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A Hybrid Red Crossbill-Pine Siskin (*Loxia curvirostra* × *Carduelis pinus*) and Speculations on the Evolution of *Loxia*

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On the morning of 27 December 1981, a strange finch appeared at Tallman's feeder in a residential backyard in Aberdeen, Brown County, South Dakota. Alone and in the company of Pine Siskins, the bird consumed sunflower seeds. It fed on the ground and also cracked seeds while perched on a sunflower head hung from a clothesline. Tallman noted that this finch, when approached, did not fly with a small siskin flock but flew alone, silently, in a straight line from the feeder. The bird exhibited aggression toward siskins feeding near it. The finch was obviously not a regular North American species, being most like a siskin but larger, less boldly streaked, and with a proportionately larger bill and head. Immediately upon recognizing the bird as an oddity, Tallman opened Potter traps and mist nets and eventually caught it in a Potter trap. The bird was then prepared as a museum skin and sent to the National Museum of Natural History, Smithsonian Institution, where Zusi identified it as a hybrid between the Red Crossbill (*Loxia curvirostra*) and Pine Siskin (*Carduelis pinus*). Apparently no previous reports of a hybrid between *Loxia* and any other genus exist (Cockrum 1952, Gray 1958).

The absence of damage to the bill, feet, or plumage suggests that the bird had not been caged. We judged the bird—a female—to be at least a year old from the completely ossified skull and the shape of its rectrices. The latter are more rounded at the tip and have broader inner vanes than those of juvenile crossbills and siskins. We therefore compared it mainly with adult females taken in December and January.

The specimen (USNM 582513) may be described as follows (see Fig. 1). Underparts whitish, streaked with gray. Sides and flanks shading to grayish olive. Patchy yellowish wash on lower throat, breast, belly, and crissum. Streaks neither bold nor sharply defined, formed from longitudinal center stripes on feathers; streaks weakest on lower throat and belly and darkest and best defined on flanks and crissum.

Upperparts dusky olive streaked or spotted with dark gray. Feathers of forehead and crown dark with whitish or yellowish edges, giving spotted effect. Longer feathers of nape, neck, and back dark gray bordered with dusky olive laterally, giving streaked effect. Rump contrasts with back in having feathers with paler olive centers and yellowish lateral edges. Upper tail coverts uniform grayish olive without pronounced center streaks, darker than rump but paler than back. Superciliary line whitish with dusky streaks. Auricular patch dusky grayish olive.

Wings sooty; median and greater wing coverts with pale, olive-whitish tips (and faint brownish cast) producing two narrow wing bars—the anterior one somewhat broken and the posterior one continuous. Narrow yellow edgings on all primaries, except outer, extending distally to point of emargination. Secondaries with short yellowish outer border toward tip (tips bilobed), becoming broader and whiter on inner, superficial secondaries. Inner vanes of primaries and secondaries with broad silvery yellowish inner border that narrows distally and ends proximal to tip (at point of emargination in primaries).

Tail strongly notched; sooty with yellow outer edges. Edges least pronounced on outer and most pronounced on inner feathers and broadest basally. Inner vanes edged narrowly with whitish.

Label data include the following: bill dark slate gray, iris dark brown, legs and feet dark brown, gape whitish, skull ossified, little to moderate fat, no molt, ovary tiny.

Measurements of wing, tail, tarsometatarsus, and bill are given in Table 1. They are compared with those of 10 specimens of *Carduelis pinus pinus* and 10 of *Loxia curvirostra sitkensis*—the smallest recognized North American race of the species. If wing length is taken as an index of body size, the hybrid is closer

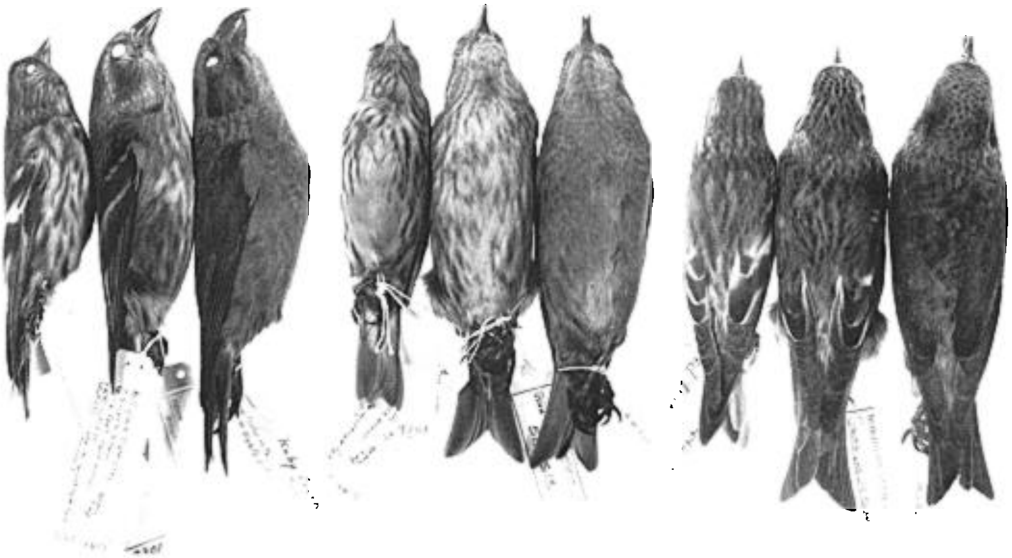

Fig. 1. Photographs of a hybrid *Loxia curvirostra* × *Carduelis pinus* and the parental species. From left to right in each photograph: *Carduelis p. pinus*, female, USNM 442040; *Loxia curvirostra* × *Carduelis pinus*, female, USNM 582513; *Loxia curvirostra sitkensis*, female, USNM 269830.

in size to the smallest crossbill than to the siskin. The tail of the hybrid is longer in proportion to wing length than that of the crossbill and similar to that of the siskin. Tarsal length of the hybrid and of the crossbill is relatively shorter than that of the siskin. The length of the bill of the hybrid is greater than that of siskins and is also greater in proportion to wing length (13.6% in hybrid, 12.3% in siskin). Comparable measurements of the bill in *Loxia* could not be made.

Several features indicate that *Loxia* is one of the parents of the hybrid. On casual inspection, the bill shows none of the asymmetry of a crossbill and resembles the conical bill of a siskin. Under magnification of a dissecting microscope, however, the right and left tomial edges of each mandible are differently shaped in dorsal or ventral view (Fig. 2). The right edge of the upper mandible is smoothly concave from base to tip; the left edge is somewhat angled near the middle of the bill. In the lower mandible the left side is smoothly concave and the right side angled. The tip of the upper mandible is deflected slightly to the right and the tip of the lower mandible slightly to the left. These features are similar to those seen in exaggerated form in right-crossed crossbills. Other crossbill features are the dark auricular patch, yellowish rump, and spotted pattern on the forehead and crown.

The White-winged Crossbill (*Loxia leucoptera*) is unlikely as a parent, because the wing bars of the hybrid are narrower, not broader, than those of a siskin, and the upper tail coverts are olive rather than blackish.

Characters of the hybrid that indicate *Carduelis pi-*

TABLE 1. Measurements (mm) of adult female *Carduelis p. pinus*, *Loxia curvirostra sitkensis*, and the hybrid *Loxia curvirostra* × *Carduelis pinus*.

	Carduelis p. pinus (*n* = 10)			*Loxia c. sitkensis* (*n* = 10)	
Measurements	Mean	SE	Hybrid	Mean	SE
Wing length	70.8	0.42	78.5	81.4	0.43
Tail length					
Inner rectrix	32.4	0.43	36.5	37.2	0.57
Outer rectrix	39.4	0.37	43.3	42.6	0.42
Tarsometatarsal length	14.2	0.05	15.1	15.5	0.19
Bill length from nostril	8.7	0.12	10.7	—	—

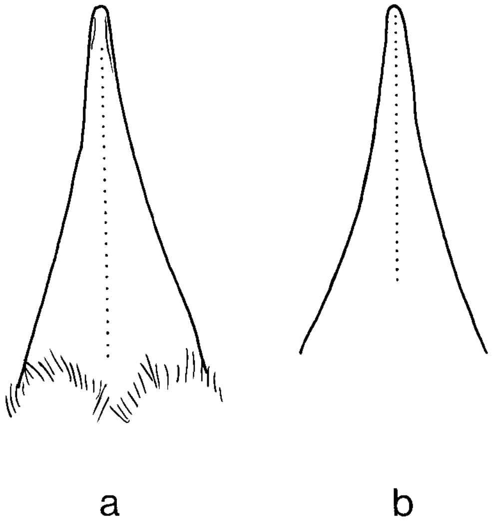

Fig. 2. Outline drawings of mandibles of a hybrid *Loxia curvirostra* × *Carduelis pinus* (USNM 582513). **a,** upper mandible in dorsal view; **b,** lower mandible in dorsal view. Dotted median lines added to emphasize asymmetry.

nus to be one of the parents are the extensively streaked, whitish underparts, the narrow (and faintly brownish) wingbars, yellow outer edges to the bases of the primaries and toward the tips of the secondaries, the broad whitish outer edgings on the innermost secondaries, and the yellowish inner vanes of the primaries and secondaries.

The pattern of wear on the bill tips of the hybrid is intriguing. Under magnification, the tips of both mandibles were noted to be smoothly rounded by wear, and the gonys and left surface near the tip of the lower mandible showed wear in the form of a slight depression with irregular longitudinal striations. This wear suggests that the bird had used its bill in a manner for which its structure was not wholly suited, such as separating cone scales by inserting the laterally compressed bill between them, with the left side of the bill toward the median axis of the cone, and then prying to the left with the partially opened lower mandible, or by using the tip of the lower mandible as a fulcrum against the inner cone scale and prying open the outer scale with the upper mandible by rotating the head. The tips of both mandibles may have been worn by pounding on tough cones. Red Crossbills are known to open pine cones by prying laterally with the opened lower mandible (Tordoff 1954).

Certain species of the genus *Carduelis* exhibit features and behavior that might have been present in the ancestor of *Loxia*. Members of *Carduelis* and *Loxia* are noted among carduelines for their habit of feeding in a variety of positions, often head down or back down, and for holding cones or other food sources with one foot while extracting seeds with the bill (Newton 1967, Palmer 1968). The bills of *Carduelis pinus*, *C. spinus* (Siskin), *C. carduelis* (European Goldfinch), *Loxia curvirostra*, and *L. leucoptera* are laterally compressed for much of their length and are provided with fine, sharp points on both mandibles. Their bills differ from the thicker bills of most other species of the Carduelinae. The tweezer-like bills of the three species of *Carduelis* mentioned above are used in part to extract seeds from cones and cone-like structures, in which scales may be forced apart by gaping. The depressor mandibulae muscle and the retroarticular process of the lower jaw are enlarged in *C. carduelis*, *C. spinus*, and *C. pinus* as part of an adaptive complex for gaping, but this is not true of other species of *Carduelis*, in which gaping does not occur (Newton 1967). These anatomical features are also found in *Loxia*, where they serve in a variety of forceful movements of the lower jaw. Thus, these three species of *Carduelis* appear to be preadapted for opening cone scales by methods other than gaping and for opening tougher and larger cones. In an ancestral form, lateral prying, as suggested for the hybrid, might favor the evolution of asymmetrical mandibles and jaw muscles and the further specializations of structure found in crossbills. An increase in bill and body size would probably have accompanied a shift to feeding on larger cones, as it has apparently in Palearctic species and races of *Loxia* (Lack 1944a, b). The North American races of *Loxia curvirostra* show more of a difference in body size than exists between the Pine Siskin and the smallest of the races of *Loxia curvirostra* (compare Table 1 with measurements in Griscom 1937), and a correlation with cone size is probable, although it has not been thoroughly documented.

The feeding adaptations typified in *Carduelis pinus* may have evolved more than once within the carduelines, but among living species they are known to occur only in the three species of *Carduelis* mentioned above. These few species may serve as a model for an intermediate stage in the evolution of *Loxia*, and they may indeed be the closest living relatives of the crossbills. This suggestion is consistent with Raikow's (1978) placement of *Loxia* and *Carduelis* on a separate branch of a cladogram based largely on appendicular myology. The Tibetan Serin (*Serinus thibetanus*) has a slender bill and is a cone feeder, but the extent of its adaptation for gaping is unknown. This species is widely regarded as a member of *Carduelis*, but it was transferred to *Serinus* by Wolters (1967) on the basis of its plumage pattern.

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The Effect of Burrow Loss on Mate Choice in the Leach's Storm-Petrel

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Long-lived seabirds often nest for many years with the same mate at the same site (Fisher and Lockley 1954, Lack 1968). Repeated pairings might result either from strong mate fidelity or from a tendency to return to the same burrow or nest site, here called site tenacity (Hildén 1965, Morse 1980). Retention of a site sometimes exceeds retention of a mate (e.g. Allan 1962, Morse and Buchheister 1979), which tentatively suggests that site tenacity is primarily responsible for repeated pairings in these instances. If repeated pairing is a consequence of site tenacity, birds deprived of their nest sites should remate randomly; if repeated pairing results from mate fidelity, birds deprived of their nest sites should retain their previous mates.

We know of no controlled experiments that assess the roles of mate fidelity and site tenacity in retaining mates from one breeding season to the next. Here, we demonstrate experimentally that retention of the same mate during successive breeding seasons by the Leach's Storm-Petrel (*Oceanodroma leucorhoa*) is largely or totally dependent on site tenacity.

This experiment was carried out on Little Duck Island, Hancock County, Maine, an island of 34 ha, located 15 km from the mainland. Pairs in 62 numbered burrows were captured and banded during June 1980. Before the arrival of birds at the colony in April 1981, 25 of these burrows were randomly selected, and their entrances were covered with a 25- × 15-cm wooden shingle. Then, a 30- × 30-cm piece of coarse metal screening (1- × 1-cm mesh) was placed over each shingle and secured with 15-cm wire spikes in each corner to prevent access to these burrows. The remaining burrows were not covered. In June 1981 the 37 burrows not covered in April were censused as in 1980, and inhabitants of neighboring burrows were captured in order to locate as many of the birds displaced from the experimental burrows as possible. In all, over 500 unnumbered burrows, those closest to the 62 numbered burrows, were searched for displaced birds.

Mate retention was strongly site-dependent. A significantly higher proportion of undisturbed individuals retained their mates from 1980 than did displaced individuals (Table 1) ($P < 0.001$ in a one-tailed Fisher Exact Probability Test).

Two groups of birds could not be used in this analysis (and thus are not included in the two right columns of Table 1), but nevertheless are consistent with this conclusion: (1) both members of six undisturbed pairs changed their burrows, and all but one of these pairs nested with a different mate; and (2) members of five displaced pairs managed to burrow under the screening into their original burrows, in spite of the efforts taken to exclude them, and all of them nested with their mates from 1980. In addition to these two groups, neither member of 10 displaced pairs or 7 undisturbed pairs was recovered, a significantly higher proportion of displaced than undisturbed pairs ($\chi^2 = 4.48$, df = 1, $P < 0.05$).