DIVERGENT SELECTION DRIVES THE ADAPTIVE RADIATION OF CROSSBILLS

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Abstract.—Knowledge of how phenotype influences fitness is necessary if we are to understand the basis of natural selection and how natural selection contributes to adaptive radiations. Here I quantify selection on a wild population of red crossbills (*Loxia curvirostra* complex) in the South Hills, Idaho. Bill depth is the target of selection and selection on bill depth is stabilizing. I then show how fitness is related to both bill depth and performance. I use these and previously published relationships to estimate a fitness surface for five species of red crossbills that are part of an ongoing adaptive radiation in western North America. The fitness surface for crossbills has distinct peaks and valleys, with each crossbill species residing on or very near the summits. This work strongly supports a key tenet of the ecological theory of adaptive radiations; namely, divergent selection for utilizing alternative resources is the ultimate cause of adaptive radiations.

Key words.—Ecological theory of adaptive radiation, feeding performance, fitness surface, *Loxia curvirostra*, morphological evolution, natural selection, stabilizing selection.

Much of the biodiversity that we observe is the result of adaptive radiations. Consequently, the extent of our understanding of adaptive radiations determines our understanding of the processes governing biodiversity (Schluter 2000). The ecological theory of adaptive radiation is the most complete theory to account for adaptive radiations and it has considerable empirical support (Schluter 2000). A central component of this theory is that divergent selection for utilizing different resources causes divergence between populations and ultimately species. The form of selection can be depicted as a fitness surface (Simpson 1953; Fear and Price 1998; Schluter 2000) where the height of the surface represents fitness and the axes represent the organism's phenotype. With sufficient knowledge, one should able to quantify a fitness surface, and, if frequency-dependent selection can be ignored (Fear and Price 1998), use the fitness surface to predict the outcome of an adaptive radiation. A test of these predictions in turn would enable us to determine both if our knowledge of the system and if the ecological theory are adequate. However, this is no simple task. Thus, only one study (Schluter and Grant 1984) has quantified a surface that has also accurately portrayed the pattern of morphological diversity.

Red crossbills (*Loxia curvirostra* complex) are an ideal study system for quantifying the links between phenotype, performance, and fitness, and for using these relationships to estimate a fitness surface. First, there is a clear and direct functional link between the morphology and ecology of crossbills and their food resources (Newton 1972; Benkman 1987a,b, 1993, 1999; Benkman and Miller 1996; Benkman et al. 2001), which is critical if we are to understand why phenotypic variation causes variation in fitness (Arnold 1983; Schluter 2000). Crossbills are highly specialized for foraging on seeds in conifer cones, and bill structure and conifer cone structure determine feeding performance (Newton 1972; Benkman 1987a,b, 1993, 1999; Benkman and Miller 1996; Benkman et al. 2001). Crossbills use their crossed mandibles to bite between overlapping cone scales and then laterally abduct their lower mandible to spread apart the scales exposing seeds at their base (Tordoff 1954; Newton 1972; Benkman 1987a; Benkman and Lindholm 1991). Bill depth,

which has a high heritability ($h^2 = 0.7$; R. Summers, pers. comm.), influences the time taken to remove seeds from cones (Benkman 1993, 1999; Benkman and Miller 1996; Benkman et al. 2001; Parchman and Benkman 2002). The width of the lateral groove in the palate is related to seed handling time (Benkman 1993). Crossbills use their tongue to secure the seed in the lateral groove of the horny palate (on the side opposite to which the lower mandible crosses), and then remove the seed coat and swallow the kernel (Newton 1972; Benkman 1993). In turn, feeding performance influences crossbill habitat and conifer use, movements, and breeding behavior (Benkman 1987b, 1989, 1990, 1992).

Second, crossbills are a recent adaptive radiation (Questiau et al. 1999; Arnaiz-Villena et al. 2001; Piertney et al. 2001) where the processes involved in population divergence may still be active. Red crossbills in North America are categorized into nine call types that are recognized by distinct vocalizations (Groth 1993; Benkman 1999). At least seven of these call types are specialized for foraging on different species of conifers that hold seeds in partially closed cones through winter (Benkman 1993, 1999; Benkman and Miller 1996; Benkman et al. 2001; Parchman and Benkman 2002), and reproductive isolation is evolving between populations that have diverged in the last 10,000 years. For example, our research in the South Hills, Idaho, shows that crossbills pair assortatively in the wild. In 2001, 161 of 163 breeding pairs of crossbills were paired assortatively (157 pairs of South Hills or ''type 9'' crossbills, four pairs of ponderosa pine or type 2 crossbills, and two hybrid pairs [Fisher's exact test, $P < 0.0001$; J. W. Smith, unpubl. data]). In addition, our preliminary analyses using amplified fragment-length polymorphism (AFLP) markers generated from three primer pairs revealed that 42 AFLP markers present in South Hills crossbills ($n = 11$ birds) at frequencies between 20 to over 50% were absent from ponderosa pine crossbills ($n = 13$ birds; and vice versa), which appears to be the sister taxa to the South Hills crossbill (Benkman et al. 2001).

Until recently phenotype could not be linked to fitness, because I had been unable to locate a resident population of crossbills where measured and marked individuals could be

followed for extended periods. How performance links phenotype to fitness and ultimately to evolution is a problem plaguing most studies using measures of performance. However, in 1997, I discovered a resident population of red crossbills that is coevolving with Rocky Mountain lodgepole pine (*Pinus contorta* ssp. *latifolia*) within a 100-km^2 pine forest in the South Hills and the adjacent Albion Mountains (Benkman 1999; Benkman et al. 2001) where I can use mark-recapture methods to estimate the form of selection. This South Hills crossbill has unique vocalizations (Benkman 1999) and has only been recorded in the lodgepole pine forests on these two isolated mountain ranges. In 1998, I began capturing, measuring, and uniquely color banding adult South Hills crossbills.

Here, I use logistic regression to determine the targets of selection on crossbills (Janzen and Stern 1998). This analysis shows that bill depth is the target of selection, which is consistent with previous analyses on foraging performance (Benkman 1993). Second, I determine the relationship between survival and bill depth, and compare it to the relationship between feeding performance and bill depth. These two relationships are similar, which indicate that feeding performance determines survival. Third, I convert measures of feeding performance of crossbills in relation to bill depth and palate structure into a fitness surface for five species of red crossbills in western North America based on the relationship between estimated survival and feeding performance. A fitness surface is the expected fitness of an individual as a function of its phenotype (Fear and Price 1998). Use of survival as a surrogate for fitness is justified because survival is consistently the single best surrogate for fitness among the various vital rates for birds and many other taxa (Crone 2001). In the presence of frequency-dependent selection, which is likely if not inevitable when there are overlapping populations, the peaks in the fitness surface do not necessarily correspond to evolutionary equilibria (Fear and Price 1998). However, an adaptive landscape, which is the mean fitness of a population in relation to its mean phenotype, has the same problem (Fear and Price 1998; Schluter 2000). The estimated fitness peaks, therefore, represent evolutionary equilibria under the assumption that frequency-dependent selection does not cause a large displacement from the peak.

METHODS

Mark Recapture/Resighting Study

We used mist nests and live decoys to capture crossbills during the summers of 1998–2001 at two sites in the South Hills. Fifty-six adult South Hills crossbills were uniquely color banded in 1998 and 2000. We used digital calipers to measure three external bill measurements to the nearest 0.01 mm: bill depth at the anterior edge of the nares; upper mandible length from the tip of the upper mandible to the anterior end of the right naris; and lower mandible length from tip of the lower mandible to where the rami meet. We measured the length of the folded wing with a ruler to the nearest 0.5 mm and body mass was measured with a Pesola scale to the nearest 0.5 gm (in 1998) and with a digital scale to the nearest 0.01 gm (in 1999–2001). Two people have measured the crossbills (CWB in all years and W. C. Holimon in 1998)

and we had nearly identical and highly repeatable bill measurements (we each measured bill depth 3–5 times per bird and used the mean). 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). Upon release, we recorded their flight calls with Sennheiser ME66 (Old Lyme, CT) shotgun microphones and Marantz PMD222 (Aurora, IL) tape recorders and analyzed the calls with Canary software (Cornell Laboratory of Ornithology, Ithaca, NY) on a Macintosh computer to confirm call type identity of every banded crossbill. We searched for and recaptured banded crossbills in 2000 and 2001, and relocated 20 (35.7%) of them one to three years after initial capture. I estimated the target of selection on crossbills using a logistic regression (Janzen and Stern 1998) assuming that relocated birds survived and those not relocated had died. I used the cube root of body mass and ln-transformed all means. The highest correlation between traits was $r = 0.52$ (between upper and lower mandible lengths). I present the logistic regression coefficients (α). I then used a cubic spline (Schluter 1988) to estimate the form of selection. All 56 crossbills were used in the cubic spline, but only 50 of them were used in the logistic regression because not all traits were measured for each bird.

Feeding Efficiency

We timed 28 captive South Hills crossbills feeding on cones from the South Hills to determine if the relationship between bill depth and feeding efficiency is similar to that between bill depth and survival. Methods for measuring feeding rates are published (Benkman 1993; Benkman and Miller 1996; Benkman et al. 2001) and are summarized below. Captive crossbills were housed in indoor aviaries (1.6 m × 2.7 m × 2.2 m or larger), and at least several days before and during the experiments, maintained at a low mass, and 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. The total time required to extract and husk (remove seed coat and swallow the seed kernel) 10 seeds, beginning after the first seed was eaten, was recorded for every bird foraging on 10–11 cones representative of the South Hills lodgepole pine. We also measured seed husking times and subtracted the mean seed husking time for each bird to provide an average time to extract a seed for each bird. I used seed extraction time in the analysis because bill size (depth) is closely related to this measure but not to seed husking time (Benkman 1993).

I estimated feeding efficiency as the inverse of the product of time taken to remove seeds from cones and estimated daily energy demands (Benkman 1993; Benkman and Miller 1996; Benkman et al. 2001). Daily energy demands were estimated as $E_{tot} = 13.05M^{0.6052}$ (*M,* body mass; Walsberg 1983). Body mass depends on a variety of factors including the amount of fat stored and, especially in captivity, the loss of flight muscle mass. Consequently, body mass was estimated from the allometric relationship between body mass (*Y,* in gm) and bill depth (*X,* in mm): $Y = -3.78 + 3.82 X$ ($r^2 = 0.68$, df

TABLE 1. Logistic regression analysis of natural selection on South Hills crossbills ($n = 50$ birds). Overall model was significant ($\chi^2 = 31.1$, $P = 0.0006$).

Character	$\alpha \pm$ SE	χ^2	P-value
Bill depth (mm)	22152.3 ± 8343.7	7.05	0.008
Bill depth^2	-4815.7 ± 1814.0	7.05	0.008
Upper mandible length (mm)	-3343.2 ± 1791.3	3.48	0.062
Upper mandible length^2	615.7 ± 329.6	3.49	0.062
Lower mandible length (mm)	2362.9 ± 1728.5	1.87	0.172
Lower mandible length^2	-477.4 ± 347.2	1.89	0.169
Wing length (mm)	-1961.7 ± 4387.6	0.20	0.655
Wing length^2	219.8 ± 484.7	0.21	0.650
Body mass (gm)	606.6 ± 3275.3	0.03	0.853
Body mass^2	-240.8 ± 1379.3	0.03	0.861

$= 77$, $P < 0.0001$), where body mass was measured at time of capture of crossbills lacking much fat. 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 (Benkman 1993; Benkman and Miller 1996; Benkman et al. 2001).

Estimation of the Fitness Surface

Crossbill feeding efficiency on five different conifers was estimated as described above for different combinations of bill depth and palate groove width, except that feeding time was the sum of the times to remove seeds from cones and to husk seeds. Five conifers were chosen because these conifers produce cone crops yearly within their geographic range and hold seeds in their cones for extended periods of time, which represent two conditions that favor specialization (Benkman 1993; Thompson 1994). Four of these conifers are widespread in the Pacific Northwest or the northern Rocky Mountains and are specialized on by the four common and widespread red crossbill call types in western North America (Benkman 1993). The fifth conifer is the lodgepole pine in the South Hills (Benkman 1999; Benkman et al. 2001). I used published equations (Benkman 1993) to estimate time to extract and husk western hemlock (*Tsuga heterophylla*) and Douglas-fir (*Pseudotsuga menziesii* ssp. *menziesii*) seeds, and to husk Rocky Mountain lodgepole pine and ponderosa pine (*Pinus ponderosa* ssp. *scopulorum*) seeds. Because crossbills drop kernel while husking ponderosa pine seeds, I adjusted husking time by dividing time per seed by the proportion of kernel consumed per seed (*adjusted husking time* = 475.28–455.20 (*groove width*) + 110.27 (*groove width*)^2, $r^2 = 0.81$, df = 10, $P = 0.0002$). I used published equations (Benkman and Miller 1996; Benkman et al. 2001) to estimate time to extract Rocky Mountain lodgepole pine seeds, and to estimate time to extract seeds from ponderosa pine and South Hills lodgepole pine cones. I lack seed husking data in relation to groove width for South Hills lodgepole pine; however, the relationships between husking time and groove width were consistent in form among the different seed types (Benkman 1993). Thus, I used the equation for husking times for Rocky Mountain lodgepole pine seeds (Benkman 1993) adjusted so that the optimum groove width corresponded to that predicted (*optimal groove width* = 1.28 + 0.21(*cube root of seed mass*), $r^2 = 0.998$, df = 2, $P < 0.002$) based on the average seed
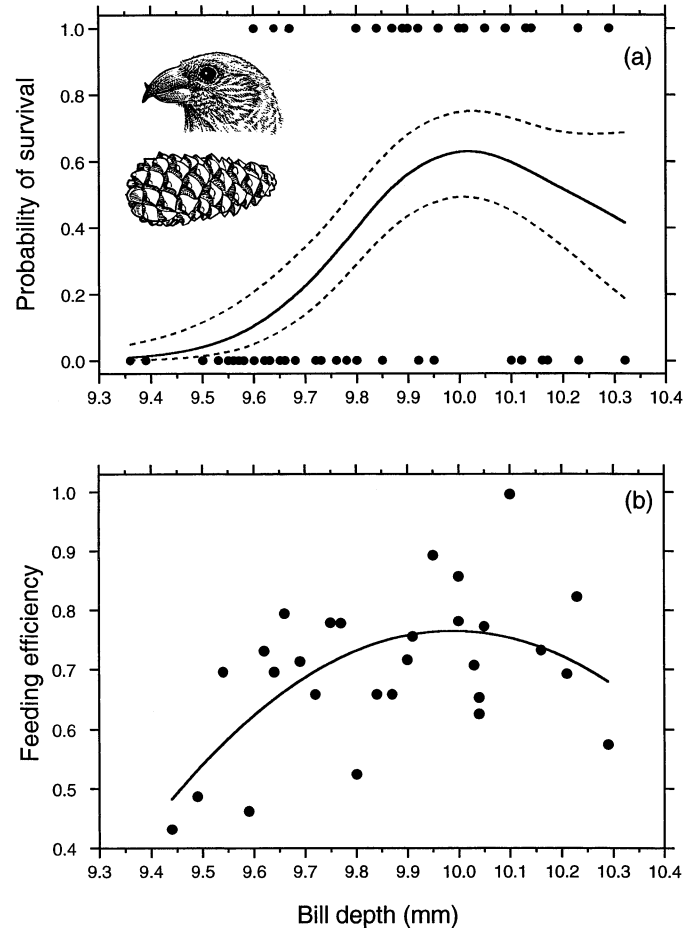
FIG. 1. The relative probability of an adult South Hills crossbill surviving at least one year (*a*) and feeding efficiency on lodgepole pine cones from the South Hills (*b*) in relation to bill depth. (*a*) The solid curve represents a cubic spline, and the dashed curves represent ± one SE (program provided by D. Schluter, University of British Columbia, Vancouver, BC; http://www.zoology.ubc.ca/~schluter/splines.html). The solid circles along the top of the figure represent uniquely marked individuals recaptured or resighted one, two, or three years after initial capture as adults ($n = 20$) and the solid circles along the bottom of the figure represent individuals not seen a year or more after initial capture ($n = 36$). Also shown is a representative crossbill and lodgepole pine cone from the South Hills. (*b*) The curve represents the quadratic equation that best fits the data (*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). A cubic spline provided a nearly identical curve. Each solid circle represents the mean for one bird timed foraging on 10 seeds from each of 10 to 11 cones.

size in the South Hills (7.01 mg; Benkman et al. 2001). I adjusted the equation for time to extract seeds from Douglas-fir cones so that the optimum corresponded to the average bill depth of the Douglas-fir crossbill (8.75 mm), because its average groove width was identical to the optimum for husking Douglas-fir seeds—implying adaptation to Douglas fir (Benkman 1993). Finally, feeding efficiency was converted into fitness using the exponential equation relating the two (see Fig. 2). Because I am unable to determine the absolute heights of adaptive peaks, I standardize their heights to one.
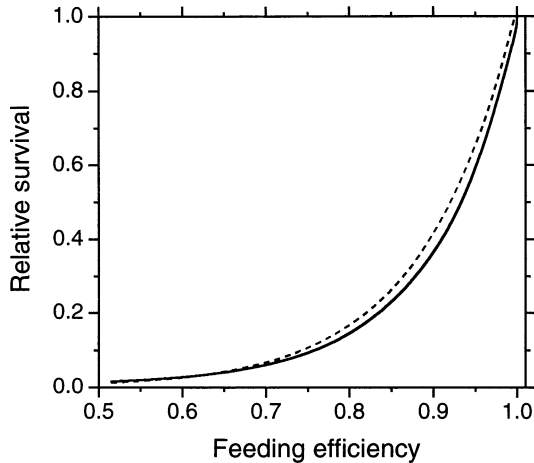
FIG. 2. Estimated relative survival in relation to estimated relative feeding efficiency (solid line), and the relationship used (dashed line; *survival* = exp[−9.032 + 9.057 *feeding efficiency*]) to convert feeding efficiency into survival (Fig. 3). We limited the analysis to bill depths ≤ 10.00 mm, because scaly leg mites (*Knemidokoptes jamaicensis*), which precluded banding, were more frequent on large-billed crossbills so that our survival estimates are best for smaller crossbills (see confidence limits in Fig. 1a).

RESULTS

The logistic regression that included all traits was significant and shows that bill depth was the target of selection (Table 1). Upper mandible length may also be a target of selection (Table 1), and if so selection may be disruptive or

at least it increasingly favored individuals as bill length increased. Upper mandible length was not a target of selection when it was the only trait included in the analysis ($P = 0.40$ for both linear and quadratic coefficients), whereas stabilizing selection on bill depth was significant ($P < 0.05$) regardless of which traits were included in the analysis and even when only bill depth was included.

Visualization of selection on bill depth further indicates that selection is stabilizing with survival highest for a crossbill having a 10.01 mm bill depth (Fig. 1a). This is similar to the optimal bill depth, 9.99 mm, based on the relationship between bill depth and foraging efficiency (Fig. 1b). Although the optimal bill depth is nearly identical to the bill depth with the highest estimated relative survival (Fig. 1), survival decreases more rapidly away from the optimal bill depth than does feeding efficiency. A plot of estimated relative survival in relation to estimated feeding efficiency shows that survival increases exponentially with increases in feeding efficiency (Fig. 2).

I used this relationship to convert feeding efficiency into fitness for five conifers in the Northwest. The result was a fitness surface characterized by ridges and peaks, representing each of the conifers, with steep slopes (Fig. 3).

DISCUSSION

Our previous results indicate that bill depth is the main trait (in addition to palate groove width) affecting feeding rates (Benkman 1993), and should be a target of selection if feeding rates affect fitness. This is supported by our multi-
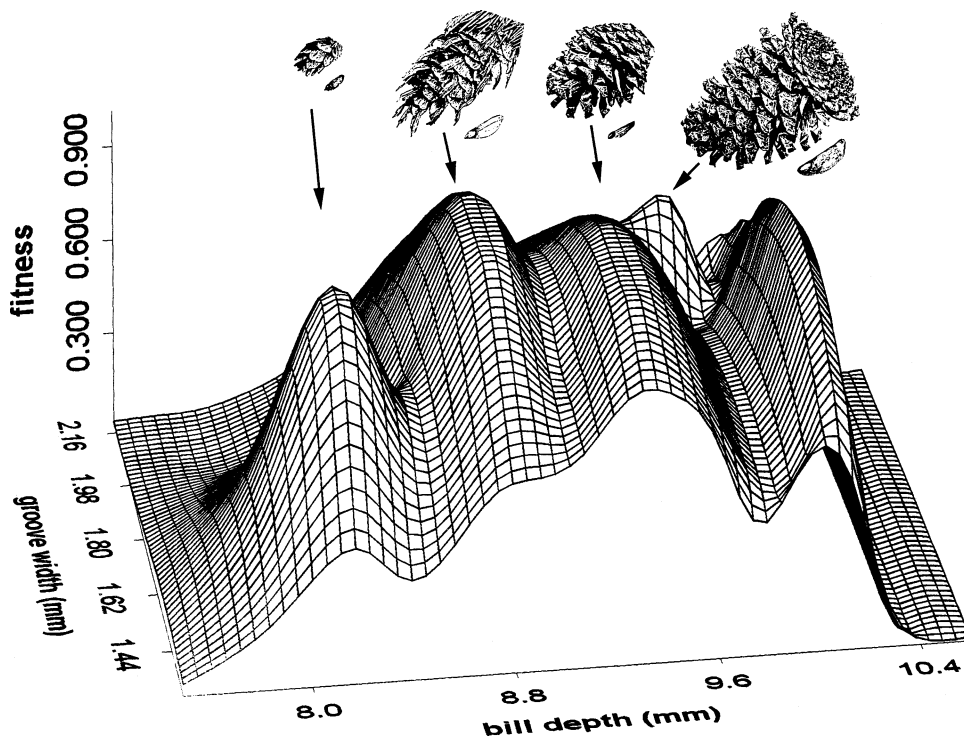

FIG. 3. A fitness surface for five different red crossbill taxa based on foraging data from the laboratory that was converted into fitness (survival) using the relationship between feeding efficiency and survival (Fig. 2). The adaptive peaks correspond to the following conifers from left to right: western hemlock, Douglas fir, Rocky Mountain lodgepole pine, ponderosa pine, and South Hills lodgepole pine, with cones and seeds (with wings) of the first four conifers drawn above to relative scale.

variate analysis of selection (Table. 1). However, upper mandible length, which is unrelated to foraging rates on Rocky Mountain lodgepole pine cones in the laboratory (in a multivariate regression [Lande and Arnold 1983] including bill depth and both upper and lower mandible lengths, $P = 0.24$ and 0.26 for upper mandible length and upper mandible length squared whereas $P = 0.002$ and 0.003 for bill depth and bill depth squared, respectively), appears at least weakly related to survival. The nearly significant quadratic coefficient (Table 1) suggests that survival accelerates as upper mandible length increases. Why longer mandibles would be favored is unclear especially when previous analyses indicate that a relatively short bill is favored for South Hills crossbills (Benkman et al. 2001). One interpretation of apparent selection on upper mandible length is that especially efficient foragers do not wear their mandibles (which are ever growing) as much as less efficient foragers and that efficient foragers are more likely to survive. Thus, both upper mandible length and survival increase as foraging efficiency increases, and mandible length and survival are correlated because each is related to foraging efficiency. This would then be a case of selection on an environmental rather than a heritable component of bill structure.

The similarity of the relationships between bill depth and feeding efficiency and survival (Fig. 1) imply that the agent of selection on crossbill bill depth is cone structure, and provides a clear link from phenotype to performance to fitness. Moreover, the curvilinear relationship between survival and performance (Fig. 2) suggests that slight reductions in feeding efficiency (and feeding rates) have substantial fitness consequences. This supports a fundamental assumption of optimal foraging theory (Stephens and Krebs 1986), and helps us understand why many aspects of crossbill behavior and ecology appear related to crossbills foraging to maximize intake rates (Benkman 1987b, 1989, 1990, 1992). The curvilinear relationship between survival and performance also causes the fitness surface (Fig. 3) to be much more rugged than a surface based on performance alone, and should result in strong divergent selection driving populations to the summits (Fear and Price 1998; Schluter 2000).

Divergent selection for utilizing alternative resources is a key component of the ecological theory of adaptive radiations (Schluter 2000), and is strongly supported by this study and one other study (Schluter and Grant 1984) that has quantified an adaptive surface that captures processes important in an adaptive radiation (Grant 1999). Indeed, the mean trait values of each of the five putative species of red crossbill reside on or very near to a summit of a peak or ridge (Benkman 1993; Benkman and Miller 1996; Benkman et al. 2001). This suggests that frequency-dependent selection has not affected the evolutionary equilibria much and implicates divergent selection between these species, and cone and seed structure as the agents of selection. This shows, perhaps more clearly than any previous study, how performance links phenotype to fitness in the wild and ultimately to evolution. We also find behavioral and genetic evidence of reproductive isolation between the crossbill taxa occupying the different adaptive peaks. If reproductive isolation is the result of divergent selection (i.e., ecological speciation), then the diversification of crossbills provides further support for the ecological theory of adaptive radiations (Schluter 2000).

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