

# A role for habitat area in the geographic mosaic of coevolution between red crossbills and lodgepole pine

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## Keywords:

divergent selection;  
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## Abstract

Understanding how resource abundance limits adaptive evolution and influences species interactions is an important step towards developing insight into the role of microevolutionary processes in establishing macroevolutionary patterns. We examined how variation in resource abundance (forest area of lodgepole pine *Pinus contorta* ssp. *latifolia*) influenced patterns of co-adaptation and coevolution between red crossbill (*Loxia curvirostra* complex) and lodgepole pine populations. First, we found that crossbill abundance increased logarithmically as forest area increased in mountain ranges lacking a preemptive competitor (pine squirrels *Tamiasciurus hudsonicus*). Second, seed defences against predation by crossbills increased with increases in crossbill density, suggesting that seed defences have likely evolved in proportion to the intensity of selection that crossbills exert. Third, the average bill size of crossbill populations increased with increasing seed defences, which implies that crossbill offenses increased with increases in seed defences. The large bill size on the largest range is the result of coevolution with lodgepole pine with this crossbill population perhaps speciating. Local adaptation of crossbill populations on smaller ranges, however, is more likely the result of resident crossbills representing a subset of the potential colonists (phenotypic sorting) than of local evolution. In the smallest range, migration and possibly more frequent extinction likely impede local adaptation and may result in maladaptation.

## Introduction

A key feature linking and defining population structure with evolutionary potential is habitat abundance. Habitat abundance is of ecological and evolutionary significance to most species because opportunity for population expansion reduces the likelihood of extinction before local adaptation can occur (Gomulkiewicz & Holt, 1995; Reznick & Ghalambor, 2001). Surprisingly few studies have examined the relationship between habitat abundance and adaptive population differentiation (e.g. Losos & Schluter, 2000). Here we provide evidence linking habitat abundance with microevolutionary processes that influence geographical variation in the outcome of the interaction between two coevolving species.

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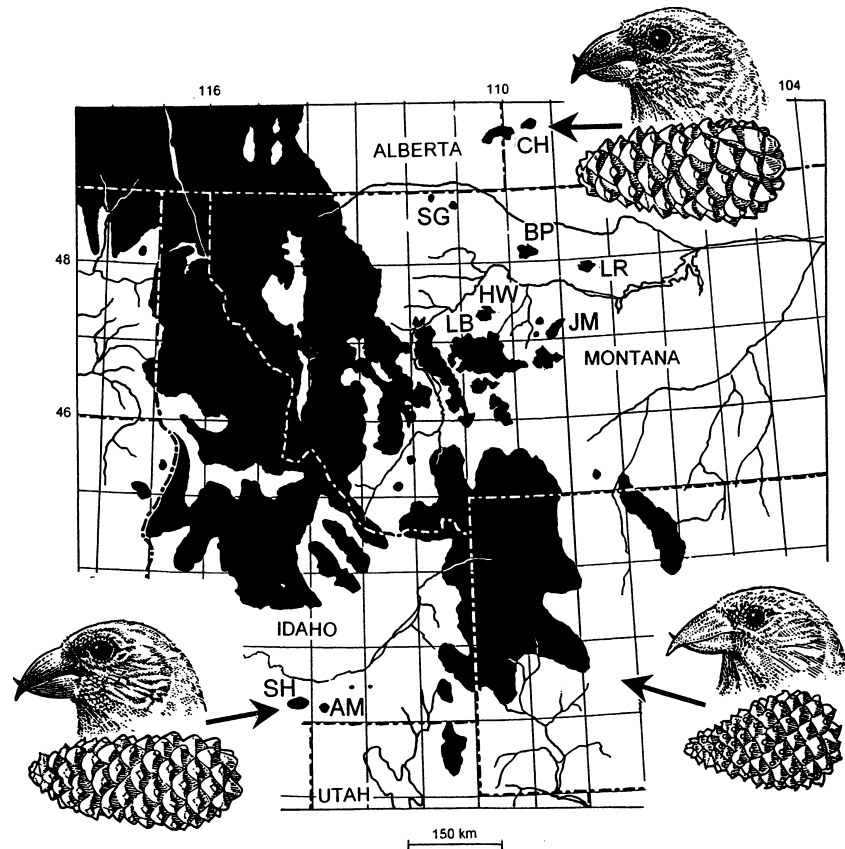
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The red crossbills (*Loxia curvirostra* complex) in isolated forest islands of lodgepole pine (*Pinus contorta* ssp. *latifolia*) east and west of the Rocky Mountains are an excellent system to examine how habitat abundance can contribute to population differentiation and coevolution. First, there is a direct functional link between the morphology, ecology and evolution of crossbills, and their key food resource, seeds in conifer cones (Benkman, 1993a). For example, variation in bill size, particularly bill depth, determines how rapidly cone scales can be spread apart and seeds removed, which in turn determines crossbill survival (Benkman, 2003). Moreover, crossbills forage on little else other than conifer seeds, thus the persistence of crossbill populations and their potential for local adaptation are likely dependent on the area of coniferous forests (Benkman, 1993b).

Second, coevolution between crossbills and lodgepole pine is replicated in isolated mountain ranges east and west of the Rocky Mountains where pine squirrels (*Tamiasciurus hudsonicus*), the main competitor to crossbills for seeds in cones, are absent (Benkman, 1999;

**Fig. 1** The distribution of lodgepole pine (black; modified from Critchfield & Little, 1966), the location of study sites and representative crossbills and cones in the Rocky Mountains (lower right), the Cypress Hills (upper right), the South Hills-Albion Mountains (lower left). The crossbills, South Hills crossbill (left) and the Rocky Mountain lodgepole pine crossbill (right), and cones are drawn to relative scale. The acronyms and estimated area of lodgepole pine (in parentheses) for sites without squirrels are: Sweetgrass Hills (SG, 5.5 km<sup>2</sup>), Bears Paw Mountains (BP, 31 km<sup>2</sup>), Little Rocky Mountains (LR, 58 km<sup>2</sup>), South Hills (SH, 80 km<sup>2</sup>) and Albion Mountains (AM, 20 km<sup>2</sup>). The acronyms and estimated area of lodgepole pine for sites currently with squirrels are: Cypress Hills (CH, 80 km<sup>2</sup>; squirrels were introduced in 1950), Highwood Mountains (HW, 96 km<sup>2</sup>), Judith Mountains (JM, <4 km<sup>2</sup>) and Little Belt Mountains (LB, >500 km<sup>2</sup>). Reproduced and modified from Benkman (1999).



Benkman *et al.*, 2001,2003). In these ranges, crossbills exert selection on lodgepole pine cone structure resulting in larger cones with thicker distal scales (Fig. 1), which impede crossbills from spreading apart the cone scales to access seeds. In response, crossbills have evolved larger and deeper bills to improve access to the seeds (Fig. 1; Benkman, 1999; Benkman *et al.*, 2001,2003). The result is a coevolutionary arms race between lodgepole pine and crossbills in mountain ranges lacking pine squirrels. Where pine squirrels are present, they out-compete crossbills for lodgepole pine seeds by preemptively harvesting and caching most of the cones soon after the seeds mature in autumn (Smith, 1970; Benkman, 1999; Benkman *et al.*, 2001,2003). Here, pine squirrels drive the evolution of seed defences because crossbills are uncommon and the selection they exert is limited because pine squirrels, by selectively harvesting a large fraction of the cones, remove much of the initial variation in cone traits (Benkman, 1999; Benkman *et al.*, 2001,2003). Although differences in cone structure among areas without squirrels are consistent with selection from crossbills, there is variation in the extent of seed defences against crossbills (Benkman, 1999; Siepielski & Benkman, 2004). Specifically, traits that have evolved as defences against crossbills (e.g. thicker distal scales) are more enhanced on larger ranges, suggesting a

role for habitat abundance (Benkman, 1999). Differences in evolutionary histories are unlikely to account for this site to site variation because most of the ranges were colonized by lodgepole pine and became isolated from other ranges at similar times in the past 12,000 years following glacial retreat (Thompson & Kuijt, 1976; Barnosky, 1989).

The goal of this paper is to further elucidate the ecological and evolutionary factors promoting population level differentiation in the geographic mosaic for red crossbills and lodgepole pine. First, we address the hypothesis that area of lodgepole pine limits crossbill population density. We test the prediction that crossbill density increases as forest area increases in the absence of squirrels. Second, we test the hypothesis that the levels of seed defences directed at crossbills in areas without squirrels are related to the density of crossbills. Although an indirect measure, higher densities of crossbills should result in greater intensities of selection on cone traits (Bell, 1997), and an evolutionary response to selection is expected because many cone traits under selection by crossbills are heritable (Benkman *et al.*, 2003). Third, we test the related hypothesis that crossbills are locally adapted for foraging on cones in the different areas. Previous research has shown that a deeper bill is an adaptation for foraging on larger crossbill-defended cones

(Benkman *et al.*, 2001,2003; Parchman & Benkman, 2002). Consequently, bill depth, which is highly heritable in birds (Merilä & Sheldon, 2001), including crossbills ( $h^2 \approx 0.7$ ; R. C. Summers, unpublished data), should be positively related to measures of seed defence if crossbills are locally adapted.

## Materials and methods

### Study areas

Eight study areas (three with squirrels and five without squirrels) within lodgepole pine dominated mountain ranges were selected in or near the northern Rocky Mountains that vary in the area of lodgepole pine (Fig. 1). Only five such ranges lacked squirrels and we sampled them all. The forested areas for the South Hills and Albion Mountains (hereafter referred to as the 'South Hills') were combined in the analyses because of their close proximity. The absence of squirrels from all but one (squirrels were introduced into the Cypress Hills in 1950; Newsome & Dix, 1968) of these ranges can be attributed to historical effects (e.g. glacial retreat and climatic effects), and not to differences in forest structure that would make the area unsuitable for colonization (Benkman, 1999; Benkman *et al.*, 2001). Indeed, the success of introduced squirrels in the Cypress Hills confirms that their absence was not the result of unsuitable habitat (Benkman, 1999). Most lodgepole pine in our study areas had serotinous cones (Benkman & Siepielski, 2004), which implies similar fire histories (Muir & Lotan, 1985) and stand characteristics (Brown, 1975). We categorized the Cypress Hills as without squirrels for cone traits because the cones were sampled from trees that germinated well before squirrels were introduced.

### Estimating crossbill density

We used point counts to estimate the density of crossbill populations in each range. Because of the overall structural similarity of the study areas and because only a single observer conducted all counts, we assumed that detection probabilities were similar among ranges and thus point counts provided a valid method to compare densities of crossbills among ranges.

Thirty 10-minute point counts were conducted once in early May and June and again in late July and early August throughout each range in each of 2 years (2001 and 2002) for a total of 120 point counts in each range. Point count locations were separated by a minimum of 250 m to maintain independence of observations (Pendleton, 1995). Although crossbills may easily move >250 m over a 10-minute time frame, we have no reason to suspect that the chance of observing a bird twice was different than the chance of not observing a particular bird; nor do we suspect variation in the occurrence of

these events among ranges. Only crossbills perched within 50 m of the observer were used in analyses. When possible, we recorded calls of crossbills heard during point counts and confirmed red crossbill call types by creating sonograms and comparing these to previously published sonograms (Groth, 1993; Benkman, 1999).

Paired *t*-tests were used to examine if there were differences in mean crossbill densities between years separately for ranges with and without squirrels. For this analysis the number of crossbills per point count was averaged across both survey periods to provide one estimate of density per range for each year. We used analysis of covariance (ANCOVA) to examine whether the presence/absence of squirrels influenced the relationship between crossbill density and forest area. In the latter analysis, we used the mean density per area averaged over all years of the study. All test assumptions were met.

### Variation in seed defences in relation to crossbill density

We used data in Benkman (1999) to characterize variation in lodgepole pine seed defences in relation to crossbill density. The correlation matrix from the ln-transformed tree means (based on three cones per tree and  $\geq 22$  trees per range) of seven cone/seed traits was used in a principal components (PC) analysis. The following traits were used: cone length, cone width, cone mass, proximal and distal scale thicknesses, total number of seeds, and individual seed mass (see Benkman *et al.*; 2003 for a detailed description). Benkman (1999) showed that the first principal component (PC1) explained 49% of the variation in cone traits among pine populations experiencing different levels of selection from crossbills and squirrels, with PC1 increasing as squirrel defences decreased and crossbill defences increased. In particular, because the time it took crossbills to remove a seed from a cone was positively correlated with PC1 ( $r = 0.42$ , d.f. = 80,  $P < 0.001$ ), we used PC1 as a measure of crossbill defences. To test the prediction that seed defences increase with increasing crossbill density, we used linear regression to test for a positive relationship between mean PC1 scores and mean crossbill densities among areas without squirrels.

The number of crossbills per point count was averaged across survey periods and years to provide one estimate of density per area. Our estimate of crossbill density in the Cypress Hills for use in this analysis only was determined in a manner requiring elaboration. Prior to the introduction of squirrels in 1950, a distinct red crossbill was common in the Cypress Hills (Godfrey, 1950; Benkman, 1999). Because we lack estimates of crossbill density there prior to the introduction of squirrels, crossbill density was estimated based on the empirical relationship between crossbill density and forest area lacking squirrels determined in this study

(crossbill density =  $-0.826 + 0.492 \ln(\text{km}^2 \text{ of lodgepole pine})$ ;  $F_{1,2} = 62.57$ ,  $r^2 = 0.97$ ,  $P < 0.05$ ).

### Variation in bill morphology

Crossbills were captured in the South Hills and in the Bears Paw and Little Rocky Mountains during the summers of 1998–2003. Crossbills were not captured in the Sweetgrass Hills because they were rarely recorded there. We measured the bill depths of museum specimens collected in the Cypress Hills in the 1930s–1940s prior to the introduction of squirrels (Benkman, 1999). One of us used digital calipers to measure bill depth to the nearest 0.01 mm of all crossbills (see Benkman, 1993a for measurement details). Calls were recorded when birds were released and analysed as described earlier to confirm call type.

### Variation in bill morphology in relation to seed defences

We used linear regression to test the prediction that mean bill depth (weighted by sex) increased with increases in seed defences (mean PC1 cone scores) among areas. We used the mean bill depth of Rocky Mountain lodgepole pine crossbills (type 5 of Groth, 1993) for an estimate of bill depth in areas with squirrels (data from Benkman *et al.*, 2001). These crossbills are generally the most common crossbill in Rocky Mountain lodgepole pine in areas with squirrels, and their bill depth approximates the optimum for foraging on lodgepole pine cones there (Benkman, 1993a; Benkman & Miller, 1996).

## Results

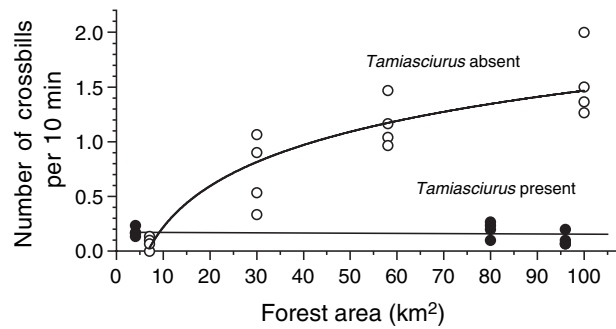
### Variation in crossbill density and call types

Differences in crossbill density between years were small, inconsistent in direction, and not significant both in areas with ( $t_3 = 0.27$ , n.s.) and without squirrels ( $t_3 = -0.71$ , n.s.).

With the exception of the South Hills, where a unique call type and perhaps species has evolved (Benkman, 1999; Benkman *et al.*, 2001), calls of crossbills in ranges without squirrels were identical to those given by ponderosa pine crossbills (type 2 of Groth, 1993). Ponderosa pine crossbills were also infrequently recorded in the South Hills. In areas with squirrels, both ponderosa pine and Rocky Mountain lodgepole pine crossbills were recorded.

### Crossbill density in relation to forest area and presence of squirrels

Variation in crossbill density among areas was largely accounted for by forest area and the presence of squirrels

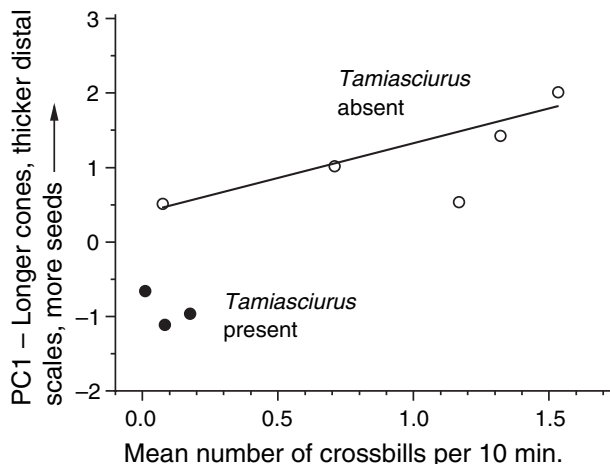


**Fig. 2** The mean number of crossbills per 10-minute point count in relation to area of lodgepole pine ( $\text{km}^2$ ) in areas with (solid circles) and without squirrels (open circles). Each point represents the mean of 30-point counts conducted in either May–June or July–August in each of 2 years (2001 and 2002). The regression equations were based on the overall mean (averaged over all periods and years) for each mountain range. Not shown is the Little Belt Mountains (mean crossbill density = 0.08,  $>500 \text{ km}^2$  lodgepole pine), however, this site was included in the analysis.

(ANCOVA full model  $F_{3,4} = 40.35$ ,  $r^2 = 0.97$ ,  $P < 0.01$ ). The interaction between area and whether squirrels were present or absent (Fig. 2: interaction term  $F_{1,4} = 61.40$ ,  $P < 0.001$ ) indicates that the influence of area depended on the absence of squirrels. Crossbill density (overall mean per area) increased logarithmically with area where squirrels were absent (Fig. 2: crossbills =  $-0.826 + 0.492 \ln(\text{km}^2 \text{ of lodgepole pine})$ ;  $F_{1,2} = 62.57$ ,  $r^2 = 0.97$ ,  $P < 0.05$ ), whereas the relationship was not significant in areas with squirrels (Fig. 2: crossbills =  $0.173 - 0.000183(\text{km}^2 \text{ of lodgepole pine})$ ;  $F_{1,2} = 2.56$ ,  $r^2 = 0.56$ , n.s.).

### Variation in seed defences in relation to crossbill density

Mean PC1 scores tended to increase as crossbill density increased in the absence of squirrels, but this trend was not significant (Fig. 3:  $\text{PC1} = 0.33 + 0.81(\text{crossbill density})$ ,  $F_{1,3} = 3.43$ ,  $r^2 = 0.53$ , n.s.). However, this analysis requires comment. Specifically, seed defences in one range, the Little Rocky Mountains, have also evolved in response to selection from lodgepole pine cone borer moths (*Eucosma recissoriana*) (Siepielski & Benkman, 2004). These moths were rare seed predators, except in the Little Rocky Mountains, where seed predation by moths was upwards of 10 times greater than in other ranges. In the Little Rocky Mountains, moths exert selection against trees producing cones with high PC1 values (Siepielski & Benkman, 2004). In consideration of this, when the Little Rocky Mountains was removed from the analysis, the relationship between PC1 and crossbill density was statistically significant (Fig. 3:  $\text{PC1} = 0.39 + 0.96(\text{crossbill density})$ ,  $F_{1,2} = 41.05$ ,  $r^2 =$



**Fig. 3** The first principal component (PC1) of seven cone measurements in lodgepole pine in relation to the mean number of crossbills per 10-minute point count. The least fit linear regression only includes areas without squirrels (open circles) and excludes the Little Rocky Mountains (see text). Each point represents the mean PC1 score for each island and mean estimated density of crossbills on each island. Areas without squirrels are from left to right (numbers in parentheses are the estimated area of lodgepole pine): Sweetgrass Hills (5.5 km<sup>2</sup>), Bears Paw Mountains (31 km<sup>2</sup>), Little Rocky Mountains (58 km<sup>2</sup>), Cypress Hills (80 km<sup>2</sup>) and South Hills (100 km<sup>2</sup> when combined with the Albion Mountains). Areas with squirrels (solid circles) are from left to right: Little Belt (>500 km<sup>2</sup>), Highwood (96 km<sup>2</sup>) and Judith mountains (<4 km<sup>2</sup>).

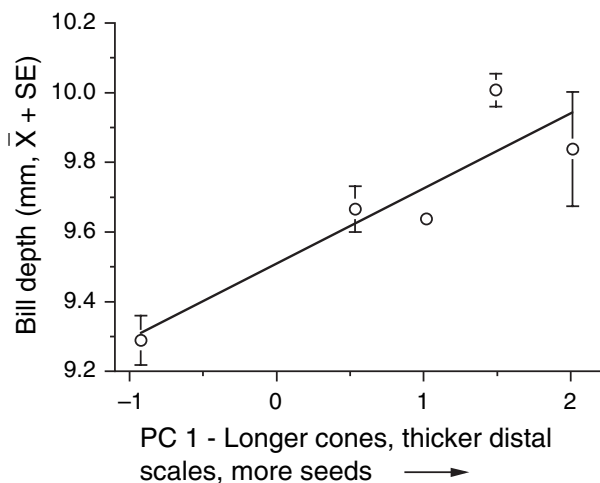
0.95,  $P < 0.05$ ); however, the significance of this relationship is tenuous as it is based on four data points one of which was estimated indirectly. Despite the small sample size, this implies that seed defences in lodgepole pine increase with increasing crossbill densities.

#### Variation in bill morphology in relation to seed defences

Mean bill depth increased as seed defences aimed at deterring crossbill predation increased (Fig. 4: Bill depth =  $9.51 + 0.22[\text{PC1}]$ ,  $F_{1,3} = 13.11$ ,  $r^2 = 0.81$ ,  $P < 0.05$ ). This indicates that increasing seed defences favour crossbills with larger bills and that cone structure has been an important feature shaping variation in bill structure among crossbill populations.

#### Discussion

Our results indicate that in the absence of squirrels, resource abundance, or habitat area, plays an important role in the geographic mosaic of coevolution for red crossbills and lodgepole pine. Below we discuss our findings in light of recent studies (Benkman, 1999; Benkman *et al.*, 2001, 2003; Parchman & Benkman, 2002) that have considered the factors determining the



**Fig. 4** Bill depth in relation to seed defences (PC1). Crossbills from left to right: Rocky Mountain lodgepole pine crossbills ( $n = 33$ ), Little Rocky Mountain crossbills ( $n = 38$ ), Bears Paw Mountain crossbills ( $n = 34$ ), Cypress Hills crossbills ( $n = 10$ ), and South Hills crossbills ( $n = 141$ ). Squirrels were absent from all the ranges except from where the Rocky Mountain lodgepole pine crossbills were measured.

geographic mosaic of coevolution for crossbills and conifers.

#### Crossbill density and competition with squirrels

Crossbill density was on average six times greater in the absence of squirrels (mean = 0.87 crossbills per point count) than in their presence (mean = 0.14; Fig. 2). Squirrels are effective competitors because their extensive harvesting of cones leaves few cones to accumulate and weather on the trees where they would become accessible to crossbills (Benkman *et al.*, 2003). Such a competitive effect is demonstrated by the decline and presumed extinction of the endemic crossbill from the Cypress Hills and the formally common Newfoundland crossbill (*L. curvirostra percna*; Benkman, 1989, 1999; Parchman & Benkman, 2002). In both these areas, crossbills became nearly (or are) extinct within 30 years of the introduction of squirrels. Alternatively, pine squirrels, which are important nest predators of open-cup nesting birds (Sieving & Willson, 1998; Bayne & Hobson, 2000; Willson *et al.*, 2003) like crossbills, could limit the abundance of crossbills. We have found that other canopy open-cup nesting birds are also less abundant in the ranges with squirrels than in the ranges without squirrels (A. M. Siepielski, unpublished manuscript). However, the breeding abundances of these eight other species were on average only about 42% higher (range among eight species: 71% increase to 14% decrease) in the absence of the squirrels than in the presence of squirrels. This is less than one-tenth the

increase found for crossbills. Thus, we doubt that nest predation can explain most of the increase in crossbill abundances in the absence of squirrels. Moreover, nest predation does not provide an explanation for the logarithmic increase in crossbill density with increases in forest area in the absence of squirrels. Consequently, we interpret our results to show a consistent and replicated pattern of the effect of competition with squirrels and, in combination with previous studies (Benkman, 1999; Benkman *et al.*, 2001), to clearly indicate that such competition limits the density of crossbills. This in turn limits the extent to which crossbills exert selection on lodgepole pine (Benkman, 1999; Benkman *et al.*, 2001,2003).

### Evolution of seed defences in relation to crossbill density

Defences aimed at deterring crossbill predation tended to increase with greater densities of crossbills (Fig. 3), suggesting that seed defences have likely evolved in proportion to the intensity of selection by crossbills. This is a reasonable inference under the assumption that more crossbills eat more seeds and cause greater selection. Although intuitive, this relationship does not directly measure selection. Rather, it only indicates that the covariance between crossbill density and seed defences is nonzero, and is but one possibility that is consistent with our understanding of selection by crossbills (e.g. Benkman *et al.*, 2003). Other evidence indicates that differences in cone traits represent genetic differences and are not the result of phenotypic plasticity (Benkman *et al.*, 2001). For example, if cone traits were plastic then cones in the Cypress Hills, where squirrels were introduced in 1950 (Newsome & Dix, 1968) and are now at densities four times higher than in the Rocky Mountains (Benkman, 1999), would express traits aimed at deterring predation from squirrels. In contrast, cones in the Cypress Hills are representative of cones that have evolved in response to predation from crossbills not squirrels (i.e., Fig. 1). Nonetheless, this leaves unanswered why crossbill densities remain paradoxically high as seed defences increase.

### Crossbill population density and habitat area

Numerous hypotheses have been proposed to explain the relationship between animal density and habitat area (Gaston & Matter, 2002). Despite many studies addressing these hypotheses, there has been little resolution. Reviews indicate that animal population density tends to be positively correlated with area (Bender *et al.*, 1998; Connor *et al.*, 2000). Our evidence for crossbills in areas without squirrels (Fig. 2) supports this finding, despite the small sample sizes. Unfortunately, there are no other comparable areas to sample. However, we suspect that our estimates of crossbill densities relative to variation in

forest area are representative and typical for this study system. This is supported by the relatively small amount of variation between our two years of surveys and a similar logarithmic relationship between crossbill density and area in the same ranges without squirrels the year before our study began (Malecki & Benkman, unpublished data). Moreover, the consistent relationship between cone traits and crossbill density (Fig. 3) indicate that the pattern of variation we observed between crossbill density and forest area has likely occurred for a long time.

Most hypotheses concerning the relationship between animal density and habitat area have been ecological (e.g. resource concentration hypothesis; reviewed in Connor *et al.*, 2000), whereas few have considered the importance of evolutionary processes. One hypothesis is that variation in crossbill densities reflects the extent of local adaptation determined at least in part by the persistence of crossbill populations and the strength of divergent selection. Because larger areas of forest support larger populations of crossbills, larger areas should facilitate local adaptation (Gomulkiewicz & Holt, 1995; Reznick & Ghalambor, 2001). Local adaptation is also favored by divergent selection (Schluter, 2000). Cones in larger areas without squirrels are more divergent from those in the Rocky Mountains than are cones in smaller ranges (Fig. 3), which causes stronger divergent selection on crossbills (Benkman, 1993a,2003; Benkman *et al.*, 2001,2003). Previous work shows that crossbills in the largest range (the South Hills) are resident, locally adapted, have diverged in vocalizations and are perhaps speciating (Benkman, 1999,2003; Benkman *et al.*, 2001).

The lower densities of crossbills in the Bears Paw and Little Rocky mountains compared with the South Hills (Fig. 2) suggest that they are less well adapted than are South Hills crossbills. The smaller areas of forest in the Bears Paw and Little Rocky mountains may not be persistent enough nor divergent selection strong enough to cause substantial differentiation. In addition, the presence of ponderosa pine (*P. ponderosa* ssp. *scopulorum*) at the lower elevations of the Bears Paw and Little Rocky mountains may further inhibit divergence by increasing gene flow. For example, crossbills periodically move out of the lodgepole pine forests in the Little Rocky Mountains to feed on the more readily accessible seeds in opening ponderosa pine cones (P. Edelaar, personal communication). Large influxes of crossbills attracted to ponderosa pine cone crops and the mixing of resident and nomadic crossbills might act to inhibit divergence and local adaptation (e.g. Hendry *et al.*, 2001,2002), especially in the absence of divergence in vocalizations that are presumably used in mate choice.

Local adaptation in these smaller ranges, as implied by the relationship between bill depth and seed defences (Fig. 4) may be the result, at least in part, of phenotypic sorting. Sorting is an ecological process whereby a subset of individuals with bills well matched to levels of seed

defences become resident. For example, large-billed European crossbills were more likely than small-billed crossbills to remain sedentary in forests dominated by Scots pine (*P. sylvestris*), because large-billed birds were more capable of extracting seeds from its cones year-round (Marquiss & Rae, 2002). Sorting would also be consistent with an observed phenotypic match to resources despite the potential for gene flow that would restrict local adaptation by evolution. Although we lack an explicit test for sorting, some additional evidence is consistent with phenotypic sorting. For instance, some individuals are resident and some are not. Resident populations of crossbills in Bears Paw and Little Rocky mountains are indicated by the consistent occurrence of crossbills in both of these ranges and the recapture/resighting of banded crossbills ( $n = 1$  of 7 in the Bears Paw, and  $n = 2$  of 38 in the Little Rocky Mountains of birds initially captured in 2000) one or more years after initial capture. That some crossbills disperse is supported by the recapture of a crossbill 300 km to the southwest 1 year after it was initially banded in the Little Rocky Mountains in 2000. Sorting may have also been important in the South Hills during the initial stages of divergence.

In the smallest range without squirrels, the Sweetgrass Hills, crossbills occurred in densities as low if not lower than where squirrels were present (Fig. 2). Such low densities argue against local adaptation by crossbills and are suggestive of a mismatch between crossbills and lodgepole pine. Such mismatches should arise when gene flow counters local adaptation (Thompson, 1994, 1999; Nuismer *et al.*, 1999) or populations go extinct before locally adapting (Thompson *et al.*, 2002). The absence of crossbills during one of the survey periods in the Sweetgrass Hills (Fig. 2) suggests that some, if not many, crossbills in the Sweetgrass Hills are transients indicating frequent turnover in the population there.

The uniformly low densities of crossbills where squirrels were present regardless of forest area (Fig. 2) suggest that population processes are different than where squirrels are absent. It presumably reflects the combination of competition by squirrels and similar levels of adaptation by crossbills in the Rocky Mountains to lodgepole pine cones that are fairly uniform in structure wherever squirrels are found (Benkman, 1999).

### The geographic mosaic

Our previous studies (Benkman, 1999; Benkman *et al.*, 2001, 2003) provided evidence for two of the three components of the geographic mosaic theory of coevolution (Thompson, 1994, 1999). This study supports and further refines those results by considering habitat abundance plus providing evidence for the third component of the theory. The first component of the theory, the selection mosaic, is influenced by the presence and absence of squirrels and the size of forest areas where

squirrels are absent. Where squirrels are present, they drive cone evolution, and crossbills are uncommon and appear to have little impact on cone evolution (Benkman, 1999; Benkman *et al.*, 2001, 2003) regardless of the forest area (a coevolutionary hotspot for squirrels but a coldspot for crossbills). Where squirrels are absent, seed defences against crossbills increase with forest area presumably because crossbill densities increase with forest area. Consequently, the extent of cone divergence and the strength of divergent selection on crossbills between areas with and without squirrels increase with forest area. The second component of the theory, the presence of coevolutionary hotspots, is dependent on concomitant increases in forest area in the absence of squirrels and divergent selection that enable and favour local adaptation and divergence of crossbill populations. In the largest forested area (South Hills) crossbills locally adapt, appear to be speciating and represent a coevolutionary hotspot. Smaller forested areas (Bears Paw and Little Rocky mountains) represent what might be called coevolutionary 'warmspots' (Thompson, 1999). Here cones have diverged because of selection by crossbills, but local adaptation by crossbills is likely limited by gene flow from immigrating nomadic crossbills and determined mostly by the efficacy of phenotypic sorting rather than by local evolution. This may lead to trait remixing and possibly maladaptation across the selection mosaic, which is the third component (e.g. Thompson, 1994, 1999). In the smallest area (Sweetgrass Hills), frequent turnover and local extinction of crossbills presumably prevent even effective phenotypic sorting so that maladaptation, as implicated by extremely low population densities, is the norm. In sum, our results are in line with the theoretical expectation that 'most geographically structured interactions will generate a mix of highly adapted, moderately adapted, and maladapted populations' (Thompson *et al.*, 2002:386).

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