



Song sharing with neighbours and relatives in a cooperatively breeding songbird



Çağlar Akçay^{a,*}, Katherine L. Hambury^a, J. Andrew Arnold^{a,b}, Alison M. Nevins^a,
Janis L. Dickinson^{a,c}

^a Cornell Lab of Ornithology, Ithaca, NY, U.S.A.

^b Department of Biological Sciences, Old Dominion University, Norfolk, VA, U.S.A.

^c Department of Natural Resources, Cornell University, Ithaca, NY, U.S.A.

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Kin recognition is important in allowing cooperative breeders to invest preferentially in helping kin, especially when helping is not restricted to the natal territory. Where spatial cues are not reliable indicators of kinship, animals can use family signatures, which may be learned or genetic. Alternatively, they can use unique signatures that are learned via prior experience in a context that identifies specific individuals as kin. Here we investigate sharing of song types between related and unrelated male western bluebirds, *Sialia mexicana*, a cooperatively breeding songbird that lives in neighbourhoods composed of a mix of kin and nonkin. Helpers only assist in raising close kin, including parents as well as brothers and grandfathers living on non-natal territories. In a previous study, we demonstrated that western bluebird males are able to recognize related males through their songs. Here we ask whether this kin recognition is based on song sharing within a family or whether western bluebird song sharing is primarily with neighbouring birds regardless of relatedness. The results indicate that western bluebirds often share with related and unrelated neighbours alike, and they rarely share any notes with non-neighbouring birds, whether they are related or unrelated. Although we cannot rule out the possibility of kin signatures that were not measurable using tools currently available for detecting vocal similarity, our findings suggest that kin recognition through song does not rely on note sharing with relatives and that western bluebirds use a more broadly applicable mechanism of vocal kin recognition compared to other cooperative breeders.

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The ability to discriminate among individuals is critical to navigating complex social environments and making fitness-enhancing decisions based on relatedness, status and outcomes of past interactions (Wiley, 2013). A prominent example of this discrimination is seen in kin-biased helping in many cooperative breeders (Cornwallis, West, & Griffin, 2009; Dickinson & Hatchwell, 2004; Hatchwell, 2009). While helping nonrelatives is common for species exhibiting mate sharing, 68% of cooperative breeders only have nonbreeding helpers-at-the-nest, and in most of these (74.7%) helpers only assist relatives (see Figure 1 in Riehl, 2013). Where locational or contextual information is unreliable, such kin-biased interactions require kin recognition, the ability of individuals to perceive family-specific signals (i.e. 'family signatures') and classify relatives using a template stored in the brain (Beecher, 1982;

Sherman, Reeve, & Pfenning, 1997). Note that we use the term kin recognition in the broad sense as any mechanism that allows individuals to distinguish kin from nonkin based on any cue (e.g. spatial cues) or signature (for the debate surrounding the term, see Grafen, 1990; Penn & Frommen, 2010).

Family- or group-specific signatures are likely to be adaptive when social interactions of animals are structured into discrete, cooperative units where insider interactions are primarily cooperative and outsider interactions are mostly competitive. In such cases, family signatures will allow rapid discrimination of group members from nongroup members. Consistent with this is the observation that, in many cooperatively breeding birds, individuals display a vocal family signature that is shared only with relatives (McDonald & Wright, 2011; Price, 1998, 1999; Sharp, McGowan, Wood, & Hatchwell, 2005). Family signatures may develop in multiple ways (Waldman, 1987). First, they may be genetically controlled such that signatures develop without significant environmental input (e.g. Hain & Neff, 2006). In such cases, a match between an individual's signature and an inherited, family-specific

* Correspondence: Ç. Akçay, Cornell Lab of Ornithology, 159 Sapsucker Rd, Ithaca, NY 14850, U.S.A.

E-mail address: caglar@uw.edu (Ç. Akçay).

template would reliably indicate the genetic relationship among individuals. Alternatively, signatures may be learned socially from parents. Social learning of vocalizations is the rule in songbirds, which makes social learning of family signatures a likely possibility (Beecher & Brenowitz, 2005; Catchpole & Slater, 2008).

In the first study that examined the development of family signatures in a cooperatively breeding bird, Sharp and colleagues (Sharp et al., 2005; Sharp & Hatchwell, 2006) found that signatures in long-tailed tits, *Aegithalos caudatus*, are learned socially from other family members. In a more recent study, Greig et al. (2012) also found that males in the cooperatively breeding splendid fairy wrens, *Malurus splendens*, learned their songs from their social father, although given the high rates of extrapair paternity (about 40%; Webster, Tarvin, Tuttle, & Pruett-Jones, 2004), song in this case acts as a cue of group membership rather than indicating actual genetic kinship with the father. Songs or calls have been found to reflect family or kin relationships in other species of cooperatively breeding birds, but the developmental underpinnings of these vocalizations have not been studied (McDonald & Wright, 2011; Price, 1998). Finally, in a recent study, Keen, Meliza, & Rubenstein (2013) found that flight calls of cooperatively breeding superb starlings, *Lamprolornis superbus*, carried group (as well as individual) signatures, but these were not correlated with actual kinship.

A further possibility is that kin recognition may rely not on family signatures but on recognition of individual-specific signatures (Kondo, Izawa, & Watanabe, 2012; McDonald, 2012; Tibbetts & Dale, 2007). If the calls or combinations of notes sung by individuals in a population are distinct, individuals can discriminate kin from nonkin by learning individual-specific signatures when they are only or mostly associating with relatives (e.g. present together at the same nest or through repeated interactions with relatives on the natal territory; Baglione, Canestrari, Marcos, & Ekman, 2003).

In contrast to cooperatively breeding birds that learn songs or calls from family members, many songbirds learn their songs from unrelated individuals that eventually become their territorial neighbours, leading to patterns of song sharing between unrelated neighbours (Beecher, Campbell, & Stoddard, 1994; McGregor & Krebs, 1982, 1989; Payne, 1983). Song sharing in these species is usually between unrelated individuals and allows birds to match each other in singing interactions, which is presumed to have a function in territory defence (Akçay, Tom, Campbell, & Beecher, 2013; Beecher, Campbell, & Nordby, 2000; Burt, Campbell, & Beecher, 2001; Krebs, Ashcroft, & van Orsdol, 1981; Vehrencamp, Hall, Bohman, Depeine, & Dalziell, 2007). More recently, the degree of song sharing among males has been found to be a target of female mate choice (Poesel, Nelson, & Gibbs, 2012).

Most songbird species for which song sharing and matching have been studied live in socially monogamous breeding units and do not have prolonged contact with their relatives, a situation that contrasts markedly with the case of cooperative breeders and animals living in kin neighbourhoods. Where family members live in close proximity, song sharing may function in kin discrimination if songs are shared primarily between relatives.

Here we examine the patterns of song sharing in the western bluebird, *Sialia mexicana*, a species in which males show delayed and localized dispersal leading to the formation of neighbourhoods composed of kin and nonkin (Kraaijeveld & Dickinson, 2001). On average, 7% of pairs (interannual range 3–16%) have between one and three adult males helping at the nest (Dickinson, Koenig, & Pitelka, 1996), and male relatives also cooperate in territorial defence (Akçay, Swift, Reed, & Dickinson, 2013; Stern, 2012). As males sometimes help at their brothers' and grandfathers' nests, in addition to nests of their parent(s), spatial information alone is insufficient to explain the observation that males only help at the

nests of relatives (Dickinson et al., 1996). In a recent study we found that males can discriminate between kin and nonkin based on their song, responding less aggressively to song from relatives than from nonrelatives (Akçay, Swift, et al., 2013).

We examine features of western bluebird song that allow for discrimination of kin testing for a kin signature and analysing the information conveyed about kinship through vocal sharing. The kin-structured neighbourhoods of western bluebirds provide a unique opportunity to test whether vocal sharing reflects relatedness, as found in other cooperatively breeding birds, or whether vocal sharing occurs regardless of relatedness, as found in many other songbirds (Beecher & Brenowitz, 2005). In particular, in studying the vocalizations of western bluebirds we have the opportunity to contrast vocal sharing of related versus unrelated neighbours, as well as neighbouring versus non-neighbouring relatives. If western bluebird males learn vocalizations from neighbours, whether or not they are related, then we predicted that song sharing would be common between neighbours but rare between non-neighbours. On the other hand, if vocalizations are learned primarily from family members, we expected that related males would share vocalizations with each other whether or not they had neighbouring territories. Note that these two hypotheses are not mutually exclusive and song sharing may reflect both kinship and spatial proximity.

METHODS

Study Species and Site

We studied a banded nestbox population of western bluebirds at Hastings Natural History Reservation, located in the upper Carmel Valley in the outer coastal range of central California. The population has been monitored for long-term research in behavioural ecology since 1983. In this population, western bluebirds form socially monogamous breeding units and a small percentage of pairs have adult male helpers that are usually offspring from previous years (Dickinson et al., 1996).

All individuals in our population are banded with a unique combination of a U.S. Fish and Wildlife Service metal band and three coloured bands for visual identification, either as nestlings, or when they immigrate to the study area. Details of the study population and monitoring methods can be found in Dickinson et al. (1996). Because of high levels of male philopatry, most males that become breeders in the population are banded as nestlings, allowing for construction of a pedigree. Although extrapair paternity accounts for about 20% of the nestlings (Dickinson & Akre, 1998; Ferree & Dickinson, 2011), there is no evidence that extrapair young are recognized as such (Dickinson, 2003, 2004; Dickinson & Akre, 1998; Leonard, Dickinson, Horn, & Koenig, 1995). Therefore, we used social pedigrees to determine relatedness among males. Universal banding provided a large sample of known nonrelatives that were banded as nestlings. We also assumed that males that were banded for the first time as yearling adults were immigrants to the study area and not related to the males already in the study area.

Western bluebirds show a two-step dispersal process (Kraaijeveld & Dickinson, 2001). In their first autumn, hatch-year males tend to stay on their natal territory, forming family groups and defending mistletoe-based territories, which provide them with a constant berry supply over the winter (Dickinson & McGowan, 2005). Daughters on the other hand, tend to disperse in the autumn, although a small percentage of females remain on their natal territory until spring. At the same time, these family groups are joined by immigrant females, and social pairing often happens in the winter group (Kraaijeveld & Dickinson, 2001). In

spring, males that acquire a mate settle onto breeding territories and often, but not always, bud off a portion of their natal territory, settling next door to their fathers. At this stage most females that stayed on their natal territory disperse and only a small proportion remain as breeders on the study area (Kraaijeveld & Dickinson, 2001). This pattern of dispersal results in related males breeding in close proximity and facilitates cooperative behaviours in which males sometimes become helpers at their parents' or brother's nest (Dickinson et al., 1996).

Recording and Equipment

Western bluebird males predominantly sing in the half-hour before dawn, and to a lesser extent during the day, usually during intense territorial stand-offs or extrapair intrusions. As such interactions are impossible to predict, we recorded males during their predawn song. Songs were recorded using a Marantz PMD 660 Digital Solid-State recorder, and Sennheiser M66/K6 or ME87 shotgun microphones. As it is too dark to see colour bands during most of the predawn singing, we verified the identities of the singers by location or colour band combination at first light or, where necessary, by radiotracking (Akçay, Swift, et al., 2013).

Repertoire and Song-sharing Analyses

The predawn song of western bluebirds consists of two distinct elements: what we call the 'pew' notes (variously described as 'kew', 'few', etc...) and 'chuck' notes (Guinan, Gowaty, & Eltzroth, 2008). The pew calls consist of frequency-modulated tonal sounds and have signatures of two distinct voices, potentially from the two sides of the syrinx (Suthers & Zollinger, 2004). The western bluebird is able to modulate these voices independently (Fig. 1). Each male has a repertoire of 5–13 pew note types (mean \pm SD: 8.26 ± 2.18) and utters these note types in immediate variety, singing each note type just once at a rate of about one note per second before switching to another note type (e.g. ABCDEF C ABE). The stream of pews is often punctuated by chuck notes every several pew notes. The chuck notes are harsher, broadband notes that are used as alarm calls during the daytime (e.g. when a human approaches the nest; Ç. Akçay, personal observations). Each bird sings one or two chuck types, although some birds do not use chucks in predawn song at all. Therefore, in what follows, we focus on the pew calls as these are ubiquitous and exhibit significantly more variation than chuck notes.

We made repertoires of pew notes for 20 males recorded in 2012 and 31 males in 2013 using the sound analysis program, Syrinx (John Burt, Seattle, WA, U.S.A.). Figure 2 shows accumulation curves of birds for which we had at least 200 notes recorded ($N = 28$). Most note types were detected within the first 50 notes, although we detected some rare notes as late as 176 pew notes from the start of the time series of recorded notes. For 82% of 28 birds, however, we did not detect new notes after scanning 100 notes. Therefore, we included the repertoires of all of the birds ($N = 20$ in 2012 and 31 in 2013) for which we had at least 100 pew notes scanned.

We printed out sonagram of each note type and compared each of these types visually with other birds' notes types. We chose this method because visual recognition of song types of western bluebird males is a task for which humans are thought to outperform and even 'teach' machines (Law & von Ahn, 2011). In particular, the nonlinear events that relate to two voices make it difficult to capture variation in songs with pitch-tracking or dynamic time-warping algorithms accurately. For instance, Fig. 1 shows two note types (rows 3 and 4) that have similar lower-frequency voices but markedly different upper-frequency voices.

Visual comparisons were made blindly with respect to the identity of the birds being compared. To achieve this, each bird was assigned a random three-letter code that was not known to the judges. Three judges independently compared the sonagram and classified each note type as either shared or unshared. Notes were classified as shared or unshared if at least two out of three judges agreed on the classification. Consensus rate (the proportion of notes where all three judges agreed) was 98%. We calculated the sharing coefficients (i.e. the level of note sharing between any given pair of birds) as $2 \times N_s / (R_a + R_b)$, where N_s is the number of note types shared, and R_a and R_b are the repertoire sizes of 'bird a' and 'bird b', respectively.

We checked whether our visual assessments indeed captured an overall similarity of note types by running spectrographic cross-correlation (Raven Pro 1.4, Cornell Lab of Ornithology; band-pass filtered from 500 Hz to 12 000 Hz) on 20 pairs of shared and non-shared note types of two birds. In this paired comparison, pairs of notes shared between two birds had significantly higher cross-correlation scores than nonshared note types (mean \pm SD: 0.71 ± 0.10 versus 0.53 ± 0.12 ; $t_{19} = 5.47$, $P < 0.0001$).

We looked for note sharing in 83 pairs of repertoires from the 20 birds recorded in 2012 and in 142 pairs of repertoires from the 31 birds recorded in 2013. These comparisons included all pairwise comparisons of relatives and immediate neighbours (sharing a direct boundary) and, for each focal bird, at least one randomly selected non-neighbour. On average, each 2013 bird was involved in 8.9 pairwise comparisons (range 6–13 comparisons) and each 2012 bird was involved in 8.3 pairwise comparisons (range 6–12 comparisons). Of these comparisons, 16 were between neighbouring relatives, 48 were between neighbouring nonrelatives, 8 were between non-neighbouring relatives and 153 were between non-neighbouring nonrelatives. All but four of the pairwise comparisons between relatives involved father–son pairings or full-brothers; three involved uncle–nephew pairings and one was between half-brothers (different mothers).

Data Analyses

As each bird was involved in multiple comparisons, the note-sharing coefficients we obtained could not be treated as independent data points. Therefore, we used permutation tests. First, we asked whether note sharing between birds was correlated with their distance from each other using Mantel tests, which determines the relationship between two distance matrices (Mantel, 1967). We ran Mantel tests on pairwise note-sharing coefficients and pairwise nestbox distances acquired from ArcGIS 10 using the function 'mantel.test' in R package 'ncf' (R Development Core Team, 2012) separately on 2012 and 2013 data (10 000 iterations). We ran a second set of permutation tests specifically on the note-sharing coefficients of related pairs, to ascertain whether the note-sharing coefficients decreased with nestbox distance. To this end, we calculated the correlation between nestbox distance and note-sharing coefficients for the 24 related pairs in our sample (collapsed across 2 years) and compared the observed correlation coefficient (Spearman) with correlation coefficients from permuted data (10 000 iterations). These analyses were also carried out in R 2.15.

Finally, we carried out a paired analysis on neighbours using the combined data set from 2012 and 2013. For each focal male that had at least one neighbouring relative and one neighbouring nonrelative, we asked whether the related neighbour shared more songs with his relative than with the unrelated neighbour. Neighbours were defined as having a shared boundary with the focal male. To this end, for each focal male, we randomly selected an unrelated neighbour and a related neighbour (usually there was only one

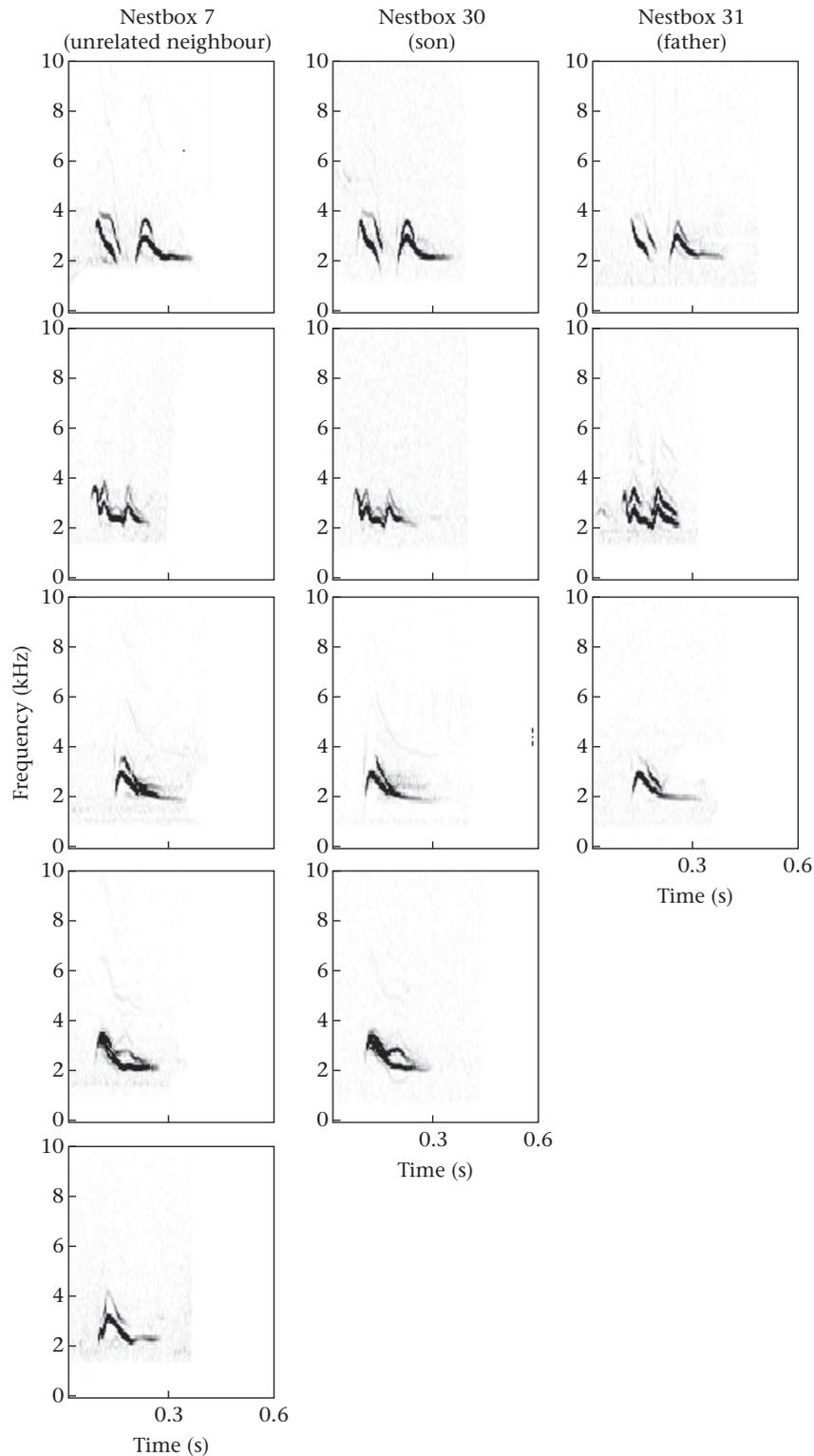


Figure 1. Partial pew note repertoires of three western bluebird neighbours that included a father–son pair and an unrelated neighbour. Notes in the same rows were shared between birds.

related bird) with the condition that each bird was used in only one pairwise comparison in each condition (i.e. a bird could be used once as a neighbouring relative and once as a non-neighbouring relative). These criteria left us with sample size of nine pairwise comparisons of note-sharing coefficients between related and unrelated neighbours.

Ethical Note

All research protocols were designed in accordance with ASAB/ABS Guidelines for the Use of Animals in Research and were approved by the Institutional Animal Care and Use Committee of Cornell University (IACUC protocol number 2005-0137).

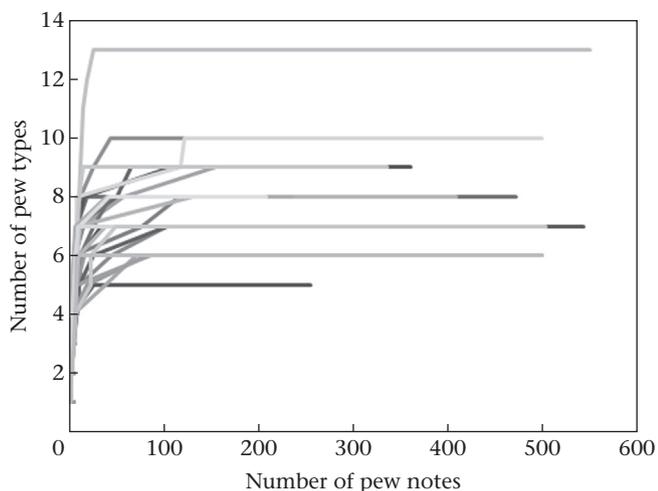


Figure 2. Accumulation curves for new pew notes in the 28 western bluebirds for whom we had at least 200 pew notes scanned. New notes were rare after 100 pew notes scanned.

RESULTS

Observed note-sharing coefficients ranged from 0 to 1. In most cases where there was sharing, sharing was incomplete: there was only one pair of males that had a sharing coefficient of 1 (a father–son pair who were also immediate neighbours in 2013). Sharing coefficients were negatively correlated with nestbox distance in both 2012 (Mantel test: $r = -0.37$, $N = 83$ coefficients, $P = 0.006$) and 2013 ($r = -0.36$, $N = 142$ coefficients, $P = 0.007$; Fig. 3). This was true even within related pairs (Spearman rank correlation: $r_s = -0.62$, $N = 24$ coefficients, $P = 0.001$; Fig. 3a).

The paired comparison between related neighbours and unrelated neighbours showed that related neighbours shared more than twice as many notes as unrelated neighbours; (mean \pm SD: 0.45 ± 0.28 versus 0.21 ± 0.14 ; $t_8 = 2.52$, $P = 0.036$). Still, a number of unrelated neighbours also showed high levels of sharing. Indeed, the range of sharing between unrelated neighbours and related neighbours overlapped almost completely (Fig. 4), and more than half of pairings with high sharing coefficients (0.5 and above) were between unrelated neighbours.

DISCUSSION

In the present study, we tested whether the pew notes in the vocal repertoires of western bluebirds are shared with relatives or neighbours. We found that vocal sharing was higher between close neighbours than between non-neighbours. Looking only at neighbouring birds that shared a territory boundary, we found significantly higher sharing between neighbours that were relatives than between neighbouring nonrelatives. Although this finding supports the idea that relatives share more songs than nonrelatives, it does not support the idea that note sharing is the basis of kin recognition, because a number of unrelated neighbours still shared notes with each other. Furthermore, in most cases relatives that were not direct neighbours did not share any notes. We discuss these results within the context of developmental processes that may lead to note sharing to shed light on the likely mechanism of kin recognition.

Signatures Underlying Kin Recognition

Our results suggest that although neighbouring relatives display high note sharing, neighbouring nonrelatives also display high

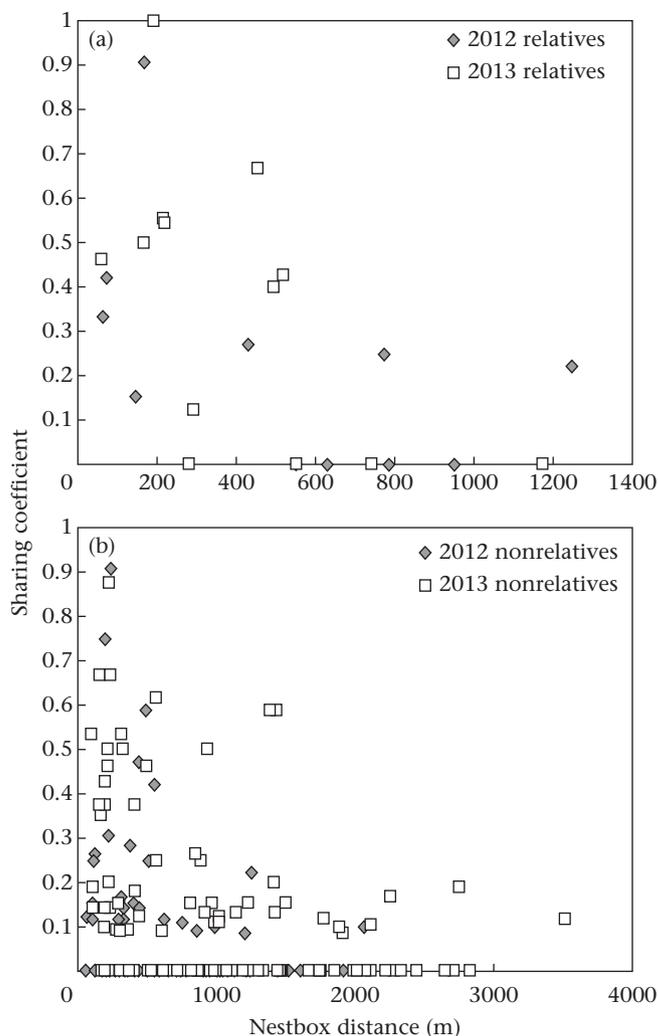


Figure 3. Scatterplot of note-sharing coefficients in western bluebird song versus nestbox distances between (a) relatives and (b) nonrelatives.

levels of sharing, making note sharing between two birds a poor indicator of actual kinship (Fig. 4). Yet, in an earlier study, we found that western bluebirds can in fact discriminate between kin and nonkin based on their song (Akçay, Swift, et al., 2013). It is possible that higher sharing among related neighbours is due to the length

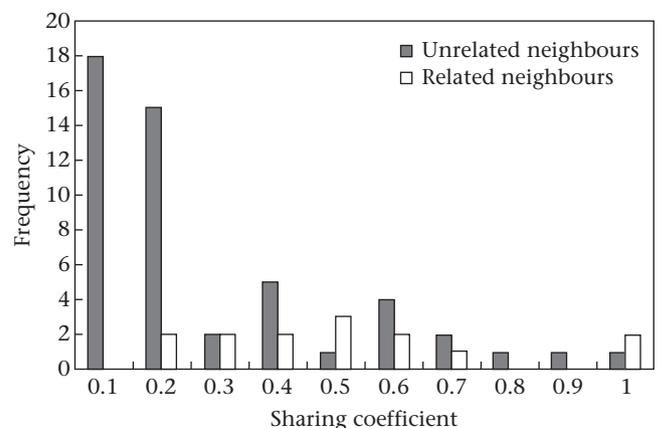


Figure 4. Frequencies of note-sharing coefficients in songs of related and unrelated western bluebird neighbours.

of time they are exposed to each other; in other words, an identical, time-dependent mechanism of song learning could potentially account for the difference in sharing between neighbouring relatives and neighbouring nonrelatives. What is clear from the current data is that simply using the degree of note sharing as a proxy for kinship would lead to frequent misclassification of neighbours as kin, which is not consistent with the fact that errors in kin-biased helping are exceedingly rare or absent (Dickinson et al., 1996).

It is important to note that we used social pedigrees to determine related and unrelated individuals. Given the frequency of extrapair paternity in this population (20%), the social pedigree is an imperfect indicator of actual genetic relatedness. This opens up the possibility that song development could be genetically controlled in western bluebirds, and that variation in actual genetic relatedness may be the reason why we see so much variation in song sharing between socially related individuals. In other words, perhaps some related males who do not share many notes with other members of their family are half-brothers. This hypothesis, while valid, is not supported based on what we have observed in western bluebirds. First, in 30 years of the western bluebird study, we have failed to gather evidence that extrapair young are recognized as such, are treated differently, or behave differently than their half-brothers in the nest. For instance, we found that fathers do not discriminate in feeding nestlings based on paternity (Dickinson, 2003), and that extrapair young are just as likely to help their social parents as within-pair young (Dickinson & Akre, 1998). These lines of evidence suggest that there is no genetically based signature that may be used by the receivers to discriminate extrapair young from within-pair young, a conclusion that is supported by a preponderance of data on other avian systems (Beecher, 1991).

A second argument against a genetically transmitted vocal signature is that males that are not putative relatives based on association as nestlings also display high levels of sharing when nesting in close proximity. Although it is true that a small portion of these nonsocially related males may in fact be genetic half-brothers as a result of one being an extrapair offspring, this is unlikely to account for the strong effect of proximity on sharing we observed, unless half-brothers from different nests settle closer to each other than do unrelated males. We find this possibility unlikely, especially given our prior evidence, in multiple contexts, indicating that extrapair young do not behave differently, nor are they treated differently, than within-pair young (Dickinson, 2003, 2004; Dickinson & Akre, 1998; Dickinson et al., 1996; Leonard et al., 1995). A more likely hypothesis is that song is learned from birds that become eventual neighbours, as has been found to be the case in several other songbirds (DeWolfe, Baptista, & Petrinovich, 1989; Nordby, Campbell & Beecher, 1999; Payne & Payne, 1993). Therefore, although we cannot rule out the genetic hypothesis conclusively without either cross-fostering or correcting pedigrees based on paternity, we do think the available evidence weighs heavily against a genetic hypothesis.

How Do Western Bluebirds Recognize Relatives through Their Vocalizations?

There are at least two nonexclusive alternative hypotheses for how western bluebirds recognize relatives. First, although song sharing is an imperfect indicator of kinship, it may be part of a more complex kin recognition system that integrates signatures, not only from vocalizations but from other modalities as well. Plumage varies significantly among individuals, although much of the variation in plumage coloration is age related (Budden & Dickinson, 2009). Odour is another possibility as recent studies showed that birds may use olfactory signatures for kin recognition (Krause, Kruger, Kohlmeier, & Caspers, 2012). Finally, an unidentified

property of the vocalizations that we have not quantified here could be important in providing a more reliable kin signature than note sharing.

Another possibility is that kin recognition through vocalizations does not rely on matching family signatures but involves learning the vocal repertoires of specific relatives as well as those of specific nonrelatives (i.e. individual signatures; Kondo et al., 2012; McDonald, 2012). Although such a mechanism can be construed as being more cognitively demanding, because it requires a template for each individual as well as some representation of the relationship with that individual, previous research in other songbirds indicates that such a mechanism is not far-fetched: there is evidence in several species that songbirds can recognize individual neighbours (Stoddard, 1996), possibly for long periods (Godard, 1991), and adaptively modify their behaviours towards them depending on recent interactions with them (Akçay et al., 2009; Godard, 1993; Olendorf, Getty, Scribner, & Robinson, 2004), and even based on eavesdropped interactions between two neighbours (Akçay, Reed, Campbell, Templeton, & Beecher, 2010). Thus, individual recognition is a plausible mechanism for explaining vocal kin discrimination. Future playback experiments can distinguish whether kin recognition in western bluebirds relies on individual recognition or levels of note sharing, for example, by controlling note sharing between kin and nonkin playback tapes.

If western bluebirds can recognize individuals based on individually distinct vocal signatures and use this recognition for kin discrimination, this raises the question of how males in this species form representations of individuals that incorporate both identity and kinship information. Given that signatures depend on where exactly the bird settles and who the bird is neighbours with, an associative learning process would be required to acquire necessary templates for these signatures and to assign relationships to them (Komdeur, Richardson, & Burke, 2004).

We do not yet have direct evidence for associative learning of individual signatures in the western bluebird. Associative learning of signatures has usually been tested with cross-fostering experiments (Beecher, 1991; Komdeur et al., 2004; Sharp et al., 2005). In the western bluebird, we also have the chance to test associative learning within the context of using individual signatures: because families persist for a few generations in the study site, we often have brothers that do not overlap in their lifetimes such that when the younger relative hatches the older male is not alive anymore. In these cases, the younger relative should not be able to discriminate between the dead relative's calls and an unrelated (also dead) male's calls. As we only had 2 years of recordings in this study we could not carry out this experiment, yet, it represents an interesting novel design for future research.

Implications for Song Learning and Function of Song Sharing

Although we did not attempt to trace song learning in the present study, the results nevertheless have important implications for song learning. First, local song sharing suggests that song is socially learned primarily from neighbours after dispersal and not inherited genetically from fathers (see above) or learned only from relatives while on the natal territory. In many cases these neighbours are also relatives. In our pairwise comparisons, the higher levels of sharing between neighbouring relatives than between neighbouring nonrelatives could be due to the fact that relatives are together longer (male relatives often reside together in winter groups) and have more time to learn from each other, or it could mean that western bluebirds prefer to learn from relatives if it is an option. Given that sharing between most relatives was not complete, a simple mechanism by which males learn indiscriminately from their neighbours based on exposure may explain this pattern.

Whatever determines song learning and song sharing in this species, we think that the western bluebird is an interesting species for further research on vocal communication. In particular, song traits such as song sharing can be examined within the context of a wide variety of life-history traits such as developmental condition, winter group composition and dispersal of males, all of which can be readily measured in this species. Thus, the present research sets the western bluebird up as an interesting model system to study vocalizations.

Acknowledgments

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