Performance Trade-Offs and Resource Availability Drive Variation in Reproductive Isolation between Sympatrically Diverging Crossbills

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ABSTRACT: Theoretical models indicate that speciation, especially when the scope for gene flow is great (e.g., sympatric speciation), is most likely when strong performance trade-offs coincide with reproduction. We tested this classic hypothesis using measures of the strength of three prezygotic reproductive isolating barriers (habitat isolation, reduced immigrant fecundity, and behavioral isolation) between two young (~2,000 years) and sympatric red crossbill (*Loxia curvirostra*) ecotypes. All three isolating barriers increased with increases in performance trade-offs, with total reproductive isolation varying between 0.72 and 1 (0 represents random mating, and 1 represents complete reproductive isolation). Strong trade-offs led to strong habitat isolation, an inability to breed in the "wrong" habitat, and more assortative flocks, with the latter leading to stronger behavioral isolation. Reproductive isolation decreased as resource availability increased relative to the demands of breeding, with higher resource availabilities eliminating the positive relationship between reproductive isolation and performance trade-offs. This latter result is consistent with previous work suggesting that increasing resource abundance dampens the effect of strong performance trade-offs on evolutionary divergence. Because many organisms, with the notable exception of host-specific phytophagous insects, rely on abundant food resources with weak performance trade-offs while breeding, our results may explain why sympatric speciation is uncommon.

Keywords: ecological speciation, *Loxia curvirostra*, reproductive isolation, resource availability, sympatric speciation, performance trade-offs.

Introduction

Thanks to renewed interest in the ecology of speciation, ample empirical evidence now supports Darwin's central hypothesis that adaptation and speciation are fundamentally linked (Schluter 2009; Schemske 2010; Nosil 2012). The power of adaptation to drive speciation is most strikingly illustrated by systems where speciation has occurred despite tremendous scope for gene flow between lineages throughout divergence (Malinsky et al. 2015; Kautt et al. 2016; Richards et al. 2018; Papadopulos et al. 2019). While it is generally accepted that adaptive divergence is essential to speciation with gene flow (Coyne and Orr 2004; Bolnick and Fitzpatrick 2007), there remain major gaps in our understanding of how adaptation, reproductive isolation, and speciation become linked when the scope for gene flow is continuous and large. Fortunately, theoreticians have developed mechanistic models relating the ecological trade-offs underlying adaptive divergence to the reproductive isolating barriers driving speciation when the potential for gene flow is high (Kopp et al. 2018).

Speciation in the face of high gene flow is possible if the ecological trade-offs underlying adaptive divergence coincide with reproduction (e.g., Bush 1975; Rice 1987; Diehl and Bush 1989; Johnson et al. 1996; Fry 2003; Kopp et al. 2018). If there is a direct coupling between ecological trade-offs and reproduction, multiple reproductive isolating barriers may "automatically" reduce gene flow between ecologically divergent groups (e.g., habitat isolation [Egan et al. 2012], temporal isolation [Bell et al. 2017], and reduced immigrant viability/fecundity [Nosil et al. 2005; Porter and Benkman 2017]). Speciation is possible under this scenario because there is little opportunity for recombination to break up genetic associations between the loci underlying adaptive divergence and assortative mating (Felsenstein 1981). Indeed, such "grouping" models are among the most conducive to sympatric speciation (Kopp et al. 2018), even without assuming the extreme conditions (e.g., very strong disruptive selection) necessary for sympatric speciation in other models (Fry 2003).

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Although grouping models have substantially influenced speciation theory, empirical evidence bearing on their consequences for speciation with gene flow is mostly based on indirect comparative patterns. For example, a key line of evidence supporting grouping models is the body of evidence for in situ speciation in host races of phytophagous insects (Berlocher and Feder 2002; Drès and Mallett 2002; Bolnick and Fitzpatrick 2007). Because many phytophagous insects mate on host plants that adults and/or larvae feed on (Bush 1975; Berlocher and Feder 2002; Drès and Mallett 2002), there is a direct coupling between reproduction and ecological trade-offs arising from adaptation to alternative hosts. By contrast, speciation requires substantial geographic isolation in most other animals (Coyne and Price 2000; Coyne and Orr 2004; Phillimore et al. 2008; Price 2008), where sympatric taxa typically show a high degree of convergence on easily accessible resources during breeding (Smith et al. 1978; Hindar and Jonsson 1982; Schoener 1982; Smith 1990; Schluter and McPhail 1992; Smith and Skúlason 1996). These patterns suggest that the lack of strong trade-offs and the resulting high ecological overlap between lineages during reproduction may inhibit reproductive isolation, thus necessitating prolonged allopatry for speciation in most taxa. However, direct tests of this hypothesis are needed.

In addition to using resources that impose weak trade-offs during breeding, most animals time breeding to coincide with periods of elevated resource availability so the energy demands of reproduction can be met (Williams et al. 2017). Variation in resource availability could in turn modulate the degree to which a given performance trade-off impedes the use of alternative resources (Poisot et al. 2011) and thereby influence reproductive isolation. For example, a wide range of phenotypes might be able to breed in the same habitat when resource availability greatly exceeds the demands of breeding even if trade-offs are strong, thus decreasing habitat isolation (e.g., Smith 1990). Whether resource availability affects reproductive isolation has received little attention but may be critical for understanding the interplay between adaptation and speciation.

Here, we take advantage of variation in both the strength of performance trade-offs and levels of resource availability to infer their effects on prezygotic reproductive isolating barriers between two sympatric ecotypes of red crossbills (*Loxia curvirostra* complex; fig. 1). In North America, red crossbills consist of nine widely sympatric ecotypes (a tenth ecotype is now recognized as a separate species: the Cassia crossbill [*Loxia sinesciuris*]) that have diversified in response to divergent selection on bill morphology for specializing on seeds of different conifer species (Benkman 1993, 2003; Benkman and Young 2020). Although the different lineages evolved to exploit the seeds of separate single "key" conifers that impose strong performance trade-offs (Benkman 1993, 2003; fig. 1*A*), few crossbills rely on

only one conifer species, often switching to forage on others if they become more profitable (Benkman 1987; Benkman and Miller 1996). Seeds in some thin-scaled conifers are especially accessible to a wide range of crossbill morphologies (fig. 1*B*), and several ecotypes often converge and breed opportunistically on large episodic cone crops of these conifers (e.g., various spruce species, especially Engelmann spruce [*Picea engelmannii*] in western North America; Groth 1993*b*).

We focus on two nomadic ecotypes that are sympatric throughout the Rocky Mountain region where their respective key conifers (Rocky Mountain lodgepole pine *Pinus contorta latifolia* and ponderosa pine *P. ponderosa*), for which their bill structures approximate the optimum for foraging on (Benkman 1993; Benkman et al. 2001), co-occur extensively (fig. S1, available online; Benkman 2007; Benkman and Young 2020). Lodgepole pine and ponderosa pine crossbills are estimated to have diverged only ~2,000 years ago (95% confidence interval: 1,200–2,900 years; C. Brock, T. L. Parchman, and C. W. Benkman, unpublished manuscript). This is consistent with various lines of evidence that a ponderosa pine crossbill could not have evolved much earlier (Benkman 1993; see also Norris et al. 2016) and indicates sympatric divergence of these two ecotypes because the distributions of lodgepole and ponderosa pine have overlapped extensively in the Rocky Mountain region for at least 5,000 years (Critchfield and Little 1966; Critchfield 1985; Norris et al. 2016); Engelmann spruce has been similarly widespread, especially within the range of lodgepole pine (Whitlock 1993; Anderson et al. 2017).

During their regular nomadic movements of hundreds to thousands of kilometers in search of developing cone crops (Benkman and Young 2020), these ecotypes experience quantifiable variation in the extent of feeding trade-offs and relative resource availability while breeding in sympatry (fig. 2). Furthermore, three prezygotic reproductive isolating barriers that are important in crossbills and other systems (habitat isolation, reduced immigrant fecundity, and behavioral isolation) are quantifiable (Smith and Benkman 2007). Thus, we can almost experimentally compare the strength of reproductive isolating barriers between the same pair of lineages as they experience temporal variation in trade-offs and resource availability during breeding. Indeed, there is little to no evidence that genetic distance (Parchman et al. 2016), bill/body size divergence (Groth 1993*b*), or vocalization divergence (Groth 1993*b*) increases with geographic distance over thousands of kilometers within the ecotypes. Therefore, comparisons of reproductive isolation in this system are unlikely to be confounded by unknown contingencies plaguing comparative studies of speciation (Seehausen 2009; Nosil 2012).

The central hypothesis we aimed to test, derived from grouping models and the natural history of crossbills, is
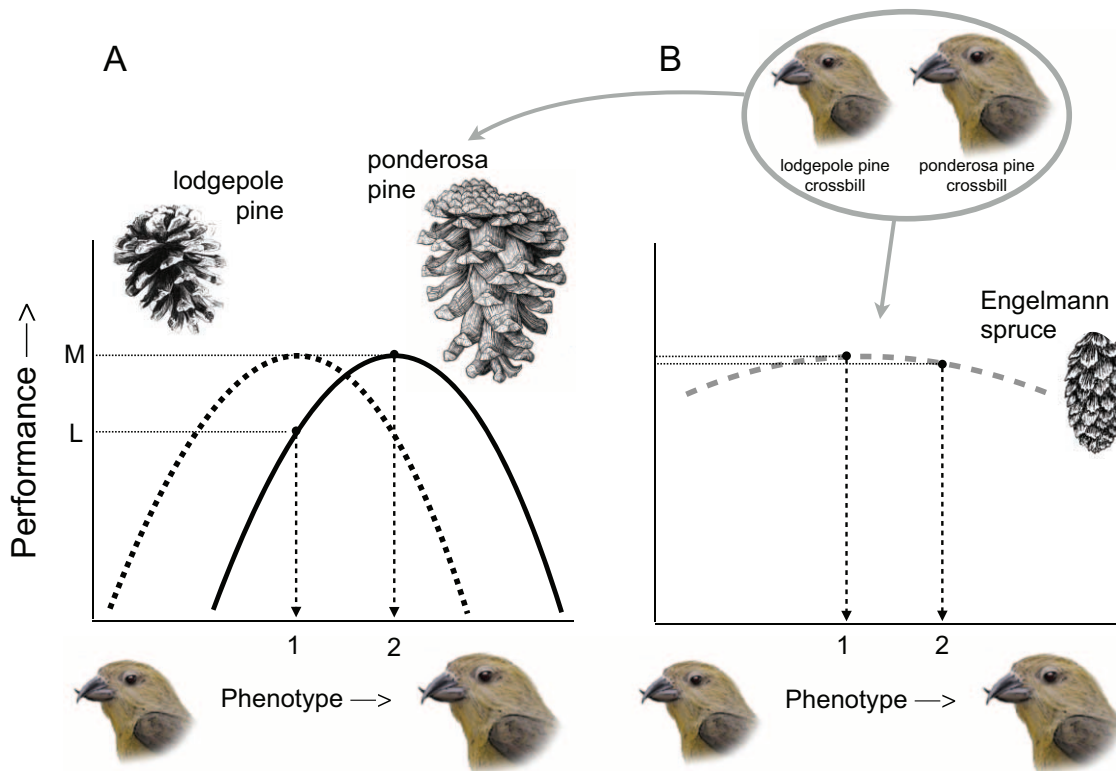
A

B

lodgepole
pine

ponderosa
pine

lodgepole pine
crossbill

ponderosa pine
crossbill

Engelmann
spruce

Performance —>

M

L

1 2

Phenotype —>

1 2

Phenotype —>

Figure 1: We took advantage of nomadism and opportunistic breeding by two crossbill ecotypes to determine how performance differentials affect reproductive isolation and assortative flocking. *A*, Both ecotypes breed in forests of mixed lodgepole and ponderosa pines. The dotted curve represents the relationship between performance and phenotype (bill depth) on lodgepole pine, and the solid curve represents the relationship on ponderosa pine. In mixed pine forests, performance differentials ($[M - L]/M$, where 1 and 2 represent the mean bill depths of lodgepole pine and ponderosa pine crossbills, respectively; M represents the performance of the more efficient ecotype; and L represents the performance of the less efficient ecotype) are large. *B*, In forests of spruce, the two ecotypes have more similar feeding abilities and small performance differentials. Increasing dissimilarity in performance (an increasing differential) between ecotypes reduces the benefit from and should reduce the propensity for heterotypic flocking (Smith et al. 1999, 2012). The locations where these crossbills breed vary yearly because of spatiotemporal variation in cone crops that crossbills track with nomadic movements.

that the conditions necessary for sympatric speciation (i.e., complete or nearly complete reproductive isolation) depend on performance trade-offs and/or the level of resource availability during reproduction. We predicted that reproductive isolating barriers would be strongest when performance trade-offs are strong and resource availability is low (fig. 2*D*). This prediction applied especially for habitat isolation and reduced immigrant fecundity because these barriers appear to be directly tied to adaptations for specializing on alternative conifers (Smith and Benkman 2007; Benkman 2017). Behavioral isolation might also increase as performance trade-offs increase, given that assortative flocking by ecotype is likely a major component of behavioral isolation in crossbills (Smith et al. 2012; Porter and Benkman 2019). Assortative flocking is thought to arise because crossbills use both their own feeding rates and those of their flockmates (i.e., public information) when assessing patch quality (Smith et al. 1999, 2012). Public in-

formation increases feeding performance when individuals have similar feeding abilities but reduces performance when individuals differ in their ability to use a shared resource (Smith et al. 1999). Thus, on resources where differences in bill morphology result in large differences in feeding performance (i.e., strong trade-offs), selection should favor flocking with individuals of the same ecotype and avoiding heterotypics (Smith et al. 1999, 2012; Porter and Benkman 2019). But during Engelmann spruce cone crops, when individuals with a wide range of bill morphologies have similar abilities to exploit the same resource (fig. 1*B*), mixed ecotype flocks may be more common. Because crossbills spend most of their lives in flocks and choose mates from within flocks (Newton 1972), an increase in mixed flocks may lower behavioral isolation (Smith et al. 1999, 2012). However, ecotypes also differ in the structure of contact calls (Groth 1993*b*; Benkman and Young 2020) and courtship songs (Porter and Smith
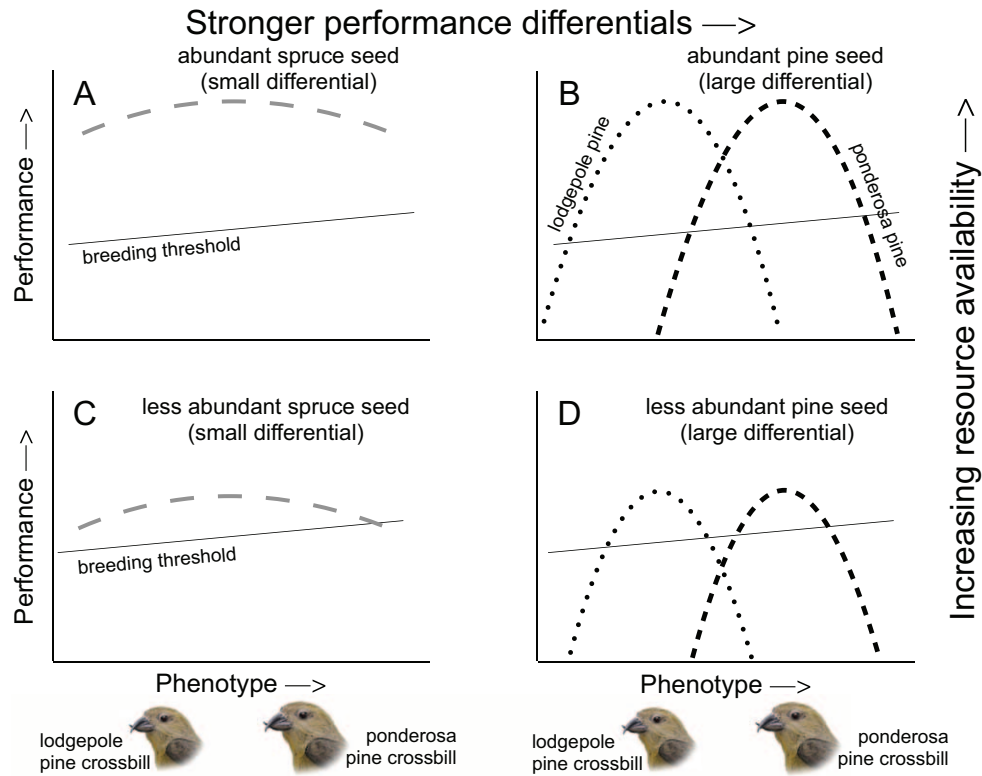
Figure 2: Illustration of the variation in performance differentials and the extent to which feeding rates exceed the threshold for breeding (i.e., relative resource availability; see "Methods"). The fine sloping line indicates the intake rate threshold for breeding (increasing slope reflects increasing demands with increasing bill depth due to body mass–bill depth allometry). *A* and *C* represent the small performance differentials for crossbills feeding on spruce, whereas the large performance differentials in *B* and *D* represent those experienced when feeding on lodgepole and ponderosa pines.

2020), which could facilitate behavioral isolation (e.g., Snowberg and Benkman 2007) regardless of the strength of performance trade-offs or the level of resource availability. Therefore, a reasonable alternative hypothesis is that the conditions necessary for sympatric speciation and the levels of reproductive isolation are unrelated to the strength of performance trade-offs or the level of resource availability.

Methods

Between 2015 and 2020 we collected data during 10 breeding periods at six locations across the southern Rocky Mountain region (fig. S1; app. 1; apps. 1–3 are available online), where crossbills are common and breed in response to large cone crops. Data were collected during the two primary periods of crossbill breeding (Benkman and Young 2020): late winter/early spring (January to April) and late summer/early fall (July to October). Although we collected data from four locations twice each (app. 1), crossbills often disperse long distances after breeding in search of new cone crops (Benkman and Young 2020), with tremendous turn-

over of individuals at a given location from year to year (Senar et al. 1993; Gómez-Blanco et al. 2019). Additionally, at two of the locations successive breeding periods were separated by 3–4 years. Therefore, individuals sampled during one breeding period at a location are likely to be mostly, if not entirely, different in a different breeding period at the same location.

Quantifying the Magnitude of Performance Differences and Relative Resource Availability

We measured crossbill feeding rates to estimate the performance of each ecotype on each conifer species. Foraging crossbills were observed with 20–60× Swarovski telescopes and timed with stopwatches. Birds were not banded, so we cannot be certain that each foraging bout is from a different crossbill. However, we suspect that multiple bouts from the same individual were uncommon in our data because we visited as many different areas as possible at a study site and the number of crossbills at most sites was in the hundreds. Feeding rates were measured by recording

the number of seeds consumed during timed intervals, as in Benkman (1987) and Smith and Benkman (2007), and are summarized in appendix 2. Birds were recorded feeding from when they were located foraging until they finished foraging on a cone (foraging bouts averaged 65 s; range: 4–508 s; SD: 63.8 s). We converted seeds consumed per second into milligrams of kernel consumed per second using the mean dry masses of seed kernels measured from at least 25 trees from each conifer species at one location (3.09, 12.31, and 2.99 mg for lodgepole pine, ponderosa pine, and Engelmann spruce, respectively). Seed size was not expected to vary much among locations because of the limited geographic extent of our study (e.g., Wells 1964; Benkman et al. 2001). Importantly, specific caloric values of conifer kernels differ little among species (Grodzinski and Sawicka-Kapusta 1970; Smith 1979), so that kernels consumed can be used as a proxy for energy intake.

We determined the extent to which one ecotype had a lower feeding rate than the other ecotype on the same conifer species (which we term the "performance differential" [PD]) as follows:

$$\text{PD} = \frac{\text{RateMoreEfficient} - \text{RateLessEfficient}}{\text{RateMoreEfficient}}, \quad (1)$$

where the rates (seeds consumed per second) are population means (fig. 1; app. 2). Two inverse performance differentials represent a performance trade-off. A single performance differential provides a useful measure when only one resource is available (e.g., during Engelmann spruce cone crops) and should influence the extent to which the less efficient lineage can occur and reproduce. Indeed, in a region with only one conifer species that imposes a strong performance differential, ecotypes with low intake rates rarely attempt to breed (Smith and Benkman 2007), instead dispersing long distances in search of cone crops where they have higher intake rates (Benkman 2017). In addition, performance differentials are the relevant currency for measuring the usefulness of public information from heterotypic flockmates (fig. 1; Smith et al. 1999).

During four of the six mixed pine breeding periods, we were able to collect feeding rates of ponderosa pine crossbills on lodgepole pine. By contrast, we rarely observed lodgepole pine crossbills feeding on ponderosa pine, and thus were unable to collect these data in most years. The relative rarity of lodgepole pine crossbills feeding on ponderosa pine likely reflects the greater difficulty that lodgepole pine crossbills have feeding on ponderosa pine than ponderosa pine crossbills have feeding on lodgepole pine (Benkman 1993). Thus, for these four breeding periods, we estimated performance differentials using the relative feeding rates of both ecotypes on lodgepole pine. However, during the winter/spring of 2015 and 2016, when particularly large

ponderosa pine cone crops were present, lodgepole pine crossbills were occasionally found feeding on ponderosa pine, whereas ponderosa pine crossbills were almost never observed feeding on lodgepole pine. Thus, we used data on the relative feeding rates of both ecotypes on ponderosa pine to estimate performance differentials during the winter/spring of 2015 and 2016 (app. 2). In other words, we were only able to estimate a single performance differential during pine breeding seasons, likely because one of the ecotypes avoided the alternative pine because its feeding rate would have been too low (e.g., Benkman 1987).

We define relative resource availability as the mean intake rate for nesting crossbills of the ecotype with the lowest intake rate divided by its estimated necessary intake rate during the most energy demanding stage of reproduction (the early nestling stage; see Benkman 1990). This provides a measure of the extent to which intake rates exceed demands of reproduction (fig. 2). Importantly, intake rates relative to demands predict whether crossbills breed (Benkman 1990) and are a direct measure of resource availability because they integrate multiple factors that determine how available resources are to an individual (e.g., resource abundance, handling time variation associated with seed defenses, and crossbill morphology). We use the rate of the ecotype with the lower intake rate to estimate relative resource availability because this is the ecotype most likely to be limited in nesting by their intake rate. Following Benkman (1990), we used standard allometric equations for energy requirements of adults and nestlings, assimilation efficiencies, and specific caloric values of seed kernels from the literature and climatic data from the field region (based on data from local SNOTEL sites) to estimate the intake rate needed by the male to feed itself plus the female and three nestlings (the average number of nestlings; Benkman and Young 2020) during the early nestling stage (see app. 3 for additional details).

The Magnitude of Reproductive Isolation

We collected data on habitat use, the occurrence of breeding, and mated pairs of crossbills to estimate key components of prezygotic reproductive isolation based on methods from a previous study of crossbills (Smith and Benkman 2007).

Habitat Isolation. Habitat isolation occurs when gene flow is reduced because lineages occupy different environments while breeding (Coyne and Orr 2004; Sobel et al. 2010; Webster et al. 2012). Habitat isolation arises in crossbills because individuals preferentially forage on the most profitable conifers (Benkman 1987), and the conifers that are most profitable depend on an individual's bill morphology (Benkman 1993, 2003), resulting in matching habitat

choice (Benkman 2017; see Edelaar et al. 2008; Berner and Thibert-Plante 2015). Habitat isolation is strong where only ponderosa pine or lodgepole pine occur, such as in extensive monotypic stands of ponderosa pine in northern Arizona, where only ponderosa pine crossbills are regularly found in large numbers (Benkman and Young 2020). However, our focus is to determine how variation in performance differentials is related to reproductive isolation, where the scope for gene flow is highest. Across much of the geographic range of the two ecotypes the distributions of lodgepole and ponderosa pine overlap (fig. S1). Yet individual forest patches tend to be dominated by one pine species, with local occurrence depending on, for example, soil type, moisture, and temperature and with lodgepole pine usually occurring at higher elevations (Knight et al. 2014).

We collected data from sites that were either a mix of lodgepole and ponderosa pine (hereafter referred to as simply "pine") or extensive Engelmann spruce (hereafter, "spruce") forests. In pine, lodgepole pine crossbills fed mostly on lodgepole pine while ponderosa pine crossbills fed mostly on ponderosa pine. However, crossbills moved long distances across the study areas daily (crossbills regularly fly several kilometers or more; Benkman and Young 2020), so that individuals had the opportunity to use either pine species. When a large spruce cone crop develops, both ecotypes may converge in their use of spruce for feeding and reproduction, ignoring even large pine cone crops nearby (C. K. Porter, personal observation).

We estimated the individual component of habitat isolation (HI) between lodgepole pine and ponderosa pine crossbills as follows (based on eq. [4A] in Sobel and Chen 2014):

$$\text{HI} = 1 - 2\left[\frac{\frac{\text{ObsNumLessEfficient}}{\text{ExpNumLessEfficient}}}{\frac{\text{ObsNumMoreEfficient}}{\text{ExpNumMoreEfficient}} + \frac{\text{ObsNumLessEfficient}}{\text{ExpNumLessEfficient}}}\right],$$
(2)

where ObsNumLessEfficient and ObsNumMoreEfficient denote the observed numbers of perched individuals of the less and more efficient ecotype counted in a given forest type, respectively, where efficiency refers to feeding efficiency as measured by feeding intake rates. ExpNumLessEfficient and ExpNumMoreEfficient denote the expected numbers of the less and more efficient ecotype in a given forest type, respectively. The expected numbers were proportional to their numbers across both forest types at a study site; in other words, expected numbers assumed that random habitat choice was occurring. For example, if there were twice as many ponderosa pine crossbills as lodgepole pine crossbills across both forest types at a study site, the expected

number of ponderosa pine crossbills in each forest type would be twice that of lodgepole pine crossbills. We searched for crossbills each day throughout the field season and distinguished the two ecotypes by their vocalizations (Groth 1993*b*; Benkman and Young 2020). While some crossbills are undoubtedly encountered more than once, these data serve as a reasonable measure of the relative frequencies of each ecotype in a forest type because there is no reason to expect a detection bias (Smith and Benkman 2007).

Habitat isolation—and each reproductive isolating barrier as well as total reproductive isolation—can range from −1 to 1, with 1 representing complete reproductive isolation, 0 representing random mating, and −1 representing complete disassortative mating. During breeding periods in pine, habitat isolation was estimated for each forest type and averaged to give an overall estimate of the strength of this barrier. We assumed that the two ecotypes should be equally abundant in spruce forest because of their similar feeding rates on spruce (app. 3). Equation (2) therefore reduces to the observed relative frequencies of each ecotype in spruce (e.g., Smith and Benkman 2007).

Reduced Immigrant Fecundity. Given the high energetic demands associated with breeding and the dependence of crossbills on conifer seeds for food (Benkman 1990), individuals that occur in the "wrong" habitat (hereafter, "immigrants") may be unable to acquire sufficient resources to breed. If less efficient ecotypes are able to survive but not breed, the probability of gene flow between ecotypes will be reduced (i.e., reduced immigrant fecundity; Porter and Benkman 2017). Because reduced immigrant fecundity is a measure of breeding by immigrants that occupy a given forest type, this barrier acts to reduce gene flow after and independent of habitat isolation (Smith and Benkman 2007). We estimated the individual component of reduced immigrant fecundity (RIF) as follows (based on a modified version of eq. [4B] in Sobel and Chen 2014):

$$\text{RIF} = 1 - 2\left[\frac{\frac{\text{ObsBrLessEfficient}}{\text{ObsNumLessEfficient}}}{\frac{\text{ObsBrLessEfficient}}{\text{ObsNumLessEfficient}} + \frac{\text{ObsBrMoreEfficient}}{\text{ObsNumMoreEfficient}}}\right],$$
(3)

where ObsBrLessEfficient and ObsBrMoreEfficient denote the observed number of breeding individuals of the less and more efficient ecotypes, respectively, in a given forest type. The number of breeding individuals of each ecotype in each forest type was tallied independently of sex and whether individuals were in a heterotypic versus homotypic breeding pair. We used the observed numbers (ObsNumLessEfficient and ObsNumMoreEfficient) from equation (2) to denote the

expected number of breeding individuals of each ecotype, assuming that ecotypes breed in proportion to their numerical occurrence. Therefore, if immigrants were less likely to breed in a given forest type than the locally adapted ecotype, the value of reduced immigrant fecundity would be positive, which would act to reduce gene flow. We note that this is likely a conservative estimate of reduced immigrant fecundity because maladapted individuals may manage to nest but produce fewer and/or lower-quality offspring than locally adapted individuals. As with habitat isolation during breeding periods in pine, reduced immigrant fecundity was estimated for each forest type and averaged to give an overall estimate.

Breeding birds were identified by observing suspected breeding pairs to detect behaviors characteristic of mated pairs (e.g., male courtship, male feeding female, allopreening, copulation, males following females that are nest building; Benkman and Young 2020). Pairs were included in analyses if they remained together for at least 20 min and exhibited at least one characteristic behavior (Smith and Benkman 2007). We assumed that birds engaging in behaviors indicative of breeding were nesting near the area where we observed them and thus in the dominant forest type at that location. Nonetheless, because crossbills may forage far from where pairs were located, there is potentially some error in this estimate.

To uniquely identify individual pairs (and thus avoid pseudoreplication), the contact calls of mated pairs were recorded with Marantz PMD661 digital recorders and Sennheiser ME 66 shotgun microphones. Contact calls differ among individuals within an ecotype (Groth 1993*b*), and mated pairs often have nearly identical call structure (Groth 1993*a*; Keenan and Benkman 2008; Sewall 2009). We visually inspected spectrograms of all pairs at each study site, and suspected duplicate recordings from the same pair were removed from subsequent analyses. To evaluate whether we could detect duplicate pairs, we conducted a blind test wherein we attempted to identify 20 intentionally duplicated spectrograms based on different calls from a given pair from a sample of 104 mated pairs recorded in the winter/spring of 2015. We detected 19 of 20 duplicated pairs in this blind test, suggesting that we were able to eliminate most duplicated pairs from our analyses.

Behavioral Isolation. If individuals of both ecotypes breed in the same habitat (i.e., if habitat isolation and reduced immigrant fecundity are incomplete), there is opportunity for interbreeding. We used data on mated pairs to determine the extent to which homotypic mated pairs were formed relative to heterotypic mated pairs. Because we consider only those individuals that are attempting to breed, this measure is sequential and independent of habitat isolation and reduced immigrant fecundity.

We estimated the individual component of behavioral isolation (BI) as follows (based on eq. [4A] in Sobel and Chen 2014):

$$\mathrm{BI} = 1 - 2\left[\frac{\dfrac{\mathrm{ObsHeterotypic}}{\mathrm{ExpHeterotypic}}}{\dfrac{\mathrm{ObsHeterotypic}}{\mathrm{ExpHeterotypic}} + \dfrac{\mathrm{ObsHomotypic}}{\mathrm{ExpHomotypic}}}\right], \quad (4)$$

where ObsHeterotypic and ObsHomotypic denote the observed number of heterotypic (i.e., mixed ecotype) and homotypic breeding pairs, respectively. ExpHeterotypic and ExpHomotypic denote the expected number of homotypic breeding pairs, respectively. Because the relative abundances of breeding lodgepole pine and ponderosa pine crossbills differed among our study sites, the random expectations for heterospecific pairing and conspecific pairing differed. We therefore used the I_{PSI} equation developed by Rolán-Alvarez and Caballero (2000) to estimate the expected numbers of each possible pairing combination relative to the observed numbers. Specifically, this equation uses data on the observed numbers of all four possible pairing combinations and the number of breeding birds of each ecotype/sex combination to calculate expected values of heterospecific and conspecific pairing (i.e., ExpHeterotypic and ExpHomotypic; for further details on the I_{PSI} equation, see tables 2 and 4 in Rolán-Alvarez and Caballero 2000). Importantly, the I_{PSI} equation is algebraically equivalent to equation (4A) of Sobel and Chen (2014), thus allowing us to incorporate it into the general framework used for calculating reproductive isolation. During breeding periods in pine, behavioral isolation was estimated for each forest type and averaged to give an overall estimate.

We assumed that breeding pairs were genetically monogamous. This assumption is reasonable in red crossbills for multiple reasons. First, Kleven et al. (2008) found no evidence for extrapair paternity among 96 offspring from 34 broods in a Norwegian population of red crossbills. Based on the similarity of breeding behavior within the red crossbill complex (Cramp and Perrins 1994; Benkman and Young 2020), the Norwegian population is unlikely to be unique. Second, extrapair paternity in red crossbills is expected to be absent to rare because males vigorously mate guard females until egg laying begins (Nethersole-Thompson 1975; Benkman and Young 2020). The presence of similar mate-guarding behavior in other Fringillidae (Billerman et al. 2020) may partly explain why this family has one of the lowest incidences of extrapair paternity in passerines (Brouwer and Griffith 2019). Third, female crossbills rely exclusively on their social mate for food for themselves and their young when they are brooding their

nestlings during the first 5 days after hatching (Benkman 1990). In bird species with similar parental care strategies, where male parental care is critical to female reproductive success, extrapair paternity is rare or absent (Møller 2000). Fourth, little to no extrapair paternity is also consistent with the relatively small testes of lodgepole pine and ponderosa pine crossbills (C. W. Benkman and C. K. Porter, unpublished manuscript), which are comparable to those of other genetically monogamous bird species with low levels of sperm competition (Møller and Briskie 1995). In the data set of Møller and Briskie (1995), only seven of 54 species had lower testis mass relative to body mass than ponderosa pine crossbills (Smith and Benkman 2007). Similarly, their relatively short sperm and elevated levels of sperm length variation within and among male red crossbills (Lifjeld et al. 2010) are consistent with little to no extrapair paternity (Lifjeld et al. 2010; Birkhead and Montgomerie 2020). Of the 55 bird species surveyed by Lifjeld et al. (2010), only one had greater sperm length variation among males than red crossbills.

Finally, some extrapair paternity need not alter our general results unless, for example, an increase in assortative pairing was countered by an increase in disassortative extrapair paternity. Few data are available on extrapair mating and interbreeding between lineages, but the available evidence suggests that social pairing behavior is strongly correlated with extrapair mating behavior in young, recently diverged bird lineages like crossbills (Vallender et al. 2007; Turbek et al. 2021). Cases of extrapair mating deviating from social pairing with respect to lineage identity have been documented in systems with severe costs of hybridization (i.e., complete intrinsic postzygotic isolation; Veen et al. 2001) or where males of one lineage are socially dominant to males of another (Reudink et al. 2006), neither of which characterizes the crossbills we studied. Although we are unable to envision a plausible scenario by which extrapair paternity alters our general conclusions, direct measures of extrapair paternity are needed to assess whether it occurs.

Total Reproductive Isolation. We used the methods outlined by Ramsey et al. (2003) to calculate the absolute contribution of each sequentially and independently acting component of reproductive isolation (AC_n) to calculate total reproductive isolation. Because habitat isolation acts first, $AC_{HI} = HI$. The absolute contribution of the second-acting barrier, reduced immigrant fecundity (AC_{RIF}), equals $RIF(1 - AC_{HI})$. The absolute contribution of behavioral isolation (AC_{BI}) equals $BI[1 - (AC_{HI} + AC_{RIF})]$. Total reproductive isolation (TI) is the sum of the absolute contributions of habitat isolation, reduced immigrant fecundity, and behavioral isolation ($TI = AC_{HI} + AC_{RIF} + AC_{BI}$). We focus on prezygotic reproductive isolating

barriers because prezygotic isolation generally appears to be most important in the early stages of divergence (Coyne and Orr 1989, 2004; Nosil et al. 2005; Lowry et al. 2008; Sobel et al. 2010; Sobel and Streisfeld 2015; Lackey and Boughman 2017; Karrenberg et al. 2019; Campillo et al. 2020; but see Irwin 2020), although extrinsic postzygotic isolation may also be important for crossbill speciation (e.g., Snowberg and Benkman 2007).

Assortative Flocking

One mechanism that could link performance differentials to behavioral isolation in crossbills is assortative flocking. To estimate the extent of assortative flocking, we recorded whether each crossbill flock encountered during fieldwork included only one ecotype or both based on contact calls heard. Using these data, we estimated the proportion of flocks that consisted of a single ecotype in each breeding period. We did not account for variation in the proportion of each ecotype in mixed flocks, as this was difficult to assess accurately, especially in large flocks with many crossbills calling simultaneously.

To experimentally test whether the propensity to join flocks of heterotypics relative to flocks of homotypics can account for the observed patterns of assortative flocking, we employed previously developed protocols using playback of crossbill contact calls (Smith et al. 2012; Sobel and Streisfeld 2015; Porter and Benkman 2019). These experiments mimic the behavior of a crossbill perched in conifers loudly calling to other crossbills flying over, an extremely common behavior that stimulates flock formation (Newton 1972). By recording whether crossbill flocks land in response to playback, we were able to assess the propensity of crossbills to associate with individuals producing either heterotypic or homotypic calls (Smith et al. 2012; Sobel and Streisfeld 2015; Porter and Benkman 2019). We used standardized recordings of lodgepole pine crossbill and ponderosa pine crossbill contact calls from a previous study of crossbill flocking behavior (Smith et al. 2012). Smith et al. (2012) used Raven Pro (ver. 1.2; Cornell Laboratory of Ornithology, Ithaca, NY) to copy and paste digitally recorded contact calls to synthesize recordings representing monotypic flocks of lodgepole pine and ponderosa pine crossbills. Each synthesized recording was made using the contact calls of a single individual, and calls from 10 individuals of each ecotype were used to make 10 synthesized recordings per call type. Individuals were chosen on the basis of the clarity of recordings. All synthesized recordings were standardized for amplitude, duration, and call rate; 30 s of calling at a rate of 88 calls per 30 s followed by a 15-s pause.

We conducted experiments at the beginning of three breeding periods (in pine during winter/spring 2016 and

summer/fall 2019 in the Laramie Range, and in spruce during summer/fall 2018 in the Snowy Range; fig. S1), when crossbills were in large flocks prior to pairing and when assortative flocking should be most consequential for mate choice and thus behavioral isolation. Recordings were broadcast between 0800 and 1100 hours using a Pignose 7-100 Legendary portable amplifier (Pignose-Gorilla, Las Vegas, NV) in 10 open areas within a study area (each separated by at least 500 m) that were adjacent to mature conifer forest with many cone-bearing trees. Recordings of both ecotypes were played at each location on separate days, and the order that the ecotypes were played was alternated at each location. The speaker was tilted upward and placed at the edge of the forest at a height of approximately 1.5 m. During each 120-min trial, calls were broadcast continuously, and we recorded whether crossbills flying over landed in the forest near the speaker or continued to fly over. We identified crossbills aurally on the basis of their distinctive contact calls. Each flock was treated as an independent sample, as in previous studies (Smith et al. 2012; Sobel and Streisfeld 2015; Porter and Benkman 2019). Of the 275 total flocks encountered during these experiments, six (2%) were mixed flocks. We excluded mixed flocks from our analyses.

Statistical Analyses

We used generalized linear mixed models with beta likelihood distributions and logit link functions in R (ver. 4.02; R Core Team 2020) using the package glmmTMB (Brooks et al. 2017) to assess the relationships between each reproductive isolating barrier and total reproductive isolation (the response variables) to performance differentials, relative resource availability, and their interaction (all fixed effects). All fixed effects were centered before analyses. We also included study site as a random effect, given that some locations were sampled multiple times. We did not have sufficient degrees of freedom to add both study location and sampling year as random effects. We suggest that study location is the more informative random effect, given that sampling year is perfectly correlated with the conifers that crossbills were feeding on in each breeding season. This is because pines and spruce usually produce seeds in alternate years and cone crops are spatially correlated over long distances (Smith and Balda 1979). In contrast, at one study location (the Front Range) crossbills were feeding on pine in one year and on spruce in another year in our data. Furthermore, there could be an effect of location if, for example, sites differed in habitat structure in some way that altered isolation (e.g., variation in the extent to which different conifers intermix on the landscape). Finally, neither sampling location nor year was significant in any comparison. We used the same approach but with the extent of as-

sortative flocking as a response variable, where the proportion of flocks that were comprised of only one ecotype was the response variable. We analyzed playback data similarly, where the response variable was the proportion of crossbills that landed in response to heterotypic calls divided by the proportion landing in response to homotypic calls. However, we did not include an interaction term or a random effect in this last analysis because we did not have sufficient degrees of freedom. In all analyses, the response variable was min-max transformed because models with beta distributions do not permit boundary values (i.e., 0 or 1).

Results

Strength of Reproductive Isolation

The magnitude of each reproductive isolating barrier varied among breeding periods, resulting in total reproductive isolation ranging from complete (i.e., total isolation $= 1$) during two breeding periods in pine to much lower total isolation (0.724) when breeding in spruce (table 1). Habitat isolation, reduced immigrant fecundity, behavioral isolation, and total reproductive isolation increased with increases in the performance differential ($P < .0152$ for all comparisons; table 2; fig. 3). We also found that reduced immigrant fecundity was negatively associated with relative resource availability ($P = .0001$; table 2; fig. 4A), as was total isolation ($P = .0034$; table 2; fig. 4B). We found no relationship between relative resource availability and the other barriers ($P > .3$ for all comparisons; table 2). Finally, we found that the interaction between the performance differential and relative resource availability influenced the strength of habitat isolation ($P = .0074$; table 2), reduced immigrant fecundity ($P < .0001$; table 2), and total isolation ($P < .0001$; table 2). These interactions are illustrated in figure 5, where the predicted relationships between reproductive isolation and performance differential are plotted separately for two levels of relative resource availability (relatively low and high), showing a strong and steep increase in reproductive isolation as the performance differential increased when relative resource availability was low but not when it was high.

Assortative Flocking

The proportion of flocks that were assortative (i.e., composed of only one ecotype) varied from 0.973 when breeding in pine to 0.583 when breeding in spruce, with the proportion assortative increasing with increases in the performance differential ($P = .0006$; table 2; fig. 6A). Similarly, crossbills were less likely to respond to playback of heterotypic calls relative to homotypic calls as

Table 1: Strength of three prezygotic reproductive isolating barriers and total isolation between ponderosa pine crossbills and lodgepole pine crossbills during each breeding period

Location and year (conifer)	Individual component of reproductive isolation			Absolute contribution to total reproductive isolation			
	Habitat isolation	Reduced immigrant fecundity	Behavioral isolation	Habitat isolation	Reduced immigrant fecundity	Behavioral isolation	Total isolation
Pike National Forest 2015 (pine)	.858	.336	.944	.858	.096	.179	.989
Laramie Range 2016 (pine)	.751	.269	.938	.751	.067	.171	.989
Grand Mesa 2016 (spruce)	.290	−.372	.717	.290	−.264	.699	.725
Snowy Range 2017 (spruce)	.261	−.515	.773	.261	−.381	.866	.746
Snowy Range 2018 (spruce)	.123	−.236	.778	.123	−.207	.844	.759
Front Range 2018 (spruce)	.130	.492	.831	.130	.432	.364	.963
Laramie Range 2019 (pine)	.824	.708	1.0	.824	.124	.051	1.0
Pike National Forest 2019 (pine)	.917	.4340	.999	.917	.036	.047	.999
Front Range 2019 (pine)	.775	.553	1.0	.775	.125	.101	1.0
Front Range 2020 (pine)	.988	.153	.9	.988	.002	.010	.999

Note: The individual component and absolute contribution to total reproductive isolation for each reproductive isolating barrier are listed.

performance differentials increased ($P = .0079$; table 2; fig. 6B) consistent with the observed variation in assortative flocking. We also found that the interaction between the performance differential and relative resource availability influenced the proportion of assortative flocks ($P = .0265$; table 2). Specifically, flocks tended to be most assortative when the performance differential was large and relative resource availability was low. However, consistent variation in response to playback was not evident in relation to relative resource availability ($P = .51$; table 2), suggesting that relative resource availability may have a negligible effect on assortative flocking. Finally, we found that the proportion of flocks that were assortative by ecotype was positively correlated with the strength of behavioral isolation ($P = .0003$; fig. 6C), thus providing a mechanistic link between performance differential varia-

tion and variation in the strength of behavioral isolation (fig. 3C).

Discussion

Our results show that prezygotic reproductive isolation between lodgepole pine and ponderosa pine crossbills increases with increases in the performance differential during breeding. When variation in bill morphology causes large differences in feeding efficiency (i.e., performance differentials are large), prezygotic reproductive isolating barriers reduce most or all gene flow between ecotypes (mean total isolation in pine = 0.996). By contrast, when conifer seeds are easily accessible to a wide range of bill morphologies (i.e., small performance differentials), each

Table 2: Summary of the generalized linear mixed models ($n = 10$ breeding seasons) testing for the effects of performance differentials and relative resource availability (observed intake rate/necessary intake rate for breeding) on individual reproductive isolating barriers, total prezygotic reproductive isolation, and assortative flocking

Response variable	β (P)		
	Performance differential	Relative resource availability	Interaction
Habitat isolation	**7.88** (<.0001)	−1.18 (.3435)	**−11.46** (.0074)
Reduced immigrant fecundity	**11.69** (<.0001)	**−5.60** (.0001)	**−19.73** (<.0001)
Behavioral isolation	**7.66** (.0151)	.51 (.8079)	−9.08 (.2121)
Total isolation	**16.60** (<.0001)	**−4.26** (.0034)	**−28.94** (<.0001)
Assortative flocking	**10.67** (.0006)	−.79 (.5578)	**−15.66** (.0265)
Response to playback	**−1.98** (.0079)	.49 (.5141)	NA

Note: Beta coefficients with $P < .05$ are highlighted in boldface. NA = not available.
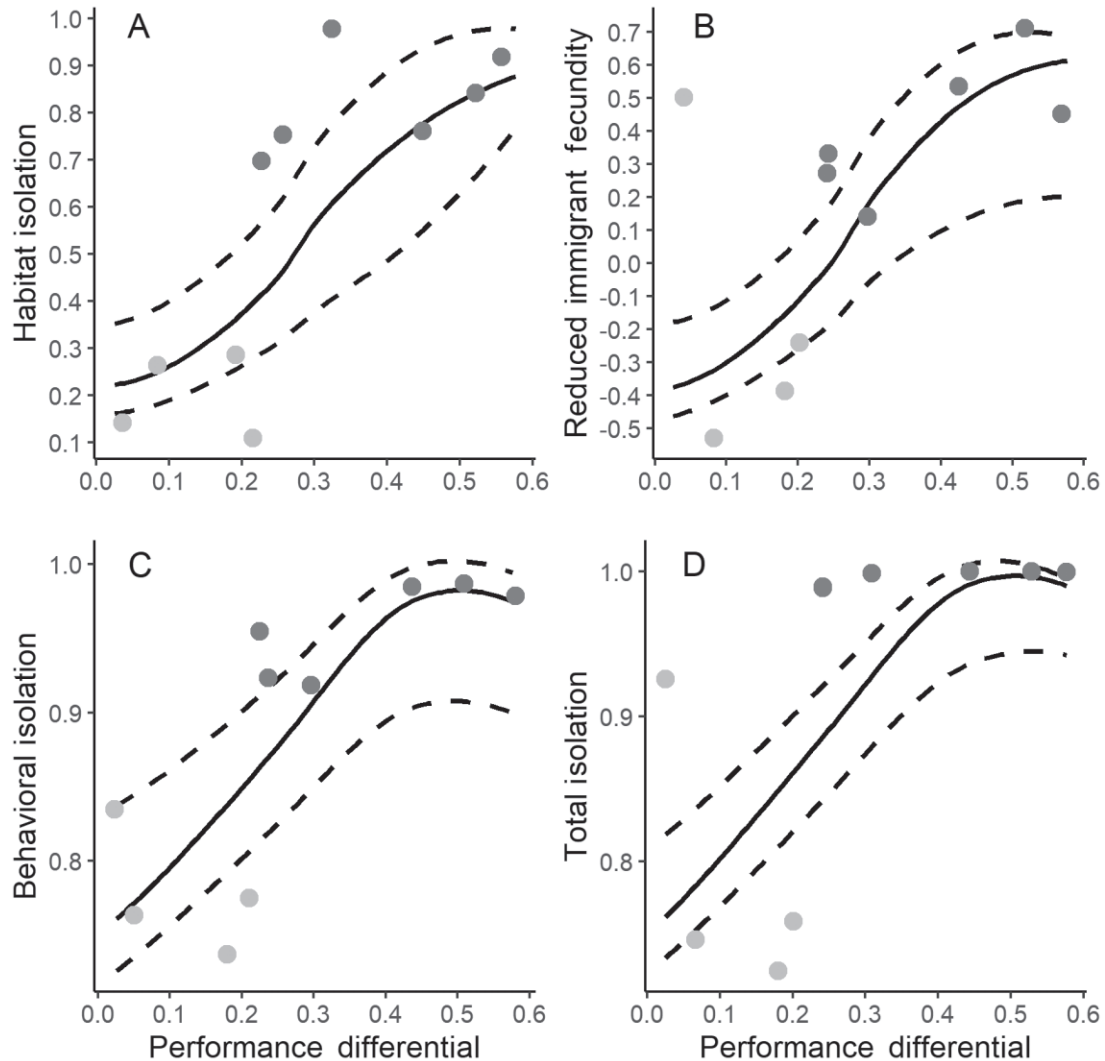
Figure 3: Premating reproductive isolation increases with increases in the performance differential. The solid curve represents model predictions from a generalized linear mixed model with a beta distribution for habitat isolation (A; $P < .0001$), reduced immigrant fecundity (B; $P < .0001$), behavioral isolation (C; $P = .0151$), and total reproductive isolation (D; $P < .0001$). Dashed lines represent model 95% confidence intervals, and individual points represent observed data. Values of reproductive isolation can range from -1 (complete disassortative mating) to 1 (complete reproductive isolation); 0 represents random mating. Dark gray points are from mixed pine breeding seasons, and light gray points are from spruce breeding seasons.

reproductive isolating barrier and total reproductive isolation are considerably smaller (mean total isolation in spruce = 0.789). We note that extrapair paternity could alter these values. However, as discussed in the methods section, we suspect that extrapair paternity is rare to absent, and if it occurred we have no reason to expect a bias that would alter our results qualitatively.

Habitat use in crossbills is driven by matching habitat choice (Marquiss and Rae 2002; Benkman 2017; Gómez-Blanco et al. 2019), wherein individuals preferentially use the conifer with the highest profitability (Benkman 1987). When conifers impose a weak performance differential,

individuals with a wide range of bill morphologies have similar intake rates and converge in their use of a single conifer and habitat type, resulting in weak habitat isolation. By contrast, when performance differentials are large, each ecotype generally uses different conifers (those on which intake rates are highest) and hence different forest patches, leading to strong habitat isolation. Nonetheless, some individuals are found in the "wrong" habitat (as indicated by the comparatively low intake rates of immigrants), resulting in incomplete habitat isolation. However, as performance differentials increase, the frequency of breeding by immigrants relative to the locally adapted ecotype
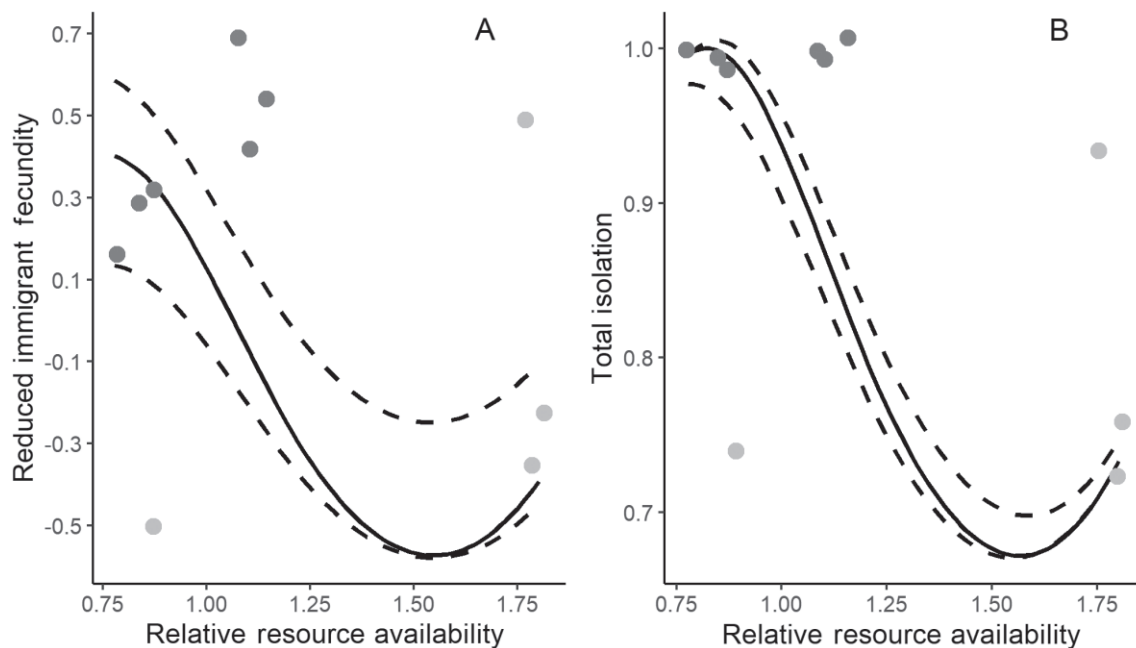
Figure 4: The strength of reduced immigrant fecundity (*A*) and total isolation (*B*) decreases as relative resource availability (intake rate/ necessary intake rate for breeding) increases. The solid curve represents model predictions from a generalized linear mixed model with a beta distribution for reduced immigrant fecundity (*A*; $P = .0001$) and total isolation (*B*; $P = .0034$). Dashed lines represent model 95% confidence intervals, and individual points represent observed data. Values of reproductive isolation can range from −1 (complete disassortative mating) to 1 (complete reproductive isolation); 0 represents random mating. Dark gray points are from mixed pine breeding seasons, and light gray points are from spruce breeding seasons. Note that the curves plotted here contain inflections that suggest a slight upward trend at the highest values of relative resource availability and the lowest values of isolation. These are likely a statistical artifact rather than a biological reality.
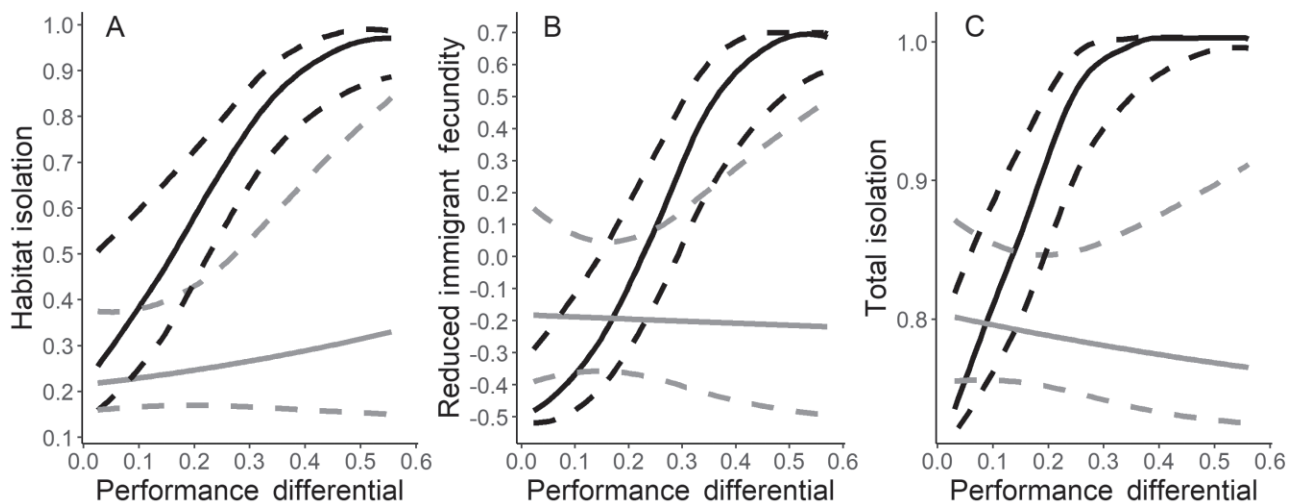

Figure 5: Habitat isolation (*A*), reduced immigrant fecundity (*B*), and total prezygotic isolation (*C*) increase with increases in the performance differential at low levels of relative resource availability (black curves) but not at high levels (gray curves; performance differential × relative resource availability: $P < .007$ for each comparison). Solid curves represent model predictions from a generalized linear mixed model with a beta distribution. Dashed lines represent model 95% confidence intervals. Low relative resource availability represented a value of 0.85 for energy intake rate divided by the intake rate estimated for the most energy-demanding nesting stage, whereas a high relative resource availability represented a value of 1.10.
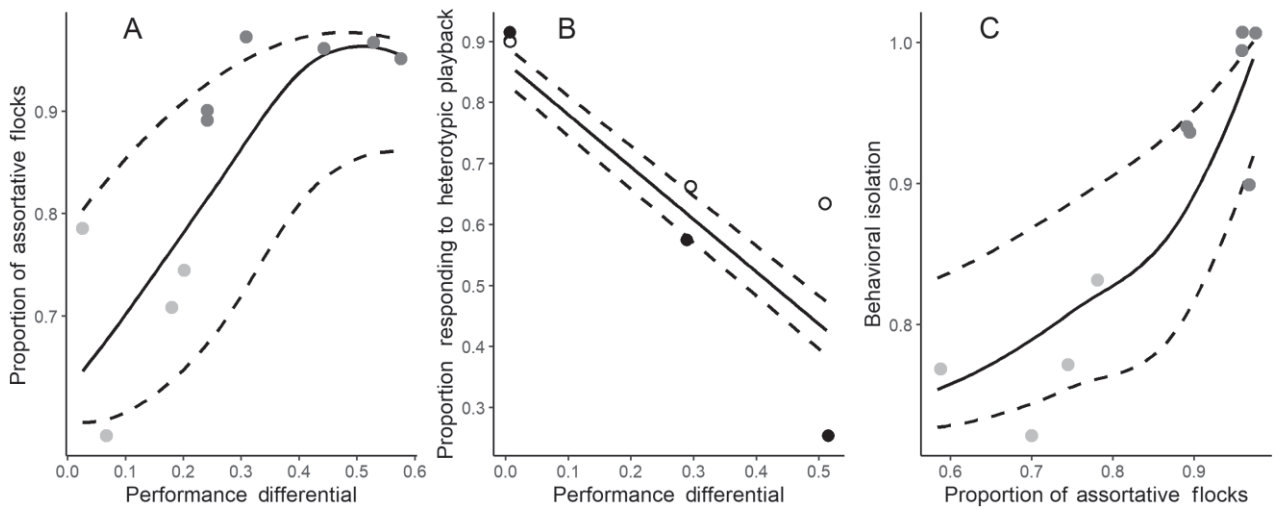
Figure 6: The proportion of flocks that were assortative by ecotype increased as performance differentials increased (*A*; *P* = .0006). This variation in the extent of assortative flocking is presumably driven by ponderosa pine crossbills (white circles) and lodgepole pine crossbills (black circles) being less likely to land in response to playback of the other ecotype's calls (relative to playback of their own ecotype) as performance differentials increased (*B*; *P* = .0079). As expected, if behavioral isolation increases with assortative flocking, behavioral isolation increased with the proportion of flocks that were assortative (*C*; *P* = .0003). In *A* and *C*, light gray points are from spruce breeding seasons, and dark gray points are from mixed pine breeding seasons. Solid curves represent model predictions, and dashed curves represent model 95% confidence intervals from a generalized linear mixed model with a beta distribution.

decreases, leading to higher levels of reduced immigrant fecundity. This likely reflects the greater energetic demands of reproduction compared with survival and maintenance (Benkman 1990; Porter and Benkman 2017). Thus, although some immigrants may persist in a forest despite low intake rates, they may struggle to acquire sufficient resources to reproduce when the performance differential is large. Finally, gene flow between ecotypes is further reduced as performance differentials increase due to increases in behavioral isolation. The lowered response to heterotypic playbacks at higher performance differentials provides a behavioral mechanism for the increase in assortative flocking at higher performance differentials. The increase in assortative flocking, in turn, appears to account for the elevated levels of behavioral isolation at high performance differentials. These patterns of association are likely driven by the greater benefits of assortative flocking at high performance differentials (Smith et al. 1999, 2012). Thus, increases in performance differentials increase reproductive isolation in multiple ways, consistent with the coupling model of reproductive isolation proposed by Butlin and Smadja (2018) and predictions of grouping models more generally (Kopp et al. 2018).

While the strength of the performance differential had the largest and most consistent effects on reproductive isolation, we also found that reduced immigrant fecundity and total isolation decreased as relative resource availability increased. Furthermore, we found that relative resource availability modulated the relationship between the performance differential and habitat isolation, reduced immigrant fecundity, and total isolation. As relative resource availability increased, the positive relationship between reproductive isolation and the performance differential weakened and levels of reproductive isolation declined. These patterns are consistent with previous work suggesting that when resource availability is high, even poorly adapted individuals can meet their energy demands on otherwise unusable resources (Poisot et al. 2011). This was evident for crossbills in the lodgepole pine forests of southern Idaho, where lodgepole pine has elevated seed defenses: in years with low resource availability, only immigrant crossbills with bill sizes near the local optimum remained for multiple years, whereas individuals with suboptimal bill sizes emigrated (Benkman 2017). In contrast, in years with high resource availability, individuals with a wider range of bill sizes remained resident (Benkman 2017) and bred (C. W. Benkman, unpublished data). Likewise, large- and small-bill morphs of black-bellied seedcrackers (*Pyrenestes ostrinus*) converged in their use of abundant small seeds that the large morph was less efficient on, resulting in high overlap in habitat use during the breeding season (Smith 1990). As the abundance of seeds declined after the breeding season, the large morph shifted to feeding on larger seeds, resulting in low diet and habitat overlap between the two morphs (Smith 1990). Our results thus add to a small body of evidence indicating that variation in resource availability can

alter the degree to which performance trade-offs promote reproductive isolating barriers.

We also found some evidence that the extent of assortative flocking was influenced by the interaction between relative resource availability and the performance differential. Specifically, we found that assortative flocking increased as relative resource availability decreased at large performance differentials, although the statistical support for this effect was notably lower than that for other model effects. However, we did not detect an effect of relative resource availability on the response to playbacks. Additionally, it is unclear to us why relative resource availability would alter assortative flocking because the feeding efficiency benefits from assortative flocking (Smith et al. 1999) should accrue regardless of relative resource availability. We note that the costs of searching for homotypic flockmates are likely minimal, given the abundance of both ecotypes at our study sites and the long-distance movements of crossbills during much of the breeding period (Benkman and Young 2020).

Behavioral isolation presumably increases as assortative flocking increases because crossbills choose mates from within flocks (Newton 1972). Indeed, female Eurasian siskins (*Spinus spinus*), a close relative of crossbills, preferred male flockmates in mate choice experiments and even preferred drab flockmates over highly ornamented nonflockmates (Senar et al. 2013). The links between performance differentials, assortative flocking, and behavioral isolation suggest that behavioral isolation may sometimes act like other reproductive isolating barriers typically assumed in grouping models of speciation (e.g., habitat isolation, temporal isolation, and reduced immigrant viability/fecundity; Kopp et al. 2018) in that it increases as the performance differential increases. Because public information use (Danchin et al. 2004) and fitness benefits associated with phenotype-based assortative social grouping (Smith et al. 1999) are taxonomically widespread (Krause and Ruxton 2002), the dynamics we document in crossbills likely apply to other systems. It may be particularly fruitful to evaluate assortative grouping as a speciation mechanism in other taxa that use public information, especially in cases where speciation is driven by resource specialization (e.g., herbivorous insects [Cocroft 2005], killer whale [*Orcinus orca*] ecotypes [Riesch et al. 2012], and threespine stickleback [*Gasterosteus aculeatus*] ecotypes [Webster and Hart 2006]).

While moderate prezygotic reproductive isolation between crossbill ecotypes exists even when performance differentials are small, there is considerable scope for gene flow to inhibit divergence. Indeed, prezygotic reproductive isolating barriers may need to be at or near completion to cause speciation when there is much scope for gene flow (Sambatti et al. 2012; Karrenberg et al. 2019; Irwin

2020). Thus, the conditions necessary for speciation with gene flow in crossbills may be met only when ecotypes are breeding while feeding on their respective key conifers that impose strong feeding trade-offs (average value of TI in pine $= 0.996$). Interestingly, this level of total prezygotic reproductive isolation is almost identical to that between the Cassia crossbill and both lodgepole pine and ponderosa pine ecotypes (average value of total reproductive isolation across six breeding seasons $= 0.999$; Smith and Benkman 2007; Benkman et al. 2009). The Cassia crossbill shows elevated levels of genomic divergence compared with the nine ecotypes and is the only reciprocally monophyletic lineage in the North American red crossbill complex (Parchman et al. 2016). The reason that Cassia crossbills, but no other North American crossbill, have speciated despite tremendous scope for gene flow throughout divergence (Parchman et al. 2016; Brock et al., unpublished manuscript) may be because Cassia crossbills do not opportunistically exploit large cone crops of conifers that impose small performance differentials (Benkman and Porter 2020; Benkman and Young 2020). Indeed, Cassia crossbills have specialized on a distinct population of lodgepole pine that is the most stable seed-producing plant in the world, with elevated cone defenses against crossbills (Benkman et al. 2003). The constant presence of a strong performance differential during breeding, combined with strong food limitation (Benkman et al. 2012), likely accounts for the consistently near-complete reproductive isolation between Cassia crossbills and sympatric red crossbill ecotypes (minimum value of total reproductive isolation across six breeding seasons $= 0.993$; Smith and Benkman 2007; Benkman et al. 2009). By contrast, the less genomically divergent red crossbill ecotypes likely experience dramatic temporal variation in the degree of reproductive isolation, resulting in regular periods of elevated gene flow.

A classic explanation for variation in progress toward speciation is that stronger divergent selection results in stronger reproductive isolation and thus further progress along the "speciation continuum" (Nosil et al. 2009). Indeed, our data support this prediction, given that reproductive isolation is stronger as the performance differential increases. However, divergent selection alone cannot explain why Cassia crossbills have speciated while other crossbills have not. If we assume a positive relationship between the magnitude of adaptive phenotypic divergence and the magnitude of divergent selection (a reasonable assumption in crossbills; Benkman 2003), Cassia crossbills are not outliers relative to other crossbills. Indeed, the magnitude of divergence in bill depth (the primary target of divergent selection in crossbills; Benkman 2003) between Cassia crossbills and ponderosa pine crossbills (the ecotype that is most abundant in sympatry with Cassia crossbills; Smith and Benkman 2007) is equal to or less than that

between most sympatric red crossbill ecotypes, including lodgepole pine and ponderosa pine crossbills (Groth 1993*b*; Benkman 1993, 2003). A similar situation occurs in European red crossbills, where the lineage that has genomically diverged the most on the European continent (*L. c. hispana*) is not especially divergent in bill morphology but occurs in a region dominated by a highly stable conifer resource (*Pinus halepensis*) that is likely to lead to a consistently strong performance differential and to limited pulses in resource availability (i.e., fig. 2*D*; Parchman et al. 2018). By contrast, sympatric European crossbills with much greater divergence in bill morphology that opportunistically breed during large Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) cone crops (i.e., fig. 2*A*) have genomically diverged little if at all (Piertney et al. 2001; Parchman et al. 2018). Therefore, temporal variation in reproductive isolation associated with variation in performance differentials and relative resource availability during breeding may best explain variation in the extent of genomic divergence among crossbill lineages.

Likewise, we suspect that the occurrence of small performance differentials and high levels of resource availability during breeding often act to prevent speciation with gene flow in other systems, including, for example, Darwin's ground finches (*Geospiza* spp.). Food limitation, and thus resource competition and divergent selection associated with resource use, is most intense during the least productive periods when species typically do not breed (Smith et al. 1978; Schoener 1982; Marshall and Wrangham 2007; Grant and Grant 2014). Thus, adaptations for exploiting alternative resources may be driven largely by resource-poor conditions in the nonbreeding season, when performance differentials are large (Smith et al. 1978; Schoener 1982; Benkman and Miller 1996; Marshall and Wrangham 2007; Grant and Grant 2014). Importantly, these alternative adaptations do not compromise the ability to exploit easily accessible abundant resources (Robinson and Wilson 1998) that many species time reproduction to coincide with (Williams et al. 2017), leading to a high degree of ecological overlap between phenotypically divergent sympatric lineages during the breeding season (Smith et al. 1978; Hindar and Jonsson 1982; Schoener 1982; Smith 1990; Schluter and McPhail 1992; Smith and Skúlason 1996). Indeed, there is often a decoupling between phenotypic and dietary variation during the breeding season (Wiens and Rotenberry 1979; Sæther 1982; Török 1993; Dumont 1995; Numi and Väänänen 2001; Lambert et al. 2004). Breeding in the presence of weak trade-offs and abundant resources may inhibit reproductive isolating barriers between sympatrically diverging lineages, leading to high levels of gene flow and necessitating extensive allopatry for speciation. This may explain why sympatric speciation is rare except possibly in systems where breeding coincides with the use of alternative resources that impose strong trade-offs, such as phy-

tophagous insects (Berlocher and Feder 2002; Drès and Mallett 2002; Bolnick and Fitzpatrick 2007) and perhaps some crossbills (Smith and Benkman 2007; Parchman et al. 2016).

Statement of Authorship

Both authors conceived of this project and obtained funding for it. C.K.P. led data collection and analyses. C.K.P. wrote the original draft and, along with C.W.B., contributed to editing and revising the manuscript.

Data and Code Availability

All data and code associated with this article are available in the Dryad Digital Repository (https://doi.org/10.5061/dryad.hqbzkh1h3; Porter and Benkman 2021).

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