NADAV NUR, AND DAVID G. AINLEY

Point Reyes Bird Observatory, Stinson Beach, California 94970, USA

The 300-m-band-transect sampling method is currently the most widely used method for counting seabirds at sea because it provides an estimate of density (birds/unit area; reviewed by Tasker et al. 1984, Haney 1985; see also Burnham et al. 1980). Density estimates derived from these counts often are affected by variation in detection rates of seabirds caused by several factors, including bird size, color and behavior, as well as weather and observer ability. However, the most critical bias results from the effect of movement by flying birds (reviewed by Tasker et al. 1984). Counts of flying seabirds are actually a measure of bird "flux" and, thus, are usually an overestimation of absolute (i.e. true) density (J. A. Wiens, D. Heine-

man, and W. Hoffman, 1978 unpubl. report to National Oceanic and Atmospheric Administration, Boulder, Colorado). Due to the effects of bird movement, Tasker et al. (1984) concluded that it was "unlikely that the conversion of raw counts of all birds seen (birds/unit time) to bird densities will ever be possible," and Haney (1985) concluded that calculations of absolute densities would not be possible without "considerable additional qualifications." Yet, a standardized approach to seabird censuses is essential for valid comparisons between studies, an important consideration in view of the recent upsurge of seabird studies at sea. Accurate density estimates are particularly critical for calculating energy fluxes and food