

A NEW SPECIES OF THE RED CROSSBILL (FRINGILLIDAE: *LOXIA*) FROM IDAHO

CRAIG W. BENKMAN^{1,4}, JULIE W. SMITH², PATRICK C. KEENAN¹, THOMAS L. PARCHMAN¹,
AND LEONARD SANTISTEBAN³

¹Department of Zoology and Physiology, University of Wyoming, 1000 E. University Ave., Laramie, WY 82071

²Department of Biology, Pacific Lutheran University, Tacoma, WA 98447

³Department of Biology, New Mexico State University, Las Cruces, NM 88003

Abstract. The Red Crossbill (*Loxia curvirostra* complex) endemic to the South Hills and Albion Mountains in southern Idaho has coevolved in a predator–prey arms race with the lodgepole pine (*Pinus contorta latifolia*). The resulting divergent selection has favored a sedentary, locally adapted crossbill population whose size and vocalizations differ from those of co-occurring Red Crossbills of other call types. It has also led to high levels of reproductive isolation between the “South Hills crossbill” and nomadic taxa with different vocalizations that move in and out of the area yearly. Genetic analyses of amplified fragment length polymorphisms (AFLP) indicate that about 5% of the loci in the South Hills Crossbill have diverged in spite of the potentially homogenizing influence of gene flow. Given these differences in genetics, morphology, and behavior, and the high level of reproductive isolation in sympatry with other call types (99% of South Hills Crossbills pair assortatively), we recommend that this crossbill be recognized as a distinct species.

Key words: Call type, lodgepole pine, *Loxia*, reproductive isolation, South Hills Crossbill, speciation.

Una Especie Nueva de *Loxia* (Fringillidae) de Idaho

Resumen. El representante del complejo de *Loxia curvirostra*, endémico de las South Hills y de las montañas Albion del sur de Idaho, ha coevolucionado mediante una carrera armamentista depredador–presa con el pino *Pinus contorta latifolia*. La selección divergente ha favorecido la evolución de una población de aves sedentaria y localmente adaptada, cuyo tamaño y vocalizaciones difieren de los de formas simpátricas del complejo que presentan tipos de llamadas diferentes. La selección también ha conducido a altos niveles de aislamiento reproductivo entre la forma de las South Hills y los taxones nómades que presentan vocalizaciones diferentes y que se mueven hacia dentro y fuera del área anualmente. Análisis genéticos de polimorfismos amplificados de longitud variable (AFLPs) indican que cerca del 5% de los loci de la población de las South Hills se han diferenciado, a pesar de la influencia potencialmente homogenizadora del flujo génico. Considerando estas diferencias en genética, morfología y comportamiento, además del alto grado de aislamiento observado en simpatria con respecto a aves que presentan tipos de llamadas diferentes (más del 99% de las aves de las South Hills se aparean asociativamente), recomendamos que esta forma de *Loxia* sea considerada como una especie diferente.

INTRODUCTION

In 1997, during studies of Red Crossbills (*Loxia curvirostra* complex) on forest islands in western North America, we discovered a resident population of Red Crossbill with distinctive vocalizations in the South Hills and Albion Mountains of southern Idaho. This crossbill feeds almost exclusively on seeds in the cones of Rocky Mountain lodgepole pine (*Pinus contorta latifolia*), and forests of this pine in the South Hills and Albion Mountains are restricted to about 100 km² within the Sawtooth National Forest (Fig. 1; Benkman 1999). The occurrence of this distinct population in a species well known for ranging widely raised the question whether it is reproductively isolated and how such isolation could have evolved.

North American Red Crossbills specialize on seeds in conifer cones and use their crossed mandibles to spread overlapping cone scales apart to expose the seeds at their base (Newton 1972, Benkman and Lindholm 1991). These birds comprise 10 call types (call types 1–10) that differ in vocalizations and overall morphology including bill size (Groth 1993a, Benkman 1999, K. Irwin, unpubl. manuscript) and palate structure (Benkman 1993, K. Irwin, unpubl. manuscript). Much of crossbill behavior and ecology is related to the birds' nomadic movements aimed at tracking and exploiting large cone crops (e.g., Benkman 1987, 1990, 1992). Nonetheless, the evolution of crossbill morphology and diversity is tied to the diversity of conifers that produce fairly regular cone crops and consistently hold seeds in closed to partly closed cones

Manuscript received 25 September 2008; accepted 27 November 2008.

⁴E-mail: cbenkman@uwyo.edu

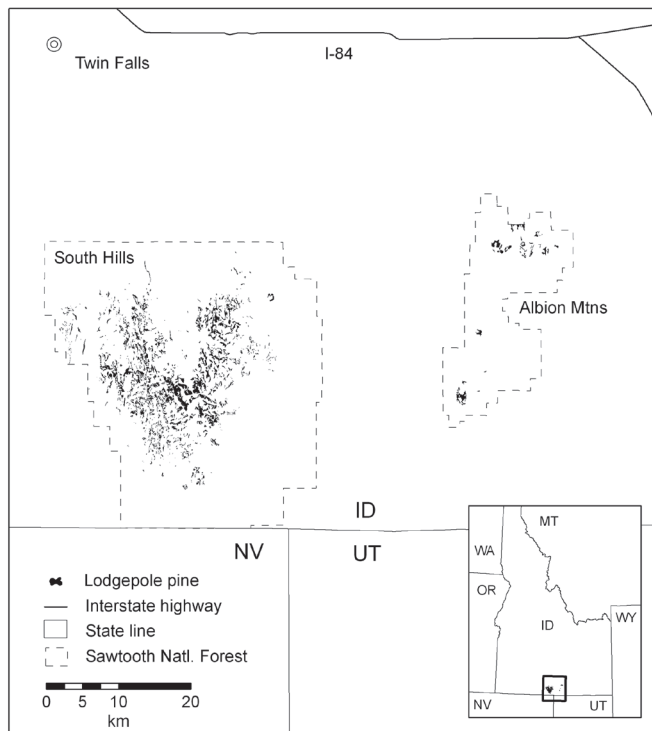


FIGURE 1. Distribution of lodgepole pine (*Pinus contorta latifolia*) in the South Hills and Albion Mountains. Lodgepole pine extends just north along part of the northern boundary of the Sawtooth National Forest in the Albion Mountains but is not shown; the lodgepole pine distribution is based on U.S. Forest Service data. Inset, location within Idaho.

through winter into spring (Benkman 1993, 2003, Benkman and Miller 1996; see Robinson and Wilson [1998] for the theoretical basis for an apparent uncoupling of ecology and evolution). At least seven of the call types are specialized for foraging on different species of conifers that hold seeds in partially closed cones through winter (Benkman 1993, 1999, Benkman and Miller 1996, Benkman et al. 2001, Parchman and Benkman 2002, K. Irwin, unpubl. manuscript). Most of the crossbills inhabiting the South Hills and Albion Mountains are of call type 9 (Sibley 2000); call types 2 and 5 also occur there regularly (Smith and Benkman 2007).

Although factors promoting divergent selection among North American Red Crossbill call types are well understood, until recently (Smith and Benkman 2007, Snowberg and Benkman 2007) little was known about whether divergent selection is promoting reproductive isolation among them. The different call types maintain morphological and vocal differences despite widespread sympatry, suggesting that they are reproductively isolated (Groth 1993a; see Knox [1990] for a similar argument for recognizing the Scottish Crossbill [*L. scotica*] as a distinct biological species). Nevertheless, direct evidence of reproductive isolation and assortative mating among the different call types has remained elusive (e.g., Groth 1993b).

In Europe, evidence for reproductive isolation of call types or even recognized species (i.e., *L. pytyopsittacus*, *L. scotica*, and *L. curvirostra*) has also remained scarce (e.g., Knox 1990, Robb 2000, Edelaar et al. 2004) until recently (Summers et al. 2007). The paucity of such data arises for two reasons. First, the variable nature of cone production of most conifers causes crossbills to engage in annual nomadic movements while tracking cone-crop fluctuations (Newton 1972, Benkman 1987, 1992, Adkisson 1996). Second, crossbills are opportunistic breeders, with timing of breeding governed by the erratic availability of conifer seeds (Newton 1972, Benkman 1990, 1992). This combination of nomadism and erratic breeding has made it difficult to observe pairing on a regular basis. One exception to this rule is found in the South Hills (Smith and Benkman 2007).

Recent observations indicate high levels of pre-mating reproductive isolation among crossbills breeding in the South Hills and two other commonly co-occurring call types (types 2 and 5; Smith and Benkman 2007; L. Santisteban and C. W. Benkman, unpubl. data). Because these estimates confirm the existence of reproductive isolation in sympatry, as was also indicated in earlier examinations of genetic, morphological, and vocal distinctiveness (Benkman 1999, Benkman et al. 2001, Parchman et al. 2006, Smith and Benkman 2007), we now feel that it is appropriate to recognize the crossbills of the South Hills as a distinct species according to the biological species concept allowing a low level of gene flow (Coyne and Orr 2004).

A RESIDENT CROSSBILL

We began color-banding adult South Hills crossbills in the South Hills in 1998 and have repeatedly captured and observed marked individuals in the same areas in successive years (Benkman et al. 2005). The longest interval between recaptures has been 8 years (two individuals initially captured as juveniles in 1999 and 2000 were recaptured 2 and 10 km from the original capture sites in 2007 and 2008, respectively). Adults show annual site fidelity remarkable for crossbills (although we recaptured one adult female that moved about 57 km from the Albion Mountains to the South Hills; Fig. 1), whereas young of the year often disperse up to 10 km or more.

Residency has been favored for two reasons. First, seed availability in the South Hills and Albion Mountains is extraordinarily stable because of the absence of the American red squirrel (*Tamiasciurus hudsonicus*), another predator of lodgepole pine seeds. Red squirrels have apparently been absent from the South Hills and Albion Mountains since the end of the Pleistocene, if not longer, because vast areas of sagebrush steppe isolate these mountains from ranges to the east that have red squirrels (Benkman 1999, Benkman et al. 2001). In the absence of red squirrels, cones accumulate on the lodgepole pines. In addition, serotinous lodgepole pine cones can

TABLE 1. Morphometrics of the three forms of Red Crossbill that breed in the South Hills, Idaho. Values sharing the same superscript letter do not differ significantly (Tukey–Kramer tests, $P > 0.05$); values bearing different letters do differ significantly.

	Males			Females		
	Call type 2	Call type 5	South Hills Crossbill	Call type 2	Call type 5	South Hills Crossbill
Body mass (g)						
Mean	34.2 ^a	32.8 ^b	34.4 ^a	33.4 ^a	33.2 ^a	34.1 ^a
SE	0.2	0.5	0.1	0.3	0.4	0.1
<i>n</i>	103	22	483	60	11	337
Range	28.8–38.6	28.6–38.6	29.2–39.4	28.2–38.6	30.0–35.3	28.8–43.9
Wing length (mm)						
Mean	92.8 ^a	93.5 ^{a, b}	93.8 ^b	90.5 ^a	91.1 ^a	91.0 ^a
SE	0.2	0.5	0.1	0.3	0.4	0.1
<i>n</i>	110	31	509	72	15	356
Range	86.0–98.5	87.0–98.0	87.5–100.0	83.0–98.5	88.5–94.0	85.0–98.0
Bill depth (mm)						
Mean	9.63 ^a	9.40 ^b	9.91 ^c	9.48 ^a	9.28 ^b	9.67 ^c
SE	0.03	0.05	0.01	0.04	0.09	0.01
<i>n</i>	120	36	471	80	14	335
Range	8.97–10.38	8.77–10.14	9.05–10.56	8.75–10.38	8.90–9.97	8.90–10.46
Bill length from nostril (mm)						
Mean	15.70 ^a	15.29 ^b	15.15 ^b	15.41 ^a	14.88 ^b	15.00 ^b
SE	0.08	0.13	0.03	0.09	0.19	0.04
<i>n</i>	105	30	446	74	14	323
Range	13.79–18.87	13.95–16.87	13.40–17.30	13.8–17.74	13.46–16.06	13.05–17.30
Bill length/depth						
Mean	1.63 ^a	1.62 ^a	1.53 ^b	1.62 ^a	1.59 ^{a, b}	1.55 ^b
SE	0.009	0.014	0.003	0.010	0.020	0.004
<i>n</i>	106	30	444	73	13	321
Range	1.40–1.93	1.43–1.75	1.32–1.74	1.40–1.80	1.46–1.69	1.35–1.80

hold seeds for decades until cones are heated by fire. In the absence of red squirrels, the frequency of serotiny has increased because red squirrels exert strong selection against serotiny (Benkman and Siepielski 2004). The result is the accumulation in the canopy of a large seed bank on which this crossbill depends (Smith and Benkman 2007). Moreover, variation in annual seed production has decreased in the absence of red squirrels so that variation in seed production from year to year (7.1% coefficient of variation of cone production measured for three branches from 78 trees; T. Fetz and Benkman, unpubl. data) is less than in any other known plant species (Benkman et al. 2003).

Second, the South Hills crossbill has become locally adapted for foraging on the distinctive cones in the South Hills and Albion Mountains, but its deep bill (Table 1) is poorly adapted relative to that of other Red Crossbills for foraging on other conifers including lodgepole pine in nearby ranges to the north and east (Benkman et al. 2001, Benkman 2003). In the absence of red squirrels, lodgepole pine in the South Hills has lost defenses against squirrels, and crossbill densities in the South Hills are about 20 times higher than in lodgepole pine forests having red squirrels (Benkman 1999, Siepielski

and Benkman 2005). Crossbills are now the main selective agent on cone structure and exert selection causing lodgepole pines to evolve seed defenses against crossbills in the form of larger, thicker-scaled cones, which in turn cause reciprocal selection favoring large-billed crossbills (Benkman 1993, Benkman and Miller 1996, Benkman et al. 2001). In response to the enhanced seed defenses South Hills crossbills have evolved bills deeper than those of other closely related crossbills (Table 1; Parchman et al. 2006, Smith and Benkman 2007). The result is a coevolutionary arms race between crossbills and lodgepole pine in the South Hills and Albion Mountains (Benkman 1999, Benkman et al. 2001, 2003, Siepielski and Benkman 2005, Edelaar and Benkman 2006).

SOUTH HILLS CROSSBILL

Loxia sinesciuris Benkman, new species

Holotype. Museum of Vertebrate Zoology (MVZ), University of California, Berkeley, No. 183381, adult female (after year of hatching) obtained by William Holimon on 25 July 1998 in the Sawtooth National Forest at Porcupine Springs, Cassia County, Idaho (latitude 42° 10' 4.4" N, longitude 114° 15' 55.3" W).

At capture, its body mass was 33.6 g, wing length 92.0 mm, bill depth 9.74 mm, and bill length (anterior edge of nares to tip of maxilla) 14.65 mm. The paratype, MVZ 183382, adult male (after year of hatching), was obtained by William Holimon at the same location on 2 August 1998. At capture, its body mass was 34.1 g, wing length 98.5 mm, bill depth 10.05 mm, and bill length 16.22 mm. Both specimens were prepared as study skins by Peter Houde. Recordings of the flight calls of these two crossbills have considerable background noise and are not shown, but they are readily identifiable as those of South Hills Crossbills (see Fig. 2).

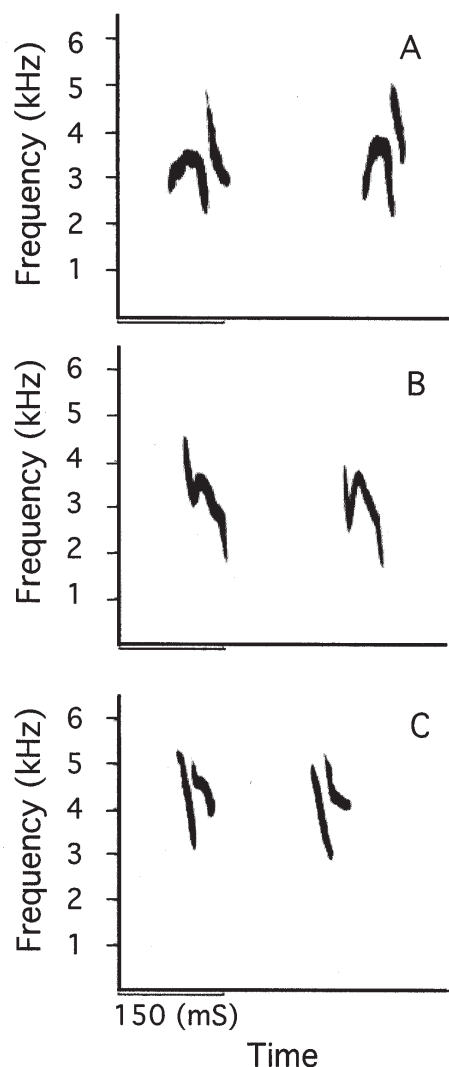


FIGURE 2. Representative flight calls from two individuals of (A) South Hills, (B) call type 2, and (C) call type 5 Red Crossbills. Flight calls of call types differ by the presence of a second element (e.g., call type 2 usually lacks it), frequency (e.g., call type 5 has highest average frequency), and slope of the frequency modulations (e.g., frequency increases in the beginning of the South Hills Crossbill call but not in the others) (Groth 1993; Smith 2005). Figure reproduced from Smith and Benkman (2007).

The only Red Crossbills collected in the South Hills or Albion Mountains prior to 1998 were two collected in the Albion Mountains by V. E. Jones in July 1939 (1256 and 1257, Idaho Museum of Natural History). One is an adult male, the other is a streaked immature male. Unfortunately, the mandibles of the adult are not occluded so that its bill depth can not be measured. The bill depth of the immature is 9.15 mm. Although both of these birds are likely South Hills Crossbills, we cannot exclude the possibility that they are call type 2 or 5.

Diagnosis. Very similar to other Red Crossbills in North America but larger (body mass and bill depth, but upper mandible relatively short) on average than other Red Crossbills currently found commonly north of Mexico (Table 1) and with distinctive vocalizations (see below; Smith and Benkman 2007). As in other Red Crossbills, males are reddish in body coloration whereas females are greenish-gray and smaller than males (Table 1; see below).

Distribution. Lodgepole pine forests in the South Hills and Albion Mountains in southern Idaho (Fig. 1). South Hills Crossbills are common year round in both ranges. During the summer months especially, Red Crossbills of call types 2 and 5 also occur in these forests but breed much less commonly than do South Hills Crossbills (Smith and Benkman 2007). Call types 4 and 7 have also been captured in the South Hills but have not been found breeding there. Although there are no confirmed records, we suspect that South Hills Crossbills will occur in other mountain ranges to the north and east at least occasionally.

MORPHOMETRICS

We captured South Hills Crossbills mostly during the summer when they were nesting or had recently completed nesting. Few individuals had observable fat (in contrast to other call types that were moving through the area), but some had recently drunk water at capture. Most individuals had worn or molting flight feathers. We captured Red Crossbills of call types 2 and 5 throughout much of the Rocky Mountain region including the South Hills and farther west; other call types in the Rocky Mountain region (e.g., call types 3 and 4) are even smaller (Benkman 1993, Groth 1993a), so we do not provide morphometrics for them.

Although South Hills Crossbills tended to have larger body masses and longer wings than crossbills of call types 2 and 5, these differences were significant only in some comparisons for males (Table 1). The bill depths of South Hills Crossbills, however, were significantly greater than those of the other call types (Table 1). The heritability of bill depth in crossbills is known to be high (Summers et al. 2007), implying a genetic basis to these differences (Table 1). The bill lengths of South Hills Crossbills were shorter than those of call type 2 and similar to those of call type 5 (Table 1). These differences show that South Hills Crossbills have relatively deep short bills compared to Red Crossbills of other call

types in the region (Benkman 1999, Benkman et al. 2001). The sexual dimorphism of the South Hills Crossbill in mandible length (males 1% larger than females) is less than in bill depth (males 2.4% larger than females), probably because of differential wear of the tips of the mandibles. Males forage more than females during nesting and thus wear their bills more (Benkman 1992).

VOCALIZATIONS

South Hills Crossbills have distinctive flight calls (Fig. 2A) that they initially learn by imitating their parents and later alter to match the call of their mates (Keenan and Benkman 2008). Flight calls of types 2 and 5 are shown (Fig. 2B, C) because Red Crossbills of these call types cluster together genetically with South Hills Crossbills (Parchman et al. 2006). They have also been found to nest in the South Hills (Smith and Benkman 2007) and in the Rocky Mountain region are the most similar in size to the South Hills Crossbill (Table 1; Benkman 1993, Groth 1993a, Smith and Benkman 2007). A principal-components analysis based on Euclidean distances among cross-correlation values (Charif et al. 1995) of flight calls of 72 individuals of these three call types showed distinct clustering of individuals by call type and, with the exception of one individual, no overlap among call types (Fig. 3; Smith 2005).

South Hills Crossbills have distinctive excitement calls with two separate elements (Fig. 4). Both harmonic elements initially rise and then fall in frequency (Fig. 4). South Hills excitement calls differ from excitement calls of call types 2 and 5 in the direction of frequency modulation and by the presence of a second harmonic element throughout the duration of the excitement call. Excitement calls of call type 2 initially drop in frequency and then rise and fall again (Groth 1993a). Although the excitement call of the South Hills Crossbill and call

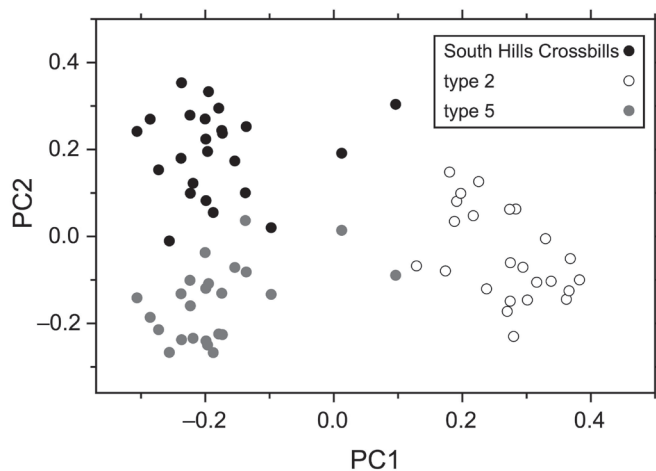


FIGURE 3. Principal-components analysis based on cross-correlation values for flight calls of 72 individuals of three call types (from Smith 2005).

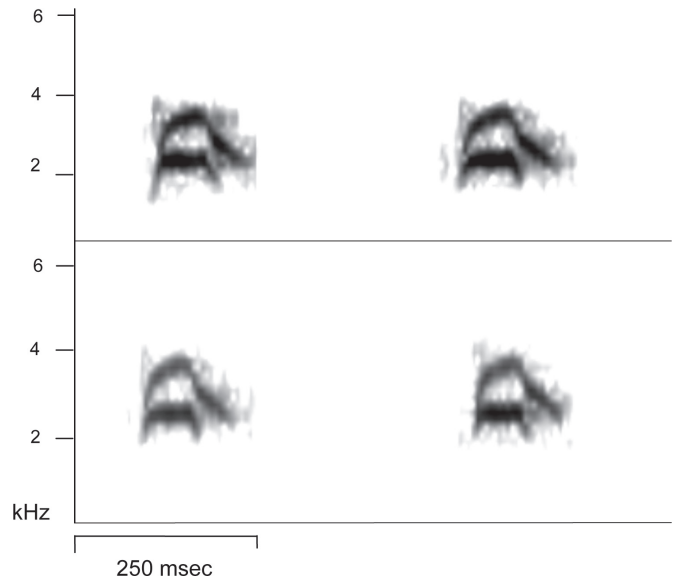


FIGURE 4. Two excitement calls from two South Hills Crossbills recorded in April and May 2002 in the South Hills, Sawtooth National Forest, Idaho.

type 2 both have a second harmonic element, in call type 2 this element is emphasized mainly in the first half of the notes (Groth 1993a). The separate elements of excitement calls of call type 5 are less separated in frequency, have less frequency modulation, and are of shorter duration than those in the excitement calls of South Hills Crossbills (Groth 1993a). The excitement calls of call type 1 are similar to the chevron-shaped lower-frequency element of the South Hills' excitement call (Fig. 4), but the excitement calls of call type 1 lack the second chevron-shaped harmonic element (Groth 1993a).

South Hills Crossbills, like other Red Crossbill call types, sing elaborate prolonged songs composed of multiple phrases separated by a few seconds of silence (Fig. 5). South Hills' songs are dominated by buzzy notes, whereas the songs of call types 2 and 5 consist predominately of shorter whistled notes (Fig. 5). South Hills' songs are more repetitive than the songs of the other two call types with fewer syllable types and more repetition of syllable types per phrase. South Hills' songs also have many unique syllables, but assessing the full extent of syllable divergence will require further investigation.

BEHAVIOR

South Hills Crossbills are similar behaviorally to Red Crossbills (e.g., see Adkisson 1996) in terms of foraging, flocking, and singing. However, their annual cycle is more seasonal than that of other crossbills and more like that of most passerines breeding in the temperate zone (Smith and Benkman 2007). As mentioned earlier, South Hills Crossbills are highly sedentary. They appear to initiate nesting at approximately the same time each year, presumably because seed availability (in terms

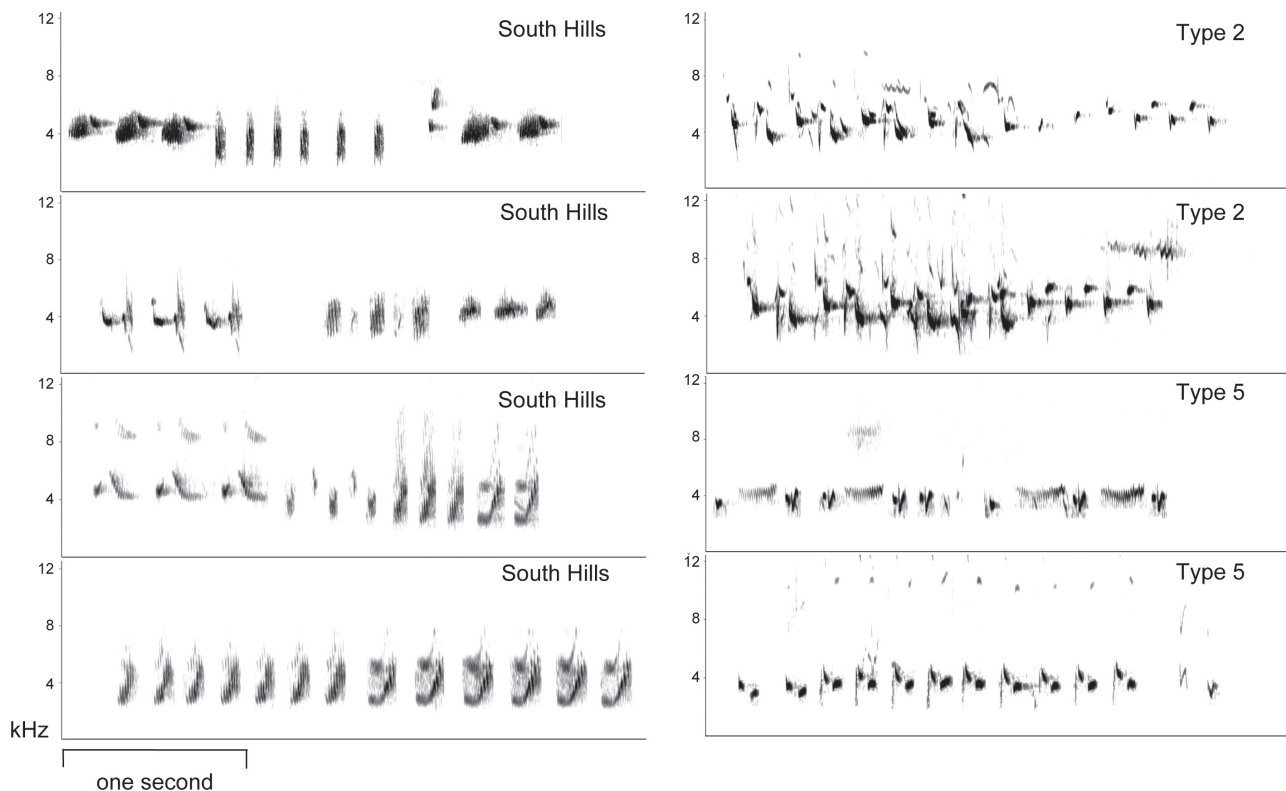


FIGURE 5. Sonograms of representative phrases from songs of four male South Hills Crossbills, two males of call type 2, and two males of call type 5. South Hills Crossbills were recorded in March, April, and June 2002 in the South Hills, Sawtooth National Forest, Idaho. Males of call type 2 were recorded in July 2007 near Beaver Lake, Okanogan National Forest, Washington. Males of call type 5 were recorded in February 2004 near Jackal Hut, White River National Forest, Colorado.

of the crossbills' food-intake rates) increases in the spring in a manner consistent from year to year (Smith and Benkman 2007). They start building nests during late March and early April and usually terminate nesting by mid to late July. South Hills Crossbills start molting in July and finish by late September (P. C. Keenan, unpubl. data). These shifts in breeding behavior and from nomadism to residency, in addition to morphological divergence from other call types, presumably results from divergent selection that is more multifarious than that between nomadic call types. This may have facilitated speciation of the South Hills Crossbill because reproductive isolation evolves more rapidly when divergent selection acts on multiple traits than when it acts on only a single trait (Rice and Hostert 1993).

ESTIMATES OF CURRENT AND PAST REPRODUCTIVE ISOLATION

Between 2001 and 2006 we recorded only 12 South Hills Crossbills paired with other call types (call types 2 and 5) out of a total of 1704 paired South Hills Crossbills (Smith and Benkman 2007; L. Santisteban and C. W. Benkman, unpubl. data), a hybridization frequency of 0.007 (annual range 0–0.02). This frequency of hybrid pairing is nearly an order of magnitude

lower than that found among the three species of crossbills recognized in Europe (0.05; Summers et al. 2007). From the behavior and relative testis size of Red Crossbills (Smith and Benkman 2007) and from the absence of extra-pair paternity in a study of Red (Common) Crossbills in Norway (Kleven et al. 2008) we assume that extra-pair paternity is rare and does not influence our estimates of hybridization. We found one instance of a female of call type 2 shifting its call to match that of its mate, a South Hills Crossbill, in successive years, but because this shift occurred only in the year following this pair's successful breeding such call shifts should affect our estimates of the frequency of hybridization only minimally (Keenan and Benkman 2008; see also Summers et al. 2007).

Strong preferences of crossbills to associate with others of their own call type were also found in the laboratory. When 18 female South Hills Crossbills, implanted with 17- β -estradiol to make them more reproductively receptive, were given a choice between associating with a male South Hills Crossbill or a male Red Crossbill of call type 2 (while differences between males in bill size and male coloration were controlled for), 15 of the females (83%) preferred to associate with the South Hills male (Snowberg and Benkman 2007).

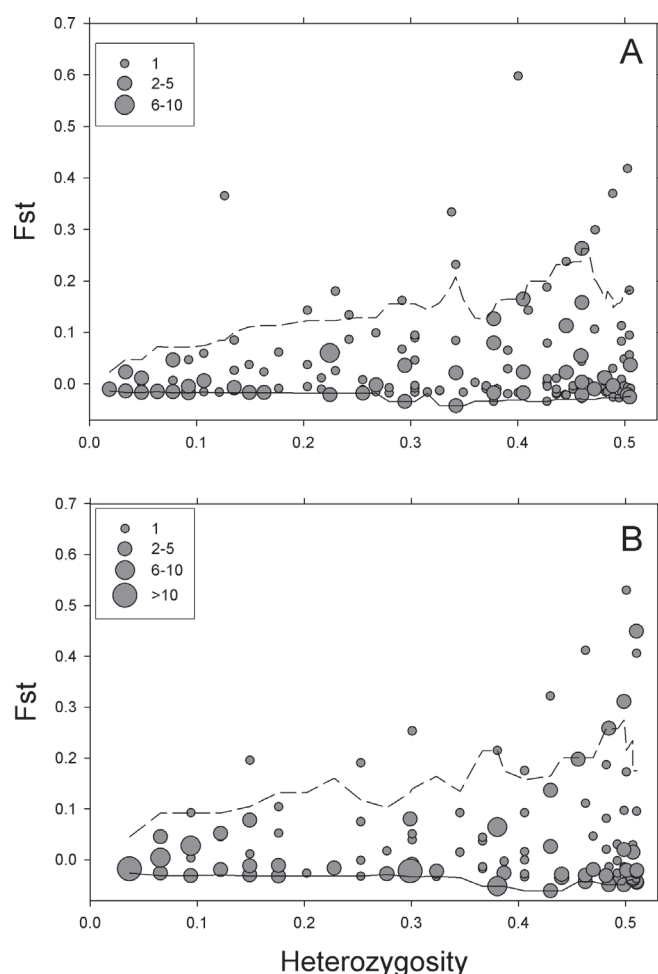


FIGURE 6. F_{ST} values estimated for 235 polymorphic AFLP loci plotted against heterozygosity (H_s) for comparisons between South Hills Crossbills and (A) crossbills of call types 2 and (B) 5. The bottom and top lines represent the 0.05 and 0.95 quantiles, respectively, estimated from simulations run in DFDIST (Beaumont and Balding 2004), representing the expected distribution of F_{ST} values for neutral loci given the weighted empirical mean. Loci occurring above the top line are considered outliers and are candidates for showing the symptoms of natural selection. Thirteen and 12 loci were outliers at $P < 0.05$ in A and B, respectively.

Using amplified fragment length polymorphisms (AFLP), we have not found fixed differences among call type 2, call type 5, and the South Hills Crossbill, but have found significant levels of genetic differentiation based on inferred variation in allele frequency and F_{ST} estimates (Parchman et al. 2006). This genetic structure is consistent with recent divergence in the face of gene flow among the call types of Red Crossbills (Parchman et al. 2006). Genetic divergence between South Hills Crossbills and crossbills of call types 2 and 5 is especially evident in about 5% of 235 AFLP loci (Fig. 6). The pattern is consistent with selection causing divergence in these regions of the genome in the face of gene flow that has homogenized the rest (Via and West 2008).

HABITAT AND CONSERVATION STATUS

South Hills Crossbills rely on consistent seed availability provided by mature stands of lodgepole pine. Their annual survivorship of adults is relatively high, averaging over 60% between 2000 and 2007 (Benkman et al. 2005; L. Santisteban and C. W. Benkman, unpubl. data). The main threats to the habitat are infestations of the mountain pine bark beetle (*Dendroctonus ponderosae*), fire, and global climate change. The last has been forecast to eliminate lodgepole pine from the region by the end of this century (Thompson et al. 2002).

ETYMOLOGY

We name this species *Loxia sinesciuris* because it occurs in an area without tree squirrels, and the absence of tree squirrels is key to its evolution. *Sine sciuris* is the Latin phrase “without squirrels.” The common name, South Hills Crossbill, refers to the main area where this crossbill resides. In previous publications it has been referred to as both the South Hills Crossbill (e.g., Benkman 1999) and call type 9 (e.g., Sibley 2000, Snowberg and Benkman 2007), because it represents the ninth call type of the Red Crossbill described in North America.

ACKNOWLEDGMENTS

We thank personnel of the Sawtooth National Forest Service and Idaho Fish and Game Department. This work was supported by National Science Foundation grants DEB-0212271 and DEB-0435923 to CWB and supplemental RET (DEB-0435923), REU (DEB-0422576, and DEB-0620261). Comments by R. Banks, P. Edelaar, A. Knox, R. Summers, M. Patten, P. Unitt, and an anonymous reviewer improved the manuscript. We thank J. Stanek for creating Figure 1. We dedicate this paper to the late Harrison B. Tor-doff, who encouraged CWB to study crossbills.

LITERATURE CITED

- ADKISSON, C. S. 1996. Red Crossbill (*Loxia curvirostra*), no. 256. In A. Poole and F. Gill [EDS.]. The birds of North America. Academy of Natural Sciences, Philadelphia.
- BEAUMONT, M. A., AND D. J. BALDING. 2004. Identifying adaptive genetic divergence among populations from genome scans. *Molecular Ecology* 13:969–980.
- BENKMAN, C. W. 1992. White-winged Crossbill (*Loxia leucoptera*), no. 27. In A. Poole, P. Stettenheim, and F. Gill [EDS.]. The birds of North America. Academy of Natural Sciences, Philadelphia.
- BENKMAN, C. W. 1993. Adaptation to single resources and the evolution of crossbill (*Loxia*) diversity. *Ecological Monographs* 63:305–325.
- BENKMAN, C. W. 1999. The selection mosaic and diversifying coevolution between crossbills and lodgepole pine. *American Naturalist* 153:S75–S91.
- BENKMAN, C. W. 2003. Divergent selection drives the adaptive radiation of crossbills. *Evolution* 57:1176–1181.
- BENKMAN, C. W., J. S. COLQUITT, W. R. GOULD, T. FETZ, P. C. KEENAN, AND L. SANTISTEBAN. 2005. Can selection by an ectoparasite drive a population of crossbills from its adaptive peak? *Evolution* 59:2025–2032.
- BENKMAN, C. W., W. C. HOLIMON, AND J. W. SMITH. 2001. The influence of a competitor on the geographic mosaic of coevolution between crossbills and lodgepole pine. *Evolution* 55:282–294.

- BENKMAN, C. W., AND R. E. MILLER. 1996. Morphological evolution in response to fluctuating selection. *Evolution* 50:2499–2504.
- BENKMAN, C. W., T. L. PARCHMAN, A. FAVIS, AND A. M. SIEPIELSKI. 2003. Reciprocal selection causes a coevolutionary arms race between crossbills and lodgepole pine. *American Naturalist* 162:182–194.
- BENKMAN, C. W., AND A. M. SIEPIELSKI. 2004. A keystone selective agent? Pine squirrels and the frequency of serotiny in lodgepole pine. *Ecology* 85:2082–2087.
- CHARIF, R. A., S. MITCHELL, AND C. W. CLARK. 1995. *Canary 1.2*. Cornell Laboratory of Ornithology, Ithaca, NY.
- COYNE, J. A., AND H. A. ORR. 2004. *Speciation*. Sinauer Associates, Sunderland, MA.
- EDELAAR, P., AND C. W. BENKMAN. 2006. Replicated population divergence caused by localized coevolution? A test of three hypotheses in the Red Crossbill–lodgepole pine system. *Journal of Evolutionary Biology* 19:1651–1659.
- GROTH, J. G. 1993a. Evolutionary differentiation in morphology, vocalizations, and allozymes among nomadic sibling species in the North American Red Crossbill (*Loxia curvirostra*) complex. *University of California Publications in Zoology* 127:1–143.
- GROTH, J. G. 1993b. Call matching and positive assortative mating in Red Crossbills. *Auk* 110:398–401.
- KEENAN, P. C., AND C. W. BENKMAN. 2008. Call imitation and call modification in Red Crossbills. *Condor* 110:93–101.
- KLEVEN, O., B. BJERKE, AND J. T. LIFJELD. 2008. Genetic monogamy in the Common Crossbill (*Loxia curvirostra*). *Journal of Ornithology* 149:651–654.
- KNOX, A. G. 1990. The sympatric breeding of Common and Scottish Crossbills *Loxia curvirostra* and *L. scotica* and the evolution of crossbills. *Ibis* 132:454–466.
- NEWTON, I. 1972. *Finches*. Collins, London.
- PARCHMAN, T. L., C. W. BENKMAN, AND S. C. BRITCH. 2006. Patterns of genetic variation in the adaptive radiation of New World crossbills (Aves: *Loxia*). *Molecular Ecology* 15:1873–1887.
- RICE, W. R., AND E. E. HOSTERT. 1993. Laboratory experiments on speciation: what have we learned in 40 years? *Evolution* 47:1637–1653.
- ROBINSON, B. W., AND D. S. WILSON. 1998. Optimal foraging, specialization, and a solution to Liem's paradox. *American Naturalist* 151:223–235.
- SIBLEY, D. A. 2000. *The Sibley guide to birds*. Knopf, New York.
- SIEPIELSKI, A. M., AND C. W. BENKMAN. 2005. A role for habitat area in the geographic mosaic of coevolution between red crossbills and lodgepole pine. *Journal of Evolutionary Biology* 18:1042–1049.
- SMITH, J. W. 2005. The role of coevolution in promoting ecological speciation in Red Crossbills (*Loxia curvirostra* complex). Ph.D. dissertation, New Mexico State University, Las Cruces, NM.
- SMITH, J. W., AND C. W. BENKMAN. 2007. A coevolutionary arms race causes ecological speciation in crossbills. *American Naturalist* 169:455–465.
- SNOWBERG, L. K., AND C. W. BENKMAN. 2007. The role of marker traits in the assortative mating within Red Crossbills, *Loxia curvirostra* complex. *Journal of Evolutionary Biology* 20:1924–1932.
- SUMMERS, R. W., R. J. G. DAWSON, AND R. E. PHILLIPS. 2007. Assortative mating and patterns of inheritance indicate that the three crossbill taxa in Scotland are species. *Journal of Avian Biology* 38:153–162.
- THOMPSON, R. S., S. W. HOSTETLER, P. J. BARTLEIN, AND K. H. ANDERSON. 2002. A strategy for assessing potential future changes in climate, hydrology, and vegetation in the western United States. US Geological Survey Circular 1153. Washington, D.C.
- VIA, S., AND J. WEST. 2008. The genetic mosaic suggests a new role for hitchhiking in ecological speciation. *Molecular Ecology* 17:4334–4345.