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Cite this article: Porter CK, Benkman CW. 2019 Character displacement of a learned behaviour and its implications for ecological speciation. *Proc. R. Soc. B* **286**: 20190761. <http://dx.doi.org/10.1098/rspb.2019.0761>

Received: 1 April 2019

Accepted: 10 July 2019

Subject Category:

Evolution

Subject Areas:

behaviour, ecology, evolution

Keywords:

character displacement, crossbills, cultural evolution, public information, reproductive isolation, speciation

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Electronic supplementary material is available online at <https://dx.doi.org/10.6084/m9.figshare.c.4579421>.

Character displacement of a learned behaviour and its implications for ecological speciation

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Cultural evolution may accelerate population divergence and speciation, though most support for this hypothesis is restricted to scenarios of allopatric speciation driven by random cultural drift. By contrast, the role of cultural evolution in non-allopatric speciation (i.e. speciation with gene flow) has received much less attention. One clade in which cultural evolution may have figured prominently in speciation with gene flow includes the conifer-seed-eating finches in the red crossbill (*Loxia curvirostra*) complex. Here we focus on Cassia crossbills (*Loxia sinesciuris*; an ecotype recently split taxonomically from red crossbills) that learn social contact calls from their parents. Previous work found that individuals modify their calls throughout life such that they become increasingly divergent from a closely related, sympatric red crossbill ecotype. This open-ended modification of calls could lead to character displacement if it causes population-level divergence in call structure that, in turn, reduces (maladaptive) heterospecific flocking. Heterospecific flocking is maladaptive because crossbills use public information from flockmates to assess resource quality, and feeding rates are depressed when flockmates differ in their ability to exploit a shared resource (i.e. when flockmates are heterospecifics). We confirm the predictions of character displacement by documenting substantial population-level divergence in Cassia crossbill call structure over just two decades and by using field experiments to demonstrate that Cassia and red crossbills differentially respond to these evolved differences in call structure, reducing heterospecific flock formation. Moreover, because crossbills choose mates from within flocks, a reduction in heterospecific flocking should increase assortative mating and may have been critical for speciation of Cassia crossbills in the face of ongoing gene flow in as few as 5000 years. Our results provide evidence for a largely neglected yet potentially widespread mechanism by which reproductive isolation can evolve between sympatric lineages as a byproduct of adaptive cultural evolution.

1. Introduction

Once thought to be unique to humans, recent decades have seen mounting evidence across the animal kingdom of culture [1] and cultural evolution [2], indicating that evolution of learned traits may play an important role in numerous biological phenomena [3]. Indeed, studies in recent decades have implicated cultural transmission in the evolution of feeding behaviour [4], habitat use [5] and migration [6]. Some studies suggest that cultural evolution of these and other behaviours may interact with and even drive genomic evolution [7,8].

Cultural evolution could have its most consequential impacts on genomic evolution through its effects on speciation, wherein gene flow between diverging lineages is reduced and eventually eliminated [9]. The rapid evolution of culturally inherited traits that affect reproductive isolation (e.g. mating signals and preferences) suggests that learning may facilitate speciation through

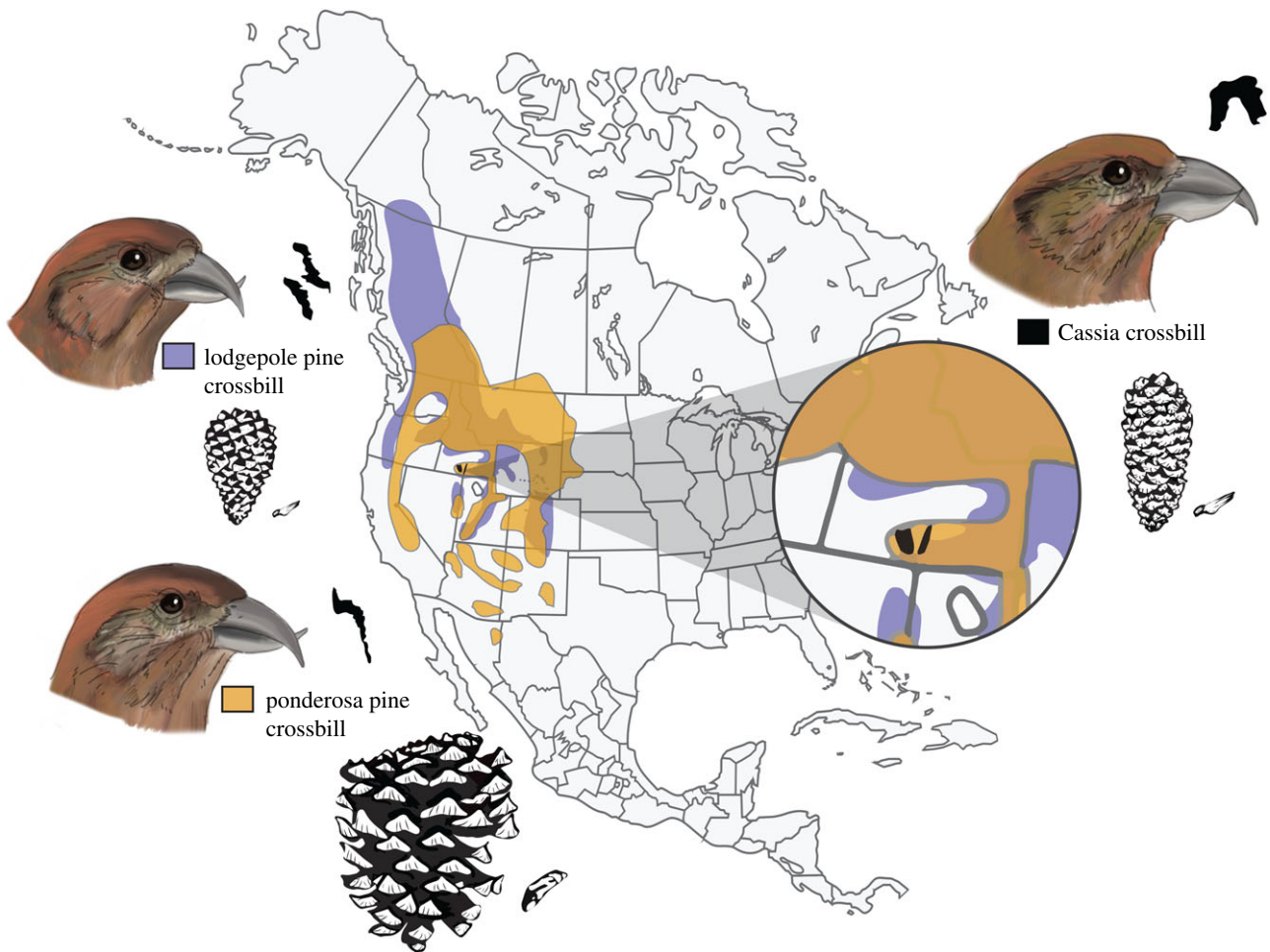


Figure 1. The distributions of lodgepole pine crossbills (purple) and ponderosa pine crossbills (orange) overlap widely and with Cassia crossbills (black in inset). Also shown are the heads of the three crossbill taxa (males), their associated conifer cones and seeds (lodgepole pine for Cassia crossbills too, but larger and better defended at the distal end against crossbills because of a coevolutionary arms race), and contact call spectrograms.

the rapid divergence of signals and preferences between populations [1,10–13]. Indeed, there is now a substantial body of theoretical and empirical evidence indicating that cultural evolution facilitates allopatric speciation ([11,14–16; but see [17]), especially through random evolutionary divergence between populations (i.e. cultural drift; [15,18,19]).

By contrast, there is much less evidence bearing on the role of cultural evolution in models of speciation with gene flow. One route to speciation with gene flow is ecological speciation, wherein reproductive isolating barriers evolve between lineages owing to divergent natural selection [20]. As lineages evolve divergent phenotypes during ecological speciation, selection may favour the evolution of signals associated with divergent phenotypes (i.e. marker traits) that reduce maladaptive ecological or reproductive interactions between lineages (i.e. character displacement; [13,21–23]). If mate choice is based on such marker traits, diverging lineages will become increasingly reproductively isolated as marker traits diverge, thus facilitating ecological speciation [23,24]. When marker traits and mate preferences for the marker trait are learned from parents rather than genetically inherited, there is no opportunity for gene flow and recombination to break up associations between the marker trait and preference for the marker trait, thus eliminating the major constraint to speciation with gene flow [24]. However, rather than facilitating ecological speciation, learning may result in signal convergence through the learning of heterospecific signals and thereby increase gene flow

between sympatric lineages [24,25]. Thus, the net effect of cultural evolution on speciation with gene flow is unclear [26].

Here, we track the evolution of learned vocalizations over time and experimentally test whether character displacement in vocalization structure could act to cause reproductive isolation between seed-eating finches known as crossbills (*Loxia* spp.; figure 1). In North America, the red crossbill (*Loxia curvirostra*) complex consists of nine widely sympatric ecotypes that have diversified in response to divergent selection on bill morphology for specializing on cone seeds of different conifer species [27]. Crossbill ecotypes have also diversified in the acoustic structure of contact calls that mediate communication and social cohesion among individuals (figure 2c; [28]), which spend most of their lives in flocks (figure 2a; [29]). Because ecotypes differ in contact calls, these calls act as a marker trait that might be an adaptation for facilitating flocking among individuals with similar bill sizes (i.e. assortative flocking; [30,31]). Crossbills use both their own feeding rates and those of their flockmates (i.e. public information) when assessing patch quality [31]. Because public information increases feeding performance when flockmates have similar feeding abilities (i.e. similar bill sizes; [27]) but reduces feeding performance when flockmates differ in their ability to feed on a shared resource, assortative flocking is adaptive [31]. Consistent with this interpretation, previous field experiments found that crossbills were increasingly likely to land in response to playbacks of sympatric ecotypes as their difference in bill

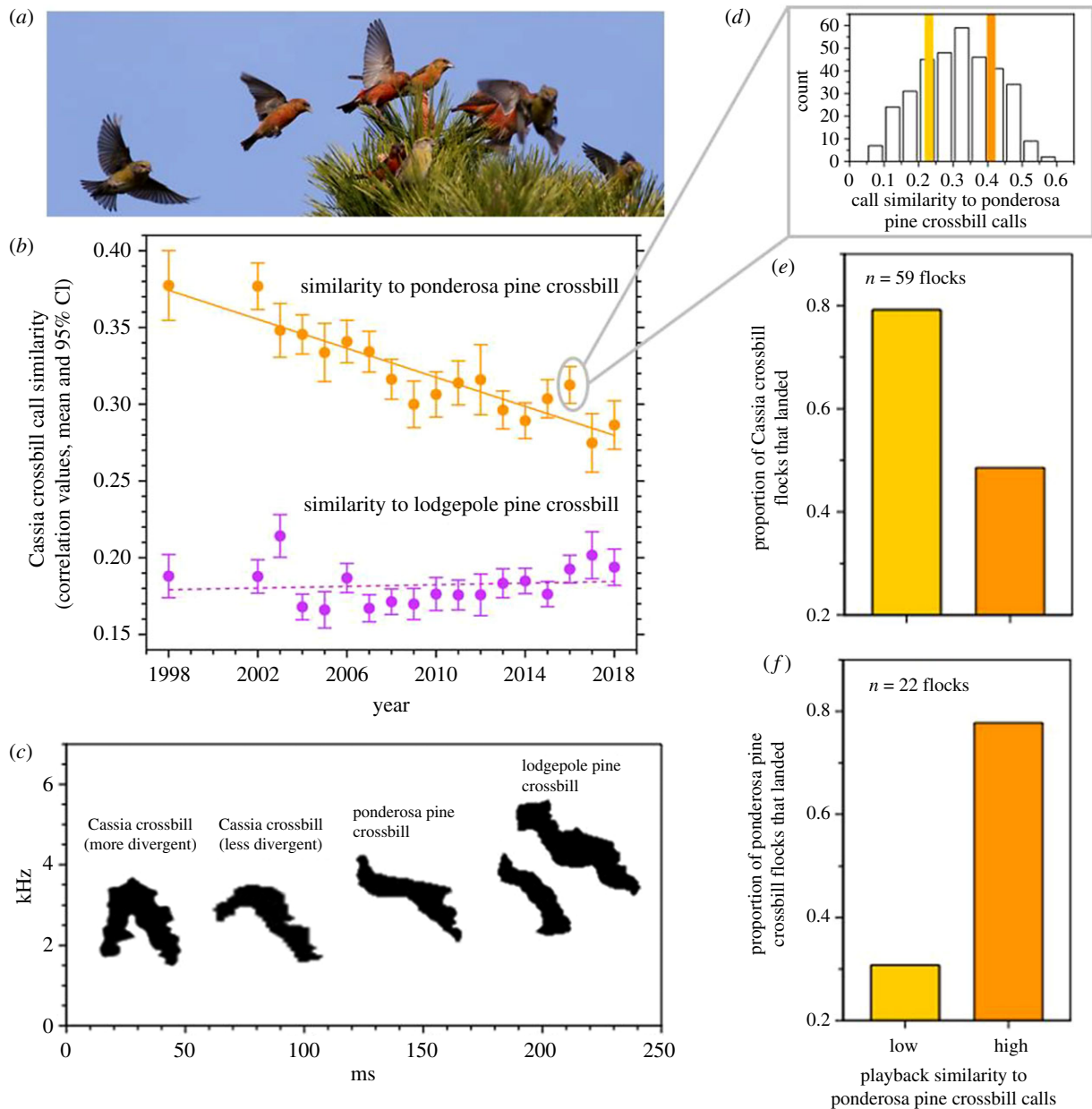


Figure 2. The divergence in Cassia crossbill contact calls from ponderosa pine crossbills over the last 20 years has led to stronger assortative flocking. (a) A flock of red crossbills landing atop a pine tree. The six red–orange individuals are males and the four yellow–green individuals are females. (Photo credit: Sam Galick.) (b) The contact calls of Cassia crossbills diverged from those of ponderosa pine crossbills (similarity decreased) between 1998 and 2018 (solid line is the least-squares regression; see text), whereas their calls did not change over time with respect to the calls of lodgepole pine crossbills. The number of Cassia crossbills recorded each year ranged from 67 to 432 with an average of 247. (c) Representative spectrograms of Cassia, ponderosa pine and lodgepole pine crossbills. The leftmost spectrogram illustrates the greater frequency modulation (greater contrast in the slopes between the ascending and descending elements) found in Cassia crossbill calls that were more divergent from ponderosa pine crossbills (similarity of representative call to ponderosa pine crossbill calls = 0.275) than Cassia crossbill calls with lower frequency modulation (similarity of representative call to ponderosa pine crossbill calls = 0.325). (d) Recordings used in the playback experiments were created by randomly choosing recordings whose call similarities to ponderosa pine crossbill calls approximated the lower quartile (light orange bar; low similarity calls) and upper quartile (dark orange bar; high similarity calls) values in the distribution of correlation values for Cassia crossbills in 2016. Contact call divergence (b) should lead to stronger assortative flocking because (e) Cassia crossbill flocks were more likely to land in response to playbacks of their calls that were more divergent from those of ponderosa pine crossbills (i.e. low similarity), whereas (f) ponderosa pine crossbills were less likely to land in response to such calls (table 1).

size decreased [30]. Because crossbills choose mates from within flocks [29], reproductive isolation between ecotypes emerges as a byproduct of assortative flocking by contact calls and thus bill size [30]. Consequently, understanding how calls are transmitted and diverge, and whether this facilitates assortative flocking is key to understanding the influence of cultural evolution in speciation.

Like other cardueline finches, crossbills imitate the contact calls of their parents and can modify calls throughout their

lives [32–34]. Previous work has shown that individuals of the Cassia crossbill (*Loxia sinesciuris*), which was described as a red crossbill ecotype but is now recognized as a distinct species [35], modified their call structure over their lifetime such that individuals' calls became more divergent from a closely related, sympatric red crossbill ecotype (call type 2 [28] or ponderosa pine crossbill; [32]). Although the exact mechanism underlying individual call modification over time is unknown, it may be an adaptive response to the

Table 1. Summary of the generalized linear mixed model testing for the effects of different variables on the probability that crossbill flocks landed in response to playback of Cassia crossbill contact calls. (The response variable was the probability of landing for each combination of variables based on the responses of 81 flocks.)

variable	z-value	d.f.	p-value
similarity to ponderosa pine crossbill calls (high or low)	−1.839	1	0.066
crossbill identity (Cassia or ponderosa pine)	−1.391	1	0.164
similarity × crossbill identity	2.864	1	0.004
playback location	1.302	9	0.193

low quality of public information provided by heterospecific flock mates (electronic supplementary material, figure S1), which results in low feeding rates [31]. This seems especially likely since crossbill behaviour is highly sensitive to variation in feeding rates [36] and crossbill flocking behaviour shows a graded response to differences in bill size between heterotypics [30]. Similar processes have been documented in other systems, where individuals alter their behaviour to reduce heterospecific interactions after experiencing maladaptive interactions with heterospecifics [37–39]. As the calls of individual Cassia crossbills diverge from those of ponderosa pine crossbills, these increasingly divergent calls would be learned by subsequent generations of Cassia crossbills, resulting in character displacement in call structure at the population level [30,32]. Furthermore, the net effect of such open-ended learning of calls is expected to be call divergence rather than call convergence, given that we found a very low frequency of heterospecific call learning (only three out of 844 individuals (0.36%) recorded in more than 1 year showed clear evidence of heterospecific learning; electronic supplementary material, figure S2).

We tested the prediction of character displacement in call structure by analysing audio recordings of Cassia crossbills in the South Hills of Idaho over a 20-year period. The South Hills is one of two small mountain ranges in southern Idaho that constitute the entire geographical range of the sedentary Cassia crossbill (figure 1; [27,40,41]). Based on multiple lines of evidence (palaeobotanical [42,43], genomic and climate-based forest reconstructions [41]), Cassia crossbills evolved in the South Hills from the widespread lodgepole pine crossbill (call type 5 [28]) as Rocky Mountain lodgepole pine (*Pinus contorta latifolia*) increased locally in abundance approximately 5000 years BP [40,41]. The Cassia crossbill evolved in the South Hills and a smaller adjacent mountain range because American red squirrels (*Tamiasciurus hudsonicus*), the dominant seed predator throughout the lodgepole pine forests in the greater Rocky Mountain region [27,40], were unable to colonize owing to the expanse of non-forested habitat surrounding these mountain ranges. In the absence of this dominant seed competitor, Cassia crossbills became engaged in a coevolutionary arms race with lodgepole pine, favouring larger bills and greater crossbill-specific cone defences than elsewhere within the extensive range of lodgepole pine [27,40]. This scenario of recent and *in situ* divergences combined with the past and widespread distribution of lodgepole pine nearby in the Rocky Mountain

region indicates that nomadic lodgepole pine crossbills (which may move hundreds of kilometres each year in search of cone crops) have occurred regularly in the region throughout the evolutionary history of Cassia crossbills. By contrast, the ponderosa pine crossbill is probably a more recent immigrant into the South Hills. Ponderosa pine crossbills presumably originated recently, diverging from lodgepole pine crossbills to specialize on Rocky Mountain ponderosa pine (*Pinus ponderosa scopulorum*) as this conifer expanded northwards (and to the east of the South Hills) from a small area in the American southwest over the last 6000 years [42]. Call divergence of Cassia crossbills from both ecotypes should be favoured if it promotes assortative flocking [30], as the smaller-billed lodgepole pine and ponderosa pine crossbills do not feed efficiently on the lodgepole pine cones in this area (the only conifer in this area that crossbills feed on; [27,40]), leading to low-quality public information and poorer feeding performance for Cassia crossbills that join heterospecific flocks (electronic supplementary material, figure S1; [31]). However, because Cassia crossbills have presumably co-occurred for less time with ponderosa pine crossbills than with lodgepole pine crossbills, Cassia crossbill calls are less likely to be in equilibrium with and more likely to be currently diverging from the calls of ponderosa pine crossbills.

In addition to testing the prediction of divergence in Cassia crossbill call structure over time, we used playback experiments of contact calls to test if the observed evolution in Cassia crossbill call structure affected the flocking behaviour of sympatric ecotypes. We also compared the call similarity of several sympatric and allopatric ecotype pairs to aid in interpreting comparisons among Cassia crossbills, lodgepole pine crossbills and ponderosa pine crossbills. Our study sheds new light on cultural evolution's role in speciation with gene flow and suggests that this has been a key diversifying force in the adaptive radiation of crossbills.

2. Material and methods

(a) Recording, preparing and analysing audio recordings

Crossbills were captured in mist nets, fitted with numbered US Fish and Wildlife bands and subsequently released, during which an audio recording of their contact call was made. Audio recordings were made with an ME-66 directional microphone (Sennheiser Electronic Corporation, Old Lyme, Connecticut) and either a PMD-222 analogue cassette recorder from 1998 to 2009 or a PMD-660 digital recorder (Marantz America, Inc., Aurora, Illinois) from 2010 to 2018. Recordings prior to 2010 were digitized at a sampling rate of 44 100 Hz using Audacity v. 2.2.1. (Audacity® software is copyright © 1999–2018 Audacity Team. The name Audacity® is a registered trademark of Dominic Mazzoni.) Only recordings of crossbills that could be unambiguously identified as producing Cassia crossbill calls were used in subsequent analyses. All recordings were saved as 16-bit WAVE files with a sampling rate of 44 100 Hz.

Spectrograms of each recording were made using the program RAVEN PRO, v. 1.5 [44]. Spectrograms were visualized and analysed with a Hann window, fast Fourier transform size of 512 points and window overlap of 50% per window step. Each recording was auditorily and visually inspected for contact calls that were not obscured by background noise. If found, one such call was saved as a separate file and used for subsequent analyses. Recordings were then bandpass-filtered in RAVEN PRO such that all noise above 7500 Hz and below 900 Hz was filtered out.

We prepared recordings of 16 individual ponderosa pine and lodgepole pine crossbill calls using the same methods described above. The 16 recordings of these ecotypes came from throughout most of their largely shared geographical range (Wyoming, Colorado, Utah, and the South Hills of Idaho) and included recordings made from 1997 to 2017. There is no evidence for geographical variation in the contact calls of lodgepole pine crossbills [28,45]. In the core range of ponderosa pine crossbills (the Intermountain West), there is no evidence for geographical variation in calls, but birds in the Appalachian Mountains and the northeastern United States frequently produce a distinctive contact call variant [45]. Because this call variant has never been recorded in the South Hills and is rarely recorded in the Intermountain West, we did not include recordings of this call variant in our analyses. Finally, the vast majority of ponderosa pine and lodgepole pine crossbills that are captured in the South Hills are not detected in subsequent years [46], and individuals of both ecotypes are primarily found in the South Hills during regular periods of long-distance dispersal by both ecotypes (late spring/early summer). After this period, ponderosa pine and lodgepole pine crossbills are uncommon in the South Hills [40]. This suggests that there is a regular movement of ponderosa pine and lodgepole pine crossbills from elsewhere in the Intermountain West into and out of the South Hills each year, with few individuals remaining year-round [46]. Thus, our use of recordings from the greater Intermountain West should be well suited for capturing the variation in calls within each ecotype that Cassia crossbills encounter.

After choosing and preparing call recordings for analysis, we calculated the average pairwise similarities of each Cassia crossbill call to the 16 recordings of both ponderosa pine and lodgepole pine crossbill contact calls using the correlation tool in RAVEN PRO [44]. The correlation tool performs a series of two-dimensional cross-correlations between two audio inputs based on temporal and frequency characteristics. A maximal correlation value between two audio inputs is estimated, which is a measure of the similarity of the two signals (values range from 0 to 1, with 1 representing identical signals; electronic supplementary material, figure S3; [44]). Cross-correlations in RAVEN PRO were run on spectrograms, correlations were biased and normalized (calculates correlation values while ignoring amplitude differences between spectrograms), linear power values were extracted and spectrogram values were not demeaned. Cross-correlation analyses are particularly well suited for comparing structurally simple and similar audio signals such as the contact calls of different crossbill taxa [44]. Furthermore, cross-correlation analyses tend to produce similar results to alternative acoustic analyses (e.g. multivariate analyses of multiple acoustic variables) yet have the advantage of directly comparing the overall similarity of audio signals and include unmeasured acoustic variables that may be important for discriminating among different audio signals [47,48].

These methods that we used to assess population-level call divergence of Cassia crossbills from ponderosa pine and lodgepole pine crossbills assume that the calls of ponderosa pine and lodgepole pine crossbills did not change relative to Cassia crossbill calls over time. To test this assumption, we ran an additional analysis that compared an independent sample of ponderosa pine and lodgepole pine crossbill contact calls made across multiple years in terms of their similarity to Cassia crossbill calls recorded in those same years. Recordings of ponderosa pine and lodgepole pine crossbills made from 1998 to 2018 across the western United States were downloaded from Xeno-canto, an online database of bird vocalization recordings. Using the previously described cross-correlation analyses, we estimated the average call similarity of each individual Cassia crossbill recorded in a given year to all ponderosa pine and lodgepole pine crossbills recorded in that year. We only made comparisons

in years that we had at least four recordings of ponderosa pine crossbills (mean number of recordings per year = 16; range = 4–45) or lodgepole pine crossbills (mean number of recordings per year = 12; range = 5–34).

To assess the degree to which Cassia crossbills change their calls over time (in terms of similarity to ponderosa pine and lodgepole pine crossbill calls), we compared the calls of individuals that were recorded in more than 1 year. Specifically, for each individual, we compared the cross-correlation value between their first recording and those of ponderosa pine and lodgepole pine crossbills to the comparable cross-correlation value from their most recent recording in order to estimate the degree of change over the longest possible time interval (mean: 1.93 years; range: 1–8 years).

Automated spectral analyses were run on all recordings using SOUND ANALYSIS PRO 2011 [49] and the default settings for zebra finches (*Taeniopygia guttata*) to test for systematic changes in syllable duration, pitch goodness (a measure of harmonic stacking), mean frequency, frequency modulation, amplitude modulation, entropy (a measure of the width and uniformity of the power spectrum) and pitch. Recordings were segmented by amplitude with a minimum stop duration of 7 ms and bouts ended when stop was greater than 10 ms. Of the measured spectral features, only frequency modulation changed in Cassia crossbill contact calls over time in a way that reduced call similarity to ponderosa pine crossbills (figure 2); no feature changed that was correlated with similarity to lodgepole pine crossbills.

(b) Comparative analysis of crossbill ecotype calls

The highly sympatric ecotype pairs (one ecotype co-occurs with another ecotype throughout much of its range) we compared were (i) ponderosa pine and lodgepole pine crossbills, which co-occur throughout most of the Intermountain West (figure 1), (ii) western hemlock and Douglas-fir crossbills (call types 3 and 4, [29] respectively), (iii) western hemlock and Sitka spruce (call type 10; [50]) crossbills, (iv) Douglas-fir and Sitka spruce crossbills, all of which co-occur in the Pacific northwest, (v) Douglas-fir and ponderosa pine crossbills, which co-occur throughout large portions of the Intermountain West and (vi) Douglas-fir and lodgepole pine crossbills, which co-occur throughout large portions of the Intermountain West. The weakly sympatric ecotype pairs we compared were (i) ponderosa pine and Appalachian (call type 1) crossbills, which sporadically co-occur in small numbers throughout Appalachia and the northeast, (ii) ponderosa pine and Sierra Madre (call type 6 [28]) crossbills, which co-occur in a small region of the US southwest and northern Mexico and (iii) lodgepole pine and Sierra Madre crossbills, which occasionally co-occur in the US southwest. The geographical distributions of these ecotypes are described in Benkman & Young [45].

These comparisons used identical methods to the previously described cross-correlation analyses. Sample sizes of recordings for these ecotypes were (in parentheses): type 1 (15), type 2 (16), type 3 (20), type 4 (17), type 5 (16), type 6 (13) and type 10 (17).

(c) Playback experiments

Two sets of Cassia crossbill recordings, representing high and low similarities to ponderosa pine crossbills, were used for playbacks. The high similarity group was created by randomly choosing 10 recordings that approximated the upper quartile value in the distribution of peak correlation values (0.40) in Cassia crossbills in 2016 (mean peak correlation value of high similarity recordings = 0.41). The low similarity group was created by randomly choosing 10 recordings that approximated the lower quartile value in the distribution of peak correlation values (0.23) in Cassia crossbills in 2016 (figure 1*d*; mean peak correlation value of low similarity recordings = 0.23). Recordings

in each group were chosen across years, such that the recordings consistently differed only in similarity to ponderosa pine crossbill calls. This design allowed us to test whether the variation in call similarity between Cassia and ponderosa pine crossbill calls within a year affected the response of crossbills to playback. Once recordings were chosen for use in playback experiments, we made synthesized recordings in RAVEN PRO by duplicating a contact call such that each recording mimicked an individual crossbill's normal calling behaviour (30 s of calling at a rate of 88 calls per 30 s followed by a 20 s pause; as in [30]). All recordings were standardized for amplitude.

Recordings were broadcast with a portable speaker to free-flying crossbills from small, isolated patches of forest containing mature, cone-bearing lodgepole pine trees (the only conifer in the South Hills that crossbills feed on) between 22 May and 3 June 2018. At 10 locations each separated by at least 500 m, calls were broadcast in the morning and the evening using a Pignose 7–100 Legendary portable amplifier (Pignose-Gorilla, Las Vegas, NV). Both high and low similarity recordings were played at each location, and the order that the recording groups were played was alternated each day so that each recording group was played with equal frequency in the morning and evening. One individual (C.K.P.) conducted all playback experiments and was blind to whether the recording was high or low similarity. During each 120 min trial, calls were broadcast continuously, and we recorded whether crossbills flying over landed in the patch of lodgepole pine near the speaker or continued to fly over. Our experimental design mimics the behaviour of a crossbill in a patch of conifers loudly calling to other crossbills flying over; an extremely common behaviour that stimulates flock formation [29,30]. Therefore, by recording whether crossbill flocks land in response to playback, we were able to assess the propensity of crossbills to associate with individuals producing different calls [30]. The speaker was tilted upwards and placed at the edge of the forest patch at a height of approximately 1.5 m. We identified each crossbill aurally based on their distinctive contact calls (Cassia and ponderosa pine crossbills represented the vast majority of crossbills detected in the South Hills during 2018, and only these taxa were present during playback experiments). All 81 flocks were homotypic. Each flock was treated as an independent sample as in a previous study [30], thus the sample size for analyses was 81 flocks.

(d) Statistics

All analyses were conducted in R [51]. All tests were two-tailed. Error bars in figures are 95% confidence intervals. No variables were transformed prior to analyses, owing to normality assumptions being met. To assess population-level change in Cassia crossbill call similarity and frequency modulation over time, linear regressions were used on the yearly means. Linear regressions were also used to evaluate the relationship between call similarity and frequency modulation. Paired *t*-tests were used to compare the similarities of the calls of recaptured Cassia crossbills to both ponderosa pine and lodgepole pine crossbill calls over multiple years. Playback data were analysed with a binomial generalized linear mixed model and logit link function in R [51] using the 'lme4' package [52]. Whether crossbill flocks landed in response to playback (yes or no) was the response variable, with similarity to ponderosa pine crossbill calls (high or low), wild crossbill flock identity (Cassia or ponderosa pine crossbill), and their interaction as fixed effects and playback location as a random effect.

3. Results

Analysis of standardized contact call recordings of 3242 uniquely banded Cassia crossbills in the South Hills from

1998 to 2018 is consistent with character displacement in call structure. The average similarity of Cassia crossbill calls to ponderosa pine crossbill calls steadily decreased from a cross-correlation value of 0.377 in 1998 to 0.287 in 2018, a decrease of 24% from the initial similarity over the 20-year interval (figure 2*b*; *mean similarity* = $9.8248 - 0.0047 * \text{year}$; $r^2 = 0.84$, d.f. = 16, $p < 0.0001$). An analysis that accounted for potential changes in ponderosa pine crossbill calls across years yielded similar results (*mean similarity* = $9.9810 - 0.0048 * \text{year}$; $r^2 = 0.70$, d.f. = 7, $p = 0.009$), including nearly identical rates of decrease in call similarity over time (0.0047 yr^{-1} in the former analysis and 0.0048 yr^{-1} in the latter analysis). This population-level divergence has been mediated apparently by an increase in frequency modulation of Cassia crossbill calls over time (figure 2*c* and figure 3*a*; *frequency modulation* = $-234.8726 + 0.1478 * \text{year}$; $r^2 = 0.47$, d.f. = 16, $p = 0.002$), given that call similarity to ponderosa pine crossbills is negatively correlated with frequency modulation of Cassia crossbill calls (figure 3*b*; *ponderosa pine call similarity* = $1.0510 - 0.0118 * \text{frequency modulation}$; $r^2 = 0.24$, d.f. = 16, $p = 0.038$). None of the six other measured acoustic variables changed in Cassia crossbills over time in a manner consistent with the changes in cross-correlation values. In contrast to the results for call similarity to ponderosa pine crossbills, the similarity of Cassia crossbill calls to lodgepole pine crossbill calls did not change over this same period (figure 2*b*; $r^2 = 0.01$, d.f. = 16, $p = 0.65$), even when accounting for potential changes in lodgepole pine crossbill calls over time ($r^2 = 0.06$, d.f. = 5, $p = 0.64$). The absence of divergence is expected given that Cassia crossbill calls are already quite dissimilar to those of lodgepole pine crossbills (figure 2*b*), presumably because of their long-term sympatry. In addition, the similarity of lodgepole pine crossbill calls to those of Cassia crossbills was unrelated to frequency modulation of Cassia crossbill calls (figure 3*b*; *lodgepole pine call similarity* = $0.1314 + 0.0008 * \text{frequency modulation}$; $r^2 = 0.01$, d.f. = 16, $p = 0.76$), and thus further divergence from (or convergence with) lodgepole pine crossbills is not expected as a byproduct of divergence from ponderosa pine crossbills.

These population-level patterns were mirrored in the within-individual changes over time. Calls of 801 Cassia crossbills recorded in multiple years became more divergent from the calls of ponderosa pine crossbills over time (paired *t*-test: $t_{779} = 5.25$, $p < 0.0001$; see the electronic supplementary material, figure S4 for examples of individual changes over time), confirming previous findings that were based on a sample of only 114 individuals [32]. The average decrease in similarity to ponderosa pine crossbill calls within individuals over the course of 1 year (0.0123 ± 0.0031 (mean \pm s.e.)) was 2.6 times larger than the average decrease over 1 year at the population level (0.0047 ± 0.0005). A smaller decrease in call similarity at the population level than at the individual level is expected because offspring do not perfectly imitate their parents' calls [32,34], resulting in the imperfect transmission of within generation changes to subsequent generations. The calls of individual Cassia crossbills did not change over time with respect to their similarity to lodgepole pine crossbill calls (paired *t*-test: $t_{779} = -0.04$, $p = 0.97$), consistent with the population-level results.

Assuming sympatry between Cassia and ponderosa pine crossbills was established comparatively recently [41–43], we predicted that their degree of call similarity would approximate that of pairs of allopatric crossbill ecotypes which

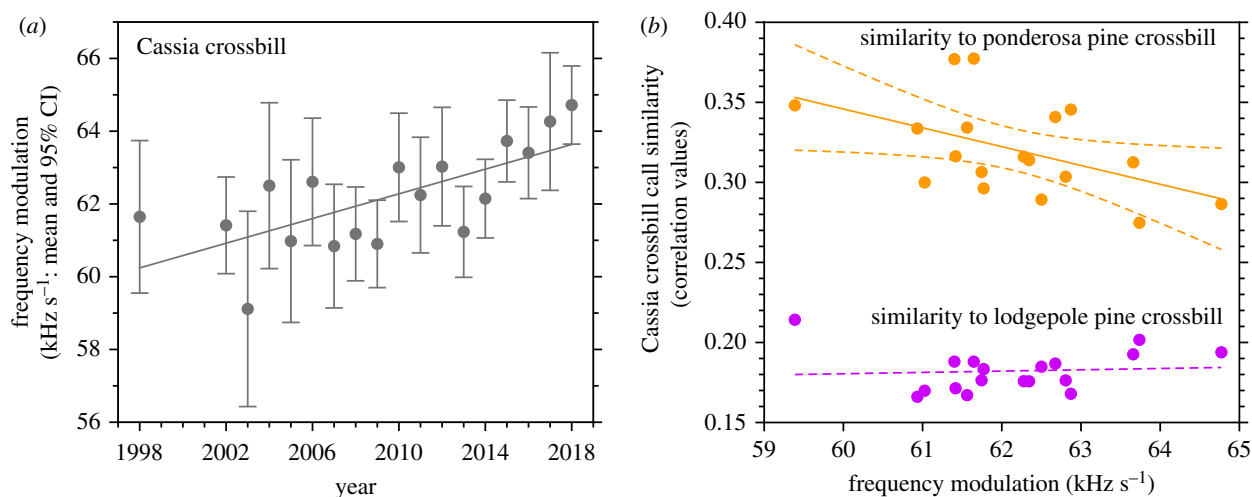


Figure 3. The observed changes in call similarity depicted in figure 2*b* appear to result from the increases in frequency modulation of Cassia crossbill calls between 1998 and 2018 (*a*), because increases in frequency modulation lead to reduced call similarity to ponderosa pine crossbills but are unrelated to call similarity to lodgepole pine crossbills (*b*); each point represents a different year as in (*a*). (Online version in colour.)

have presumably not undergone character displacement in call structure. Indeed, we found that the initial call similarity between Cassia and ponderosa pine crossbills in 1998 (0.377) is comparable to call similarity between three primarily allopatric pairs of crossbill ecotypes (mean: 0.317; range: 0.161–0.403; electronic supplementary material, figure S5). By contrast, the range of call similarities between Cassia and lodgepole pine crossbills over the last 20 years (0.166–0.214) is more comparable to call similarity between six highly sympatric pairs of crossbill ecotypes (mean: 0.259; range: 0.206–0.350; electronic supplementary material, figure S6), which have probably undergone character displacement in call structure over extended periods of time.

The key prediction of character displacement is that call divergence reduces maladaptive heterospecific flocking [30], which, because crossbills choose mates from within flocks [29], should also increase assortative mating [30]. As predicted if the observed call divergence reduces heterospecific flocking, there was an interaction between call similarity to ponderosa pine crossbills and flock identity ($p = 0.004$; table 1): as Cassia crossbill calls diverged from ponderosa pine crossbills, the propensity of ponderosa pine crossbills to land in response to playback declined relative to the responses by Cassia crossbills as Cassia crossbill calls diverged from ponderosa pine crossbills (shift from high to low call similarity in figure 2*e,f*). These results suggest divergence in call structure over just two decades (figure 2*b*) reduced heterospecific flocking between Cassia and ponderosa pine crossbills, with the potential to increase assortative mating as a byproduct [30].

4. Discussion

Our results indicate that parent–offspring learning combined with an open-ended modification of calls causes call divergence rather than call convergence (figure 2*b*). Consistent with other lines of evidence (palaeobotanical [42,43], genomic and climate-based forest reconstructions [41]), comparative analyses of call structure of sympatric and allopatric pairs of red crossbill ecotypes indicate that sympatry between Cassia and ponderosa pine crossbills is more recent than sympatry between Cassia and lodgepole pine

crossbills. This presumably explains why the calls of Cassia crossbills are still diverging from those of ponderosa pine crossbills but not from lodgepole pine crossbills (figure 2*b*). Playback experiments show that these changes in Cassia crossbill call structure over time act to reduce heterospecific flocking with ponderosa pine crossbills (figure 2*e,f*; table 1), which is expected to increase assortative mating and thus promote speciation because crossbills choose mates from within flocks [29,30]. The inference that assortative flocking promotes speciation is supported by preliminary data revealing that behavioural isolation [9] between ponderosa pine and lodgepole pine crossbills in the Rocky Mountains increased with increases in the frequency of assortative flocking ($r^2 = 0.72$, $p = 0.033$, $n = 6$ breeding seasons and 254 mated pairs, C. K. Porter 2019, unpublished data).

If the rate of Cassia crossbill call divergence from ponderosa pine crossbills observed between 1998 and 2018 (figure 2*b*) occurred earlier, this would imply that divergence began less than a century ago (electronic supplementary material). However, character displacement is expected to be rapid only at intermediate levels of trait overlap (i.e. call similarity) and especially if heritability is low [53], as appears evident for Cassia crossbill calls [32]. Therefore, the rapid divergence of Cassia crossbills from ponderosa pine crossbills (figure 2*b*) may be a recent phenomenon that followed a period of slow call divergence in the earliest stages of sympatry between these lineages when call similarity was higher. How long divergence was initially slow is unknown, but the extent of recent call divergence that we measured indicates that regular and common co-occurrence of ponderosa pine and Cassia crossbills might be even more recent than we envisioned.

In contrast to most cases of ecological speciation, we suspect that the fitness benefits of signal divergence are not because of reductions in maladaptive interspecific mating (i.e. reinforcement; [54]). Rather, we suspect that the fitness benefits of contact call divergence in crossbills are owing to reductions in interspecific flocking (figure 2*e,f*; table 1); conspecific flockmates provide higher quality public information on resource availability than do heterospecifics (electronic supplementary material, figure S1) leading to higher feeding rates in conspecific flocks [31]. Flocking with heterospecifics may also be detrimental because food-deprived crossbills

only produce stress hormones if their flockmates are also food deprived [55]. Therefore, individuals experiencing low feeding rates on a given resource might respond less adaptively when flocking with heterospecifics than with conspecifics if heterospecifics are more efficient foragers on the resource. Furthermore, the low frequency of interspecific mating between Cassia and ponderosa pine crossbills (0.7% of 1704 breeding pairs from 2001 to 2007 in the South Hills; [40,56]) combined with an estimated 12% reduction in fitness of hybrids between these taxa [57] would result in weak natural selection against interspecific mating that is probably insufficient to account for the observed call divergence (figure 2*b*). Therefore, we suggest that the fitness benefits of grouping with conspecifics (electronic supplementary material, figure S1), not selection against interspecific mating, is the primary adaptive mechanism driving recent call evolution.

As noted above, interbreeding between Cassia and ponderosa pine crossbills was already quite low from 2001 to 2007 [40], when their calls were more similar (mean similarity: 0.346) than they were in 2018 (0.287). Consequently, further reductions in interbreeding arising from recent call divergence (figure 1*b*) and its associated reductions in heterospecific flocking (figure 2*e,f*) are not likely to be large in an absolute sense (i.e. in tenths of a per cent, and thus extremely difficult to detect without massive sample sizes of mated pairs). However, this does not mean that even slight reductions in interbreeding are inconsequential for speciation of Cassia crossbills, because even low rates of introgression in systems with near-complete reproductive isolation can impede speciation [58–61]. Additionally, if the call divergence we document leads to increased assortative mating, this may be especially important, because further increases in reproductive isolation become progressively more difficult as isolation nears completion [62–64]. As such, evolutionary processes that increase assortative mating when reproductive isolation is very strong yet incomplete can be particularly important in speciation.

The character displacement in call structure between sympatric lineages that we document (figure 2*b*) emerged from individuals altering their behaviour (open-ended learning of contact calls; [32]) presumably to reduce heterospecific interactions after experiencing reduced feeding rates with heterospecifics when in feeding flocks (electronic supplementary material, S1). These increasingly divergent vocalizations are imitated by offspring [32,34], leading to call divergence at the population level (figure 2*b*) and reduced heterospecific

flocking (figure 2*e,f*). Contact calls therefore act as marker traits that mediate group formation and diverge by adaptive cultural evolution. Because crossbills flock year-round and choose mates from within flocks [29], increased reproductive isolation is probably a byproduct of character displacement in call structure. Interestingly, while ours is the first study we are aware of that comprehensively demonstrates this evolutionary process and its role in ecological speciation with gene flow, a very similar process has been hypothesized, though not directly demonstrated, to explain sympatric ecotype formation in sperm whales [65,66] and bottlenose dolphins [66,67] and ecological speciation with gene flow in killer whales [66,68,69]. Because the individual components of this evolutionary process have been described in a wide range of animals [37–39,70–75], the scenario we describe in crossbills may figure prominently in diversification more generally. Thus, while most research on the role of cultural evolution in population divergence and speciation has historically focused on random cultural drift in allopatric lineages as the mechanism by which reproductive isolation arises [10–12,14–19,25,26,54], our results and others suggest a route to ecological speciation with gene flow driven by adaptive cultural evolution that could be common in social taxa that exhibit resource specialization.

Ethics. The experiment in this study meets the conditions of the University of Wyoming Institutional Animal Care and Use Committee.

Data accessibility. Call similarity data, acoustic measurements, playback experiment data, simulation results and R code associated with all analyses are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.6s57c73> [76].

Authors' contributions. C.K.P. and C.W.B. conceived of the study, participated in banding and recording crossbills and wrote the manuscript. C.K.P. performed field experiments and analysed the data.

Competing interests. We declare we have no competing interests.

Funding. A Dean's Graduate Scholars Award from the University of Wyoming awarded to C.K.P., and the Robert Berry Chair Endowment and National Science Foundation grant nos. DEB-0212271 and DEB-0435923 awarded to C.W.B. provided financial support for this research.

Acknowledgements. We thank N. Behl, J. Hart, P. Keenan and J. Sales for multiple years of help with banding and recording crossbills. J. Podos provided valuable advice on sound analyses. J. Golcher-Benavides provided illustrations of pine cones and created figure 1. D.J. McNeil provided illustrations of crossbills used in figure 1. C. Akcali, P. Edelaar, J. Golcher-Benavides, D. Irwin, T. Parchman, J. Podos, C. Wagner and anonymous reviewers provided comments that greatly improved this manuscript.

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