



## Limited adult vocal learning maintains call dialects but permits pair-distinctive calls in red crossbills

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### ARTICLE INFO

#### Article history:

Received 27 October 2008  
Initial acceptance 27 November 2008  
Final acceptance 8 January 2009  
Published online 19 March 2009  
MS. number: A08-00702

#### Keywords:

call  
*Loxia curvirostra*  
red crossbill  
vocal learning

Vocal imitation can inform receivers about the social background of signallers because shared signals reflect learning experiences. Open-ended imitation can generate shared signals that indicate current social affiliation, whereas limited vocal plasticity in adulthood can permit signals to reflect an individual's origin. I examined the relations between vocal learning, signal sharing and social dynamics in red crossbills, *Loxia curvirostra*. Two levels of shared variation exist within crossbills' contact calls: discrete call variants distinguish ecologically diverged crossbill forms, and within these variants, some bonded pairs produce calls with nearly identical structures. Assessment of vocal and social behaviour of experimentally housed birds revealed that some adult crossbills converged on calls shared with companions of their own form, but no birds learned new, categorically distinct call variants. Also, while the process of call convergence within the bounds of discrete variants was associated with affiliation, birds that produced different contact call variants interacted less frequently and less amicably. These results suggest that call learning is limited in adult crossbills, generating calls with two levels of shared variation and multiple social functions: discrete contact call variants reflect birds' ecological forms, while pair-distinctive calls within those discrete variants reflect current social affiliation. Thus, a single social call concurrently reflects bonding among conspecifics of common origin and promotes the social isolation of ecologically diverged forms of red crossbills.

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The social interactions of many group-living animals are mediated by vocalizations referred to as calls (pinnipeds: [Insley et al. 2003](#); cetaceans: [Janik & Slater 1998](#); birds: [Marler 2004](#); primates: [Maurello et al. 2000](#); elephants: [McComb et al. 2000](#); bats: [Wilkinson & Boughman 1998](#)). A particular class of calls, termed contact calls are involved in the coordination of movement and cohesion of social units ([Marler 2004](#)), giving them unique potential to influence the organization of social groups and even the structure of populations. Historically, calls were thought to be innate ([Thorpe 1961](#)), but there is increasing evidence that they may be learned, especially in birds ([Marler 2004](#)). Here, I explored the relations between adult call learning, contact call variability and social dynamics in a gregarious songbird.

Variation within contact calls sometimes takes the form of signature calls, which are individually distinctive and facilitate individual recognition ([Cheney & Seyfarth 1982](#); [Sayigh et al. 1999](#); [McComb et al. 2000](#); [Aubin & Jouventin 2002](#); [Insley et al. 2003](#)). In some cases, shared call structures have also been reported among

conspecifics and may be evidence that call production is learned ([Mundinger 1979](#); [Tyack 2008](#)). It is possible, however, that social companions could share call structures if animals with previously existing call similarities assort preferentially ([Moravec et al. 2006](#)). In most species studied to date, shared call structures do, in fact, result from vocal modification and imitation ([Mundinger 1979](#); [Nowicki 1989](#); [Elowson & Snowdon 1994](#); [Farabaugh et al. 1994](#); [Boughman 1998](#); [Janik 2000](#); [Miller et al. 2004](#); [Tyack 2008](#)). Vocal imitation may take the form of copying or convergence. Copying occurs when a single individual alters its call production to generate a new contact call variant with nearly the same structure as the existing call of a companion. In contrast, convergence occurs when two or more birds modify their calls to produce a more similar call variant that is distinct from their original calls. Shared signal variants that emerge through either form of imitative learning can provide additional information about an individual's social background because they reflect prior learning experiences. The timing and process of vocal learning are factors that determine the pattern of variation within contact calls and circumscribe the range of potential roles contact calls may play in social dynamics. Shared call structures could emerge if animals imitate family or population-specific calls early in life and assort preferentially with companions that produce calls like their own. In these cases, calls

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will reflect an individual's family or population of origin and may impede social interaction among conspecifics from different backgrounds. In contrast, open-ended copying or convergence will permit calls to reflect current social associations, perhaps facilitating social interaction and intermixing. Shared contact call variants have been described at two levels of social organization: (1) 'group or pair-distinctive calls' are shared among close social companions and (2) 'call subtypes' are common to members of a lineage or population. The social relevance of these shared call variants depends upon the process by which they develop.

Group- and pair-distinctive contact call variants are identified when members of a social unit produce calls that share acoustic features. Calls shared among close companions have been reported in primates (Elowson & Snowdon 1994), cetaceans (Tyack 1986; Janik 2000; Miller et al. 2004; Watwood et al. 2004), bats (Boughman 1997), parrots (Farabaugh et al. 1994; Wright 1996; Wanker & Fischer 2001; Baker 2003; Cortopassi & Bradbury 2006) and songbirds (Mundinger 1970, 1979; Marler & Mundinger 1975; Samson 1978; Mammen & Nowicki 1981; Groth 1993a; reviewed in: Tyack 2008). The production of pair- and group-distinctive calls is thought to facilitate the identification of companions and the coordination of shared behaviours such as foraging and the care of young (Mundinger 1970, 1979; Nowicki 1983; Farabaugh et al. 1994). In most cases studied to date, calls shared among close companions emerge through open-ended call modification, which is associated with social bonding. It has been suggested that vocal copying is a prerequisite for group membership and serves to reduce aggression (Baker 2003), whereas convergence is generally associated with mutual affiliation (Farabaugh et al. 1994). Both forms of open-ended learning may permit birds to communicate more effectively with new companions and become integrated into new social groups (Tyack 2008). And resulting group- and pair-distinctive calls can indicate an individual's current social bonds (Wright & Wilkinson 2001; Baker 2003).

In a handful of taxa, shared contact calls have been associated with particular lineages (Ford 1991; Weilgart & Whitehead 1997; Price 1998; Sharp & Hatchwell 2006) or with morphological and ecological variation among populations or subspecies (Adkisson 1981; Groth 1993b; Baker 2000; Sewall et al. 2004; Runciman et al. 2005). I refer to calls shared among conspecifics that have common origins but not necessarily immediate social contact as 'call subtypes'. Like song dialects, call subtypes are generally stable over time, and the acoustic features of calls from different lineages, populations or subspecies vary discretely. Call subtypes may be considered to include call dialects because subtypes do not necessarily have geographical boundaries; individuals producing different call subtypes can sometimes co-occur (Adkisson 1981; Groth 1993b; Sewall et al. 2004). The potential for call subtypes to shape social and population dynamics is determined by the learning processes that generate and maintain them (ten Cate 2004; Freeberg & White 2006; Price 2008). Call subtypes, like some song dialects, could reflect an individual's current population if vocal imitation of calls facilitates social integration and occurs after an animal leaves its natal group. Alternatively, call subtypes could reflect an individual's origin and serve to impede social intermixing and gene flow if animals do not learn new call subtypes later in life. Examining contact calls in species in which both call subtypes and pair-distinctive calls exist could provide insight into the relations between learning, signal diversity and the social and evolutionary consequences of variation within calls. Here, I report on a series of studies of the vocal and social behaviour of red crossbills, a bird species in which both call subtypes and pair-distinctive calls have been described.

Red crossbills exist as several sympatric, ecologically diverged morphs (ecomorphs, see methods in: Groth 1993b; Benkman

2003). Variation in beak size and shape among morphs is thought to permit specialization on different conifer resources (Benkman 2003). Each ecomorph is best identified by a discrete contact call subtype, though, and call structure is essential to Groth's (1993b) original crossbill taxonomy. Although the morphological and genetic differences are relatively modest (Groth 1993b; Questiau et al. 1999; Parchman et al. 2006), researchers have proposed that crossbill ecomorphs may be either ecologically diverged cryptic species (Groth 1993b), or sympatric incipient species in the process of diverging (Parchman et al. 2006). It has been proposed that call subtypes serve as neutral marker traits for crossbills' ecological specializations, which are thought to be under ecological selection (Snowberg & Benkman 2007). This would require that crossbills produce the same call subtype throughout life. However, cross-fostering studies have shown that contact calls are initially learned through imitation (Groth 1993b; Sewall 2008). Furthermore, field studies have shown that members of wild mated pairs produce calls with nearly identical structures (Groth 1993a; Keenan & Benkman 2008), suggesting that some degree of vocal plasticity extends into adulthood. Plasticity in call production could facilitate pair bonding among adult birds but may result in changes in call subtypes, as well as pair-distinctive calls. For call subtypes to reliably reflect individuals' ecomorphs, call production learning in adult red crossbills would have to be constrained. That is, after learning their initial call subtype early in development (Groth 1993b; Sewall 2008), crossbills' call production must be fixed at the level of call subtypes. Here, I examined the learning processes underlying contact call diversity in red crossbills to help determine the social function and potential evolutionary effects of contact call variants. I experimentally housed adult birds with a companion of either the same or a different call subtype and ecomorph and examined their calls before and after pairing to assess the nature of call modification and the degree of call similarity achieved. In addition, I observed the behavioural interactions of each pair to determine how call similarity and subtypes affected their social interactions.

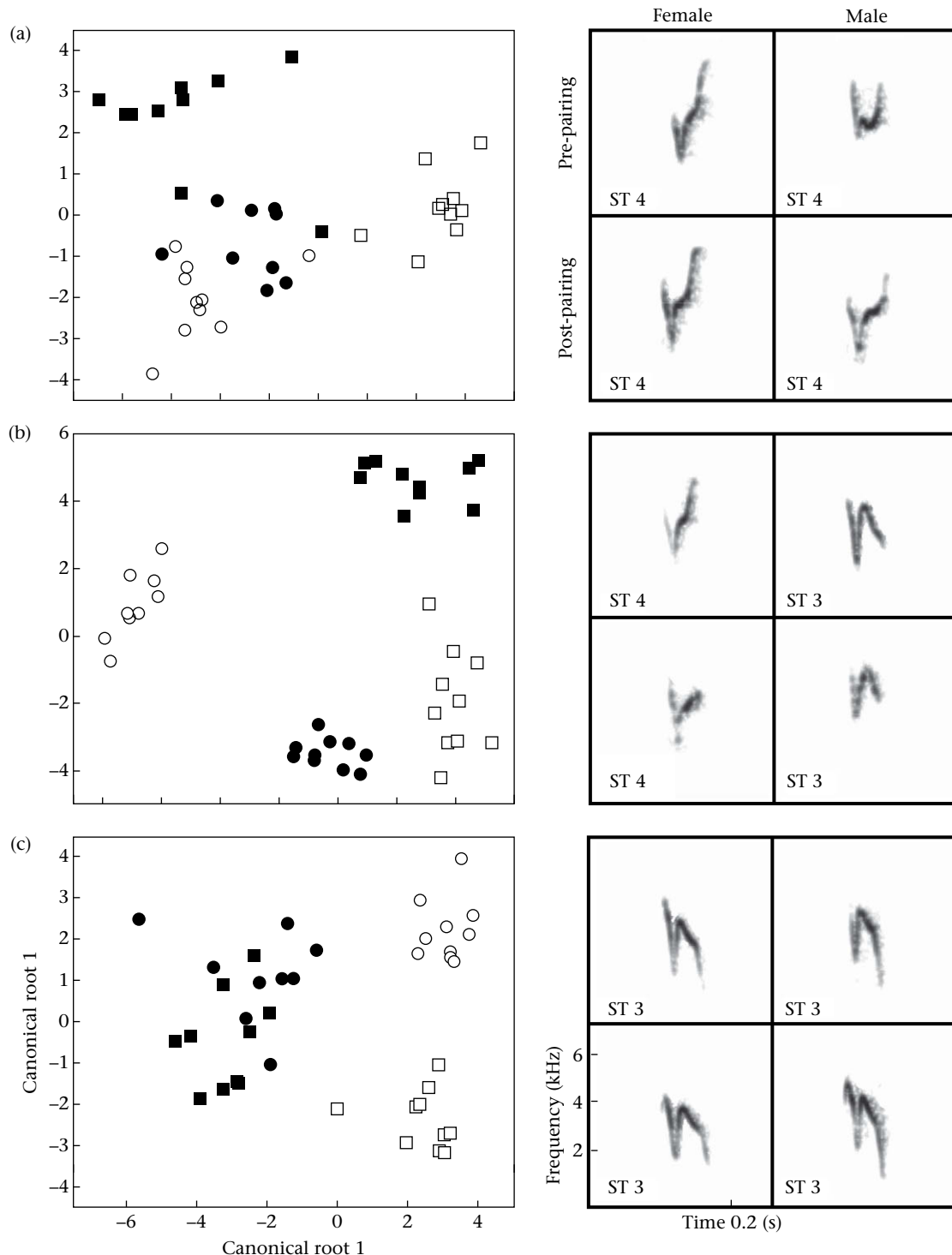
## METHODS

The vocal, morphological and ecological variation within red crossbills was originally described by Groth (1993b, 1988), who designated crossbill variants as 'types', numbered in the order in which they were discovered. Groth used both learned calls and morphological measurements to define 'types'. Here, to distinguish the vocalizations (i.e. the behaviour) from the ecological and morphological forms of crossbills (i.e. the taxa), I refer to Groth's 'types' as ecomorphs and the contact call variants that the different ecomorphs produce as call subtypes.

### *Subjects and Housing*

I captured 27 wild ecomorph-3 and 15 wild ecomorph-4 crossbills in Washington and Oregon, U.S.A., during the summers of 2003 and 2004. Ecomorph-3 is the smallest North American form with a small bill that facilitates efficient foraging on conifers with soft cones and small seeds (Benkman 1993; Groth 1993b). Ecomorph-4 is a medium-sized bird that performs better on medium-sized cones (Benkman 1993; Groth 1993b). Ecomorphs-3 and -4 often co-occur but their contact calls are highly distinctive (Fig. 1 for example spectrograms).

Initially, I housed birds in large indoor aviaries (3.6 × 3 × 1.8 m aviaries; Corners, Limited, Kalamazoo, MI, U.S.A.) at the University of California, Davis, U.S.A., with birds of the same sex and ecomorph. The aviaries were within a single room such that, as sometimes occurs in nature, all birds could hear conspecifics of



**Figure 1.** Canonical plots of linear discriminant analysis (LDA) of the acoustic parameters of calls from (a) a same-subtype pair that converged vocally but did not achieve statistically indistinguishable shared calls, (b) a mixed-subtype pair that converged vocally and (c) a same-subtype pair that converged sufficiently to achieve a shared call structure, and representative spectrograms of calls from each pair. The subtype (ST) of each bird, as determined by expert classification, is indicated in the bottom left corner of each spectrogram. Symbols in each of the LDA plots represent the following: open circles = female's calls before pairing; solid circles = female's calls after pairing; open squares = male's calls before pairing; solid squares = male's calls after pairing.

their own and other call subtypes prior to the study. The study spanned 2 years; four experimental and five control pairs were included in the first year of the study (2003) and seven experimental and five control pairs were included in the second year of the study (2004; total of 11 experimental and 10 control pairs). Almost all of the birds were adults; two were physically mature but

had juvenile plumage when captured. These birds were probably born the previous winter (capture age estimated about 7 months, based on plumage and skull pneumatization). Ten of the 24 birds in the second year of the study had been housed in captivity for 1 year before the experiment. These birds were housed with companions of their same call subtype. I included time in captivity, housing

prior to and during the study, and the age, sex and ecomorph of the focal birds as variables in statistical analyses. None of these factors were significant and they were dropped from subsequent analyses.

During the experiment, birds were paired with an unfamiliar companion of the opposite sex and housed in separate cages ( $60 \times 30 \times 45$  cm). I housed same-ecomorph (control) and mixed-ecomorph (experimental) pairs in a single room in the first year of the study. In the first year, all of the birds heard one another but had visual and physical contact exclusively with their companion. In the second year of the study, I housed mixed-ecomorph and same-ecomorph pairs in separate sound-attenuation chambers (7 experimental pairs divided among three chambers, 5 control pairs among three chambers; IAC mini booths, Industrial Acoustics, Bronx, NY, U.S.A.) such that subjects could hear the other birds within the chamber but only see and physically interact with their companion. I examined possible vocal imitation among birds that had vocal but not physical contact to address this housing constraint (see below). Experimental pairing began in late autumn (when foraging winter flocks form), continued through winter (when crossbills are likely to select mates from within their small flocks) and into early spring (when breeding generally peaks in ecomorph-3 and -4 birds) (Adkisson 1996; Hahn 1998). Birds were held on natural photoperiod with ad libitum access to food (Roudybush, Woodland, CA, U.S.A.), water, grit and sunflower seed.

#### *Vocalizations and Social Behaviour*

I recorded individuals before and after ( $10 \pm 2$  weeks in year 1;  $15 \pm 3$  weeks in year 2) the experiment by transferring each bird to a sound-attenuation chamber equipped with a Sennheiser ME62 omnidirectional microphone. The number of weeks required to assess each pair varied because it often took multiple sessions to record numerous high-quality calls from both pair members. I made recordings using a Sony TCM 5000EV tape recorder and subsequently digitized them at a 22 050 kHz sampling rate (maximum frequency of crossbill calls is 8 kHz) using Syrinx bioacoustics software (Burt 2006).

I observed the behavioural interactions of each pair at the end of the experimental period ( $X = 2.5$  h, minimum of 1 h). I tallied the number of affiliative (bill touch, courtship feeding) and aggressive interactions (open bill threat, chase, attack; Tordoff 1954) and calculated rates of affiliative and aggressive interactions, as well as the rate of total social interactions for each pair (intrarater behavioural sampling was 94% reliable). I also gave each pair a bonding classification ('bonded' or 'not bonded'). This qualitative bonding classification was consistent with the rates of affiliative and aggressive interactions of these pairs; 'bonded' pairs engaged in more affiliative than aggressive interactions, whereas pairs classified as 'not bonded' engaged in relatively equal rates of affiliative and aggressive behaviours (bonding classification  $\times$  rate of aggressive/affiliative interactions post hoc ANOVA:  $F_{1,19} = 9.662$ ,  $P = 0.006$ ).

#### *Acoustic and Statistical Analysis*

I assessed both the process of call modification and the overall similarity of pair members' calls using two approaches: spectrogram cross-correlation (SPCC, Avisoft bioacoustics software; Specht 2007) and linear discriminant analysis (LDA) of acoustic parameter measurements (Wanker & Fischer 2001). I used the results of SPCC to make comparisons among pairs, and the results of LDA to assess the process of vocal modification within pairs. In addition, I had experts in crossbill classification categorize birds' calls by subtype. Finally, I combined the results of all three analyses and gave each pair two qualitative classifications; pairs were classified for vocal

change (converged/did not converge) and final similarity (shared calls achieved/shared calls not achieved; see definitions below). I conducted all measurements and classifications using spectrograms of 5 to 12 (mode = 10) calls from each pair member just prior to and at the termination of pairing (FFT length: 256; Hamming window; temporal resolution: 2.903 ms; frequency resolution: 86 Hz).

#### *Spectrogram cross-correlation*

I used SPCC  $R$  values to compare call similarity among pairs before and after the experimental pairing (Tchernichovski & Mitra 2001; Baker & Logue 2003). Spectrogram cross-correlation generates an  $R$  value for two spectrograms by sliding them over one another along the time axis to achieve the greatest possible overlap (Clark et al. 1987; Nowicki & Nelson 1990; Baker & Logue 2003). I averaged the SPCC  $R$  values for all possible comparisons of calls from pair members at a given point in time to generate two mean SPCC  $R$  values for each pair, one pre- and one post-pairing. I conducted repeated measures ANOVA of SPCC  $R$  values for pairs from different treatments (mixed/same-ecomorph pairs) using mean SPCC  $R$  values from the beginning and the end of the study as repeated measures and treatment as the between-subjects factor. This permitted me to assess effects of experimental pairing on final call similarity and to look for evidence that pairing treatment affected call convergence over the course of the study (i.e. an interaction between treatment and pre- and post-pairing similarity values). I conducted two additional repeated measures ANOVAs of SPCC  $R$  values, one for mixed-subtype pairs and one for same-subtype pairs, in which mean SPCC  $R$  values from the beginning and the end of the study were the repeated measures and the qualitative bonding classification (bonded/not bonded) was the between-subjects factor. This permitted me to determine whether the bonding classification (bonded/not bonded) affected final call similarity and whether bonding was associated with change in call similarity (i.e. whether there was an interaction between pre- and post-pairing similarity values and bonding classification within treatment groups). I used Fisher least significant difference (LSD) post hoc tests to identify significant differences between groups.

#### *Linear discriminant analysis*

I conducted linear discriminant analysis (LDA) of acoustic parameters for each pair individually to track call modification over time, within pairs. I also conducted LDA of the acoustic parameters of calls from all birds in vocal contact (all birds in year 1 of the study; birds in each chamber in year 2 of the study) to examine pairs relative to one another and to determine whether birds modified their calls to generate a call that was more similar to that of a conspecific, on the basis of vocal contact alone.

For each call, I measured the duration and the entropy and frequency at four equidistant points using the automated measurement function in Avisoft (Specht 2007). I then conducted LDA on these acoustic measures (Statistica Version 6.0, Statsoft, Tulsa, OK, U.S.A.; forward stepwise LDA was conducted following StatSoft 2001). Linear discriminant analysis effectively mapped the calls of each bird onto principal components space that represented the acoustic space used by each pair of birds and, in the large models, all birds in vocal contact with one another.

#### *Expert classification by subtype*

Neither SPCC nor LDA of acoustic parameter measurements is capable of imposing qualitative classifications of call subtype. Therefore, I had two experts in the field of crossbill identification, in addition to myself, classify six calls from each bird in the mixed-ecomorph pairs by subtype; three calls that were recorded before and three calls that were recorded after the experimental pairing



(total of 396 calls). Experts made classifications using printed spectrograms and, in a separate assessment, audio recordings, both presented in a blinded manner. The three experts agreed in their spectrographic classification of calls by subtype 100% of the time and in their aural classification of calls by subtype 96% of the time.

#### *Classification of vocal change and final similarity*

I used the classification of cases generated through the large LDA models of all birds within vocal contact of each other to determine whether pair members modified their calls sufficiently to achieve shared calls. I defined 'shared calls' statistically as calls of different individuals that were discriminable via LDA before, but not after, experimental social pairing. I also classified each pair for vocal change (as converging vocally, or not), because pairs could converge vocally yet fall short of achieving calls classified as being shared based on my definition. I classified pairs as converging vocally if the Mahalanobis distances (MDs, measures of distance between calls from different individuals at different time points generated through LDA) for both pair members indicated vocal modification and both the MDs and SPCC *R* values for pair members were smaller and reflected greater similarity at the end of the study. I conducted a chi-square test using the number of same- and mixed-ecomorph pairs in each vocal modification classification (converged/did not converge) to determine whether mixed- and same-ecomorph pairs were equally likely to converge vocally.

#### *Ethical Note*

This research was conducted under an approved Institutional Animal Care and Use protocol (no. 12092, University of California, Davis, U.S.A.) and scientific collecting permits from the Oregon, Washington and California Departments of Fish and Game. Methodologies were guided by animal care and use guidelines of the Animal Behavior Society.

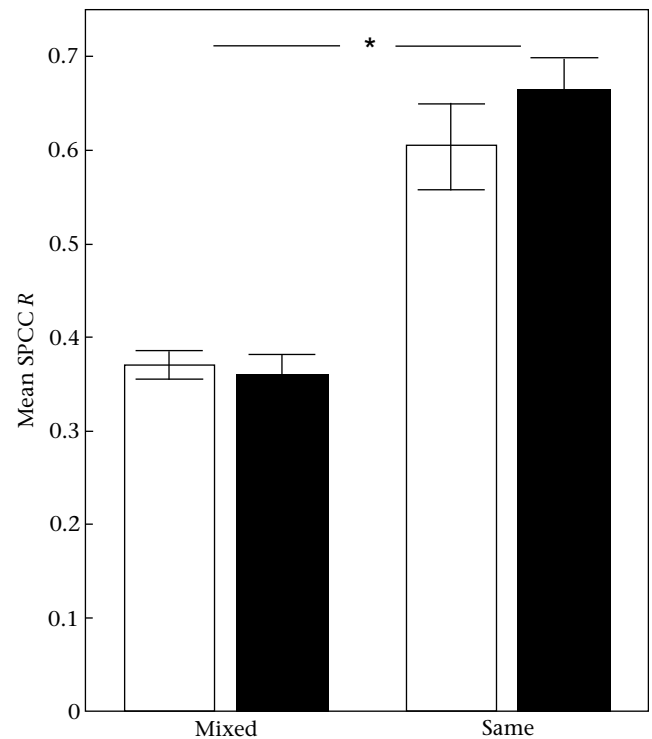
## RESULTS

#### *Convergence within Call Subtypes*

All birds made vocal modifications over the course of the study (Fig. 1; also see [Supplementary Material, Figs S1, S2](#)). But the calls of birds in same-ecomorph pairs were more similar both before and after pairing than were the calls of mixed-ecomorph pairs according to SPCC similarity values (treatment, ANOVA:  $F_{1,19} = 92.046$ ,  $P < 0.001$ ; Fig. 2). Thus, the calls of same-ecomorph pairs were more similar on average. Furthermore, significantly more same-ecomorph than mixed-ecomorph pairs were classified as producing calls that were more similar after pairing (see classification criteria, above; 8 of 10 same-ecomorph versus 3 of 11 mixed-ecomorph pairs; Yates corrected chi-square:  $\chi^2_1 = 3.92$ ,  $P = 0.048$ ). Case-by-case examination of LDA analysis and MDs revealed that increased call similarity was achieved through vocal modification by both pair members, which is consistent with vocal convergence (LDA: Fig. 1; [Supplementary Material, Figs S1, S2](#)).

#### *No Categorical Change in Call Subtype*

None of the birds made categorical changes in their call structure to produce a new call subtype according to both the spectrographic and aural classification of calls by experts. And only same-ecomorph pairs vocally converged sufficiently to be classified as achieving shared, pair-distinctive calls (4 of 10 same-subtype pairs; Figs 1, 3, also see [Supplementary Material, Figs S1, S2](#)).



**Figure 2.** Mean  $\pm$  SE SPCC *R* values for same- and mixed-subtype pairs before (open bars) and after (closed bars) pairing.

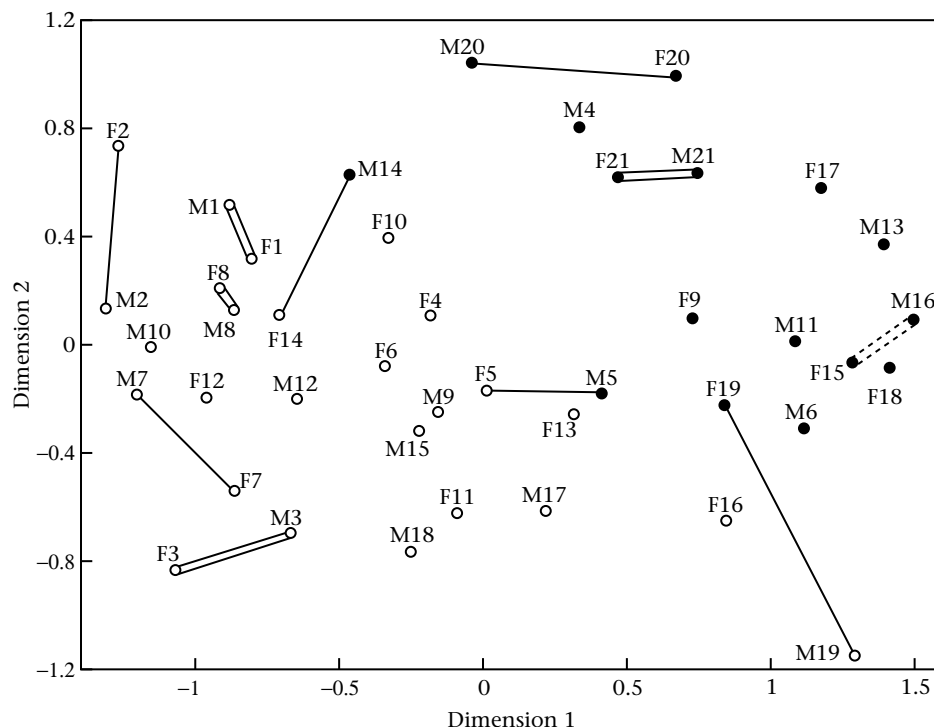
#### *Call Subtype Affects Social Interaction*

Mixed-subtype pairs had a lower frequency of affiliative interactions than birds in same-subtype pairs ( $\bar{X}_{\text{same}} \pm \text{SE} = 0.122 \pm 0.026$  affiliative interactions/min;  $\bar{X}_{\text{mixed}} \pm \text{SE} = 0.063 \pm 0.011$  affiliative interactions/min; independent samples *t* test:  $t_{19} = -2.147$ ,  $P = 0.045$ ), probably because birds in mixed-subtype pairs interacted less frequently than same-subtype pairs overall, even though they were in close physical proximity ( $\bar{X}_{\text{same}} \pm \text{SE} = 0.193 \pm 0.033$  total interactions/min;  $\bar{X}_{\text{mixed}} \pm \text{SE} = 0.111 \pm 0.021$  total interactions/min; independent samples *t* test:  $t_{19} = -2.142$ ,  $P = 0.045$ ).

#### *Bonding is Associated with Vocal Change*

Overall, same-ecomorph pairs that were classified as being bonded had more similar call structures at the end of the study than pairs that were classified as 'not bonded' (time  $\times$  bonding classification; repeated measures ANOVA:  $F_{1,17} = 7.311$ ,  $P = 0.019$ ; Fig. 4a, b). Unbonded pairs did not converge on more similar call structures, overall (Fig. 4b). Interestingly, same-ecomorph pairs that were classified as being bonded at the end of the study had less similar calls at the beginning of the study than did same-ecomorph pairs that were later classified as 'not bonded' ( $\bar{X}$  SPCC<sub>bonded</sub> = 0.516;  $\bar{X}$  SPCC<sub>not bonded</sub> = 0.690; independent samples *t* test:  $t_8 = -2.321$ ,  $P = 0.049$ ; Fig. 4a, b).

Note that two ecomorph-4 birds in mixed-subtype pairs within the same chamber (year 2) converged on statistically indistinguishable calls (Fig. 5). That is, two birds that produced the same call subtype converged on shared calls when they had acoustic but not physical contact. Neither of these birds was bonded with their cagemate of a different ecomorph and one bird was male and the other was female; they did not have prior physical social experience with one another.



**Figure 3.** Canonical plot of the centroids of calls from all birds at the end of experimental pairing. Open circles = subtype-3 birds' calls; solid circles = subtype-4 birds' calls; double black lines: experimental pairs that achieved statistically indistinguishable shared calls; double dashed lines = single pair that converged on shared calls within a chamber; single black lines = pairs that converged vocally but did not achieve shared calls. Note that this figure represents the calls of every bird in the 2-year study; the distinctiveness of pair members' calls would appear greater if calls of birds within social contact were graphed separately.

## DISCUSSION

The process of imitative vocal learning can determine the scope of potential social functions that shared communication signals may have. If shared signals emerge when animals copy or converge upon vocalizations with new companions, signals will reflect current social associations. Alternatively, limited vocal plasticity after a critical period of early learning can generate signals that reliably reflect an individual's lineage or population of origin. There are two levels of shared variation in the contact calls of red crossbills, and the present study suggests that limited learning in adulthood explains this diversity. Furthermore, the dual levels of variation in red crossbills' contact calls have the potential to serve two separate but concurrent social functions: call subtypes, learned early in development, can serve as reliable indicators of ecological specialization and facilitate assortment by ecomorph, while vocal plasticity within the boundaries of call subtypes permits pair-distinctive calls to emerge throughout life, which may facilitate interaction with close social companions of the same ecomorph.

### *Stable Production of Distinct Call Subtypes*

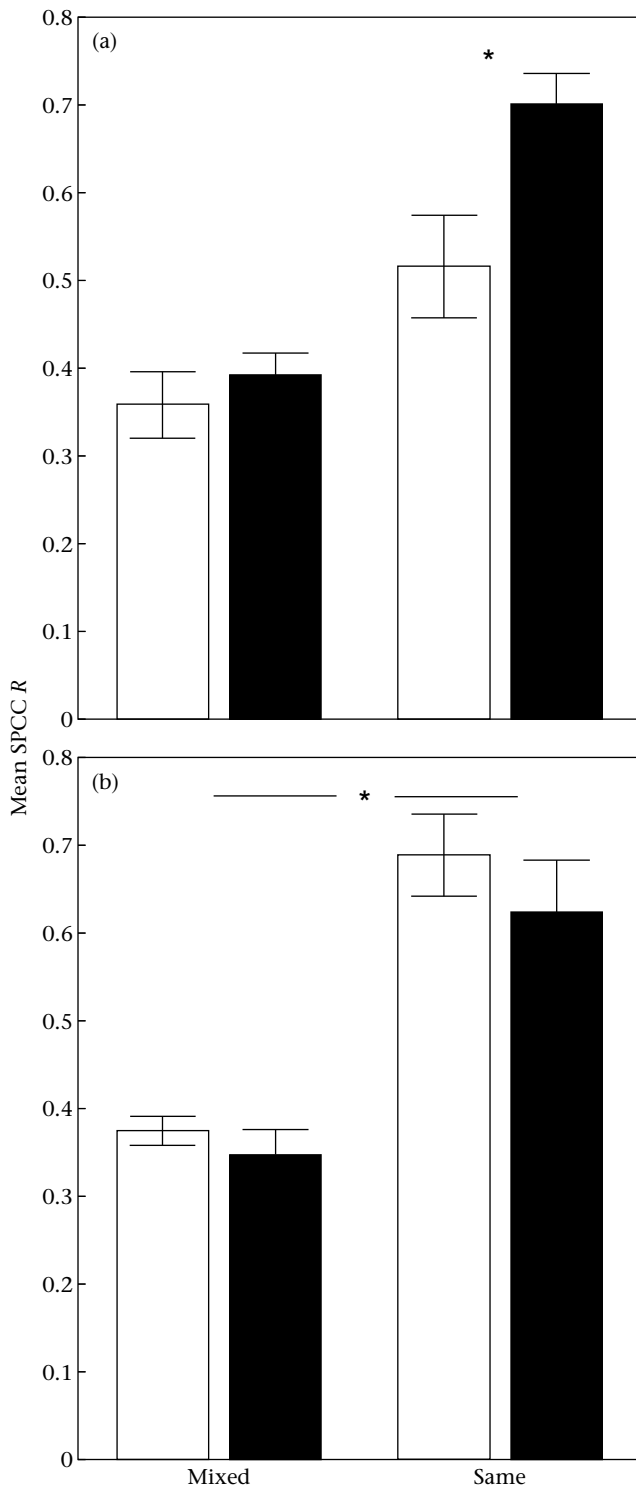
Adult red crossbills in this study only readily converged to the point of achieving calls shared with companions of their own ecomorph and call subtype. Crossbills learn their contact calls through imitation early in development and, very early in life, are able to copy the contact calls of adoptive parents of different ecomorphs (Groth 1993b; Sewall 2008). However, the adult birds in this study did not make categorical shifts in the structure of their calls sufficient to produce a different call subtype. It is possible that hearing conspecifics of the same call subtype impeded vocal modification in experimental birds. However, birds that are extreme minorities in the wild have been reported to maintain

production of their distinctive call subtypes, even if they pair with a mate of a different call subtype and ecomorph (Adkisson 1996). Thus, there is evidence that the limited call modification observed in adult crossbills in this study is mirrored in the wild.

Behavioural observations suggest that persistent production of subtypes could permit these categorically distinct call variants to impede social intermixing of crossbill ecomorphs. Birds that produced different call subtypes were less likely to interact when they were already in close physical proximity. Similarly, previous studies have shown that adult red crossbills respond selectively to individuals that produce calls of their subtype (Snowberg & Benkman 2007) and to playbacks of contact calls of their own subtype (Sewall & Hahn 2009). Red crossbills are thought to benefit from flocking with companions that share their ecological preferences because companions pool information about foraging success, increasing foraging efficiency (Smith et al. 1999). Furthermore, crossbills are likely to select mates from within their foraging flocks (Adkisson 1996), and hybrid offspring are argued to suffer reduced fitness (Benkman 1993, 2003). Thus, persistent production of call subtypes could improve both foraging and reproductive success by ensuring assortment with companions with common ecological specializations.

### *Vocal Convergence on Calls Shared with Close Companions*

While adult crossbills did not make categorical changes in the discrete call subtypes they produced, contact calls shared with companions did emerge through the process of vocal convergence within the boundaries of subtypes. Both male and female adult red crossbills are capable of vocal learning, as increased similarity in call structures was achieved when both pair members made vocal modifications (Fig. 1, Supplementary Material, Figs S1, S2). The observation that a male and female that had vocal contact but were



**Figure 4.** Mean  $\pm$  SE SPCC  $R$  values for (a) bonded mixed- and same-ecomorph pairs and (b) unbonded same- and mixed-ecomorph pairs. Bonded same-ecomorph pairs produced calls that were more similar after pairing (closed bars) than before pairing (open bars).

physically housed with companions of different ecomorphs still converged on pair-distinctive calls, suggests that crossbills preferentially converge on pair-distinctive calls with companions of their same call subtype (Fig. 5).

The vocal convergence that occurred among same-ecomorph pairs was associated with social affiliation (Fig. 4), just as it is in

many other species (Mundinger 1970, 1979; Farabaugh et al. 1994; Bartlett & Slater 1999). The interesting finding that same-ecomorph pairs that bonded had less similar calls within the scope of subtypes at the beginning of the study seems inconsistent with previous studies in other species (Moravec et al. 2006) and with evidence that crossbills avoid interaction with conspecifics that produce categorically distinct calls (Sewall & Hahn 2009). I offer the explanation that crossbills may prefer prospective mates with less similar calls because crossbill families share call structures (Keenan & Benkman 2008; Sewall 2008), and selecting a mate with a different call structure within the bounds of shared call subtype could be a mechanism for avoiding inbreeding.

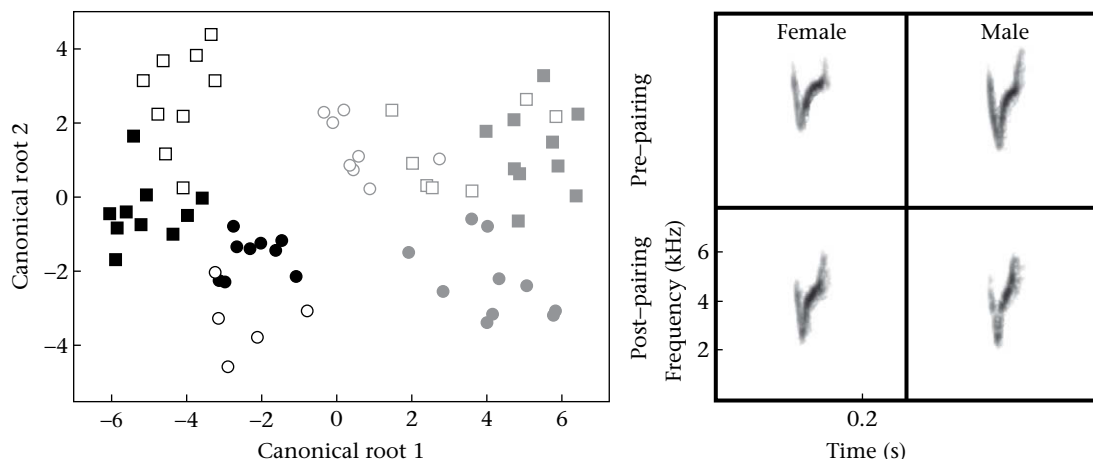
A number of adaptive explanations could account for companions' convergence on shared call structures. It has been proposed that shared calls may facilitate the identification of mates and companions (Mundinger 1970; Nowicki 1983), especially in noisy environments (Tyack 2008). Improved recognition of a mate's call, in particular, could permit pair members to maintain contact even when they vocalize only rarely or at lower amplitudes than usual, which could be important during nesting or when young are vulnerable to predators (Mundinger 1970). Red crossbills, like other cardueline finches, often nest in semicolonial groups, and males provision incubating and brooding females at the nest (Adkisson 1996). Breeding pairs that converge upon shared calls may better coordinate their behaviour around the nest and draw less attention from predators (Mundinger 1970).

Another adaptive explanation for call convergence is that the learning ability essential to achieve shared calls with close companions may reflect an individual's quality. Nowicki et al. (2002) proposed that variation in the precision of song imitation by male songbirds reflects variation in male quality (see also repertoire size: Catchpole & Slater 1995; Hile et al. 2005). Similarly, the precision of call sharing with prospective mates could provide information about a companion's quality. Alternatively, variation in the precision of call sharing could reflect the prospective mate's motivation and commitment to pairing, because achieving a close vocal match with a companion should prevent the sharing of call features, and perhaps also bonding, with other conspecifics (Hile et al. 2000). That is, convergence to the point of sharing a companion's call structure may reflect commitment to a specific social bond.

#### Consequences of Limited Call Modification

In contrast to red crossbills, adult pine siskins, *Carduelis pinus*, held under conditions similar to those in the present study have been reported to make categorical shifts in their contact call structures to copy the calls of a companion from a different population or species (Mundinger 1979; T. P. Hahn, unpublished data). The apparent open-ended vocal learning in this close relative of the red crossbill suggests that limited vocal imitation in adulthood may be a derived adaptation in red crossbills, which occur as sympatric ecologically diverged morphs (Benkman 1993; Groth 1993b).

It could be hypothesized that reduced social interactions and motivation impede shifts in call subtype production because vocal convergence is associated with bonding, and birds of different ecomorphs interact less frequently and less amicably. However, three mixed-ecomorph pairs showed evidence of social bonding yet failed to achieve shared calls, inviting speculation that limited call modification is the result of learning constraints, not motivation or social context. Constrained call production learning in adult red crossbills may be most analogous to the learning of song dialects in some birds (Baker & Cunningham 1985; Catchpole & Slater 1995). Some male songbirds learn their songs through imitation of adult males early in development and, although they may make subtle modifications to their songs across seasons, males do not



**Figure 5.** Representative spectrograms of calls from two subtype-4 birds (one female, one male) in separate mixed-ecomorph pairs housed within the same chamber. The male and female converged on statistically indiscriminable shared calls. The linear discriminant analysis shows the acoustic space used by all the birds in the chamber. Black circles = converging female's calls; black squares = converging male's calls; grey symbols = calls of experimental subtype-3 companions of the converging birds; open symbols = pre-experiment; solid symbols = post-experiment.

acquire songs of different dialects in adulthood, probably as the result of limited neural plasticity (Catchpole & Slater 1995; Kroodsma & Miller 1996). It is not known whether the neural systems that regulate song learning also mediate call learning, nor is it clear whether song learning is open- or closed-ended in red crossbills. Future studies of the neural mechanisms of call learning will inform our understanding of the conditions that promote call modification.

Whether limited call modification results from dampened motivation or learning abilities, closed-ended learning of call production, like song production, can theoretically contribute to the reproductive isolation of diverged or allopatric populations (Grant & Grant 1996; Freeberg 2000; MacDougall-Shackleton & MacDougall-Shackleton 2001; Ellers & Slabbekoorn 2003; Lachlan & Servedio 2004; Price 2008). Limited adult learning of call subtypes that are specific to ecologically diverged groups may promote social isolation in red crossbills because of the role of contact calls in social assortment. If red crossbill ecomorphs are cryptic or incipient sympatric species, as some researchers have suggested (Groth 1993b; Parchman et al. 2006), limited call learning in adulthood could ultimately promote assortment by ecological specialization and contribute to sympatric speciation.

## Acknowledgments

I thank T.P. Hahn, P.R. Marler, G.L. Patricelli, V.V. Pravosudov and S.A. MacDougall-Shackleton. Funding was provided by the Animal Behavior Society, the American Ornithologist's Union, the University of California (UC), Davis, Department of Neurobiology Physiology and Behavior and the UC Davis Animal Behavior Graduate Group.

## Supplementary Material

Supplementary Material for this article may be found, in the online version, at doi:10.1016/j.anbehav.2009.01.033.

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