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THE INFLUENCE OF A COMPETITOR ON THE GEOGRAPHIC MOSAIC OF COEVOLUTION BETWEEN CROSSBILLS AND LODGEPOLE PINE

CRAIG W. BENKMAN,[1] WILLIAM C. HOLIMON, AND JULIE W. SMITH
Department of Biology, MSC 3AF, New Mexico State University, Las Cruces, New Mexico 88003-8001
[1]*E-mail: cbenkman@nmsu.edu*

Abstract.—The geographic mosaic theory of coevolution posits that the form of selection between interacting species varies across a landscape with coevolution important and active in some locations (i.e., coevolutionary hotspots) but not in others (i.e., coevolutionary coldspots). We tested the hypothesis that the presence of red squirrels (*Tamiasciurus hudsonicus*) affects the occurrence of coevolution between red crossbills (*Loxia curvirostra* complex) and Rocky Mountain lodgepole pine (*Pinus contorta* ssp. *latifolia*) and thereby provides a mechanism giving rise to a geographic mosaic of selection. Red squirrels are the predominant predispersal seed predator and selective agent on lodgepole pine cones. However, in four isolated mountain ranges east and west of the Rocky Mountains, red squirrels are absent and red crossbills are the main predispersal seed predator. These isolated populations of pine have apparently evolved without *Tamiasciurus* for about 10,000 to 12,000 years. Based on published morphological, genetic, and paleobotanical studies, we infer that cone traits in these isolated populations that show parallel differences from cones in the Rocky Mountains have changed in parallel. We used data on crossbill and conifer cone morphology and feeding preferences and efficiency to detect whether red crossbills and lodgepole pine exhibit reciprocal adaptations, which would imply coevolution. Cone traits that act to deter *Tamiasciurus* and result in high ratios of cone mass to seed mass were less developed in the isolated populations. Cone traits that act to deter crossbills include larger and thicker scales and perhaps increased overlap between successive scales and were enhanced in the isolated populations. In the larger, isolated mountain ranges crossbills have evolved deeper, shorter, and therefore more decurved bills to exploit these cones. This provides crossbills with higher feeding rates, and the change in bill shape has improved efficiency by reducing the concomitant increases in body mass and daily energy expenditures that would have resulted if only bill size had increased. These parallel adaptations and counter adaptations in red crossbills and lodgepole pine are interpreted as reciprocal adaptations and imply that these crossbills and pine are in coevolutionary arms races where red squirrels are absent (i.e., coevolutionary hotspots) but not where red squirrels are present (i.e., coevolutionary coldspots).

Key words.—Ecomorphology, geographic mosaic, *Loxia curvirostra, Pinus contorta,* predator-prey, seed predation, *Tamiasciurus hudsonicus.*

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The view that coevolution is a prominent evolutionary process has been contentious. Nonetheless, evidence from diverse areas of evolutionary biology indicate that coevolution is a fundamental process in evolution and that a better understanding of the coevolutionary process is critical for progress in evolutionary biology, conservation, and health-related issues (Thompson 1994, 1999a,b). One recent advance in coevolutionary theory has risen from the recognition that the form of an interaction between species often varies across a landscape (e.g., Thompson and Pellmyr 1992). This geographic variation forms the basis of the geographic mosaic theory of coevolution (Thompson 1994, 1999a).

Three components are central to the geographic mosaic theory of coevolution. First, the form of selection between interacting species varies across a landscape (i.e., selection mosaics). Second, coevolution is an important and active process in some locations (i.e., coevolutionary hotspots), but not in others (i.e., coevolutionary coldspots). Third, gene flow between locations causes trait remixing that can result in mismatches in the traits of interacting species. Much recent evidence shows that these three components characterize a variety of interspecific interactions. For example, a given interspecific interaction often varies in outcome from one area to another (e.g., Thompson and Pellmyr 1992; Thompson 1997, 1999a; Berenbaum and Zangerl 1998), coevolution is prominent in some areas but not others (e.g., Brodie and Brodie 1999; Lively 1999), and gene flow can affect the outcomes of interactions (e.g., Burdon and Thrall 1999).

One example that highlights how geographic variation in the strength of interactions might arise is the interaction between red squirrels (*Tamiasciurus hudsonicus*), red crossbills (*Loxia curvirostra* complex), and Rocky Mountain lodgepole pine (*Pinus contorta* spp. *latifolia*; Benkman 1999). In brief, crossbills are relatively uncommon in the presence of *Tamiasciurus* because crossbills are outcompeted for seeds in lodgepole pine cones. Red squirrels are the predominant seed predator and drive cone evolution, and crossbills have adapted to the average cone (i.e., a coevolutionary coldspot for crossbills). In isolated mountain ranges east and west of the Rocky Mountains, red squirrels are absent and crossbills are abundant and coevolve with lodgepole pine (i.e., a coevolutionary hotspot for crossbills). The difference in cone structure between coevolutionary hotspots and coldspots causes divergent selection between crossbill populations. This study illustrates how the presence and absence of one key species determines the geographic selection mosaic and location of coevolutionary hotspots and coldspots for its competitor.

Benkman (1999) showed that the overall change in cone structure (as measured by the first two principal components characterizing variation in seven cone and seed traits) in areas where red squirrels are absent was consistent with evolution in response to selection by crossbills. In particular, the changes in cone structure were predicted if the benefits of defenses, in terms of time per seed for foraging crossbills, were maximized relative to the costs of the defenses, in terms of mass of cone divided by total seed mass. In addition, the extent of change was greatest in larger mountain ranges, where crossbills are most abundant and resident and have evolved larger and more decurved bills, than in smaller mountain ranges, where crossbills are less common or perhaps less persistent and have apparently not adapted locally (Benkman 1999). Although this last line of evidence indicates that selection by crossbills has at least affected the rate of change, the direction of change was not very different from that predicted if trees had simply reduced the amount of cone mass compared with that devoted to seed mass.

The goal of this paper is to further evaluate whether crossbills and lodgepole pine coevolve when red squirrels are absent. First, we address the hypothesis that the differences in cone traits between geographic areas are the result of selection and relaxation of selection by *Tamiasciurus* and the result of selection by red crossbills where red squirrels are absent. Two predictions can be tested: (1) traits that act to deter *Tamiasciurus* and result in a reduction in seed production (i.e., result in an increase in cone mass relative to seed mass) should differ between areas where red squirrels are present and absent in a manner consistent with selection and relaxation of selection by *Tamiasciurus,* respectively; and (2) some differences in cone traits are related to selection by crossbills and are not related to selection and relaxation of selection by *Tamiasciurus.* For example, traits that result in an increase in cone mass, and are thus costly to the plant, might be more developed in the absence of *Tamiasciurus* if these traits act to deter crossbills. An alternative hypothesis is that differences in cone traits between geographic areas are simply the result of selection and relaxation of selection by *Tamiasciurus.* This hypothesis would be supported if the results were consistent with only the first prediction of the first hypothesis. Finally, we test the hypothesis that the bill structure of the crossbills on the largest isolated mountain ranges is an adaptation to foraging on cones in these mountain ranges.

METHODS

The Study System

Throughout the Rocky Mountains, red squirrels are the main seed predators of lodgepole pine. Red squirrels harvest many lodgepole pine cones and cache them in the ground in middens soon after the seeds mature in late summer and early autumn, but before the cone scales begin opening (Smith 1968, 1970, 1981; Elliott 1988); insects consume less than 0.1% of the seed crop (Miller 1986). Seeds in these cached cones provide the main winter food for *Tamiasciurus* and are unavailable to crossbills and other seed predators (Smith 1968, 1970, 1981). In the Rocky Mountains from the Yukon to Colorado, cones are short, are wide at the base (Fig. 1), have few seeds, and have an especially high ratio of cone mass to seed mass (nearly 100 to 1) that reflects selection by *Tamiasciurus* (Smith 1970; Elliott 1974, 1988; Wheeler and Guries 1982b; Benkman 1999). Red squirrels tend to avoid cones that are wide at the base because wide cones are difficult to bite off the branch (Smith 1970; Elliott 1974, 1988). After cones are removed from the branch, red squirrels forage for seeds by biting off successive scales at their base starting at the proximal end of the cone. Seeds are mostly located under the distal scales, so when cones have few seeds and when cone mass is large relative to seed mass red squirrels need to bite through more scale mass before reaching seeds.

Red crossbills in North America are categorized into about eight call types that are recognized by distinct vocalizations (Groth 1993; Benkman 1999). At least six of these call types are each specialized for foraging on different species of conifers (Benkman 1989b, 1993, 1999; Benkman and Miller 1996). One call type is specialized for foraging on seeds in lodgepole pine cones in the Rocky Mountains (call type 5 of Groth 1993; see also Benkman 1993; Benkman and Miller 1996). Another call type is endemic to the South Hills and Albion Mountains of Idaho and appears to be specialized for foraging on lodgepole pine cones in these mountains (Benkman 1999). In isolated ranges east and west of the Rocky Mountains, including the South Hills and Albion Mountains, where red squirrels are absent (see Fig. 1), red crossbills are the main seed predators of seeds in lodgepole pine cones. In the largest isolated ranges crossbills are resident, have distinct bill morphologies, and are up to 20 times more abundant than in comparable habitat in the Rocky Mountains (Benkman 1999, unpubl. data).

These large isolated ranges have lodgepole pine cones that are predominantly (>90%) serotinous (C. W. Benkman, pers. obs.). Serotinous cones remain closed until sufficient heat melts the resinous bonds holding the cone scales together (Johnson and Gutsell 1993) and serotinous cones are characteristic of areas where stand-replacing fires are common (Muir and Lotan 1985). South Hills crossbills mostly feed upon 3–7-year-old serotinous cones that accumulate in the absence of *Tamiasciurus* (C. W. Benkman, pers. obs.). The relative scarcity of these cones where red squirrels are present explains why crossbills are common in Rocky Mountain lodgepole pine forest only in the absence of *Tamiasciurus.* Crossbills rely on seeds in these older cones presumably because their scales have opened slightly or their resinous bonds have weathered; crossbills cannot easily remove seeds from serotinous lodgepole pine cones whose resinous bonds are intact. Only after the cone scales open further can other vertebrate seed predators (e.g., *Parus gambeli* and *Carduelis pinus*) reach the seeds, but by then many of the seeds have been shed or eaten by crossbills. In these isolated ranges, cones are longer, relatively narrower, have more and larger seeds and thicker distal scales than where red squirrels are present (Benkman 1999).

The ranges lacking *Tamiasciurus* have been isolated from the Rocky Mountains by nonforested habitat for about 12,000 years or less. The lodgepole pine forests in the South Hills and Albion Mountains in Idaho (Fig. 1) were likely connected to lodgepole pine forests in adjacent ranges more than 10,000 years ago (Wells 1983; O. K. Davis, pers. comm.; see also Bright 1966; Davis et al. 1986). How long red squirrels have been absent is unclear, but it is probably less than 10,000 years. Allozyme studies of lodgepole pine (Wheeler and Guries 1982a; Dancik and Yeh 1983) are consistent with the hypothesis that lodgepole pine, widespread in the western United States near the end of the Pleistocene (Critchfield 1985), spread from the northern Rocky Mountains and colonized the Cypress Hills in southern Canada (Fig. 1) after glaciers retreated 12,000 years ago (see Thompson and Kuijt

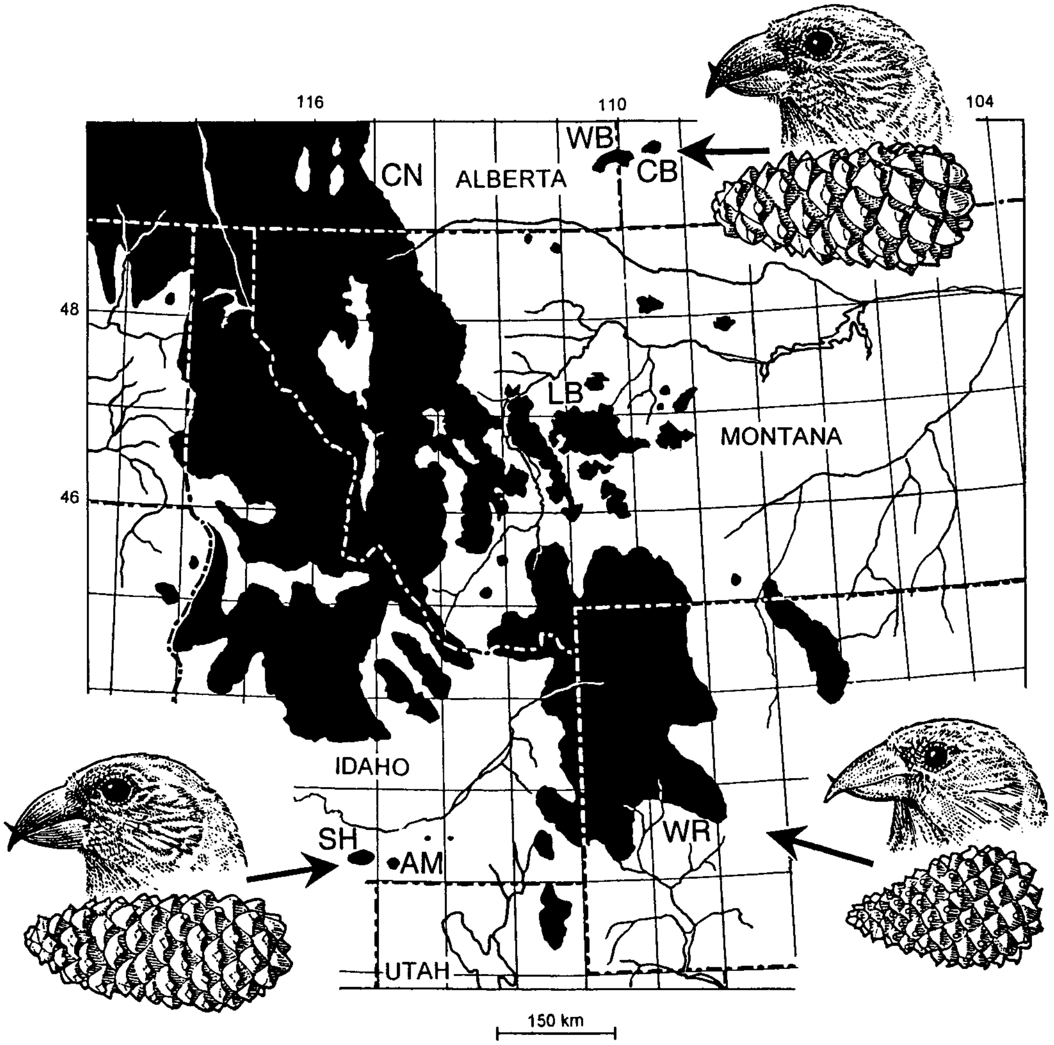

FIG. 1. The distribution of lodgepole pine (black), locations of study sites, and representative crossbills and cones in the Rocky Mountains (lower right), in the Cypress Hills (upper right), and in the South Hills and Albion Mountains (lower left; modified from Benkman 1999). The crossbills and cones 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) and Albion Mountains (AM). Red squirrels were absent from the West Block (WB) and Centre Block (CB) of the Cypress Hills until being introduced in 1950. One Rocky Mountain study site not shown was near Twin Lakes, Colorado approximately 650 km south-southeast of the Wind River Range (WR) site. The two other Rocky Mountain study sites were Crow's Nest Pass (CN) and Little Belt Mountains (LB).

1976). Crossbills likely became resident in the Cypress Hills only in the last 6800 years, when lodgepole pine became common (Sauchyn and Sauchyn 1991) in apparent response to cooler and wetter conditions in the region (Barnosky 1989). Pine was probably too rare to support a population of *Tamiasciurus* prior to 6800 years ago, and *Tamiasciurus* would not have been able to colonize the Cypress Hills because extensive grassland steppe surrounded the Cypress Hills during the last 10,000 years (Ritchie 1976; Thompson and Kuijt 1976; Barnosky 1989).

Based on the above information, we assume that lodgepole pine independently colonized the South Hills and the Cypress Hills and had cones similar to those that characterize lodgepole pine throughout the Rocky Mountains. This implies, therefore, that all the differences between cones in the Rocky Mountains and these isolated ranges represent changes that have occurred in the isolated ranges in the past 12,000 years. This might seem like a short time, especially for lodgepole pine (average generation time probably exceeds 100 years; e.g., Muir 1993), to evolve substantial differences. However, rapid and extensive evolution of quantitative traits, including cone structure, has occurred in other populations of lodgepole pine (Aitken and Libby 1994; Xie and Ying 1995). Moreover, many of the measured lodgepole pine cone traits are heritable. Heritability in the broad sense (H^2) equals 0.53 for cone length, 0.30 for cone width, 0.25 for cone mass, 0.43 for seed mass, and 0.37 for the number of seeds per cone (T. S. Kimbrell, C. C. Smith, J. S. Pontius, and P. F. Elliott, unpubl. ms.).

Cone Variation

We used discriminant function analysis (DFA) to find which cone traits most strongly distinguish geographic areas where predation on cones is dominated by *Tamiasciurus* from areas where predation is dominated by crossbills. DFA is successful when few cases are misclassified. We used jackknifed classification so that the resulting classification was not based on the same cases used in developing the classification equations. We limited analyses to serotinous cones from four locations in the Rocky Mountains (*Tamiasciurus* present) and four isolated ranges without *Tamiasciurus* where crossbills are known to have been or are common. Most lodgepole pine trees at the study sites had serotinous cones (C. W. Benkman and W. C. Holimon, pers. obs.). The four locations with *Tamiasciurus* are Crow's Nest Pass, Little Belt Mountains, Wind River Range, and Twin Lakes (Fig. 1). The four locations without *Tamiasciurus* were the South Hills, Albion Mountains, and the West Block and Centre Block of the Cypress Hills (Fig. 1). Although red squirrels were introduced into the Cypress Hills in 1950 (Newsome and Dix 1968) and are now common (Benkman 1999), all the cones sampled in the Cypress Hills came from trees that germinated before 1950.

We measured three cones from each of 22–30 trees from each of the eight sites. We selected trees haphazardly with the constraint that cones could be reached with a 9-m extension pole with a clipper attached at the end. Only cones without apparent deformities were measured. The following cone and seed traits were measured: closed cone length, maximum width of closed cone, the thickness at 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 (the six 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, hereafter seed kernel), and the individual masses of five filled seeds. All length measurements were made to the nearest 0.01 mm with digital calipers. All mass measurements were made to the nearest 0.1 mg with a digital scale after the cones and seeds were oven-dried at 60–70°C for more than 2 days. We analyzed seven of the eight measured traits (ln-transformed tree means) in the DFA. The number of full seeds was not used because it is highly correlated with the total number of seeds ($r = 0.88$) and the percentage of full seeds is influenced by the frequency of outcrossed pollen (Smith et al. 1988), which is not a characteristic of interest in this analysis. We used two-level nested ANOVA on each cone trait (ln-transformed, unless noted otherwise) to test for differences between areas and among sites within areas with and without *Tamiasciurus.* Regression and ANCOVA were used to control for size changes to further characterize variation between cone traits that contributed most to differentiating areas with and without *Tamiasciurus.* Trees were the experimental units, so we used the mean value from each tree in these analyses.

Squirrel Preferences

Red squirrels are considered important selective agents on lodgepole pine cones (Smith 1970; Elliott 1974, 1988; Benkman 1999). To quantify which cone traits might deter *Tamiasciurus,* we contrasted cones from trees that were extensively harvested by *Tamiasciurus* to cones from trees that were avoided. We gathered three cones, recently cut by *Tamiasciurus,* from the base of 30 lodgepole pine trees on 30 different *Tamiasciurus* territories in the West Block of the Cypress Hills in September 1994. These trees (i.e., harvested trees) generally had few cones remaining on their branches (cf. Elliott 1988). We compared cones from these harvested trees to three cones gathered from trees that were near the harvested tree and from which red squirrels had harvested few cones (many closed cones from many previous years were attached to the branches). Because red squirrels are more selective of cone traits with increasing distance from middens (Elliott 1988), we selected pairs of trees (> 12 m tall) that were approximately equidistant from the nearest midden. We measured the same cone traits as above and used the mean from each tree in the analyses. We used DFA to contrast cones from trees that had been harvested or avoided by *Tamiasciurus* as described above, except that we used the number of full seeds rather than the total number of seeds.

Cone Traits that Impede Crossbills

We used partial correlation between crossbill feeding rates in captivity and various cone traits to determine which cone traits might serve as a defense against crossbills. Crossbill feeding rate is a good measure of seed defense, because crossbills maximize feeding rates when foraging (Benkman 1987b, 1989a) and therefore avoid trees where time per seed is high. Evidence that would indicate that certain cone traits serve as a defense against crossbills include a significant correlation between the cone trait and crossbill feeding rates in the partial correlation analyses and patterns of geographic variation in these same cone traits that are consistent with variation in the selection intensity by crossbills. We excluded cone mass from the analysis because it was strongly correlated with both cone length and width ($r = 0.66$ and 0.77, respectively). Once it was excluded, the highest correlation was between cone length and distal scale thickness ($r = 0.51$).

Captive crossbills were housed in indoor aviaries (1.6 m × 2.7 m × 2.2 m or larger). The birds were provided with a constant supply of grit and water. Fresh cones were provided daily, supplemented with Mazuri Chow (PMI Seeds Incorporated, St. Louis, MO). Crossbills remained in excellent condition. At least several days before and during the experiments, crossbills were maintained at a low mass by monitoring their diet and were required to forage mostly on seeds in lodgepole pine cones. To ensure consistent and high motivation for foraging, we removed all food from the aviary about 15 h before the experiments. During foraging experiments, the focal crossbill was isolated from other crossbills by a screen partition. The presence of other crossbills isolated by a screen eliminated variation that might arise from time spent scanning for predators and competitors (Benkman 1997). All foraging experiments were conducted between November 1997 and October 2000.

Eight red crossbills (call type 2 of Groth 1993) were timed foraging on serotinous lodgepole pine cones from 82 trees. Call type 2 crossbills (hereafter ponderosa pine crossbills; Benkman 1993) are intermediate in bill depth between lodgepole pine crossbills from the Rocky Mountains (call type 5 of Groth 1993) and from the South Hills (see Table 3). Thus, the cone traits that hinder ponderosa pine crossbills are likely the same traits that hinder South Hills crossbills and crossbills ancestral to them. Ponderosa pine crossbills, therefore, are appropriate subjects to use to determine which cone traits impede foraging crossbills and which traits may have experienced selection by crossbills.

The total time required to extract (prying time) and handle (remove seed coat and swallow the seed kernel) 10 seeds, beginning after the first seed was eaten (see Benkman 1987a, 1993), was recorded for one cone from each tree for each bird. The tree was the experimental unit, so we used the overall mean feeding rate of the eight crossbills from each tree in the partial correlations. We also measured seed handling times for cones from 60 of the trees. Thus, we could estimate prying time (total time per seed minus average time to handle a seed) for 60 of the trees.

Cones were selected from trees, including 42 trees used in the analyses of cone variation described earlier and 40 trees from other mountain ranges, whose previously measured cones represented much of the variation in lodgepole pine cone traits (Benkman 1999). Cones were given to crossbills in random order with respect to cone traits. We assumed that the cones used in the foraging experiments had the same average cone traits as those measured for the tree. This assumption is reasonable given that within-tree variance in cone traits is significantly smaller than the between-tree variance (Smith 1968; Elliott 1974). To reproduce cones that crossbills rely on in the wild (i.e., resinous bonds between scales broken or weathered), each cone was placed in boiling water for about 30 sec to remove the resinous bond and open the scales. The cones were then stored in plastic bags in a freezer and thawed before the experiments. Moisture in the bags kept the scales reclosed.

Have Crossbills Adapted to Lodgepole Pine Cones in the South Hills?

To determine if crossbills have adapted to lodgepole pine, we tested one quantitative and two qualitative predictions. The first qualitative prediction is that each crossbill type should have a higher feeding rate on cones from its respective habitat. To test this prediction, we measured the feeding rates of 10 South Hills crossbills and five Rocky Mountain lodgepole pine crossbills on lodgepole pine cones from the South Hills and from the Rocky Mountains. Feeding rates were measured as detailed above, and each crossbill was timed foraging on 10 cones representative of the South Hills and 10 cones representative of the Rocky Mountains. We used *t*-tests on the average feeding rates of each crossbill to test for differences in feeding rates between the two types of crossbills on cones from each area. To determine if there was a trade-off between adapting to cones from each area, we used ANOVA to test for a significant interaction between crossbill type and cone type.

The quantitative prediction is that average bill depth of the South Hills crossbill approximates the optimum for foraging on cones from the South Hills. We measured the feeding rates of 28 South Hills crossbills to quantify the relationship between bill size (depth) and feeding efficiency on lodgepole pine cones from the South Hills (for justification for using bill depth, see Benkman and Miller 1996). Feeding rates were measured as detailed above and every bird was timed foraging on 10 or 11 cones representative of the South Hills to provide an average feeding rate for each bird. The bill depth that is most efficient at meeting energy demands (i.e., the optimal bill depth) was estimated as the bill depth that minimizes the foraging time necessary to meet daily energy demands. We estimated feeding efficiency as the inverse of the product of prying time and estimated daily energy demands (Benkman 1993; Benkman and Miller 1996). We used prying time because bill size (depth) is closely related to prying time but not seed husking time (Benkman 1993). Daily energy demands were estimated as $(\text{body mass})^{0.6052}$ (Walsberg 1983). Body mass depends upon a variety of factors including the amount of fat stored and, especially in captivity, the loss of flight muscle mass. The crossbills used in this experiment varied in body fat at time of capture. Consequently, body mass was estimated from the allometric relationship between body mass (Y, in g) and bill depth (X, in mm): $Y = -3.78 + 3.82X$ ($r^2 = 0.68$, df $= 77$, $P < 0.0001$), where body mass was measured at time of capture of crossbills lacking much fat.

The second qualitative prediction is that the South Hills crossbill has evolved a bill shape that is adaptive for foraging on lodgepole pine cones in the South Hills. To test this prediction, we used bill depth and length measurements to quantify bill shape. Then we used comparative feeding efficiency data to test whether differences in bill shape are adaptive. Bill depth was measured at the anterior end of the nares. The mean of the upper and lower mandible lengths was used to estimate bill length. Upper mandible length was measured from the tip of the upper mandible to the anterior end of the right naris. Lower mandible length was measured from the tip of the lower mandible to the base where rami meet. Bills were measured to the nearest 0.01 mm with digital calipers. C. W. Benkman and W. C. Holimon measured the crossbills. Our bill measurements (we each measure bill depth 3–5 times per bird and use the mean) are nearly identical and highly repeatable. For example, of the 17 South Hills crossbills that we both independently measured about one month apart, the average difference in bill depth was 0.001 mm (repeatability $= 0.992$, $F = 245.1$; Lessells and Boag 1987). We used the foraging data on 17 South Hills crossbills gathered to test the quantitative prediction described above and in the same manner we measured and analyzed feeding rates of 14 ponderosa pine crossbills.

RESULTS

Cone Variation

Cones from areas with *Tamiasciurus* differed significantly (DFA: eigenvalue $= 3.58$, $F_{7,202} = 103.4$, $P < 0.0001$) from cones from areas without *Tamiasciurus.* Areas without *Tamiasciurus* had positive canonical scores, and the canonical discriminant functions correctly classified 97% and 96% of the trees (jackknifed classification) from areas with and without *Tamiasciurus* ($n = 97$ and 113 trees), respectively. Individually, all cone traits differed significantly between areas with and without *Tamiasciurus* (Table 1). Significant differences were also found among sites within each area, with the exception of distal scale thickness (Table 1). Although most

TABLE 1. Mean cone measurements for sites with and without *Tamiasciurus*. The *P*-values give the significance of the differences between areas (i.e., sites with or without *Tamiasciurus*) and of the differences among sites within areas with and without *Tamiasciurus* based on two-level nested ANOVAs (ln-transformed data except for seed mass/cone mass, which was arcsine transformed). The ratio seed mass/cone mass is individual seed mass (in mg) times number of full seeds per cone divided by cone mass (in mg). Analyses were based on the mean for each tree, and three cones were measured from each tree.

	Tamiasciurus present				*Tamiasciurus* absent[1]				Between areas with and without *Tamiasciurus*		Among sites with and without *Tamiasciurus*	
Measurement	Crow's Nest Pass	Little Belt Mountains	Twin Lakes	Wind River Range	Albion Mountains	South Hills	Centre Block	West Block	*F* (df = 1, 6)	*P*	*F* (df = 6, 202)	*P*
Cone length (mm)	35.13	37.45	36.21	37.17	46.82	49.60	43.86	43.61	313.9	<0.0001	7.36	<0.0001
Cone width (mm)	24.16	26.75	23.10	23.59	24.94	26.00	25.94	26.68	25.5	<0.0001	7.36	<0.0001
Proximal scale thickness (mm)	2.71	3.01	2.97	2.96	2.37	2.43	2.60	2.59	46.3	<0.0001	2.95	0.0088
Distal scale thickness (mm)	2.53	2.52	2.63	2.68	2.82	2.98	2.98	2.84	35.1	<0.0001	1.20	0.31
Cone mass (g)	6.69	5.71	6.21	6.42	8.27	9.04	9.36	9.56	155.1	<0.0001	2.28	0.038
Number of seeds/cone	26.0	23.0	19.2	21.0	43.2	62.7	43.2	43.2	155.9	<0.0001	5.45	<0.0001
Number of full seeds/cone	19.1	16.6	15.1	14.9	33.4	50.0	36.8	34.6	185.1	<0.0001	4.37	0.0004
Individual seed mass (mg)	3.89	4.62	4.47	4.69	6.08	7.01	6.58	7.14	321.0	<0.0001	5.93	<0.0001
Seed mass/cone mass	0.012	0.013	0.011	0.011	0.025	0.040	0.026	0.025	118.4	<0.0001	9.14	<0.0001
Number of trees sampled	28	22	23	24	25	29	30	29				

[1] Red squirrels were introduced into the Centre Block and West Block of the Cypress Hills in 1950.

cone traits had larger values in areas without *Tamiasciurus* than in areas with *Tamiasciurus*, cones where red squirrels are absent were not simply larger versions of cones where red squirrels are present.

Based on the canonical discriminant functions, areas without *Tamiasciurus* were characterized by larger and more slender cones with thinner basal scales, thicker distal scales, and larger seeds. These differences can be readily seen in bivariate plots. For example, a plot of cone width in relation to cone length (Fig. 2A) shows that cones in areas without *Tamiasciurus* were longer and also relatively more slender than in areas with *Tamiasciurus*. Cone width was linearly related to cone length ($P < 0.0001$) within areas where red squirrels are present and within areas where red squirrels are absent (Fig. 2A), however, the slopes of these two regressions differed significantly (ANCOVA, $F = 9.7$, df = 1, $P = 0.002$).

Distal and proximal scale thickness were linearly related ($P < 0.001$) within areas where red squirrels are present and within areas where red squirrels are absent (Fig. 2B). The slopes of the regressions between distal and proximal scale thickness did not differ between areas with and without *Tamiasciurus* (ANCOVA, $F = 1.1$, df = 1, $P = 0.30$), but their intercepts did differ (ANCOVA, $F = 104.2$, df = 1, $P < 0.0001$). These results show that distal scales are relatively thick and proximal scales are relatively thin in areas without *Tamiasciurus* compared with areas with *Tamiasciurus*.

Seed mass was linearly related to cone mass ($P < 0.0001$) within areas where red squirrels are present and within areas where red squirrels are absent (Fig. 3A). The slopes of the regressions between seed mass and cone mass did not differ between areas with and without *Tamiasciurus* (ANCOVA, $F = 0.6$, df = 1, $P = 0.42$), but their intercepts did differ (ANCOVA, $F = 101.9$, df = 1, $P < 0.0001$). The difference in intercept indicates that differences in seed mass between areas with and without *Tamiasciurus* have occurred independently of changes in cone size. The number of seeds (total and full) per cone was also linearly related to cone mass ($P < 0.03$) within areas where red squirrels are present and within areas where red squirrels are absent. The slopes of the regressions between the number of seeds (total and full) per cone and cone mass did not differ between areas with and without *Tamiasciurus* (ANCOVA: $F < 0.2$, df = 1, $P > 0.67$). However, the intercepts of these regressions differed ($F > 45.8$, df = 1, $P < 0.0001$) so that the number of seeds per cone was significantly greater in areas without *Tamiasciurus* than in areas with *Tamiasciurus*. Larger individual seed masses and more seeds per cone resulted in a substantially greater total seed mass relative to cone mass (Fig. 3B) in areas without *Tamiasciurus* than with areas with *Tamiasciurus* (ANCOVA: for slope $F = 0.0001$, df = 1, $P = 0.99$; for intercept $F = 136.4$, df = 1, $P < 0.0001$).

Squirrel Preferences

Cones from trees intensively harvested by *Tamiasciurus* differed significantly (DFA: eigenvalue = 0.67, $F_{7,52} = 5.0$, $P = 0.0002$) from cones from trees avoided by *Tamiasciurus*. The canonical discriminant functions correctly classified 77% and 63% of the trees (jackknifed classification) from trees harvested and avoided by *Tamiasciurus* ($n = 30$ and 30 trees), respectively. Slender cones with many seeds characterized trees intensively harvested by *Tamiasciurus*. These results were consistent with previous analyses of the same data (Benkman 1999), which showed that red squirrels preferentially harvested cones that had a small ratio of cone width to cone length, more full seeds, and a higher total seed mass relative to cone mass.

Cone Traits that Impede Crossbills

Five cone traits were significantly correlated (partial correlation) with foraging time (Table 2). First, distal scale thickness was positively correlated with time per seed (Table 2). Most seeds are located in the distal half of the cone and this is where crossbills forage. Second, larger seeds take longer to extract from the cone than small seeds (Table 2). This correlation arises presumably because larger scales surround larger seeds (McGinley et al. 1990), which provide greater resistance to the forces exerted by crossbills. Alternatively, larger seeds take longer to handle. However, a similar and even stronger relationship was found between prying time per seed, which excludes seed handling time, and seed mass (Table 2). Third, time per seed increased as cone width increased (Table 2). Cone width near the distal end of the cone would provide a measure of the amount of scale mass covering a seed. However, cone width was measured at the widest part of the cone, which was usually near the proximal end (see Fig. 1). We assume that cone width provides a rough measure of the width of the cone near the distal end. Fourth, foraging time increases with decreasing cone length (Table 2). We interpret the inverse relationship between foraging time and cone length in terms of the amount of scale overlap and therefore the number of scales that impede crossbills when they are trying to extract a given seed. If other cone variables like scale thickness and seed size (which is about equal to scale length and width; McGinley et al. 1990) are controlled by partial correlation, shorter cones have greater overlap between adjacent scales than longer cones. Fifth, prying time increases with increases in the number of empty seeds (Table 2). Crossbills cannot distinguish empty seeds from full seeds until they are secured in the bill. Thus, increases in empty seeds result in an increase in time between full seeds.

Have Crossbills Adapted to Lodgepole Pine Cones in the South Hills?

South Hills crossbills had significantly higher feeding rates on South Hills lodgepole pine cones than did lodgepole pine crossbills from the Rocky Mountains (Fig. 4; $t = -2.93$, df $= 13$, $P = 0.012$). Conversely, lodgepole pine crossbills from the Rocky Mountains had significantly higher feeding rates on Rocky Mountain lodgepole pine cones than did South Hills crossbills (Fig. 4; $t = 3.33$, df $= 13$, $P = 0.005$). These two results in combination show a strong trade-off between adapting to cones from the South Hills and the Rocky Mountains (ANOVA, interaction between cone and crossbill types: $F = 19.6$, df $= 1$, $P = 0.0002$), and that both crossbill types have adapted to the cones in their respective ranges. Finally, feeding rates for both crossbill types were significantly lower on cones from the South Hills than on cones from the Rocky Mountains (ANOVA, $F = 67.5$, df $= 1$, $P < 0.0001$). This result suggests that cones in the South Hills have enhanced defenses directed at crossbills.

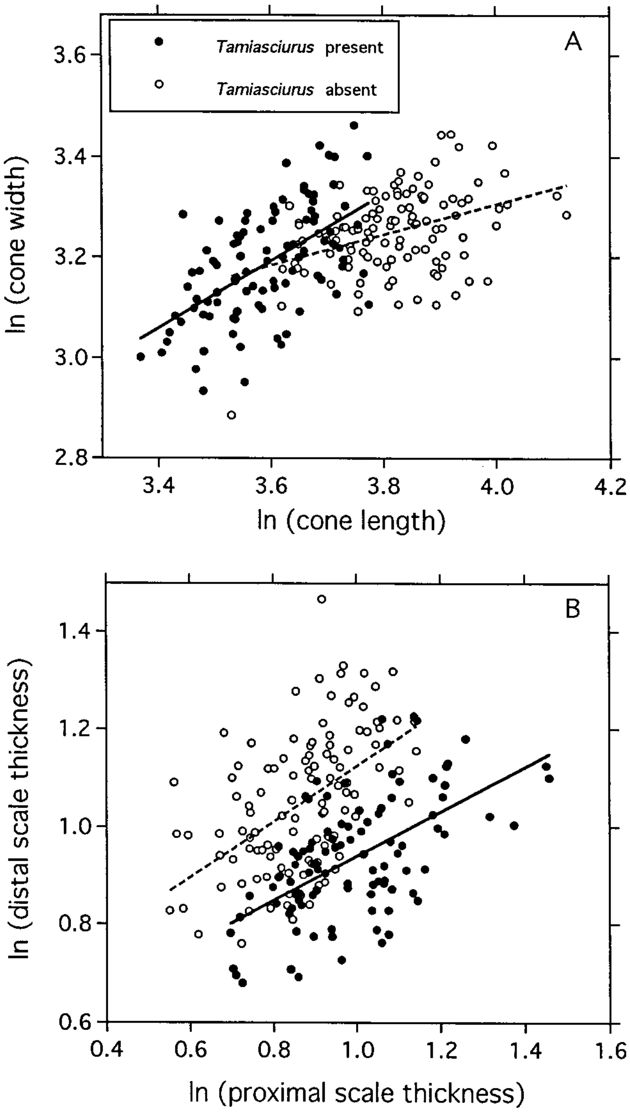

FIG. 2. Cone width in relation to cone length (ln transformed) and distal scale thickness in relation to proximal scale thickness (ln transformed). (A) The linear relationships between ln cone width (Y) and ln cone length (X) were highly significant for areas where red squirrels are present (solid line: $Y = 0.79 + 0.67X$, $r^2 = 0.34$, df $= 95$, $P < 0.0001$) and where red squirrels are absent (dashed line: $Y = 2.08 + 0.31X$, $r^2 = 0.15$, df $= 111$, $P < 0.0001$). (B) The linear relationships between ln distal scale thickness (Y) and ln proximal scale thickness (X) were significant for areas where red squirrels are present (solid line: $Y = 0.48 + 0.46X$, $r^2 = 0.33$, df $= 95$, $P < 0.0001$) and where red squirrels are absent (dashed line: $Y = 0.55 + 0.57X$, $r^2 = 0.27$, df $= 111$, $P < 0.0001$). Each symbol represents the means from one tree.

Prying time (Y, in sec) on South Hills lodgepole pine cones is curvilinearly related to bill depth (X, in mm) for South Hills crossbills ($Y = 1460.9 - 290.9X + 14.5X^2$, $r^2 = 0.48$, df $= 25$, $P = 0.0002$, $P = 0.0037$ for quadratic term). We used this relationship in combination with allometric relationships to estimate daily energy expenditures and to esti-

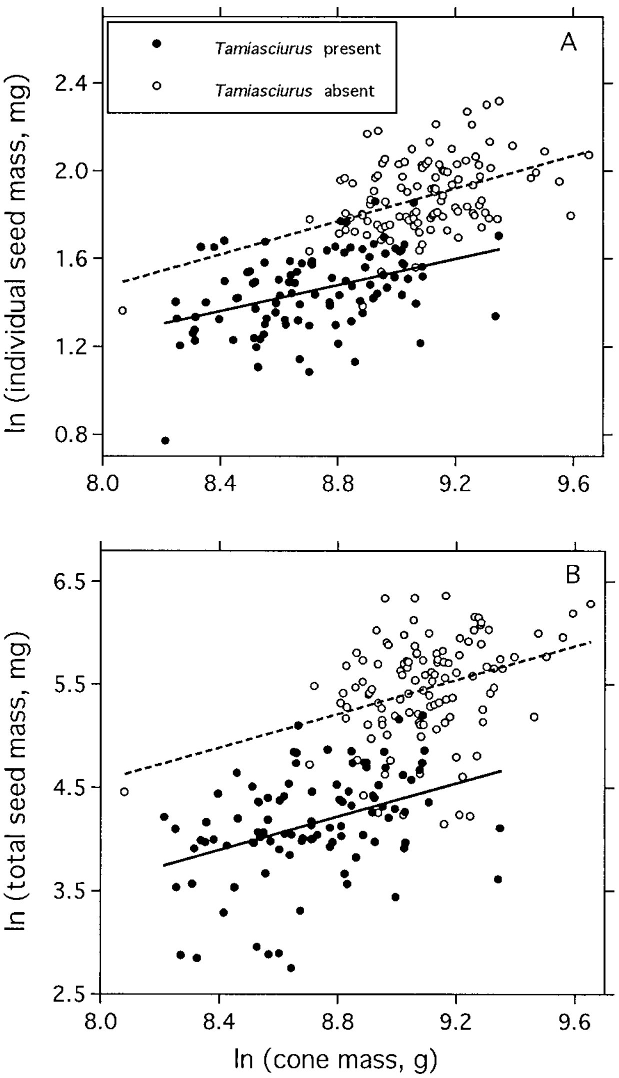

FIG. 3. Individual seed mass and total seed mass (the product of individual seed mass and the number of full seeds per cone) in relation to cone mass (ln transformed). (A) The linear relationships between ln individual seed mass (Y) and ln cone mass (X) were significant for areas where red squirrels are present (solid line: $Y = -1.11 + 0.29X$, $r^2 = 0.16$, df = 95, $P < 0.0001$) and where red squirrels are absent (dashed line: $Y = -1.54 + 0.38X$, $r^2 = 0.19$, df = 111, $P < 0.0001$). (B) The linear relationships between ln total seed mass (Y) and ln cone mass (X) were significant for areas where red squirrels are present (solid line: $Y = -2.90 + 0.81X$, $r^2 = 0.15$, df = 95, $P < 0.0001$) and where red squirrels are absent (dashed line: $Y = -1.93 + 0.81X$, $r^2 = 0.11$, df = 111, $P = 0.0003$). Each symbol represents the means from one tree.

mate the most efficient or optimal bill depth (see Methods). Based on the quadratic relationship between foraging efficiency and bill depth (Fig. 5), the optimal bill depth is 9.99 mm. The average bill depth for South Hills crossbills is 9.87 mm (Table 3). This is smaller than the estimated optimum, but is larger than the two largest other crossbills in the region (Table 3). These results show that the South Hills crossbill has adapted to lodgepole pine cones in the South Hills, but may not have the optimal bill depth.

The South Hills and Cypress Hills crossbills have deeper and relatively shorter bills compared to lodgepole pine and ponderosa pine crossbills (Fig. 6). The shorter the bill for a given bill depth, the more decurved the mandibles (see Fig. 1). One result of more decurved mandibles is that greater biting forces can be withstood (as compression rather than shearing forces) and therefore exerted at their tips (see Grant and Grant 1989). This could enable the short-billed South Hills crossbill to have a smaller optimal bill depth, which would be adaptive if it allows a smaller body with lower energy requirements. A comparison of the estimated feeding efficiencies of South Hills and ponderosa pine crossbills supports this hypothesis (Fig. 5). Feeding efficiency for ponderosa pine crossbills on South Hills lodgepole pine cones does not appear to level off within the measured bill range, whereas feeding efficiency peaks at a bill depth of about 10 mm for the South Hills crossbill. This hypothesis also requires that body mass is allometrically related to bill depth

TABLE 2. Partial correlation coefficients between various Rocky Mountain lodgepole pine cone traits and prying time ($n = 60$ trees) and foraging or total time per seed ($n = 82$ trees; all ln-transformed) for eight ponderosa pine red crossbills.

	Prying time per seed	Total time per seed
Cone length	−0.176	−0.322***
Cone width	0.092	0.300***
Distal scale thickness	0.156	0.256*
Proximal scale thickness	−0.165	0.009
Individual seed mass	0.335**	0.239*
Number of full seeds	0.193	0.111
Number of empty seeds	0.329**	0.172

* $P < 0.05$; ** $P < 0.02$; *** $P < 0.01$.

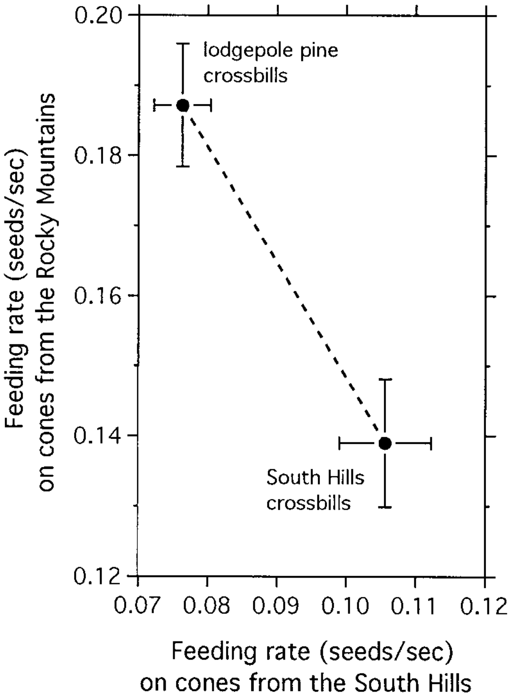

FIG. 4. Feeding rates (mean ± SE) of South Hills crossbills ($n = 10$ birds) and lodgepole pine crossbills ($n = 5$ birds) on lodgepole pine cones from the South Hills and Rocky Mountains.

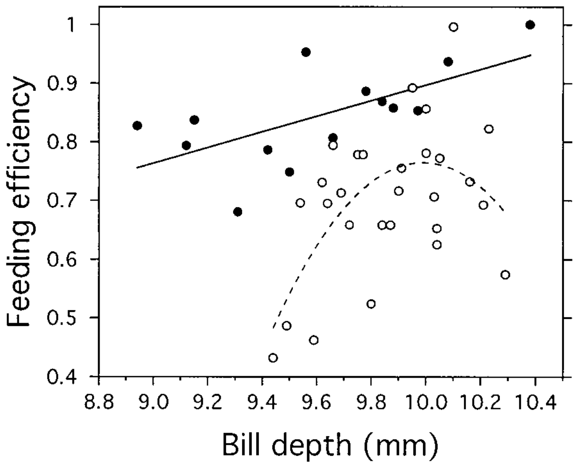

FIG. 5. Estimated feeding efficiencies of South Hills crossbills (open circles) and of ponderosa pine crossbills (solid circles) on South Hills lodgepole pine cones. The dashed curve represents the quadratic equation that best fits the data for South Hills crossbills (feeding efficiency $= -92.94 + 18.76$ (bill depth) $- 0.94$ (bill depth)^2, $r^2 = 0.35$, df $= 25$, $P = 0.005$, $P = 0.020$ for quadratic term). The solid line represents the best-fit linear regression for ponderosa pine crossbills (feeding efficiency $= -0.44 + 0.13$ (bill depth), $r^2 = 0.42$, df $= 12$, $P = 0.012$). Feeding efficiency was standardized within each type of crossbill; thus, comparisons between individuals in different types are inappropriate.

TABLE 3. The predicted optimal and observed bill depths (in mm) for red crossbills in the northern Rocky Mountain region. The observed bill depths are weighted by sex.

Conifer	Optimal bill depth	Observed bill depth[1]	
		$\bar{x}$	n
South Hills lodgepole pine	9.99	9.87	95
Rocky Mtn. lodgepole pine	9.28[2]	9.29	32
Rocky Mtn. ponderosa pine	9.56[3]	9.64	60

[1] Measurements for the crossbill call type predicted to be adapted to respective conifer.

[2] From Benkman and Miller (1996).

[3] Based on unpublished data for 16 crossbills timed foraging on Rocky Mountain ponderosa pine (*Pinus ponderosa* ssp. *scopulorum*); foraging efficiency $= -103.3 + 21.8$(bill depth) $- 1.1$(bill depth)^2, $r^2 = 0.44$, df $= 14$, $P = 0.018$, $P = 0.014$ for quadratic term.

and that this allometric relationship is the same for South Hills and ponderosa pine crossbills. Such an allometric relationship was presented in the Methods. A similar allometric relationship was also found between the mean body mass and mean bill depth (weighted by sex) of six different North American red crossbill call types ($r = 1.000$, $P < 0.0001$; data from appendix D in Groth 1993). Finally, the slopes and the intercepts of the relationships do not differ between South Hills and ponderosa pine crossbills (ANCOVA: for slope $F = 0.4$, df $= 1$, $P = 0.51$; for intercept $F = 0.3$, df $= 1$, $P = 0.61$).

DISCUSSION

Our results indicate that in the absence of *Tamiasciurus* lodgepole pine has evolved in response to relaxation of selection by *Tamiasciurus.* This alone could lead to a selection mosaic for crossbills, with crossbills experiencing different selection pressures in the different areas as a result of geographic variation in cone traits. However, our results show that in the absence of *Tamiasciurus,* lodgepole pine has also evolved in response to selection by crossbills and that crossbills in turn have evolved in response to the increases in cone defenses. That is, variation in the presence and absence of *Tamiasciurus* provides the mechanism determining whether coevolution occurs between crossbills and lodgepole pine, and thus determines the geographic selection mosaic for both crossbills and lodgepole pine. Below we discuss the evidence for reciprocal adaptation between crossbills and lodgepole pine.

Evolution in Lodgepole Pine in Response to Seed Predators

Before considering the differences in cone traits between areas as evolutionary responses to selection by seed predators, we need to consider the alternative that the differences are the result of adaptive phenotypic plasticity in response to seed predation. Three lines of evidence rule out this alternative. First, as mentioned earlier the various cone traits have fairly high broad-sense heritabilities. Second, *Tamiasciurus* has been the dominant seed predator in the Cypress Hills since 1950 (when red squirrels were introduced), yet the cones in the Cypress Hills are similar to cones in other areas where crossbills are the dominant seed predator (Table 1; Benkman 1999). Third, if cone characters are phenotypically plastic in response to seed predation, then trees that are harvested by *Tamiasciurus* year after year should over time develop cone traits that characterize areas where red squirrels are the dominant seed predator. Conversely, trees whose cones are avoided (not harvested) year after year should over time develop cone traits that characterize areas where red squirrels are absent. The exact opposite was found. Lodgepole pines whose cones have been consistently avoided by *Tamiasciurus* in the Cypress Hills, as compared to trees that have been consistently harvested by *Tamiasciurus,* have cone traits that better characterize regions where red squirrels are present (Benkman 1999). We assume, therefore, that dif-

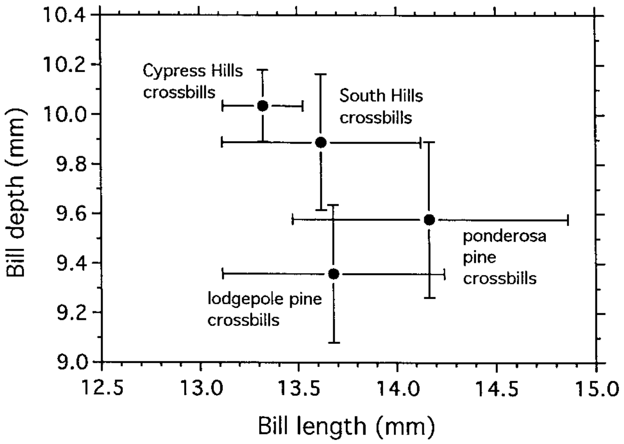

FIG. 6. Bill depth in relation to bill length (mean ± SD) for four different taxa of red crossbills. Sample sizes were 27 lodgepole pine crossbills, 61 ponderosa pine crossbills, 10 Cypress Hills crossbills, and 57 South Hills crossbills. All crossbills were alive when measured except the Cypress Hills crossbills.

ferences in cone traits between areas represent genetic differences.

Benkman (1999) showed that the overall change in lodgepole pine cone structure in the absence of *Tamiasciurus* could be explained if trees were maximizing defenses directed at crossbills (i.e., benefits) relative to the costs of the defenses. The analyses here complement these results by being more explicit about which traits change and why. For example, some cone traits are related to deterring predation by *Tamiasciurus.* In the absence of *Tamiasciurus,* these cone traits evolve to be less costly by having high values of seed mass relative to cone mass (Fig. 3B). These changes include decreases in cone width (Fig. 2A) and proximal scale thickness (Fig. 2B), which are easy to understand. Wider cones with thicker proximal scales are more difficult for *Tamiasciurus* to remove and more difficult to bite through (Smith 1970; Elliott 1974, 1988). When red squirrels are absent, the extra cone mass at the base serves no defensive function against crossbills because they forage in the distal parts of the cone.

Cones with more seeds are preferred by *Tamiasciurus* because they harvest and cache whole cones. Furthermore, feeding rates are higher on cones with more seeds (Elliott 1988) because to reach the distal half of the cone where seeds are most numerous red squirrels have to remove each successive and often sterile scale starting at the base of the cone. In contrast, the number of full seeds per cone has a negligible affect on crossbill feeding rates (Table 2), because crossbills avoid the parts of the cone with sterile scales. Consequently, in the absence of *Tamiasciurus,* lodgepole pine benefits because the number of seeds increases, resulting in an increase in the ratio of seed mass to cone mass. Similar differences in the ratio of seed mass to cone mass and in the number of seeds per cone between areas without *Tamiasciurus* in comparison to areas with *Tamiasciurus* are found in limber pine (*P. flexilis*; Benkman 1995). The number of seeds per cone is 2.0 and 2.2 times greater, and the amount seed mass relative to cone mass is 2.3 and 2.4 times greater for limber pine and lodgepole pine, respectively, in areas without *Tamiasciurus* than in areas with *Tamiasciurus.* In contrast, lodgepole pine cones are about 45% larger, whereas limber pine cones are about 30% smaller in areas without *Tamiasciurus* than in areas with *Tamiasciurus.* One important difference between lodgepole and limber pine is that the seeds of limber pine ($\sim$ 90 mg) are too large for crossbills to handle (C. W. Benkman, pers. obs.). We believe that lodgepole pine cones are greater in mass in the absence of *Tamiasciurus* rather than smaller as found in limber pine because of selection by crossbills.

Cone traits that act to deter crossbills should increase the cone's resistance to the forces crossbills exert while separating overlapping cone scales to extract individual seeds. Thus, for example, scale size in the distal end of the cone where most of the seeds are located should be greater in areas without *Tamiasciurus* than in areas with *Tamiasciurus.* Thicker distal scales impede crossbills from separating overlapping cone scales to retrieve the underlying seeds and characterize cones from areas where crossbills presumably exert strong selection. With just relaxation of selection by *Tamiasciurus,* we would expect a reduction in distal scale thickness, as found for proximal scale thickness. In addition, proximal and distal scale thickness are positively correlated within all eight study sites ($P < 0.05$), so the increase in distal scale thickness in the absence of *Tamiasciurus* is not a correlated response to a reduction in proximal scale thickness.

We suggested that the difference in seed size in areas where red squirrels are absent is the result of selection by crossbills favoring an increase in individual scale size, and that seed size increases as a correlated trait (see McGinley et al. 1990). In further support, variation in seed size between ranges without *Tamiasciurus* is related to the area of lodgepole pine and perhaps the intensity of selection by crossbills. The smallest seeds (mean = 5.44 mg, SE = 0.10, $n = 2$ sites, 52 trees sampled) are found in the smallest ranges, the West Butte and East Butte of the Sweetgrass Hills (3 km^2 and 4 km^2 of lodgepole pine, respectively; Benkman 1999). There, red crossbills do not appear resident or very common (C. W. Benkman, pers. obs.). Seeds are largest (mean = 6.70 mg, Table 1) in the largest ranges, the South Hills and Cypress Hills (100 km^2 and 80 km^2, respectively), and there crossbills are very common and have evolved endemic races that at least in the South Hills harvest seeds from a large fraction of the cones.

One alternative hypothesis for the geographic variation in seed size is that selection by *Tamiasciurus* favors smaller seed size so that in the absence of *Tamiasciurus* seed size increases. This hypothesis is not supported because seed size is not related to lodgepole pine cone preferences by *Tamiasciurus* (Smith 1970; Elliott 1974, 1988; Benkman 1999). In addition, limber pine seed mass does not differ between areas with and without *Tamiasciurus* (Benkman 1995), suggesting that *Tamiasciurus* has not influenced seed size evolution in other pines.

A second alternative explanation for the geographic variation in seed size is selection during the seedling stage. For example, seedlings from larger seeds might be favored during drought or if competition or shading is great during the very early stages of growth (Westoby et al. 1996). Although we do not have measures of drought experienced by seedlings, we do have measures of annual precipitation from near 11 of the 16 study sites where we have seed mass data (means or ranges of annual precipitation, in which case we use the mean of the range). Individual seed mass is not correlated with annual precipitation ($r = 0.08$, df = 9, $P = 0.80$). We also estimated average precipitation for each of the 16 study sites during June and July from climate data from 1950 to 1995 (http://www.cdc.noaa.gov:80/USclimate/). (We assumed similar precipitation patterns in southern Canada to those in adjacent areas in Montana.) We were not able to account for topographic or local variation in precipitation, although all the study sites were located at mid to upper elevations on mountains. June and July were chosen because drought conditions then are known to cause high mortality in lodgepole pine seedlings (Lotan and Perry 1983). Although these analyses are based on crude estimates of drought, no relationship was found between individual seed mass and precipitation during June and July ($r = 0.00$, df = 14, $P = 0.87$). We do not have measures of competition experienced by seedlings, although when most of the trees in a stand have serotinous cones (most trees from all sites had serotinous cones and only serotinous cones were sampled) seeds generally germinate after a stand-replacing fire (Muir and Lotan 1985). In the absence of a relationship between measures of precipitation and seed mass, and given that the seedlings generally develop in full sun following a fire, we have no evidence that conditions during early growth have differentially favored large seeds in the absence of *Tamiasciurus.*

We believe that cones are longer in areas where selection by crossbills predominates (and red squirrels are absent) because of relaxation of selection by *Tamiasciurus* favors more seeds per cone and selection by crossbills favors larger scales. That cone length would increase as the number of seeds and scale size increase is consistent with the results of the multiple regression between lodgepole pine cone length (Y) and the number of seeds per cone (X) and individual seed mass (Z; all ln-transformed). This regression accounted for 67% of the variation in cone length: $Y = 2.87 + 0.10X + 0.31Z$ ($R^2 = 0.67$, $n = 210$ trees, $P < 0.0001$). Such an explanation is also consistent with crossbill foraging behavior on Scots pine (*Pinus sylvestris*) in Scotland. There, crossbills preferentially forage on trees with shorter cones apparently because the cones have thinner scales (Summers and Proctor 1999). In contrast, our partial correlation analysis suggests that crossbills might select for shorter cones. Our interpretation is that selection by crossbills favors increased scale overlap, not decreased cone length. Because the partial correlation controls for the other cone variables like scale thickness and seed size (about equal to scale length and width), cone length perhaps more closely reflects the amount of overlap between adjacent scales. If scale overlap increases as cone length decreases in the partial correlation, then the number of scales that impede crossbills when they are trying to extract a given seed should increase as cone length decreases. We need direct measures of cone preference and of scale overlap to test this hypothesis.

Cone width where seeds are located would be one of best linear measures reflecting the forces required by crossbills to separate cone scales. We measured cone width where the cone was widest, which was usually near the proximal end where few seeds occur. Nevertheless, maximum cone width should be roughly correlated with the width of the cone where seeds are located. Such a positive correlation would explain why cone width was positively related to time per seed. Unfortunately, we do not have other measures of cone width. However, the cones in Figure 1 illustrate well the general shape differences between areas. Cones have much wider distal halves in areas where red squirrels are absent than where they are present. This needs to be better quantified.

Increases in the number of empty seeds could also act to deter crossbills (Table 2). For example, juniper titmice (*Baeolophus griseus*) avoid feeding on juniper (*Juniperus osteosperma*) trees with relatively high frequencies of empty seeds (Fuentes and Schupp 1998). However, empty seeds in lodgepole pine are the result of self-fertilization so that the frequency of empty seeds is related to stand density (Smith et al. 1988). Consequently, the number of empty seeds is likely to have low heritability, and variation in the number of empty seeds is unlikely the result of selection by seed predators.

In sum, with relaxation of selection by *Tamiasciurus* east and west of the Rocky Mountains, lodgepole pine has fewer defenses directed at *Tamiasciurus* and allocates more resources to seed mass relative to cone mass. As a result, lodgepole pine is able to produce more seeds for a given amount of resources. As the proportion of cone mass decreases relative to seed mass, however, seeds have become less accessible to crossbills (Fig. 4). In fact, a larger bill is favored for foraging on cones in the South Hills than in the Rocky Mountains (Table 3). This suggests that lodgepole pine cones have not simply lost seed defenses, but have also changed in ways that are related to selection by crossbills. These changes, however, are less straightforward in part because we mostly measured whole cone traits that are relevant to *Tamiasciurus,* which harvest cones whole, but less relevant to crossbills, which extract seeds individually. The cone traits that have increased in apparent response to selection by crossbills are larger and thicker cone scales and perhaps greater overlap of scales. These traits would increase the resistance against crossbills trying to spread apart overlapping scales to expose underlying seeds. Seed mass has also increase presumably as a correlated trait to scale size (McGinley et al. 1990). Larger seed size might also be advantageous in more arid environments, but our data are not consistent with the hypothesis that this advantage differentially affects lodgepole pine in areas with and without *Tamiasciurus.* The increases in seed and scale size and the increase in the number of seeds per cone have in combination caused cone length and mass to increase greatly in the absence of *Tamiasciurus.*

Reciprocal Evolution in Crossbills in Response to Changes in Cone Structure

Our evidence indicates that red crossbills in the South Hills and Cypress Hills have evolved large, strongly decurved bills as an adaptation for foraging on lodgepole pine cones. The average bill of the South Hills crossbill (9.87 mm) is not as large as the predicted optimum for foraging on cones in the South Hills (9.99 mm), but is larger than the next largest crossbill in western North America (Table 3). The average bill depth of crossbills collected in the Cypress Hills in 1945–48, where cones are very similar to those in the South Hills, was 10.01 mm ($n = 10$ birds; Benkman 1999). This suggests that the Cypress Hills crossbill had a bill depth that approximated the optimum and that the South Hills crossbill has evolved near to the optimum. Alternatively, these distinct bill sizes and shapes could be the result of phenotypic plasticity. However, phenotypically plastic responses have not been noted when crossbills have been raised on atypical foods (Benkman 1993) and bill size is generally highly heritable in birds (Boag and van Noordwijk 1987; Grant and Grant 1989). Moreover, crossbills have been used to typify organisms for which adaptive phenotypic plasticity is unlikely to evolve (Schlichting and Pigliucci 1998).

The relatively short and more decurved bill of the South Hills and Cypress Hills crossbills is an important adaptation because it enables crossbills to exert stronger biting forces at the tip than could a straighter bill for a given depth. Greater mandible decurvature in turn shifts the optimal bill depth to a smaller size, which enables South Hills and Cypress Hills crossbills to have a smaller body mass and lower daily energy expenditures. This assumes a strong allometric relationship between bill depth and body mass in crossbills and that it acts as a constraint. Body mass is highly correlated with bill depth among red crossbills. Strong correlations are also found within other taxa of seed-eating birds, with body mass larger relative to bill depth in taxa that experience higher predation pressure (Schluter 1988; Benkman 1991; Smith 1997). Thus, reductions in body mass without concomitant decreases in bill depth might increase vulnerability to predators (Benkman 1991). This would act as an allometric constraint on body size evolution.

In the past, we have stressed bill depth as an important determinant of the forces that can be exerted by crossbills in large part because the crossbills we studied varied little in bill decurvature (see Benkman 1993). However, the results in this study make it clear that bill decurvature is also important, especially in determining the biting forces that can be withstood (as compression rather than shearing forces) and exerted at the tip of the bill (see Grant and Grant 1989). After all, the ability to exert strong biting forces with pointed and opposing bill tips is why crossbills have crossed mandibles (see Benkman 1987a; Benkman and Lindholm 1991).

Conclusions

Many studies have explored the ecological and evolutionary consequences of shared resources and shared predators (e.g., Taper and Case 1992; Holt and Lawton 1994; Wootton 1994; Denno et al. 1995; Menge 1995). These studies have usually focused on the indirect effects resulting from short-term changes in the abundance or distribution of prey (resources) or predators. Although these studies are and will continue to be critical to our understanding of ecological communities, future studies will benefit from examining the evolutionary significance of these interactions (Wootton 1994; McPeek 1996). For example, one predator species may alter not only the abundance and distribution of its prey, but also its evolution (e.g., McPeek et al. 1996). How, in turn, this affects other predator or competitor species and their interactions with their prey are rarely considered (but see McPeek 1998). Here we showed that the presence and absence of a dominant preemptive competitor, *Tamiasciurus*, determines the geographic selection mosaic and location of coevolutionary hotspots and coldspots for its competitor the red crossbill.

Interspecific interactions often vary geographically in outcome (e.g., Thompson and Pellmyr 1992; Thompson 1997, 1999a; Berenbaum and Zangerl 1998). In at least some cases (e.g., Thompson and Pellmyr 1992) the variation in outcome is the result of the presence and absence of other species. Crossbills, for example, coevolve with lodgepole pine in the absence of *Tamiasciurus*, but not when they are present. We suspect that dominant competitors often impede coevolutionary arms races between subordinate competitors and the shared prey. Given that competition is usually an asymmetric interaction (Levins 1979; Connell 1983; Schoener 1983; Denno et al. 1995), variation between the geographic distributions of competitors has the potential to have dramatic effects on the geographic selection mosaics for many species.

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LITERATURE CITED

Aitken, S. N., and W. J. Libby. 1994. Evolution of the pygmy-forest edaphic subspecies of *Pinus contorta* across an ecological staircase. Evolution 48:1009–1019.

Barnosky, C. W. 1989. Postglacial vegetation and climate in the northwestern Great Plains of Montana. Quat. Res. 31:57–73.

Benkman, C. W. 1987a. Crossbill foraging behavior, bill structure, and patterns of food profitability. Wilson Bull. 99:351–368.

———. 1987b. Food profitability and the foraging ecology of crossbills. Ecol. Monogr. 57:251–267.

———. 1989a. Intake rate maximization and the foraging behaviour of crossbills. Ornis Scand. 20:65–68.

———. 1989b. On the evolution and ecology of island populations of crossbills. Evolution 43:1324–1330.

———. 1991. Predation, seed size partitioning and the evolution of body size in seed-eating finches. Evol. Ecol. 5:118–127.

———. 1993. Adaptation to single resources and the evolution of crossbill (*Loxia*) diversity. Ecol. Monogr. 63:305–325.

———. 1995. The impact of tree squirrels (*Tamiasciurus*) on seed dispersal adaptations of limber pine. Evolution 49:585–592.

———. 1997. Feeding behavior, flock-size dynamics, and variation in sexual selection in crossbills. Auk 114:163–178.

———. 1999. The selection mosaic and diversifying coevolution between crossbills and lodgepole pine. Am. Nat. 154:S75–S91.

Benkman, C. W., and A. K. Lindholm. 1991. The advantages and evolution of a morphological novelty. Nature 349:519–520.

Benkman, C. W., and R. E. Miller. 1996. Morphological evolution in response to fluctuating selection. Evolution 50:2499–2504.

Berenbaum, M. R., and A. R. Zangerl. 1998. Chemical phenotype matching between a plant and its insect herbivore. Proc. Natl. Acad. Sci. USA 95:13743–13748.

Boag, P. T., and A. van Noordwijk. 1987. Quantitative genetics. Pp. 45–78 *in* F. Cooke and P. A. Buckley, eds. Avian genetics: a population and ecological approach. Academic Press, New York.

Bright, R. C. 1966. Pollen and seed stratigraphy of Swan Lake, Southeastern Idaho: its relation to regional vegetational history and to Lake Bonneville history. Tebiwa 9:1–47.

Brodie, E. D., III, and E. D. Brodie Jr. 1999. Predator-prey arms races. Bioscience 49:557–568.

Burdon, J. J., and P. H. Thrall. 1999. Spatial and temporal patterns in coevolving plant and pathogen associations. Am. Nat. 153: S15–S33.

Connell, J. H. 1983. On the prevalence and relative importance of interspecific competition: evidence from field experiments. Am. Nat. 112:661–696.

Critchfield, W. B. 1985. The late Quaternary history of lodgepole and jack pines. Can. J. For. Res. 15:749–772.

Dancik, B. P., and F. C. Yeh. 1983. Allozyme variability and evolution of lodgepole pine (*Pinus contorta* var. *latifolia*) and jack pine (*P. banksiana*) in Alberta. Can. J. Genet. Cytol. 25:57–64.

Davis, O. K., J. C. Sheppard, and S. Robertson. 1986. Contrasting climatic histories for the Snake River Plain, Idaho, resulting from multiple thermal maxima. Quat. Res. 26:321–339.

Denno, R. F., M. S. McClure, and J. R. Ott. 1995. Interspecific interactions in phytophagous insects: competition reexamined and resurrected. Annu. Rev. Entomol. 40:297–331.

Elliott, P. F. 1974. Evolutionary responses of plants to seed-eaters: pine squirrel predation on lodgepole pine. Evolution 28: 221–231.

———. 1988. Foraging behavior of a central-place forager: field tests of theoretical predictions. Am. Nat. 131:159–174.

Fuentes, M., and E. W. Schupp. 1998. Empty seeds reduce seed predation by birds in *Juniperus osteosperma.* Evol. Ecol. 12: 823–827.

Grant, B. R., and P. R. Grant. 1989. Evolutionary dynamics of a natural population: the large cactus finch of the Galápagos. Univ. of Chicago Press, Chicago, IL.

Groth, J. G. 1993. Evolutionary differentiation in morphology, vocalizations, and allozymes among nomadic sibling species in the North American red crossbill (*Loxia curvirostra*) complex. Univ. California Publication in Zoology, no. 127, Berkeley.

Holt, R. D., and J. H. Lawton. 1994. The ecological consequences of shared natural enemies. Annu. Rev. Ecol. Syst. 25:495–520.

Johnson, E. A., and S. L. Gutsell. 1993. Heat budget and fire behavior associated with the opening of serotinous cones in two *Pinus* species. J. Veget. Sci. 4:745–750.

Lessells, C. M., and P. T. Boag. 1987. Unrepeatable repeatabilities: a common mistake. Auk 104:116–121.

Levins, R. 1979. Asymmetric competition among distant taxa. Am. Zool. 19:1097–1104.

Lively, C. M. 1999. Migration, virulence, and the geographic mosaic of adaptation by parasites. Am. Nat. 153:S34–S47.

Lotan, J. E., and D. A. Perry. 1983. Ecology and regeneration of lodgepole pine. U.S. Dept. of Agriculture Forest Service, Agriculture Handbook no. 606, Washington, DC.

McGinley, M. A., C. C. Smith, P. F. Elliott, and J. J. Higgins. 1990. Morphological constraints on seed mass in lodgepole pine. Funct. Ecol. 4:183–192.

McPeek, M. A. 1996. Linking local species interactions to rates of speciation in communities. Ecology 77:1355–1366.

———. 1998. The consequences of changing the top predator in a food web: a comparative experimental approach. Ecol. Monogr. 68:1–23.

McPeek, M. A., A. K. Schrot, and J. M. Brown. 1996. Adaptation to predators in a new community: swimming performance and predator avoidance in damselflies. Ecology 77:617–629.

Menge, B. A. 1995. Indirect effects in marine rocky intertidal interaction webs: patterns and importance. Ecol. Monogr. 65: 21–74.

Miller, G. E. 1986. Insects and conifer seed production in the Inland Mountain West: a review. Pp. 225–237 *in* R. C. Shearer, comp. Proceedings—Conifer tree seed in the Inland Mountain West symposium, General Technical Report INT 203, U.S. Dept. of Agriculture, Forest Service, Ogden, UT.

Muir, P. S. 1993. Disturbance effects on structure and tree species composition of *Pinus contorta* forests in western Montana. Can. J. For. Res. 23:1617–1625.

Muir, P. S., and J. E. Lotan. 1985. Serotiny and life history of *Pinus contorta* var. *latifolia.* Can. J. Bot. 63:938–945.

Newsome, R. D., and R. L. Dix. 1968. The forests of the Cypress Hills, Alberta and Saskatchewan, Canada. Am. Midl. Natur. 80: 118–185.

Ritchie, J. C. 1976. The late-Quaternary vegetational history of the western interior of Canada. Can. J. Bot. 54:1793–1818.

Sauchyn, M. A., and D. J. Sauchyn. 1991. A continuous record of Holocene pollen from Harris Lake, southwestern Saskatchewan, Canada. Palaeogeogr., Palaeoclimatol., Palaeoecol. 88:13–23.

Schlichting, C. D., and M. Pigliucci. 1998. Phenotypic evolution: a reaction norm perspective. Sinauer Associates, Inc.: Sunderland, MA.

Schluter, D. 1988. Character displacement and the adaptive divergence of finches on islands and continents. Am. Nat. 131: 799–824.

Schoener, T. W. 1983. Field experiments on interspecific competition. Am. Nat. 122:240–285.

Smith, C. C. 1968. The adaptive nature of social organization in the genus of tree squirrels, *Tamiasciurus.* Ecol. Monogr. 38: 31–63.

———. 1970. The coevolution of pine squirrels (*Tamiasciurus*) and conifers. Ecol. Monogr. 40:349–371.

———. 1981. The indivisible niche of *Tamiasciurus*: an example of nonpartitioning of resources. Ecol. Monogr. 51:343–363.

Smith, C. C., J. L. Hamrick, and C. L. Kramer. 1988. The effects of stand density on frequency of filled speeds and fecundity in lodgepole pine (*Pinus contorta* Dougl.). Can. J. For. Res. 18: 453–460.

Smith, T. B. 1997. Adaptive significance of the mega-billed form in the polymorphic black-bellied seedcracker *Pyrenestes ostrinus.* Ibis 139:382–387.

Summers, R. W., and R. Proctor. 1999. Tree and cone selection by crossbills *Loxia* sp. and red squirrels *Sciurus vulgaris* at Abernethy Forest, Strathspey. For. Ecol. Manage. 118:173–182.

Taper, M. L., and T. J. Case. 1992. Coevolution among competitors. Oxf. Surv. Evol. Biol. 8:63–109.

Thompson, J. N. 1994. The coevolutionary process. Univ. of Chicago Press: Chicago.

———. 1997. Evaluating the dynamics of coevolution among geographically structured populations. Ecology 78:1619–1623.

———. 1999a. Specific hypotheses on the geographic mosaic of coevolution. Am. Nat. 153:S1–S14.

———. 1999b. The evolution of species interactions. Science 284: 2116–2118.

Thompson, J. N., and O. Pellmyr. 1992. Mutualism with pollinating seed parasites amid co-pollinators: constraints on specialization. Ecology 73:1780–1791.

Thompson, L. S., and J. Kuijt. 1976. Montane and subalpine plants of the Sweetgrass Hills, Montana, and their relation to early postglacial environments of the northern Great Plains. Can. Field-Nat. 90:432–448.

Walsberg, G. E. 1983. Avian ecological energetics. Pp. 161–220 *in* D. S. Farner, J. R. King, and K. C. Parkes, eds. Avian biology. Vol. 7. Academic Press, New York.

Wells, P. V. 1983. Paleobiogeography of montane islands in the Great Basin since the last glaciopluvial. Ecol. Monogr. 53: 341–382.

Westoby, M., M. Leishman, and J. Lord. 1996. Comparative ecology of seed size and dispersal. Phil. Trans. R. Soc. Lond. B 351: 1309–1318.

Wheeler, N. C., and R. P. Guries. 1982a. Biogeography of lodgepole pine. Can. J. Bot. 60:1805–1814.

———. 1982b. Population structure, genic diversity, and morphological variation in *Pinus contorta* Dougl. Can. J. For. Res. 12: 595–606.

Wootton, J. T. 1994. The nature and consequences of indirect effects in ecological communities. Annu. Rev. Ecol. Syst. 25:443–466.

Xie, C., and C. C. Ying. 1995. Genetic architecture and adaptive landscape of interior lodgepole pine (*Pinus contorta* ssp. *latifolia*) in Canada. Can. J. For. Res. 25:2010–2021.

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