

Social experience modifies behavioural responsiveness to a preferred vocal signal in red crossbills, *Loxia curvirostra*

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Although plasticity in signal production is well recognized as a means for animals to modify their communication systems, modifying responsiveness to signals could be equally important. We examined plasticity of responsiveness to social signals that mediate group formation and cohesion in red crossbills. The red crossbill is composed of several ecologically diverged forms, defined by variation in morphology, ecological specialization and vocal behaviour; each form is associated with a distinct variant of the species 'contact call.' To understand how plasticity in response to signal variants may influence social dynamics, we examined the response of red crossbills to distinct call variants before and after experimental pairing with a companion of a different form. In a playback study conducted soon after birds were captured we found that adult crossbills responded more to calls that were similar to their own calls. However, social experience with a companion that produced a different contact call variant eroded this response selectivity; at the end of the study birds experimentally housed with a companion that produced a different call variant responded equally to all species-typical calls, but control birds continued to respond selectively to calls that were similar to their own. The observed form of response plasticity may permit birds to gain information from a wider range of conspecifics but is unlikely to facilitate the social intermixing of crossbills of different forms; birds that respond to all crossbill call variants probably would not gain acceptance into flocks of other forms.

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Vocal communication repertoires are generally composed of multiple, acoustically discrete call types. Diverse call repertoires composed of many such discrete call types permit communication about a wide range of intentions, events and referents (Seyfarth & Cheney 2003; Marler 2004). Detailed study of any call repertoire generally also reveals some degree of graded variation within calls of a given type, however. Variation within a call type can be just as important to the social lives of animals as the distinct call types that make up a species' repertoire (Hauser & Marler 1993; Fischer et al. 2001). For example, referential call variants can reflect food availability (Hauser & Marler 1993; Evans & Evans 1999; Freeberg & Lucas 2002), the relative threat of predators (Seyfarth et al. 1980; Evans et al. 1993; Templeton et al. 2005) or the intentions of conspecifics (Baker et al. 1991; Kajikawa & Hasegawa 2000; Fischer et al. 2001, 2002; Wanker et al. 2005).

Social experience can increase the diversity of vocal communication signals that animals produce and also shape response to those signals, as animals must come to discriminate among and

respond differently to distinct signals (Hauser & Marler 1993; Janik & Slater 2000). One form of social learning, vocal imitation (Freeberg 2000; Janik & Slater 2000), can generate within-call-type variants shared among companions. These shared call variants may reflect membership to a social group or population. Within the category of signals known as 'contact' calls, imitative vocal learning can generate two forms of shared variation, each specific to a particular social class. 'Group or pair-specific calls' vary subtly within a population and are shared by members of pairs, families and social groups (bats: Boughman 1997; primates: Elowson & Snowdon 1994; cetaceans: Ford 1991; Weilgart & Whitehead 1997; Janik 2000; Watwood et al. 2005; birds: Mundinger 1970, 1979; Marler & Mundinger 1975; Samson 1978; Groth 1993a; Farabaugh & Dooling 1996; Wright 1996; Price 1998; Baker et al. 2000; Baker 2003). In contrast, 'call subtypes' are discrete contact call variants shared by individuals of a particular population or subspecies (Adkisson 1981; Snowdon 1985; Groth 1993b; Wright 1996; Baker 2000, 2003; Sewall et al. 2004; Runciman et al. 2005). Call subtypes are similar to dialects, but animals that produce different call variants often co-occur (Adkisson 1981; Groth 1993a; Sewall et al. 2004).

Contact calls serve to coordinate movements and to initiate and maintain contact among conspecifics (Marler 2004). Plasticity in responsiveness to contact call variants in adulthood therefore has

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the potential to influence social assortment and even population dynamics. Plasticity in responsiveness to call variants could persist throughout life such that an animal can come to respond selectively to the group-specific calls or call subtypes that are currently predominant in a social environment. Such plastic selectivity for contact call variants could facilitate movement among social groups and populations. Alternatively, because responsiveness must be somewhat plastic to accommodate changing social environments, social context can have the effect of eroding selectivity for particular signal variants but not reversing selectivity. The result of eroded response selectivity is that animals become equally responsive to a range of social cues and conspecifics (Sockman et al. 2002; Swaddle & Page 2007). In this study we examined plasticity of responsiveness to contact call subtypes found in red crossbills.

Red crossbills exist as at least nine sympatric, ecologically diverged morphs (ecomorphs: see *Methods*; Groth 1993b; Benkman 2003). Crossbill ecomorphs show variation in body size and beak morphology, thought to reflect adaptation to different conifer resources (Groth 1988, 1993b; Benkman 2003). Distinct contact call subtypes are associated with each size class and constitute the most conspicuous difference between ecomorphs. Crossbills learn their call subtype production early in development (Groth 1993b; Sewall 2008), and there is strong evidence that the call subtype a bird produces then remains stable throughout adult life (Groth 1993b; Adkisson 1996; Keenan & Benkman 2008; Sewall 2008). Contact call subtypes are therefore well positioned to reflect birds' ecological adaptations and permit crossbills to classify conspecifics by ecomorph (Snowberg & Benkman 2007). The degree of adult crossbills' plasticity in responsiveness to different call subtypes is one factor that will determine the nature of their interaction with birds of different ecomorphs. We conducted a series of playback studies over 2 years to mature, wild-caught red crossbills with the aim of describing adult plasticity of responsiveness to different call subtypes.

METHODS

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

We captured 31 wild ecomorph-3 and 24 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 small seeds and papery scales, such as western hemlock, *Tsuga heterophylla* (Groth 1993b; Benkman 2003). Ecomorph-4 is a medium-sized bird that performs better on medium-sized cones such as Douglas-fir, *Pseudotsuga menziesii* (Groth 1993b; Benkman 2003). We also used flight calls from birds of ecomorph-2 in our playback experiment. Ecomorph-2 is one of the larger crossbill forms with a robust bill that permits efficient foraging on large tough cones such as ponderosa pine, *Pinus ponderosa* (Groth 1993b; Benkman 2003). Birds of ecomorph-4 commonly co-occur with both ecomorph-3 and ecomorph-2, but ecomorphs-2 and 3 co-occur infrequently in the wild, presumably owing to their more distinct foraging preferences (T. R. Kelsey & T. Hahn, personal communication).

Experimental Design

Two studies were conducted over 16 months. In the autumn of the first year (2003), we tested 21 ecomorph-3 and 6 ecomorph-4

crossbills soon after capture for selectivity for call subtypes. In a separate two-part experiment in the second autumn (2004), we tested 16 ecomorph-3 and 21 ecomorph-4 birds for baseline selectivity in the 'pre-pairing playback' study. Then, to assess the nature of plasticity in responsiveness to call subtypes, we immediately paired 36 of these birds with an unfamiliar companion of the opposite sex of either their own call subtype (control condition) or a different call subtype (experimental condition) for approximately 4 months. In this second study the birds' response selectivity for call subtypes was reassessed in a 'post-pairing playback' at the end of the captive pairing period. Mixed sex pairs were chosen for the experimental housing between the pre- and post-pairing playback studies because this condition is known to promote vocal learning (Mundinger 1979; Hile et al. 2000; Sewall 2008). We housed experimental and control pairs in cages within separate sound-attenuation chambers (3 pairs per chamber, 3 chambers per treatment, 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. Only 21 of the 36 birds responded in both the pre- and post-pairing trials. Furthermore, to avoid potential nonindependence of pair members' responses, we excluded the results from the member of each pair that had been in captivity the longest when analysing the post-pairing playback (N control = 11, N experimental = 5). Four subjects, three ecomorph-3 and one ecomorph-4 bird, were included in the playback studies in both years (i.e. all three studies). These birds were held in captivity with companions of their same ecomorph for approximately 1 year between the studies. The other 12 subjects in the second year had been captured within 8 weeks of the beginning of the study. Time in captivity was included as a variable in all statistical analyses (see below).

Playback Protocol: Year 1

Initially, birds were housed in large sex- and ecomorph-specific groups in indoor aviaries at the University of California Davis ($3.7 \times 3 \times 1.8$ m aviaries, Corners, Limited, Kalamazoo, MI, U.S.A.). The aviaries were within a single room so all birds could hear calls of their own and other subtypes prior to the study, as often occurs in nature.

In the first year of study, subjects were played stimulus files of subtype 3 and subtype 4 calls; subtypes designated as 'own' and 'other' for analytical purposes. Subjects had been exposed to the other call subtype in captivity and probably in the wild. Each bird in this study heard the same 20 stimulus files (10 of each call category) in randomized ABAB or BABA order in a single, 20 min trial (Kroodsma 1990; Vicario et al. 2001; Table 1).

We generated stimulus files that were 30 s long with mean calling rates of one call per 1.5 s by pasting single exemplar calls into a template that mimicked a natural calling bout using Syrinx software (Burt 2006). This procedure ensured that calling rate and duration were controlled across stimulus files. We also

Table 1
Experimental design for the playback study in year 1

	Exemplar subtype	Subject 1	Subject 2	Subject 3
Exemplar A	3	X	X	X
Exemplar B	3	X	X	X
Exemplar C	3	X	X	X
Exemplar X	4	X	X	X
Exemplar Y	4	X	X	X
Exemplar Z	4	X	X	X

The number of playback exemplars is the sample size ($N = 20$), the subtype of each exemplar is the between-subjects dependent factor and the response of each focal bird to each exemplar is the sample point.

bandpass-filtered (1/10 kHz) and normalized each call exemplar for amplitude using Avisoft software (Specht 2007). Each exemplar call had been recorded from a wild crossbill previously captured and banded at a different location and in a different year, making it improbable that subjects had prior experience with the specific exemplar calls. We presented each 30 s stimulus file once, with 30 s of silence between files for a total of 20 min of playback exposure.

On each day of testing we transferred the focal bird into a testing cage in a separate sound-attenuation chamber (IAC, Industrial Acoustics) and allowed it to acclimate for 15 min. Trials were initiated only when birds were sitting quietly in the chamber. We recorded all trials using a Sony TCM 5000EV tape recorder and Sennheiser ME66 short-shotgun microphone. As a measure of call subtype discrimination, we digitized and made spectrograms (spectrogram resolution of 86 Hz, 2.903 ms, 85% overlap, FFT size 256, Hamming window) of all trial recordings using Syrinx software (Burt 2006). We then quantified the number of contact calls produced by each focal bird during the presentation of a stimulus file and during the 30 s of silence following the stimulus.

Playback Protocol: Year 2

In the second year of the study we included 20 exemplars each of three call subtypes in both the pre- and post-pairing playbacks: (1) own subtype, (2) other subtype and (3) odd subtype. The 'other' subtype was either subtype 3 or subtype 4, depending upon the call of the focal bird. For experimental birds the 'other' subtype was also the call subtype of their companion (post-pairing playback). For all subjects the 'odd' call subtype was subtype 2, a call variant that all subjects had been exposed to in captivity but which they had not heard in at least 4 months at the time of the post-pairing playback.

In the pre-pairing and post-pairing playbacks each subject heard only one of 20 exemplars of each call subtype in randomized order on consecutive trial days (Kroodsma 1990; Table 2). Each exemplar was played to one subject of each ecomorph (except for eight exemplars that were used twice in the pre-pairing playback). As in the first year, we generated 30 s stimulus files of each call exemplar. We repeated each stimulus file 10 times with 30 s of silence between repetitions for a total of 10 min of stimulus exposure. Trials were conducted, recorded and scored as they were in the first year (see above).

Statistical Analysis

The interindividual variation in calling rate was significant in all three playback studies (number of response calls: range 1–1425) leading to non-normal distributions among subjects but not between treatment groups (second year). We addressed this through two approaches. In the first year we transformed data by the natural log (plus one, to accommodate the fact that some individuals only responded to exemplars of one subtype) to achieve normality (Kolmogorov–Smirnov: $P > 0.05$). In the second year we used the total number of calls that a focal individual produced

across all trials to calculate the proportion of calls given in response to each call subtype. We then arcsine-transformed those proportions to achieve normality.

We assessed discrimination among call subtypes in the first year playback using two ecomorph-specific repeated measures ANOVAs (Kroodsma 1990). In this first analysis the number of exemplars was the sample size because all subjects heard all of the playback files (Kroodsma 1990; Kroodsma et al. 2001; Searcy et al. 2003). Exemplar subtype (own, other) was the between-subjects factor, and the number of response calls by the focal bird to each exemplar was the sample point (Table 1; Searcy et al. 2003). The number of exemplars was the level of replication in this analysis. The nesting of exemplars within the category of 'subtype' controlled for between-exemplar variation in response to signal classes. We used ln-transformed total number of calls produced by each subject in response to each exemplar in this first analysis because the proportion of total calls that a given exemplar received was small and relatively uniform across all exemplars.

In the pre- and post-pairing playbacks, each subject of a particular ecomorph heard a different exemplar of each call subtype (with the exception of 8 birds in the pre-pairing playback). We used the number of subjects as the sample size and each subject's response to an exemplar of a given subtype as a sample point (Table 2; Searcy et al. 1997, 2003). This approach permitted evaluation of responsiveness across the pre- and post-pairing playback and evaluation of treatment effects (see below). We used the arcsine-transformed proportion of the total number of calls that a bird produced during playback of an exemplar of a particular call subtype to achieve normality in this second analysis.

We assessed baseline discrimination among call subtypes in the pre-pairing playback using ANOVA, with exemplar subtype as the dependent within-subjects factor. Then, to test for plasticity in response to call subtypes, we conducted a repeated measures ANOVA including both the pre- and post-pairing playback. Treatment was the between-subjects factor in this large model, responses to exemplars of each subtype were sample points, and pre- and post-pairing trials were repeated measures (Table 2). We also conducted ANOVA of the post-pairing trial alone to specifically assess the effect of social housing condition on call responsiveness at the end of the study. The age, sex, ecomorph and time in captivity of each bird were included in the analysis; none of those factors had significant effects either before or after pairing ($P > 0.05$). We used Fisher LSD post hoc tests to identify significant factors in ANOVAs.

RESULTS

Soon after capture and prior to any pairing manipulations, crossbills responded more to contact calls of their own subtype than to other subtypes with which they had some prior auditory experience in captivity and probably in the wild. In the preliminary playback study, subtype 3 exemplars elicited more response calls from ecomorph-3 birds than did subtype 4 exemplars (exemplar subtype, ANOVA: $F_{1,20} = 14.227$, $P = 0.001$; Fig. 1a). Likewise, subtype 4 exemplars elicited more total calls from ecomorph-4 birds than did subtype 3 exemplars (exemplar subtype, ANOVA: $F_{1,5} = 7.660$, $P = 0.013$; Fig. 1b).

The finding that wild-caught crossbills responded selectively to calls of their own subtype was corroborated in the second year. In the pre-pairing playback, adult wild-caught crossbills called more in response to exemplars of their own subtype than they did to the other two subtypes (exemplar subtype, ANOVA: $F_{2,36} = 10.123$, $P = 0.0001$; Fig. 2).

Social housing had a significant effect on responsiveness to calls of different subtypes (time \times call exemplar subtype \times social condition, repeated measures ANOVA: $F_{2,23} = 4.219$, $P = 0.021$; exemplar subtype \times social condition, post-pairing ANOVA:

Table 2
Design of pre- and post-pairing playback studies in year 2

Category	Own			Other			Odd		
	A	B	C	A	B	C	A	B	C
Exemplar	A	B	C	A	B	C	A	B	C
Subject 1	X	–	–	X	–	–	X	–	–
Subject 2	–	X	–	–	X	–	–	X	–
Subject 3	–	–	X	–	–	X	–	–	X

With only eight exceptions each focal bird of a given ecomorph heard a different exemplar of each call subtype; the focal birds were the sample size. Housing condition (same versus mixed subtype) was the between-subjects dependent factor, the response of each subject to an exemplar of a given call subtype was the sample point and the pre- and post-pairing playbacks were the repeated measures.

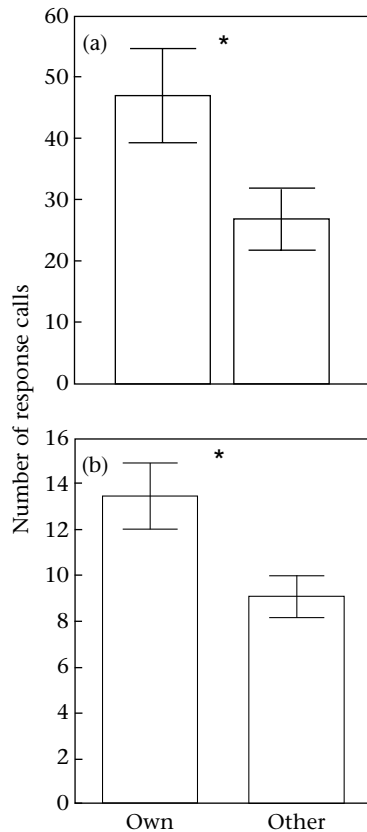


Figure 1. Mean \pm SE number of response calls produced by wild-caught (a) ecomorph-3 crossbills ($N = 21$) and (b) ecomorph-4 crossbills ($N = 6$) during the playback of contact calls of their own call subtype and a call subtype that they had substantial prior experience with in captivity and probably in the wild.

$F_{2,23} = 5.086$, $P = 0.01$; Fig. 3). That is, birds' responsiveness to calls of different subtypes changed as a function of their housing condition. Both control and experimental birds responded selectively to calls of their own subtype prior to pairing. Control birds

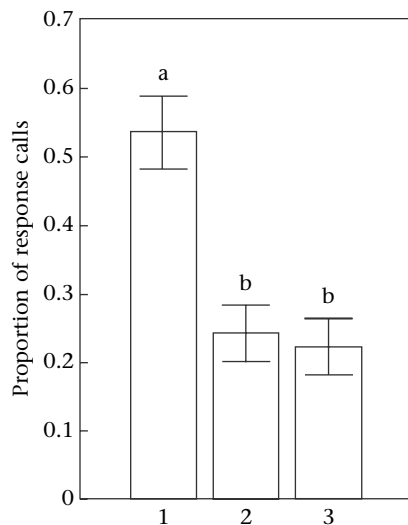


Figure 2. Mean \pm SE proportion of total response calls produced by wild-caught crossbills ($N = 37$) during playback of three contact call variants prior to any social pairing: (1) calls of their own subtype, (2) calls of a subtype that they had recent experience with in captivity and probably in the wild and (3) calls of a subtype that they had only some recent experience with (subtype 2). Lowercase letters indicate statistically significant differences between groups, as determined by post hoc tests.

continued to respond selectively to their own call subtype after pairing and called much less to the two call subtypes they had not heard for the 4 months of the study. Experimental birds, in contrast, called relatively equally in response to their own call subtype, the call subtype of their companion and a third call subtype that they had no recent experience with; experimental birds did not respond selectively to any call subtype in the post-pairing trial (Fig. 3).

DISCUSSION

Our results show that wild-caught adult crossbills of two sympatric ecomorphs respond selectively to contact calls of their own subtype (Figs. 1, 2). This finding is consistent with previous studies of crossbills from a resident population in South Hills, Idaho, U.S.A. (Snowberg & Benkman 2007) and with field playbacks to free-living nomadic ecomorphs (K. B. Sewall, unpublished data).

Most previous playback studies of shared contact call variants in birds have focused on group- or pair-specific calls, which emerge when companions copy or converge on shared call structures. Selective responsiveness to contact calls that are shared with mates, family members or group members has been documented in American goldfinches, *Carduelis tristis* (Mundinger 1970), Cassin's finches, *Carpodacus cassinii* (Samson 1978), stripe-backed wrens, *Campylorhynchus nuchalis* (Price 1999) and black-capped chickadees, *Poecile atricapillus* (Nowicki 1983). It has been inferred from these patterns of selective response that pair- and group-specific calls mediate social cohesion, help coordinate group movement and facilitate shared activities such as foraging and breeding (Mundinger 1970; Nowicki 1983; Wilkinson & Boughman 1998).

In contrast to group-specific calls that are shared with close social companions, red crossbills' contact call subtypes are learned early in life and are shared more broadly with unfamiliar individuals that have common ecological specializations (Groth 1993b). Pine grosbeaks, *Pinicola enucleator*, which are close relatives of crossbills, also display morphological variation, and birds of different classes produce distinct contact call subtypes (Adkisson 1981). Field playbacks of pine grosbeak contact call subtypes show that free-living birds respond selectively to call exemplars of their own subtype (Adkisson 1981; see also orange-fronted conures, *Aratinga canicularis*: Vehrencamp et al. 2003; yellow-naped amazon parrots: *Amazona auropalliata*: Wright & Dorin 2001). Just as selective responsiveness for group-specific calls can facilitate social cohesion, selective responsiveness for call subtypes could mediate assortment by morphology and ecological specialization.

Our research suggests that social experience can erode red crossbills' response selectivity for call subtypes. After experimental birds in the present study had social experience with a companion that produced a different contact call subtype, they responded relatively equally to contact calls of all subtypes, even exemplars of a call subtype that they had not heard during the 4 months of the pairing experiment (Fig. 3). Under the experimental social conditions in the present study, adult crossbills did not come to respond selectively to calls of their new companion's subtype. Rather, adult red crossbills became responsive to all species-typical contact calls.

We suggest that the erosion of selective responsiveness for call subtypes in red crossbills is similar to female songbirds' preferences for mates and song variants. Although some female birds, such as cowbirds, modify their preferences for song variants in adulthood and come to prefer the songs of current companions (Freeberg 2000; West et al. 2006), females often develop preferences early in life for signals specific to populations or classes of individuals, through an imprinting-like process (Miller 1979; Irwin & Price 1999; Freeberg 2000; Hernandez & MacDougall-Shackleton 2004). However, females that acquire song preferences early in life still show some plasticity in response to song types in adulthood as a result of their social environment. When females lack the

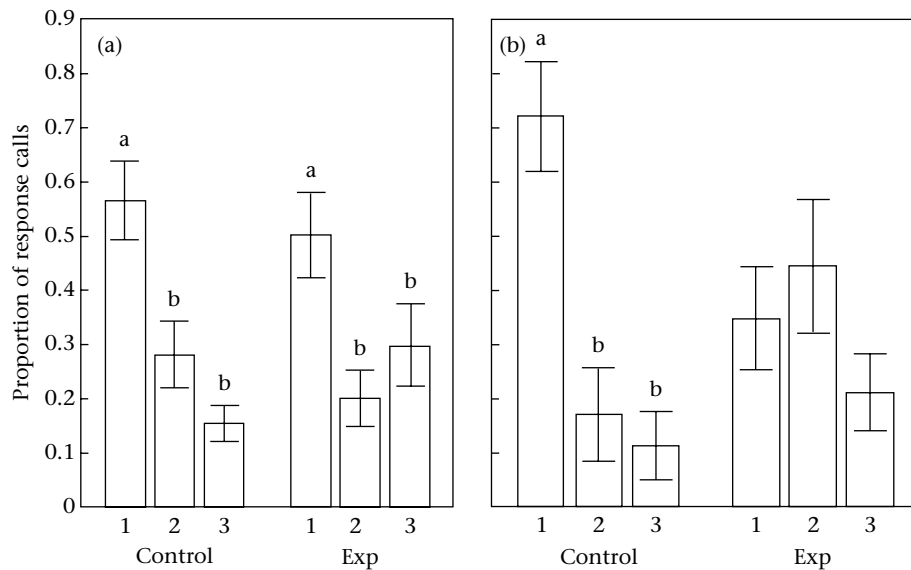


Figure 3. Mean \pm SE proportion of total response calls produced by control ($N = 11$) and experimental ($N = 5$) crossbills before (a) and after (b) pairing. Three contact call variants were included: (1) their own call subtype, (2) another call subtype that they had prior experience with, also the subtype of experimental birds' companions and (3) a call subtype that they had not heard in 4 months at the time of the post-pairing playback. Lowercase letters indicate statistically significant differences between groups, as determined by post hoc tests.

opportunity to select mates that produce preferred songs, their selectivity is eroded and they come to respond to a wider range of males (Price 2008). For instance, although female European starlings, *Sturnus vulgaris*, show neural and behavioural selectivity for complex songs early in life, adult females exposed exclusively to less preferred song variants become equally responsive to all song types (Gentner & Hulse 2000; Sockman et al. 2002). The same seemed to be true for red crossbills in the present study. Birds that had exclusive physical social contact with a companion that produced a different contact call subtype became responsive to all crossbill contact calls, even calls of a subtype that they had not heard in at least 4 months. In contrast, birds housed with a companion that produced their same call subtype responded selectively to their own call subtype, just as wild-caught birds do (Figs 2, 3).

Although we cannot rule out the possibility that crossbills express greater plasticity in responsiveness under different circumstances, we argue that the natural history of red crossbills should favour erosion but not reversal of responsiveness to call subtypes. Red crossbills are believed to pool information about foraging success and choose mates from within flocks (Adkisson 1996; Smith et al. 1999). Thus, crossbills are thought to benefit from assorting with companions of their same ecological specialization whenever possible (Smith et al. 1999). If crossbills reversed their selectivity as adults and came to respond preferentially to calls of a subtype that differed from their own, they would probably approach conspecifics of a different ecomorph and suffer reduced foraging performance (Smith et al. 1999) and reproductive success (Snowberg & Benkman 2007). In contrast, eroded selectivity for ecomorph-specific call subtypes could permit birds to adjust to adverse social conditions but would not result in preferential contact and interaction with birds of a different ecomorph. Generalized responsiveness to crossbill calls of any subtype could permit birds to gain more information from conspecifics and perhaps accrue nonforaging-related benefits of group membership (Smith et al. 1999). This generalized responsiveness could be especially beneficial when a particular ecomorph is a minority, as sometimes occurs during irruptive migrations or in mixed forests (Adkisson 1996). Plasticity in response to call subtypes despite

stable production of calls could, in fact, explain rare observations of mixed-subtype pairs in the wild (Adkisson 1996). Although crossbills have elaborate songs, plasticity in response to call subtypes may also play a role in mediating functional plasticity in mate choice when preferred mates are not available. Eroded response selectivity may not frequently result in mixed flocking though, because the majority of crossbills would still respond selectively to conspecifics that produce their own call subtype. Furthermore, crossbills interact less often and less amicably with conspecifics that produce different call subtypes when they are housed together in captivity (Sewall 2008). Thus, birds that respond equally to all crossbill call subtypes might not gain acceptance into flocks of other ecomorphs on the basis of their call production, which does not readily change (Adkisson 1996; Keenan & Benkman 2008; Sewall 2008).

The songbird literature may provide a basis for predicting the evolutionary impact of eroded selectivity for contact call subtypes, described here in crossbills. Although cultural signals alone probably do not promote social and genetic isolation, learned communication signals that differ between ecologically diverged groups can theoretically reinforce genetic divergence (Price 2008). Constrained plasticity in responsiveness to song variants is one factor that can promote reproductive isolation among diverged or allopatric populations (MacDougall-Shackleton & MacDougall-Shackleton 2001; Lachlan & Servedio 2004; Price 2008). The same may be true of responsiveness to contact call subtypes that are specific to ecologically diverged crossbill forms, because of the role that these calls play in social assortment. That is, selective responsiveness to contact call subtypes may promote the social, and eventually even the genetic isolation, of ecologically diverged groups.

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