

Reciprocal Selection Causes a Coevolutionary Arms Race between Crossbills and Lodgepole Pine

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ABSTRACT: Few studies have shown both reciprocal selection and reciprocal adaptations for a coevolving system in the wild. The goal of our study was to determine whether the patterns of selection on Rocky Mountain lodgepole pine (*Pinus contorta* spp. *latifolia*) and red crossbills (*Loxia curvirostra* complex) were concordant with earlier published evidence of reciprocal adaptations in lodgepole pine and crossbills on isolated mountain ranges in the absence of red squirrels (*Tamiasciurus hudsonicus*). We found that selection (directional) by crossbills on lodgepole pine where *Tamiasciurus* are absent was divergent from the selection (directional) exerted by *Tamiasciurus* on lodgepole pine. This resulted in divergent selection between areas with and without *Tamiasciurus* that was congruent with the geographic patterns of cone variation. In the South Hills, Idaho, where *Tamiasciurus* are absent and red crossbills are thought to be coevolving with lodgepole pine, crossbills experienced stabilizing selection on bill size, with cone structure as the agent of selection. These results show that crossbills and lodgepole pine exhibit reciprocal adaptations in response to reciprocal selection, and they provide insight into the traits mediating and responding to selection in a coevolutionary arms race.

Keywords: geographic selection mosaic, *Loxia curvirostra*, *Pinus contorta* ssp. *latifolia*, predator-prey interaction, seed predation, *Tamiasciurus hudsonicus*.

Many evolutionary biologists believe that predator-prey interactions, particularly coevolution, have played a pivotal role in evolution. This stems from the intuitive notion that few animals are not either predator or prey, so that the

evolution of reciprocal counterdefenses and offenses is often expected (Abrams 2000). Accordingly, the development of numerous models and theoretical arguments (e.g., Dawkins and Krebs 1979; Abrams 1986, 2000; Vermeij 1987, 1994) has paved the road for examining how predator-prey relationships fit into the general scope of evolutionary biology. For example, many recent studies have shown that divergent selection may be a common outcome of coevolution (Thompson and Pellmyr 1992; Thompson 1997, 1999*a*, 1999*b*; Lively 1999; Brodie et al. 2002; Thompson and Cunningham 2002) and could be responsible for promoting population divergence and perhaps speciation (Benkman 1999; Benkman et al. 2001; Parchman and Benkman 2002). Such spatial heterogeneity in species interactions is most clearly articulated by Thompson (1994, 1999*a*, 1999*b*, 2001) in the framework of the geographic mosaic theory of coevolution. This theory posits that coevolution is prominent in some areas (coevolutionary hot spots) but not in others (coevolutionary cold spots; Benkman 1999; Lively 1999; Benkman et al. 2001; Brodie et al. 2002; Parchman and Benkman 2002), that the outcome of an interaction can vary between areas (Thompson and Pellmyr 1992; Thompson and Cunningham 2002), and that gene flow can affect the outcome of interactions (Burdon and Thrall 1999).

Despite the importance of predator-prey coevolution, we lack much quantitative evidence for one of its salient predictions: namely, that reciprocal selection between predators and prey causes reciprocal adaptations. Here we provide quantitative evidence for traits mediating reciprocal selection between predator and prey populations in a coevolutionary arms race in the wild. We also show that selection between predator and prey populations is divergent and leads to a geographic selection mosaic. Elsewhere, we provide evidence for reciprocal adaptations between these predator and prey populations (Benkman 1999; Benkman et al. 2001).

The interaction between red squirrels (*Tamiasciurus hudsonicus*), red crossbills (*Loxia curvirostra* complex), and Rocky Mountain lodgepole pine (*Pinus contorta* spp. *latifolia*; fig. 1) is one example of how geographic variation

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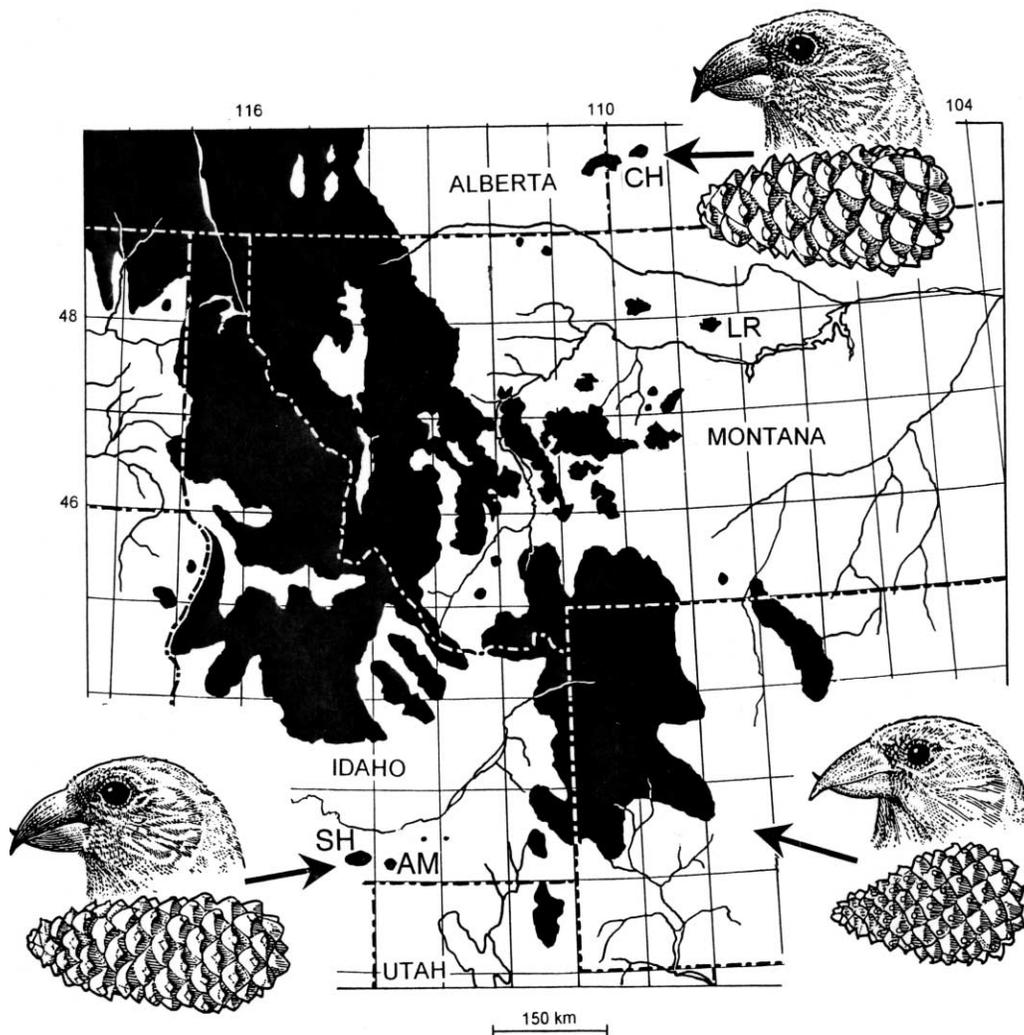


Figure 1: Distribution of lodgepole pine (black), locations of study sites, and representative red crossbills (*Loxia curvirostra* complex) and cones in the Rocky Mountains (lower right), in the Cypress Hills (upper right), and in the South Hills and Albion Mountains (lower left; modified from Benkman 1999). The crossbills and cones are drawn to relative scale. Red squirrels (*Tamiasciurus hudsonicus*) are found throughout the range of lodgepole pine except in some isolated mountains, including the South Hills (SH), Albion Mountains (AM), and Little Rocky Mountains (LR). *Tamiasciurus* were absent from the Cypress Hills (CH) until they were introduced in 1950.

in the strength and outcome of interactions might arise (Benkman 1999; Benkman et al. 2001). Where *Tamiasciurus* are present, they act as the dominant seed predator and drive lodgepole pine cone evolution. These areas represent a coevolutionary hot spot for *Tamiasciurus* and pine but a coevolutionary cold spot for crossbills. Here crossbills adapt to cones (fig. 1) whose evolution is largely the result of selection by *Tamiasciurus*. Where *Tamiasciurus* are absent, however, crossbills act as the primary seed predators, and they drive the evolution of lodgepole pine cone traits. In these areas, crossbills exhibit reciprocal adaptations implicating coevolution as an active process, making

such areas coevolutionary hot spots for crossbills (fig. 1). The result is divergent selection between populations of crossbills and pine in hot spots and cold spots.

This scenario is based on behavioral, morphological, genetical, and paleobotanical evidence that indicate replicated reciprocal adaptation and coevolution between crossbills and lodgepole pine east and west of the Rocky Mountains in the past 10,000 yr (fig. 1; Benkman 1999; Benkman et al. 2001). However, direct measures of natural selection on lodgepole pine by crossbills and reciprocal selection by lodgepole pine on crossbills are lacking. Earlier studies (Benkman 1999; Benkman et al. 2001) inferred

selection on lodgepole pine and on crossbills from variation in crossbill foraging rates in aviaries in relation to cone traits and bill depth, respectively. Although these inferences are reasonable given that crossbills forage so as to maximize feeding intake rates (Benkman 1987, 1989), direct measures of selection in the wild are preferable and would strengthen previous findings substantially. Moreover, this example is of particular interest because examples of predator-prey coevolution are few (Abrams 2000). Some examples of predator-prey coevolution are compelling (e.g., Brodie et al. 2002; Geffeney et al. 2002); however, none has provided quantitative evidence of both reciprocal adaptations and selection in the wild that can account for these adaptations. This knowledge is necessary if we are to eliminate other alternatives to coevolution, such as predators responding to selection from other factors in their environment (e.g., their enemies) and prey in turn evolving in response to this variation in the predators (Vermeij 1994).

The first goal of our study was to quantify selection by crossbills on lodgepole pine in an area where *Tamiasciurus* are absent, the Little Rocky Mountains, Montana (fig. 1). Second, we determined whether selection by crossbills was divergent from that imposed by *Tamiasciurus* by quantifying in a similar manner the form of selection exerted by *Tamiasciurus* on lodgepole pine using previously published data (Benkman 1999; Benkman et al. 2001). If the forms of selection by crossbills and *Tamiasciurus* were congruent with the patterns of cone evolution, this would indicate that variation in selection by these two seed predators was largely responsible for the geographic patterns of variation in cone structure. Such an evolutionary response to selection would be expected because many of the lodgepole pine cone traits analyzed are heritable (T. S. Kimbrell, C. C. Smith, J. S. Pontius, and P. F. Elliott, unpublished manuscript). We assume that if selection on a trait by *Tamiasciurus* results in a reduction in seed production (i.e., results in a decrease in the ratio of seed mass to cone mass), then in the absence of such selection (i.e., relaxation of selection), counterselection should prevail. For example, if selection by *Tamiasciurus* favors a reduction in the number of seeds per cone and an increase in cone mass per seed, then, in the absence of *Tamiasciurus*, trees producing cones with more seeds and less cone mass per seed would be favored.

Finally, we quantified the form of selection on crossbills in the South Hills, Idaho, where crossbills are resident and are thought to be coevolving with lodgepole pine in the absence of *Tamiasciurus* (fig. 1; Benkman 1999; Benkman et al. 2001) to determine whether selection was reciprocal between crossbills and lodgepole pine. If the bill depth favored by selection was similar to the one that is most efficient at meeting estimated daily energy demands

(Benkman et al. 2001), this would implicate cone structure as the primary agent of selection on crossbills. Such an inference is strengthened given the clear and direct functional link between the morphology and ecology of crossbills and their food resources, seeds in conifer cones. For example, feeding performance influences crossbill habitat and conifer use, movements, and breeding behavior (Benkman 1987, 1989, 1990), and bill size and cone structure determine feeding performance (Benkman 1993, 1999; Benkman and Miller 1996; Benkman et al. 2001). We focus on bill depth because earlier analyses of foraging data revealed that other measures of bill size (e.g., upper and lower mandible lengths) were weakly related to foraging times and explained little variation when bill depth was excluded from the analyses (Benkman 2003; C. W. Benkman, unpublished data). Moreover, bill depth is heritable in red crossbills ($h^2 \approx 0.7$; R. Summers, personal communication), so an evolutionary response to selection is expected.

Methods

Seed Predation and the Targets and Form of Natural Selection by Crossbills

Serotinous cones were collected from 150 trees in a lodgepole pine-dominated forest in the Little Rocky Mountains (fig. 1) from July 12 to 24, 2000, in order to examine how cone traits were related to seed predation by crossbills. Trees were sampled atop a ridge (elevation 1,440 m) 3.8 km north-northeast of Zortman, Montana. The first 55 trees were sampled haphazardly under the constraint that three upper branches with cones could be cut; the upper branches of most trees along the ridge could be reached with a branch cutter attached to a 9-m extension pole. The remaining 95 trees were chosen to increase the number of trees sampled that were either foraged heavily on by crossbills or completely avoided by them to help detect the form of selection by increasing phenotypic variation (Schluter 1988).

One of us (T.L.P.) cut three branches with at least 6 yr of cones from three different sides of each tree. All trees examined in the study area had serotinous cones, which remain closed until sufficient heat melts the resinous bonds holding the cone scales together (Johnson and Gutsell 1993). These cones were attached firmly to branches, and cones commonly remain closed and attached for 15–20 yr (Crossley 1956; Elliott 1988a) and some for up to 80 yr (Critchfield 1957). The cut branches in our study held up to 14 yr of cones. A successive whorl of cones is usually produced each year; thus, cones can be aged by counting the number of cone whorls starting from cones that matured in the autumn of 1999 (designated cone age

1 yr; the cones produced in 2000 were developing and were not counted). After cutting three branches from a tree, T.L.P. recorded for each branch the number of cones produced each year and the number of cones showing signs of crossbill foraging (scales bent back to expose underlying seeds), and he visually estimated the percentage of each cone foraged on by crossbills. The percent of the cone foraged on by crossbills was scored categorically for each cone with values of 0%, 20%, 40%, 60%, 80%, or 100% depending on the percent of the scales bent back. We assume that this measure was proportional to the percent of the seeds eaten by crossbills, and we refer to this value as percent seed predation.

One of us (A.F.) measured three cones from each of the 150 trees from which crossbill seed predation data were gathered. The three cones measured represented the average cone width and length (selected by visual inspection) of five to 10 cones from each tree. We assumed that the cones foraged on or avoided by crossbills had the same average traits as those measured for the tree. This assumption is reasonable given that within-tree variance in lodgepole pine cone traits is significantly smaller than the between-tree variance (Smith 1968; Elliott 1974). If crossbills were selective of cones within a tree, then our measurements should bias us against detecting trends among trees foraged on and avoided by crossbills. The following cone traits were measured (fig. 2) as described by Benkman et al. (2001): closed cone length, maximum width of closed cone, the thickness of the distal end of six scales in the middle of the distal third of the cone and in the middle of the proximal third of the cone (scales were selected approximately equidistant around the cone), cone mass with seeds removed, number of seeds and number of full seeds (i.e., filled with female gametophyte), and the individual masses of five full seeds without their wings (<5 seeds were measured from 43 of the 450 cones). The number of scales that fall along the vertical axis of the cone in two different planes (fig. 2) and the length of six scales from the distal third of the cone were also measured. All length measurements were made to the nearest 0.01 mm with digital calipers. All mass measurements were made to the nearest 0.01 mg with a digital scale after the cones had been oven dried for ≥ 2 d in a 60°–70°C oven. One composite cone trait requires elaboration. Seed mass/cone mass was the total seed mass in milligrams in the cone (mean number of full seeds times mean seed mass) divided by the mean cone mass in milligrams. Average trait values were calculated for each cone, and these values were used to calculate mean tree values, which were used in further analyses.

We limited analyses to the 120 trees for which 10 yr of cones were present and to data from the most recent 10 yr of cones. We restricted the analyses to trees with the

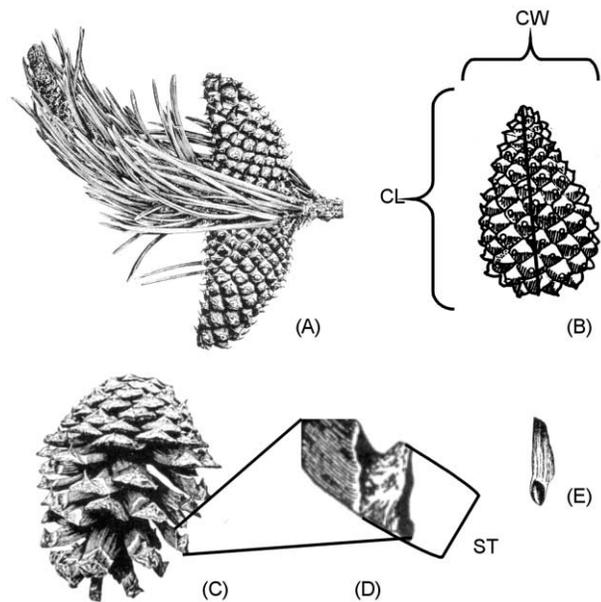


Figure 2: Lodgepole pine cones from the Rocky Mountains. *A*, Two closed cones attached to a branch. *B*, A closed cone to illustrate cone length (*CL*) and cone width (*CW*) and an illustrative line along the cone axis used to count the number of scales. *C*, An open cone. *D*, A cone scale to show where scale thickness was measured (*ST*). *E*, A seed with wing attached.

same range of cone ages because cone predation increased with cone age. We chose trees with at least 10 yr of cones as a compromise between having more trees with fewer years of cones and more years of cones but fewer trees. We chose 29 of these 120 trees haphazardly. For each tree, we calculated a mean percent seed predation for each year and used the means for the 10 yr to calculate the overall mean percent seed predation. We used Spearman's rank correlations between mean percent seed predation per tree, which was nonnormal (see fig. 4), and the various cone traits to determine whether net selection by crossbills (direct selection and indirect selection because of trait correlations) favored increases or decreases in the traits. We used cubic splines (Schluter 1988) to check for stabilizing selection by crossbills and *Tamiasciurus* on cone traits. No evidence of stabilizing selection on any cone trait was found.

We used Spearman's partial correlations to determine the targets of selection, that is, which traits were directly under selection by crossbills. Partial correlation coefficients are analogous to the selection gradients (β), the strength of direct selection on a trait (Lande and Arnold 1983). We included cone width divided by cone length instead of either character alone and excluded scale length to reduce multicollinearity. The highest trait correlation

in the analysis was $r_s = .46$ (table 1). We ln-transformed all cone and seed measurements for all analyses.

*The Targets and Form of Natural
Selection by Tamiasciurus*

We estimated the targets and form of selection on lodgepole pine by *Tamiasciurus* using logistic regression (Janzen and Stern 1998) on most of the above-mentioned cone traits from trees foraged intensively on or largely avoided by *Tamiasciurus*. Benkman (1999) gathered and measured three cones, recently cut by *Tamiasciurus*, from the base of 30 lodgepole pine trees on 30 different *Tamiasciurus* territories in the west plateau of the Cypress Hills, Alberta (fig. 1), from September 15 to 19, 1994. These trees generally had few if any cones remaining on their branches, indicating that *Tamiasciurus* had repeatedly harvested cones from these trees and that seeds from these trees were unlikely to survive (Smith 1970). We compared these cones with three cones gathered from 30 trees that were near the harvested tree and from which few cones had been harvested by *Tamiasciurus*. Such contrasting levels of predation between trees by *Tamiasciurus* have been noted in the Rocky Mountains (Elliott 1974). We assigned trees harvested intensively (completely) and rarely fitnesses of 0 and 1, respectively. The number of scales and scale length were not measured, but the rest of the cone and seed traits were measured in a manner identical to those measured above (fig. 2). We used the cube roots of cone and seed mass and ln-transformed all means. The highest correlation between the cone traits used in this analysis was $r_s = .45$. We present the logistic regression coefficients (α) and estimate the selection gradient (β), as described by Janzen and Stern (1998).

The Form of Natural Selection on Crossbills

We used mist nests and live decoys to capture crossbills during the summers of 1998–2001 in the South Hills. Fifty-six adult South Hills crossbills were uniquely color banded in 1998 and 2000. South Hills crossbills have distinctive vocalizations, and they have been recorded only in the South Hills and adjacent Albion Mountains. Other red crossbill call types (e.g., types 2 and 5 [Groth 1993]) are commonly found in the South Hills from late spring to fall but are rare in winter and thus appear to be mostly summer residents and transients. We used digital calipers to measure bill depth to the nearest 0.01 mm. Two people measured the crossbills (C.W.B. in all years and W. C. Holimon in 1998), and we had nearly identical and highly repeatable bill measurements (we each measured bill depth three to five times per bird and used the mean). For example, of the 17 South Hills crossbills that we both independently measured about 1 mo apart, the average difference in bill depth was 0.001 mm (repeatability = 0.992 [Lessells and Boag 1987]). On release, we recorded their flight calls with Sennheiser shotgun microphones and Marantz tape recorders and analyzed the calls with Canary software on a Macintosh computer to confirm call type identity of every banded crossbill. In subsequent years (1999–2001), we searched for and recaptured banded crossbills and relocated 20 (35.7%) of them 1–3 yr after initial capture. We used a cubic spline (Schluter 1988) to estimate the form of selection in relation to bill depth, assuming relocated birds survived (fitness = 1) and those not relocated had died (fitness = 0).

We do not have direct measures of survival for crossbills in the Rocky Mountains for comparison to the South Hills crossbills. However, we can convert measures of feeding efficiency on Rocky Mountain cones into estimated relative

Table 1: Spearman's pairwise correlations (r_s) between various cone traits (ln-transformed, $n = 120$ trees) in the Little Rocky Mountains, Montana

	Cone		Scale thickness		Scale		Seed mass	Number of seeds	
	Width	Mass	Distal	Proximal	Length	Number		Full	Empty
Cone length (mm)	.500***	.795***	.340***	.316***	.664***	.439***	.310***	.183*	.132
Cone width (mm)		.795***	.116	.677***	.448***	.167	.390***	.128	.037
Cone mass (gm)			.234**	.458***	.598***	.442***	.421***	.197*	.127
Distal scale thickness (mm)				.274**	.424***	-.199***	.100	-.150	-.058
Proximal scale thickness (mm)					.326***	-.063	.258	-.030	-.009
Scale length (mm)						.051	.383***	.032	-.056
Number of scales							.083	.311***	.197*
Seed mass (mg)								.267**	-.155
Number of full seeds									-.139

* $P \leq .05$.

** $P \leq .01$.

*** $P \leq .001$.

survival on the basis of the relationship between survival in the South Hills and feeding efficiency on South Hills cones (survival = $\exp[-9.03 + 9.06(\text{feeding efficiency})]$, $r^2 = .96$; Benkman 2003). We used published equations for feeding efficiency in relation to bill depth for crossbills foraging on lodgepole pine cones from the Rocky Mountains (feeding efficiency = $-17.63 + 3.99[\text{bill depth}] - 0.22[\text{bill depth}]^2$, $r^2 = 0.69$, $df = 24$, $P < .0001$; Benkman and Miller 1996) and from the South Hills (feeding efficiency = $-92.94 + 18.76[\text{bill depth}] - 0.94[\text{bill depth}]^2$, $r^2 = 0.35$, $df = 25$, $P = .005$; Benkman et al. 2001). We standardized the heights of the feeding efficiency curves to 1 before converting them into estimates of survival.

Results

Annual Cone Production

The mean and median number of cones produced per tree in the Little Rocky Mountains was similar during each of the last 9 yr (fig. 3A), with evidence of a slight reduction in cone production during the most recent 3 yr (the number of cones of ages 1, 2, or 3 were each less than in year 4; Kruskal-Wallis tests, $\chi^2 > 4.3$, $P < .04$). The decline in the number of cones between ages 9 and 10 (fig. 3A; Kruskal-Wallis test, $\chi^2 = 33.8$, $P < .0001$) was most likely an artifact of selecting younger branches that could be cut near the top of the tree. These results show that annual cone production was stable over the last 9 yr (coefficient of variation [CV] = 5.1%), and observations of cones on older branches indicate that these 9 yr were not atypical.

Patterns of Seed Predation and Natural Selection by Crossbills

Seed predation by crossbills varied with cone age (fig. 3B) and among trees (fig. 4) in the Little Rocky Mountains. Predation increased with cone age (fig. 3B), especially between years 3 and 4 and after year 7, presumably because of weathering of both the scales and the resin bonds holding the scales together, making it easier for crossbills to access seeds. The variation in percent predation among trees was correlated to differences in cone traits (table 2; Spearman's rank correlations). In particular, crossbills tended to prefer smaller, shorter cones with proportionately more seed mass and short and thinner distal scales. Although these correlations indicate selection on cone traits by crossbills (trees with larger, longer, relatively narrow cones with proportionately less seed mass and longer and thicker distal scales had a selective advantage), they do not show which traits were the targets of selection. The partial correlations (table 2) indicate that crossbills

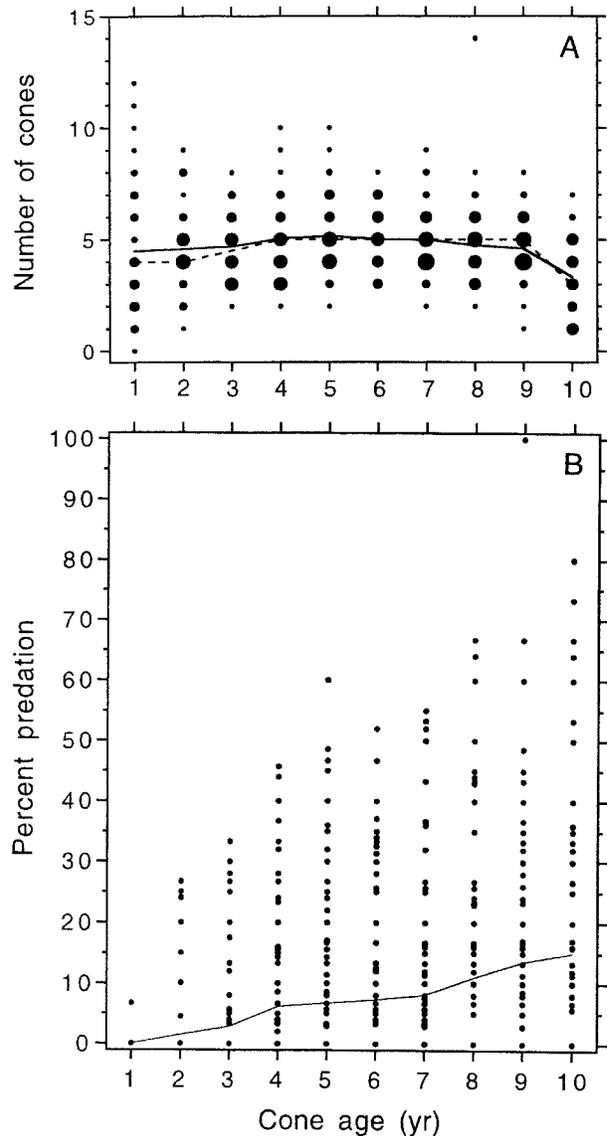


Figure 3: A, Number of cones per tree (sum of three branches) and (B) mean percent of each cone foraged on by crossbills in relation to cone age in the Little Rocky Mountains, Montana. A, The solid line connects the means, the dashed line connects the medians, and the size of solid circles is proportional to number of trees (1–5, 6–10, 11–15, ..., 36–40 trees). B, The solid line connects the overall means, and the circles represent one or more trees ($n = 120$ trees).

avoided heavier, relatively long and narrow cones with few scales. That is, the targets of selection were cone and scale size, with crossbills avoiding large cones with large scales (see cones in fig. 1).

Natural Selection by *Tamiasciurus*

Three cone traits were under direct selection by *Tamiasciurus* in the Cypress Hills (table 3; multiple regression).

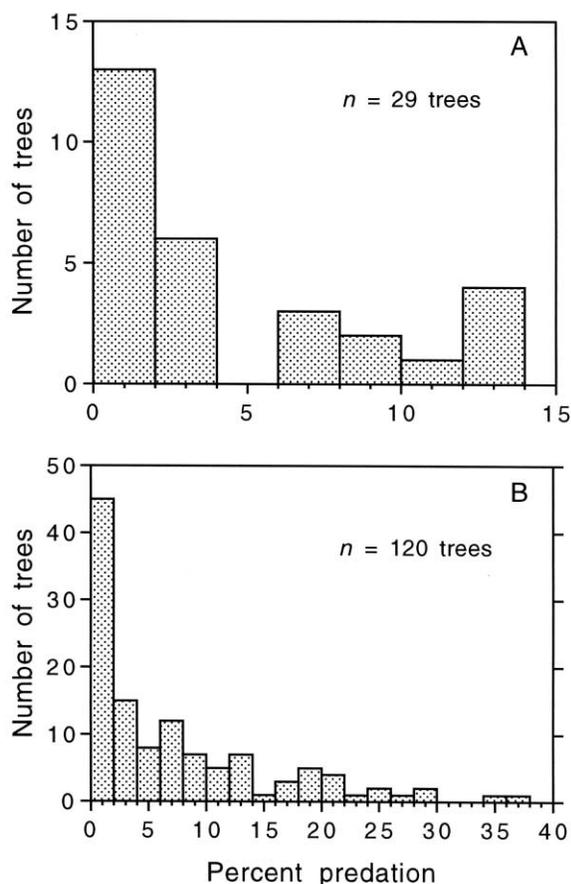


Figure 4: Number of trees with different mean overall percentages of cone predation by crossbills. A, The 29 trees sampled haphazardly. B, All 120 trees used in the analyses, including 29 trees sampled haphazardly and 91 trees sampled to increase the range of predation levels.

Tamiasciurus preferentially harvested cones that were relatively narrow and had more and larger full seeds. This resulted in selection (direct and indirect) that favored trees producing cones with few seeds, were wide relative to their length, and produced relatively little seed mass compared with the amount of cone mass (table 4; pairwise regressions).

The Form of Selection on Crossbills

The form of survival in relation to bill depth indicates that selection is stabilizing, with survival probability highest for a South Hills crossbill having a 10.01-mm bill depth (fig. 5). Selection on crossbills in the South Hills is strongly divergent from the estimated selection in the Rocky Mountains (fig. 6), where the optimal bill depth for crossbills

foraging on lodgepole pine is 9.28 mm (Benkman and Miller 1996).

Discussion

Coevolution is the evolution of one species in response to selection by another species, followed by evolution in the second species in response to reciprocal selection exerted by the first species (Janzen 1980). Such reciprocal selection should result in reciprocal adaptations if the traits under selection are heritable. An increasing number of studies of wild populations have shown evidence of coevolution (e.g., Davies and Brooke 1989a, 1989b; Pellmyr and Huth 1994; Pellmyr et al. 1996; Dybdahl and Lively 1998; Clayton et al. 1999; Brodie et al. 2002; Thompson and Cunningham 2002). Nonetheless, relatively few studies provide evidence of both reciprocal selection and adaptation (Davies and Brooke 1989a, 1989b; Berenbaum and Zangerl 1998; Dybdahl and Lively 1998). Our results, which reveal natural selection and the targets of selection by crossbills and *Tamiasciurus* on lodgepole pine, the form of selection on crossbills, and earlier studies showing evidence of replicated reciprocal adaptation and evolution in the same heritable traits undergoing selection (Benkman et al. 2001) are important because we have been able to quantify both reciprocal selection and adaptation. An important and perhaps unique aspect of our studies is that they provide an understanding of the traits mediating and responding to selection (i.e., the phenotypic interface of coevolution [E. D. Brodie III, personal communication]), which has been difficult to attain in studies of wild populations. We discuss the patterns of cone production and predation by crossbills

Table 2: Spearman's rank and Spearman's partial correlations between tree fitness, because of seed predation (100 - % seed predation by crossbills), and various cone traits (ln-transformed, $n = 120$ trees) in the Little Rocky Mountains, Montana

Trait	Spearman's rank correlations		Spearman's partial correlations	
	r_s	P	r_s	P
Cone length (mm)	.423	<.0001
Cone width (mm)	.179	.051
Cone width/length (mm)	-.224	.014	-.215	.022
Cone mass (gm)	.333	.0002	.356	.0001
Distal scale thickness (mm)	.236	.0096	.045	.633
Proximal scale thickness (mm)	.078	.40	-.068	.476
Scale length (mm)	.291	.0016
Number of scales	.002	.99	-.211	.025
Seed mass (mg)	.116	.21	.022	.818
Number of full seeds	-.082	.38	-.084	.374
Number of empty seeds	.105	.26	.053	.575
Seed mass/cone mass (mg)	-.186	.042

Table 3: Pairwise and multiple logistic regression analyses of natural selection on lodgepole pine from seed predation by *Tamiasciurus* in the Cypress Hills, Alberta ($n = 60$ trees)

Trait	Pairwise logistic regression		Multiple logistic regression		
	α (\pm SE)	P	α (\pm SE)	P	β
Cone length (mm)	-5.08 (2.99)	.090
Cone width (mm)	1.53 (2.92)	.60
Cone width/length (mm)	28.47 (11.18)	.01	.98 (.44)	.025	.24
Cone mass (gm)	-.65 (1.33)	.63	1.11 (.63)	.079	.27
Distal scale thickness (mm)	4.36 (2.88)	.13	-.05 (.44)	.91	-.01
Proximal scale thickness (mm)	1.96 (2.00)	.33	.39 (.47)	.40	.10
Seed mass (mg)	-.77 (1.45)	.59	-1.30 (.53)	.014	-.32
Number of full seeds	-3.81 (1.02)	.0002	-2.52 (.73)	.0005	-.62
Number of empty seeds	-.38 (.49)	.44	.66 (.44)	.13	-.16
Seed mass/cone mass (mg)	-252.08 (63.68)	<.0001

Note: The whole multiple regression model is significant (maximum likelihood ratio test, $\chi^2 = 37.01$, $df = 7$, $P < .0001$).

and *Tamiasciurus*. Then we discuss the targets and the patterns of divergent selection and cone evolution in light of our findings. Finally, we consider how reciprocal selection is imposed on crossbills and its implications on patterns of crossbill divergence and the dynamics of coevolution.

Patterns of Cone Production

Cone production is remarkably stable from year to year (fig. 3A). Stable cone production by Rocky Mountain lodgepole pine has been noted before (e.g., Smith 1970; Smith and Balda 1979); however, the year-to-year consistency in cone production shown here is even greater than previously reported. The coefficient of variation (CV) of annual cone production in our study (5.1%) is substantially lower than any CV reported for 175 plant species, including Rocky Mountain lodgepole pine (CV = 61% and 92% in two studies in Wyoming and Colorado, respectively; Kelly and Sork 2002). We suspect that the extremely low variation in cone production is related to the rarity or absence of certain seed predators, such as insects and squirrels, that are unable to track temporal and spatial fluctuations in cone crops and would thus select for fluctuating cone crops (Hulme and Benkman 2002). Insects are uncommon seed predators of Rocky Mountain lodgepole pine (usually <0.1% of seed crop; Lotan and Perry 1983; A. M. Siepielski and C. W. Benkman, unpublished data), which probably accounts for the low variation in the size of its annual cone crops (Lotan and Perry 1983). The absence of *Tamiasciurus* from isolated ranges like the Little Rocky Mountains and South Hills may explain why lodgepole pine cone crops there may fluctuate even less (this study; T. Fetz and C. W. Benkman, unpublished data)

than in the Rocky Mountains. These results also suggest that enhanced pollination success from masting (Kelly and Sork 2002) does not play as dominant a role as seed predation in the evolution of cone crop fluctuations in lodgepole pine.

Such cone crop stability is important to our study for two reasons. First, stable cone crops, and especially holding seeds in cones for extended periods of time, allow crossbills to be resident (Senar et al. 1993; Benkman et al. 2001; Parchman and Benkman 2002), maintain stable population densities from year to year (T. Fetz, A. M. Siepielski, and C. W. Benkman, unpublished data), and have a continuous relationship with lodgepole pine in the absence of *Tamiasciurus*. This in turn has led to patterns of reciprocal

Table 4: Direction of selection exerted by crossbills (from table 2) and *Tamiasciurus* (from table 3) on various lodgepole pine cone traits and the observed changes in these cone traits when *Tamiasciurus* are absent and crossbills are more abundant

	Selection by		Observed change
	Crossbills	<i>Tamiasciurus</i>	
Cone length	+	-*	+
Cone width	+*	0	+
Cone mass	+	0	+
Distal scale thickness	+	0	+
Proximal scale thickness	0	0	-
Seed mass	0	0	+
Number of full seeds	0	-	+
Cone width/length	-	+	-
Seed mass/cone mass	-	-	+

Note: From Benkman et al. (2001). Pluses and minuses refer to selection favoring increases and decreases in a cone trait, respectively. Zero means there was no statistical support for selection on the trait.

* Marginally insignificant (.08 > P > .05).

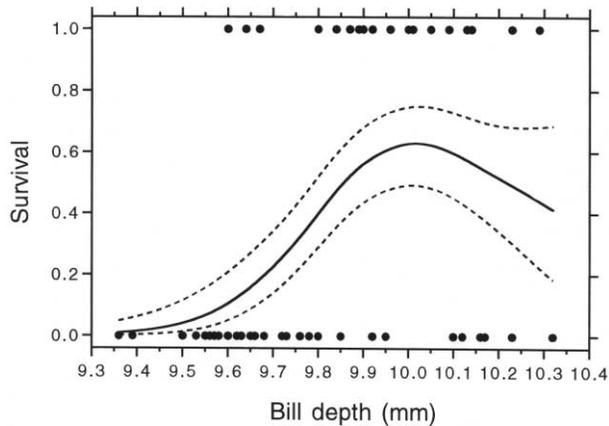


Figure 5: Probability of an adult South Hills crossbill surviving at least 1 yr in relation to bill depth. The solid curve represents a cubic spline, and the dashed curves represent ± 1 SE (software program provided by D. Schluter). The solid circles along the top of the figure represent uniquely marked individuals recaptured or resighted 1–3 yr after initial capture as adults ($n = 20$), and the solid circles along the bottom of the figure represent individuals not seen a year or more after initial capture ($n = 36$) and assumed not to have survived.

selection between crossbills and lodgepole pine. Second, the stability of the cone crop indicates that the patterns of predation and selection we observed are representative of a stable pattern over time that justifies inferences about the long-term form of selection.

Patterns of Seed Predation and the Targets of Selection

The differences in foraging behavior between crossbills and *Tamiasciurus* are important in understanding the patterns of seed predation and why certain cone traits are the targets of selection of each seed predator. Crossbills extract seeds from cones by prying apart scales at the distal end of the cone while it remains attached to the tree. Consequently, crossbills prefer shorter cones that have small scales (relatively short cones with many scales) because they would presumably require less force to pry apart than would cones with large scales. A preference for shorter cones with presumably smaller scales has also been found for crossbills foraging on Scots pine (*Pinus sylvestris*) in Scotland (Summers and Proctor 1999). Crossbills also prefer older cones. As cones age, the resinous bonds and cone scales weather and deteriorate so that cones become softer and often open partially (Elliott 1988b). This weathering is critical and presumably explains the increase in predation by crossbills, because the forces required to separate cone scales that are sealed are 30 times greater than those required to separate scales for which the seal is broken (Lotan 1975). Nevertheless, only a few trees suffered from seed predation levels

>15%, and these trees were only sampled when we actively searched for such trees (cf. fig. 4A, 4B). This value, however, underestimates the overall proportion of seeds eaten by crossbills because predation by crossbills appears to increase as cones age further (C. W. Benkman, personal observation). Regardless, in forests dominated by trees with serotinous cones, crossbills rely on cones that have remained in the trees for a number of years—a canopy seed bank.

In contrast, *Tamiasciurus* harvest a much larger fraction of the seeds. For example, Elliott (1988a) found that *Tamiasciurus* removed all the closed cones from 62% of the trees (530 of 856 trees) on the two territories studied. *Tamiasciurus* harvest many cones and cache them in the ground in middens soon after the cones mature in late summer and early autumn (Smith 1968, 1970, 1981; Elliott 1988a). Moreover, cones that are not harvested the first year are often harvested by *Tamiasciurus* in later years after the cones have weathered (Elliott 1988b). This leaves few cones to weather on the trees for crossbills and illustrates why crossbills are rare in lodgepole pine forests when *Tamiasciurus* are present (Benkman 1999) and why selection by *Tamiasciurus* overwhelms selection by crossbills.

Tamiasciurus bite cones off the branch and then, after removal, forage on the seeds by biting off successive scales at their base, starting at the proximal end of the cone. *Tamiasciurus* avoid cones that are relatively wide at the base because this makes it difficult for them to bite the cone off the branch (Smith 1970; Elliott 1974, 1988a). Cones are also avoided when seeds are few and small, because then *Tamiasciurus* are rewarded by less kernel mass after biting through the sterile scales at the cone base. In

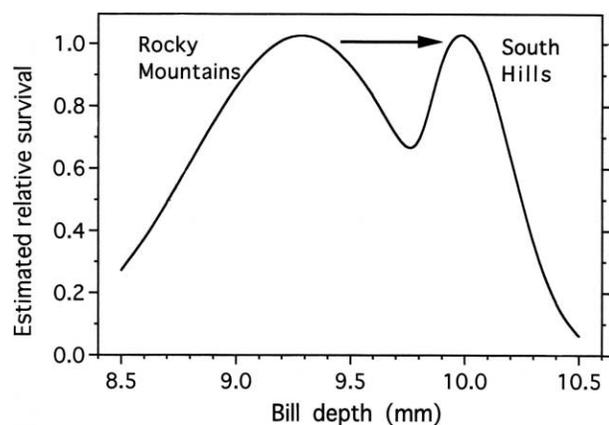


Figure 6: Estimated relative survival of crossbills foraging on lodgepole pine in the Rocky Mountains (*Tamiasciurus* present) and in the South Hills (*Tamiasciurus* absent). The difference between the peaks represents the change in selection on crossbills (arrow) as the result of coevolution in the South Hills.

contrast to *Tamiasciurus*, crossbills do not preferentially forage on cones with more seeds because crossbills forage at the distal end of the cone where seeds are common. Prior univariate analyses of cone selection by *Tamiasciurus* in British Columbia, Colorado, and the Cypress Hills revealed similar results but did not show that *Tamiasciurus* preferentially harvested cones with larger seeds (Smith 1970; Elliott 1974, 1988a; Benkman 1999). Presumably, direct selection on seed mass was erased by selection on other correlated traits (i.e., indirect selection).

Patterns of Cone Evolution in Relation to Forms of Selection

The consistent differences between cones from eight isolated mountains where *Tamiasciurus* have been absent during the past 10,000 yr and cones from the numerous ranges with *Tamiasciurus* (fig. 1; Benkman 1999; Benkman et al. 2001) can be largely accounted for by selection by crossbills and by relaxation of selection by *Tamiasciurus* (table 4). For example, cone length has increased and the ratio of cone width/length has decreased in the absence of *Tamiasciurus* because of increased selection by crossbills and because of the relaxation of counterselection by *Tamiasciurus*. Cone width, cone mass, and distal scale thickness have increased because of increased selection by crossbills, whereas the number of full seeds per cone has likely increased simply from relaxation of selection by *Tamiasciurus*. However, individual seed mass presumably increased because it was positively correlated with other traits (table 1) under positive selection by crossbills (table 2) and undergoing relaxation of selection by *Tamiasciurus* (table 3). For example, seed mass may have increased in the absence of *Tamiasciurus* because it is positively correlated with scale size and the number of seeds per cone, both of which increased. Seed size is strongly correlated with scale size (McGinley et al. 1990), and as the number of seeds per cone increases, proportionately fewer of the seeds will be located in the distal end of the cone where scales and seeds are smaller (McGinley et al. 1990).

Proximal scale thickness is the one trait that cannot be explained so simply. It decreased even though it was not under selection (tables 2, 3) and was positively correlated with the various measured cone traits (table 1) under positive selection. Proximal scale thickness may have decreased because it was positively correlated with cone width/cone length ($r_s = .318$, $n = 120$ trees, $P = .0004$), which decreased because of relaxation of selection by *Tamiasciurus* and selection by crossbills.

Finally, the ratio of total seed mass to cone mass was larger in the absence of *Tamiasciurus* than in their presence even though selection by both crossbills and *Tamiasciurus* favored a decrease in this ratio. Presumably, counter-

selection favors an increase in the ratio of seed mass to cone mass (i.e., proportionately more seeds can be produced) so that the equilibrium value is larger in the absence of *Tamiasciurus* because selection by crossbills was weaker (table 2) than selection by *Tamiasciurus* (table 3).

Reciprocal and Divergent Selection on Crossbills

The bill depth favored by selection (fig. 5; 10.01 mm) is similar to the optimal bill depth for foraging on lodgepole pine cones in the South Hills (9.99 mm) on the basis of foraging efficiency data (Benkman et al. 2001; Benkman 2003), implicating cone structure as the agent of viability selection. The steep decline in estimated survival probability away from the peak (fig. 5) indicates that selection should rapidly drive the South Hills crossbill to the peak and that it should experience stabilizing selection. Indeed, we have found that the average bill depth approximates the predicted optima for foraging on single species of conifers in three other populations or species of red crossbills (Benkman 1993; Benkman and Miller 1996; Benkman et al. 2001). In addition, the Cypress Hills crossbill, which relied on lodgepole pine cones much like those in the South Hills (fig. 1; Benkman 1999; Benkman et al. 2001), had an average bill depth (10.01 mm; Benkman et al. 2001) that is identical to that predicted on the basis of selection in the South Hills (fig. 5). The average bill depth of the South Hills crossbill, however, is smaller (9.88 mm, $n = 179$ birds). This indicates that South Hills crossbills, although close to the peak, experience a combination of stabilizing and directional selection from lodgepole pine.

We have identified another source of selection on South Hills crossbills, which has perhaps only recently shifted their bill depth distribution. About 27% of the adult South Hills crossbills that we captured between 1997 and 2001 (49 of 179 birds) had scaly leg mites (*Knemidokoptes jamaicensis*) and were excluded from the survival analyses because they had swollen legs and thus were not banded. Because scaly leg mites likely cause mortality in birds (Pence et al. 1999; Latta and Faaborg 2001), and because for unknown reasons a disproportionate number of crossbills with scaly leg mites had deep bills, directional selection from scaly leg mites favored smaller-billed crossbills. This can account for much of the deviation of the South Hills crossbills from that predicted on the basis of survival in the absence of mites (C. W. Benkman, unpublished data). One of us (C.W.B.) has captured hundreds of crossbills throughout much of North America and has never found scaly leg mites besides in the South Hills. We suspect that the occurrence of mites in the South Hills is recent and that in the absence of mites the South Hills crossbill would experience stabilizing selection from lodgepole pine. Regardless of the effect of mites, crossbills in areas without

Tamiasciurus are experiencing selection from lodgepole pine that is divergent from selection experienced in areas with *Tamiasciurus* (i.e., a geographic selection mosaic) in line with the different bill sizes of crossbills found in these areas (Benkman 1999; Benkman et al. 2001).

Asymmetrical Selection

Asymmetries are often thought to arise in coevolutionary arms races (e.g., Dawkins and Krebs 1979; Vermeij 1994; Brodie and Brodie 1999; Abrams 2000) so that one species may lag in its evolutionary response relative to the other. One reason is different generation times, with the species having a longer generation time lagging behind the other. This is consistent with the observation that lodgepole pine, with the longer generation time, experiences directional selection from crossbills, whereas crossbills experience mostly stabilizing selection from lodgepole pine. If lodgepole pine is lagging behind crossbills, then this coevolutionary interaction is not at equilibrium, and pine defenses should continue to increase and crossbills should continue to adapt. Alternatively, the differences in the forms of reciprocal selection might merely reflect the importance of the other organism as a selective agent (Dawkins and Krebs 1979; Vermeij 1994; Brodie and Brodie 1999; Abrams 2000). Crossbills rely almost exclusively on seeds in conifer cones, and the South Hills crossbill is no exception. However, various factors in addition to predation by crossbills may influence the reproductive success of lodgepole pine, especially given that crossbills eat a relatively small proportion of the seeds (fig. 4). For example, cone serotiny is negatively correlated with twig diameter presumably because slender twigs increase flammability (Schwilk and Ackerly 2001). Selection favoring slender twigs in serotinous lodgepole pines might result in selection against larger cones. For instance, larger cones might cause the slender twigs to break or bend and reduce photosynthetic efficiency. Other trade-offs could limit cone evolution, such as when the reduction in seed production from increasing defenses balances the gains from reductions in seed losses to predators. However, this trade-off may be unimportant because the ratio of seed mass to cone mass has increased more than twofold in the absence of *Tamiasciurus* (Benkman et al. 2001).

One of the costs to crossbills from adaptations to the increased defenses of lodgepole pine is the allometric increase in body size and energy requirements with increases in bill size. Some of these costs have apparently been reduced by changes in bill shape to a more decurved bill, which has resulted in greater power for a given bill depth (Benkman et al. 2001). However, unlike structural cone defenses where further increases likely deter seed predators further, increases in bill size much beyond the optimum

in terms of meeting energy demands decrease the rate at which seeds can be extracted from cones (Benkman et al. 2001). Consequently, at equilibrium, reciprocal selection will favor increased defenses by lodgepole pine but will not favor increased offenses (at least within this range of variation) by crossbills. The coevolutionary equilibrium, therefore, is set by the relative costs and benefits of increased defenses to lodgepole pine.

Conclusions

Our results further support the hypothesis that the presence and absence of *Tamiasciurus* are the key elements underlying the geographic selection mosaic for crossbills and lodgepole pine because *Tamiasciurus* are effective preemptive competitors for conifer seeds and drive cone evolution when present (Benkman 1999; Benkman et al. 2001). In particular, we show that in areas without *Tamiasciurus*, crossbills and lodgepole pine impose reciprocal selection on each other that is divergent from the selection experienced in areas with *Tamiasciurus*. As a result, crossbills and lodgepole pine have coevolved in isolated ranges and diverged from populations in the Rocky Mountains. These results support the first two components of the geographic mosaic theory of coevolution (Thompson 1994, 1999a, 1999b, 2001): coevolution is prominent in some areas but not others, and the outcome of an interaction varies between areas. Our studies to date provide little evidence for or against the third component: that gene flow affects the outcome of the interactions. However, given that coevolution appears to be leading to a reduction in gene flow and perhaps speciation in crossbills (Benkman 1999; Benkman et al. 2001), models of the geographic mosaic of coevolution (e.g., Nuismer et al. 1999) might benefit from considering the evolution of reproductive isolation to capture the full range of possibilities and to further delimit the conditions when gene flow is likely to affect the outcome of interactions.

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