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Craig W. Benkman; Richard E. Miller

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## BRIEF COMMUNICATIONS

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### MORPHOLOGICAL EVOLUTION IN RESPONSE TO FLUCTUATING SELECTION

CRAIG W. BENKMAN<sup>1</sup> AND RICHARD E. MILLER<sup>2</sup>

*Department of Biology, New Mexico State University, Las Cruces, New Mexico 88003-8001*

<sup>1</sup>*E-mail: cbenkman@nmsu.edu*

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A central issue in the study of evolution in natural populations is how morphology evolves in response to environmental complexity, especially when environmental variation results in contrasting selective pressures (Levins 1968; Boyce 1979; Gomulkiewicz and Kirkpatrick 1992). In birds, contrasting selective pressures associated with seasonal fluctuations are common (e.g., Fretwell 1972; Newton 1972; Baker and Baker 1973; Price and Grant 1984; Schluter and Smith 1986). Here, we explore the consequences of seasonal fluctuations on the evolution of morphological traits related to foraging in the red crossbill (*Loxia curvirostra*).

Crossbills are highly specialized for foraging on seeds in conifer cones (Benkman 1988, 1993; Benkman and Lindholm 1991) and rely on conifer seeds year-round (Newton 1972; Benkman 1987a, 1990, 1992). In seed-eating birds, bill size is the likely target of selection and so provides a logical focal trait for a study of the evolution of morphology related to foraging (e.g., Grant 1986). Here, we consider the evolution of bill size of one sibling species of red crossbill (*L. curvirostra* complex) that Groth (1993) designates as type 5. ("Call types" are recognized by their vocalizations, but also differ in bill and body size; Groth 1993.)

Morphological traits associated with avian foraging ecology are, with few exceptions (e.g., Smith 1993), polygenically inherited (Boag and van Noordwijk 1987; Grant and Grant 1989). To make predictions concerning the evolution of quantitative traits, estimates of both the amount of genetic variation for the trait and the pattern of selection acting on the trait are needed. In this study, we assume that evolution of bill size is not genetically constrained and is determined mostly by selection. Based on the results of other studies of seed-eating birds (Boag and van Noordwijk 1987; Grant and Grant 1989) this simplifying assumption is unlikely to interfere with our predictions.

The form of selection depends on the relationship between the trait and fitness. Field estimates of fitness are difficult to obtain for nomadic species such as red crossbills. Therefore, we make use of the partitioning suggested by Arnold (1983) where first the relationship between the trait and some measure of performance is estimated and then performance is related to fitness. We use the time to extract seeds from cones as a measure of performance, which can be measured in aviaries (Benkman 1993). Furthermore, we adjust foraging ef-

iciency to be in terms of the ability to meet daily energy demands (see Stephens and Krebs 1986).

Determining the relationship between performance and fitness (fitness gradient) is more problematic. In this study, we make the simplifying assumption that foraging efficiency provides an estimate of fitness. Seed intake rates are likely to be correlated with fitness given that, at least occasionally, they approach the estimated minimum necessary intake rate for survival (Benkman 1987a, 1992) and they influence the occurrence and success of breeding (Benkman 1990). In addition, in zebra finches (*Taeniopygia guttata*) where this relationship has been examined directly, seed intake rates have been shown to correlate with fitness (Lemon 1991, 1993; see also Schluter 1995).

Less certain is how selection varies at different stages of the life cycle. Selection has been found to differ between juveniles and adults in some seed-eating birds (Price and Grant 1984; Schluter and Smith 1986; but see Grant and Grant 1989). In one species of Darwin's finch (*Geospiza fortis*) smaller body size is favored in the first several months of life apparently because of the reduction in daily energy demands (Price and Grant 1984). Smaller bodied juvenile crossbills may also be favored. Selection for smaller body size in juvenile crossbills would likely result in correlated selection for smaller bill size; the genetic covariance between bill and body size is unknown in crossbills, but bill and body size are phenotypically positively correlated (Groth 1993).

Type 5 red crossbills forage on different species of conifers during different times of the year (Benkman 1993). During the summer and early autumn (2–4 mo) they usually forage for seeds in cones of Engelmann spruce (*Picea engelmannii*). From mid to late autumn to the following summer (8–10 mo) they forage on seeds in lodgepole pine (*Pinus contorta* var. *latifolia*) cones (Benkman 1993, unpubl. data). The cone scales of pine are thicker and denser than those of spruce (Fig. 1), so that a different bill structure is predicted to be optimal for foraging on each of these conifers (see Benkman 1987b, 1989, 1993). The seeds of these two conifers, however, are similar in size (Fig. 1). Consequently, a similar palatal structure is expected to be optimal for foraging on seeds of both conifers (Benkman 1993).

Researchers have nearly unanimously concluded that animals are adapted for exploiting resources relied upon during periods of food scarcity (e.g., British finches [Newton 1967, 1972], North American shorebirds [Baker and Baker 1973], African cichlids [McKaye and Marsh 1983], Central American cichlids [Liem and Kaufman 1984], Darwin's finches

<sup>2</sup> Present address: Department of Zoology, Duke University, Durham, North Carolina 27708-0325. E-mail: rmiller @ men-del.zoo.duke.edu.

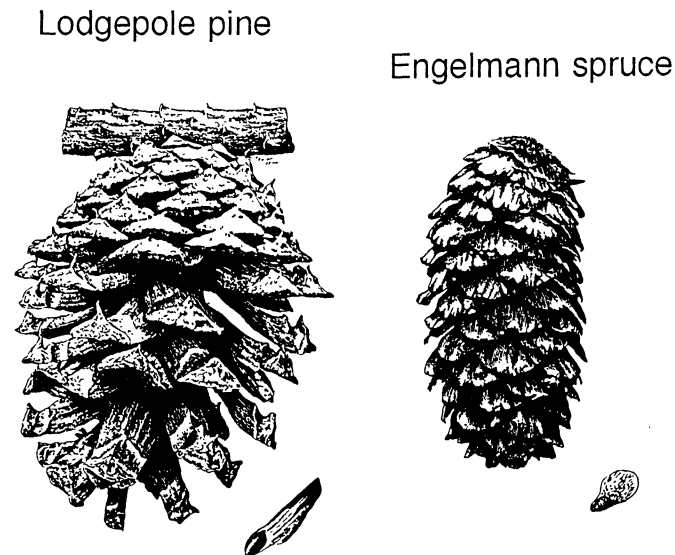


FIG. 1. Cones and seeds (with attached seed wings) of lodgepole pine and Engelmann spruce drawn to relative scale (reproduced from Sudworth 1967). The average seed masses minus their wings are 3.2 mg for lodgepole pine (Biro 1978) and 3.4 mg for Engelmann spruce (Schopmeyer 1974).

[Schluter and Grant 1984; Grant 1986], African seedcrackers [Smith 1990, 1991]; but see Greenberg 1979, 1981). This conclusion is consistent with the results of studies on selection that have found the selection gradient to be steepest during periods of resource scarcity (Price et al. 1984; Schluter and Smith 1986; Grant and Grant 1989, 1993). However, attempts to measure selection related to foraging on summer and winter, or breeding and nonbreeding resources have rarely been conducted. For example, it was shown that four types of red crossbills have bill and palatal structures that approximate the predicted optima for foraging on the conifers they most use during winter (Benkman 1993; unpubl. data), suggesting that selection on bill structure was more intense during the winter. In one case, where the optima for both winter and summer were estimated, the optima were found to differ by only 0.05 mm. Although the average bill depth of this Red Crossbill (type 3), which forages on western hemlock (*Tsuga heterophylla*) year-round, was identical to the optima for winter, the similarity between the two optima does not warrant conclusions regarding relative selection gradients. In this study, we estimate the performance gradients for red crossbills foraging on Engelmann spruce and lodgepole pine cones. A prediction consistent with previous work is that the average observed bill depth for type 5 red crossbills will be identical to the optimum estimated from the performance of birds foraging on their winter food resource, lodgepole pine cones.

## MATERIALS AND METHODS

### Aviary Experiment

Six male and four female red crossbills (type 5) were captured on 18 and 19 September 1993 in a lodgepole pine-Engelmann spruce forest near Aspen, Colorado. They were

housed in a room that included a 1.6 m × 2.7 m × 2.2 m aviary. The birds were provided with a constant supply of grit and water containing vitamins and calcium supplement. Fresh cones, usually ponderosa pine (*Pinus ponderosa* var. *scopulorum*), were provided daily, supplemented with sunflower seeds. Fresh conifer branches were provided weekly. The crossbills remained in excellent condition.

Feeding rates on lodgepole pine and Engelmann spruce cones were measured between 3 and 17 November 1993 by one of us (CWB). The lodgepole pine cones (mean cone length = 48.5 mm, SD = 3.5 mm,  $n = 112$  cones) were serotinous. To represent cones that had opened but reclosed from moisture (winter food), scales were opened by placing cones in an oven at 100°C for about 10 min, and then briefly soaked in water to reclose the scales. Engelmann spruce cones (mean cone length = 52.0 mm, SD = 2.8 mm,  $n = 84$  cones) were still green and unopen (summer food). These cones were stored in a freezer and then thawed prior to the experiments. We selected average-sized cones of similar size and shape from each conifer, to minimize environmentally induced variation in feeding rates.

During foraging experiments only one bird occupied an aviary to eliminate interference between birds. Birds were deprived of seeds for c. 15 h before the experiments. The time required to extract (prying time) and to husk 10 seeds, beginning after the first seed eaten (see Benkman 1987b, 1993), was recorded for a total of 10 cones of each conifer species for each bird. All times were recorded to the nearest 0.1 s.

We used bill depth as a measure of bill size because it (1) is not subject to wear; (2) has the largest weighting on the first principal component of four bill measurements (Benkman 1993; also see Groth 1993); (3) should be proportional to the maximum force a crossbill can exert when biting between the cone scales (Benkman 1987b; also see Wiens 1989); and (4) is closely related to the ability of four different types of red crossbills, including type 5, to extract seeds from conifer cones (Benkman 1993). Bill depth was measured with digital calipers at the anterior end of the nares to the nearest 0.01 mm. Four to six measurements per bird were used to estimate bill depth.

### Estimating Performance Gradients

Performance gradients were estimated using regression analyses between feeding rates and bill depth for birds feeding on both lodgepole pine and Engelmann spruce cones. Feeding rates were calculated as the inverse of mean prying time per bird. Relative feeding rates (mean = 0) were then calculated as individual feeding rates divided by the mean feeding rate (analogous to relative fitness).

Bill depth was standardized prior to the analyses, so that the performance gradients could be expressed in standard deviation units. The forces of directional selection and stabilizing selection were estimated as the coefficients of the linear and quadratic terms, respectively, from regression analyses between relative feeding rate and bill depth (Lande and Arnold 1983). The significance of the quadratic terms was examined using *F*-tests for adding this term to the second-order models.

Following these analyses we further adjusted the perfor-

TABLE 1. Estimates of performance gradients using regression analyses between relative feeding rates (based on the mean time for individual crossbills to extract seeds) and bill depth. For each analysis, first-order and second-order models are compared. *F*-tests show how the models are improved by adding either bill depth or (bill depth)<sup>2</sup> when the other variable is in the model. Bold indicates best model. A and B represent regressions on data gathered from the same 10 type 5 red crossbills, and C represents regressions on data gathered in an earlier study (Benkman 1993) on type 2, 3, and 4 red crossbills.

	<i>F</i>	<i>P</i>	<i>R</i> <sup>2</sup>	$\beta' \pm SE$	<i>F</i> adding variable	<i>P</i>	<i>N</i>
A. Engelmann spruce							
First-order model	<b>7.67</b>	<b>0.024</b>	<b>0.49</b>	—	—	—	10
bill depth	—	—	—	<b>-0.14 ± 0.05</b>	—	—	10
Second-order model	3.97	0.071	0.53	—	—	—	10
bill depth	—	—	—	-0.13 ± 0.06	5.15	0.058	10
(bill depth) <sup>2</sup>	—	—	—	0.04 ± 0.05	0.62	0.456	10
B. Lodgepole pine							
First-order model	3.33	0.106	0.29	—	—	—	10
bill depth	—	—	—	0.11 ± 0.06	—	—	10
Second-order model	2.28	0.173	0.39	—	—	—	10
bill depth	—	—	—	0.08 ± 0.06	1.85	0.216	10
(bill depth) <sup>2</sup>	—	—	—	-0.06 ± 0.06	1.17	0.316	10
C. Lodgepole pine							
First-order model	19.31	0.0002	0.44	—	—	—	27
bill depth	—	—	—	0.15 ± 0.03	—	—	27
Second-order model	<b>39.27</b>	<b>0.0001</b>	<b>0.77</b>	—	—	—	27
bill depth	—	—	—	<b>0.19 ± 0.02</b>	<b>65.41</b>	<b>0.0001</b>	27
(bill depth) <sup>2</sup>	—	—	—	<b>0.12 ± 0.02</b>	<b>33.86</b>	<b>0.0001</b>	27

mance gradients to account for differences in daily energy requirements as affected by body mass. The adjustment was made to link performance more closely to the ability of the birds to meet their energy demands. Body mass varies depending on the amount of fat stored, whether a meal was recently consumed and, if so, how large a meal was eaten. The crossbills used in the experiment were caught at a site that they were visiting for grit. Because these birds varied in the amount of visible fat, and some of these birds had recently eaten a meal and grit, we used data from an earlier

study (Benkman 1993) to estimate body mass for an individual of a given bill depth:  $Y = -7.770 + 4.214X$  ( $r^2 = 0.84$ ,  $df = 12$ ,  $P < 0.01$ ), where  $Y$  is body mass (in grams) at time of capture of crossbills lacking much fat and  $X$  is bill depth (in millimeters). Daily energy demands can be estimated based as (body mass)<sup>0.6052</sup> (Walsberg 1983). Feeding efficiency is inversely proportional to the amount of prying time necessary to meet daily energy demands. Consequently, we estimated feeding efficiency as the inverse of the product of prying time and estimated daily energy demands. Each estimate was then standardized by dividing by the maximum estimated feeding efficiency. This adjustment to the performance gradient was then used in a graphical analysis to identify the bill depth that achieved the maximum feeding efficiency.

#### RESULTS AND DISCUSSION

Mean bill depth was 9.29 mm (SD = 0.27) for 30 type 5 red crossbills (includes 10 birds from this study and 20 measured in other studies) and the distribution of bill depths was not significantly different from a normal distribution (using the Shapiro-Wilk's statistic).

Significant directional selection was detected for crossbills feeding on Engelmann spruce cones, indicated by the significant first-order model in the regression analysis of bill depth on feeding rate (Table 1). Relative feeding rate increased with decreasing bill depth (Fig. 2), so that small-billed type 5 crossbills extracted seeds from cones more quickly than those with larger bills.

Neither significant directional selection nor significant stabilizing selection was detected for crossbills feeding on lodgepole pine cones, although the second-order model provided the best fit to the data (Table 1). Fortunately, we were also able to examine data from an earlier study involving

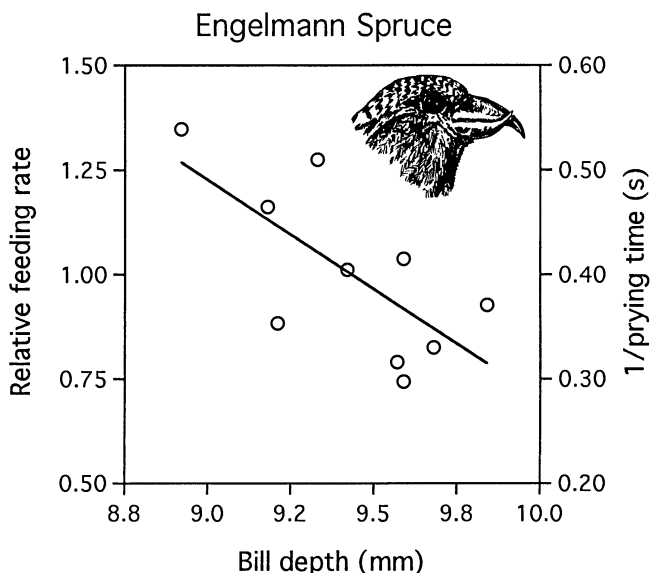


FIG. 2. The relative feeding rates and the inverse of mean prying time per Engelmann spruce seed in relation to bill depth. Cones were green and closed. Line represents least squares regression.

three other types of red crossbills (types 2, 3, 4) (Benkman 1993). Using methods similar to those used here, feeding rates were measured for these birds on lodgepole pine. These data include nearly three times as many birds with over two and a half times wider range of bill sizes (7.87–10.36 mm versus 8.92–9.84 mm bill depths). It should be noted, however, that these crossbill types do not specialize on lodgepole pine in the wild (Benkman 1993), so the performance gradient described using these data represents a more general relationship between crossbill bill morphology and feeding rate on lodgepole pine cones. On the other hand, using the larger data set with a wider range follows the general suggestion of Schluter (1988) that artificially increasing the phenotypic variation may allow a better estimate to be made of the selection gradient, or in this case, the performance gradient for red crossbills feeding on lodgepole pine cones.

The form of the relationship between feeding rate and bill depth for type 2, 3, and 4 red crossbills feeding on lodgepole pine cones (Fig. 3B) was similar to the relationship for the type 5 crossbills (Fig. 3A). This result supports the idea that there is a general relationship between relative feeding rate and bill depth for these morphologically similar red crossbill types. The regression analysis, which includes a larger sample and a greater range of bill depths, detected significant directional and stabilizing selection (Table 1). This selection is indicated by the second-order model providing the best fit to the data, with both the linear and quadratic terms being significant. It is also noteworthy that the directional component here is positive and opposes the direction of selection for birds foraging on Engelmann spruce.

The significant second-order model demonstrates significant curvature to the relationship between relative feeding rate and bill depth. The estimated optimum for bill depth where relative feeding rate is maximized is 9.43 mm. To eliminate the possibility that other optima may exist beyond the range of the data, we performed further analyses with the data transformed in various ways (e.g.,  $\ln$ , sine, tangent, exponential, arcsine) (see Mitchell-Olds and Shaw 1987), and in all cases the quadratic term remained highly significant ( $P < 0.0001$ ). We also performed a constrained regression analysis (Mitchell-Olds and Shaw 1987; Simms 1990) where we forced the optimum to be outside the range of the data, to see if we could distinguish between these alternative fitness curves and the observed relationship. In both cases, with the optimum set above the range of the data ( $P < 0.0001$ ) and with the optimum set below ( $P = 0.0054$ ), the unconstrained regression with the intermediate optimum provided the better fit.

To examine the relationship between bill depth and feeding efficiency, the performance gradient for type 5 crossbills feeding on Engelmann spruce and the performance gradient for the type 2, 3, and 4 red crossbills feeding on lodgepole pine, were adjusted to account for differences in daily energy demands. These adjustments steepen the decline in feeding efficiency on Engelmann spruce as bill size increases (Fig. 4). The adjustments for energy demands when feeding on lodgepole pine also reaffirm that the maximum feeding efficiency is achieved by birds with an intermediate bill depth. The most efficient bill depth for feeding on lodgepole pine from the graphical analysis is 9.28 mm. This result provides

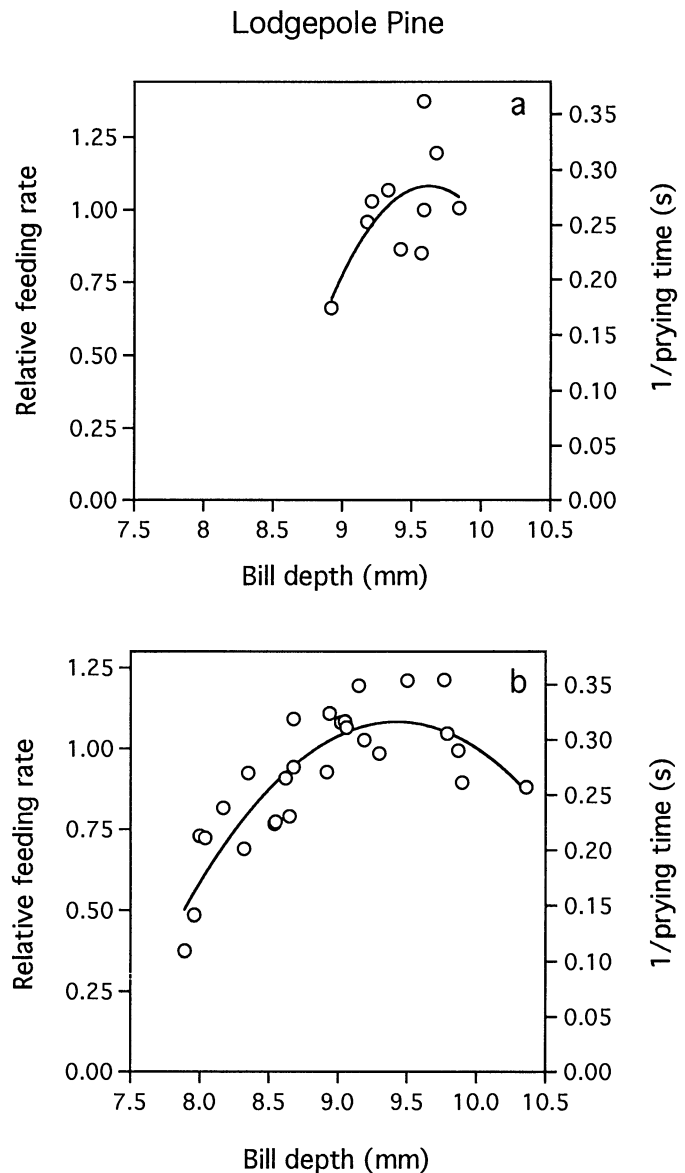


FIG. 3. The relative feeding rates and the inverse of mean prying time per lodgepole pine seed in relation to bill depth. Curves represent quadratic equations fit to data; (A) data from the 10 type 5 Red Crossbills used in the experiments; and (B) data from an earlier experiment (Benkman 1993), representing crossbills from three call types other than type 5.

a remarkably close fit to the observed mean value for bill depth in type 5 crossbills—9.29 mm.

By incorporating estimates of daily energy demands, which are a function of body mass, into our measure of foraging efficiency, we may have been able to account for any correlated selection that may have occurred if body size was also the target of selection. The effect of the adjustment was to shift the optimum bill depth based on feeding rate alone from 9.43 mm to 9.28 mm. Either way, the estimated optima are very close to the observed mean bill depth.

The close correspondence between the average bill depths for type 5 crossbills and the optimum bill depth based on feeding efficiency on lodgepole pine provides strong support

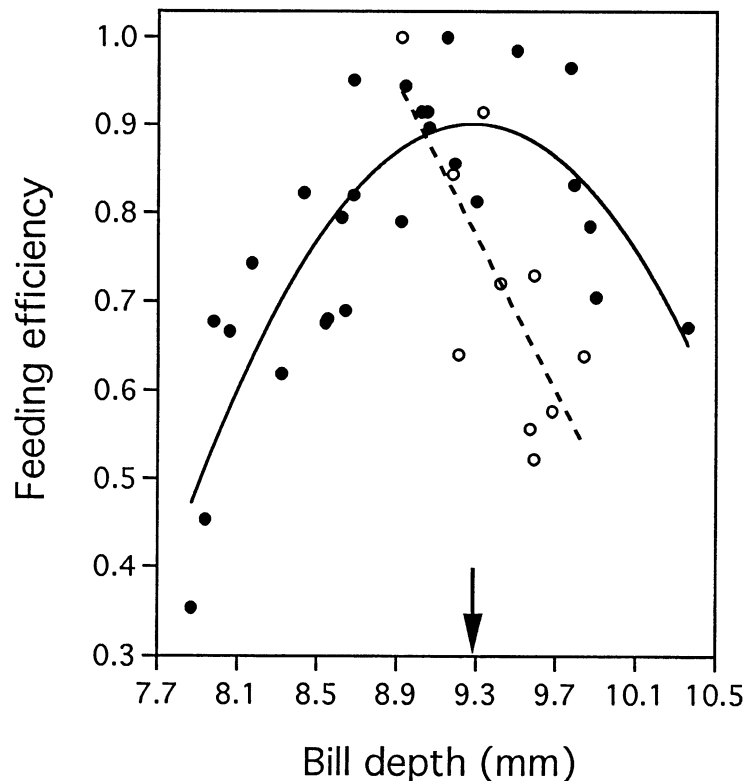


FIG. 4. Feeding efficiency gradients of Red Crossbills as estimated by their efficiency at meeting daily energy requirements while foraging on Engelmann spruce (dashed line and open circles;  $Y = 4.83 - 0.44X$ ,  $r^2 = 0.56$ ,  $df = 8$ ,  $F = 10.31$ ,  $P = 0.01$ ) and lodgepole pine (solid curve and filled circles;  $Y = -17.63 + 3.99X - 0.22X^2$ ,  $r^2 = 0.69$ ,  $df = 24$ ,  $F = 26.93$ ,  $P < 0.0001$ ; the quadratic term is highly significant [ $P < 0.0001$ ] even when the data are transformed, e.g.,  $\ln$ , sine, tangent, exponential, arcsine). The arrow indicates the mean bill depth of type 5 red crossbills.

for our initial hypothesis that foraging morphology represents an adaptation to feeding on resources that are available when food is scarce. This observation implies that selection from feeding on lodgepole pine outweighs the directional selection from feeding on Engelmann spruce. The results also suggest that our initial simplifying assumptions did not interfere with our prediction. That is, evolution of bill size in crossbills is not genetically constrained and is determined mostly by selection, and performance gradients may translate directly into selection gradients during winter and spring.

In this study we were able to test the prediction that fitness differences are much greater during periods of food scarcity based on measured performance gradients and the observed mean trait values. In systems such as nomadic crossbills where individuals cannot be followed for very long, such indirect measures of fitness may be the only ones possible. However, the prediction was also based on a thorough knowledge of crossbill ecology (Benkman 1992, 1993 and references therein), without which the appropriate hypotheses could not have been formulated.

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Corresponding Editor: A. Larson

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## NATURAL FORMATION OF IRIS HYBRIDS: EXPERIMENTAL EVIDENCE ON THE ESTABLISHMENT OF HYBRID ZONES

SCOTT A. HODGES,<sup>1</sup> JOHN M. BURKE, AND MICHAEL L. ARNOLD<sup>2</sup>  
*Department of Genetics, University of Georgia, Athens, Georgia 30602*  
<sup>2</sup>E-mail: arnold@dogwood.botany.uga.edu

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Studies of animal and plant hybrid zones have been used to examine the early stages of speciation and mechanisms of

reproductive isolation, as well as the interactions between genetic and ecological features of differentiated populations (Barton and Hewitt 1989; Arnold 1992; Harrison 1993). Despite the widespread use of hybrid zones for studies of evolutionary processes, little is actually known about the early

<sup>1</sup> Present address: Department of Ecology, Evolution, and Marine Biology, University of California, Santa Barbara, California 93106.