

Original Article

Vocal kin recognition in kin neighborhoods of western bluebirds

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In most cooperatively breeding birds, individuals direct helping behavior to close relatives. Western bluebirds live in family groups in winter and show a high degree of male philopatry. Sons disperse locally forming kin neighborhoods and occasionally help at their parents' or brothers' nests. Although the pattern of kin-directed helping is well established in birds, the mechanism of recognition is known in only a few cases. Here, we report on an experiment with western bluebirds (*Sialia mexicana*) that investigates the role of vocalizations in kin recognition, a species that even when breeding on its own often maintains lifelong connections with kin. We presented western bluebirds with songs recorded from equidistant kin and nonkin living on other territories, conducting playback near their nests on 2 consecutive days. We found that male western bluebirds responded more aggressively to playback of nonkin song compared with kin song. These results suggest that vocal signatures serve as a kin recognition cue in western bluebirds. We discuss these results within the context of other systems in which vocal kin recognition has been demonstrated and discuss the potential for further research to examine signal development and to distinguish kin signatures from individual signatures, which can also be used to recognize kin.

Key words: cooperative breeding, kin recognition, signature, song learning. [*Behav Ecol*]

INTRODUCTION

Social animals exhibit kin-biased interactions in a diversity of behavioral contexts ranging from nepotistic alarm calling (Sherman 1977; Griesser and Ekman 2004) to cannibalism (Pfennig et al. 1993), incest avoidance (Koenig et al. 1998), and cooperative breeding (Dickinson and Hatchwell 2004). Although the pattern and fitness consequences of kin-biased behaviors have been the subject of extensive studies in numerous species of animals, our understanding of the mechanisms by which individuals recognize kin has been incomplete. Only recently have researchers begun to harness the power of field studies of vocal recognition in kin neighborhoods to better understand the form and function of vocal kin recognition in birds (Hatchwell et al. 2001; Sharp et al. 2005).

There has been much debate over the term kin recognition (e.g., Grafen 1990)—here we use the term in the broad sense as any mechanism that functions to discriminate kin from nonkin based on contextual cues or individual signatures (Waldman 1987; Sherman et al. 1997; Penn and Frommen 2010). At the most basic level, contextual cues that correlate significantly with relatedness may allow individuals to bias their behavior toward relatives. A good example of this is the tendency of most birds to feed any offspring in their own nest (Kempenaers and Sheldon 1996), the nest being the

contextual cue. Such contextual cues, however, can be rendered unreliable by multiple factors such as high levels of extrapair paternity (EPP) or colonial nesting where offspring can intermix with non-offspring or move between nests (Beecher 1982). Furthermore, contextual cues are likely to be rendered unreliable by the process of dispersal when individuals intermix with the larger population and start interacting with kin and nonkin alike. Kin recognition in these cases requires a recognition system that involves perception and discrimination of signatures from different individuals as kin versus nonkin (Sherman et al. 1997). These signatures can be in any modality. In birds, particularly in songbirds, vocalizations are the most commonly studied signature modality for a wide range of social behaviors (Halpin 1991; Komdeur and Hatchwell 1999).

Vocal signals play a significant role in the social life of songbirds, and songbird vocalizations have been a focus of intensive research in animal behavior (Catchpole and Slater 2008). Although nestling vocalizations and their role in kin recognition at the early stages of life have been subject to extensive research (Beecher 1982, 1991), use of adult vocalizations for kin recognition is not well studied. Typically, songbirds learn their songs from unrelated neighbors after dispersing away from their natal site (Catchpole and Slater 2008), and there are only few exceptions where the song is learned from the father (e.g., Immelmann 1969; Clayton 1987; Grant and Grant 1996). In most species, young birds do not have extended interactions with their kin throughout the period for vocal development, meaning that they might not have much opportunity to learn family-specific

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vocalizations. On the other hand, there are exceptional species in which offspring, usually males, disperse locally resulting in kin neighborhoods where prolonged interactions with relatives should select for kin recognition mechanisms (Komdeur and Hatchwell 1999; Kraaijeveld and Dickinson 2001; Cornwallis et al. 2009).

Although most cooperatively breeding birds show delayed dispersal and kin-structured populations (Ekman et al. 2004; Hatchwell 2009), it is the localized dispersal of kin and the potential for continuation of kin interactions after dispersal that provides opportunities for separating experimentally the use of vocal signals of kinship from use of spatial or other contextual cues. In particular, local dispersal of kin allows asking whether individuals recognize close relatives when they are no longer living on the same territory.

Only a few studies to date have addressed the use of vocalizations in kin recognition experimentally. In the first such study, Sharp and colleagues found that in the cooperatively breeding long-tailed tit (*Aegithalos caudatus*), nestlings learned their vocalizations from parents attending the nest. These vocalizations were then used as cues in kin recognition after the offspring left the nest and moved to other nearby territories (Sharp et al. 2005; Sharp and Hatchwell 2006). In the stripe-backed wren, *Campylorhynchus nuchalis*, male and female calls show high levels of similarity across different breeding groups with male and female relatives, respectively (Price 1998), and males can discriminate between unrelated birds and their own relatives using these calls (Price 1999). In this case, calls seem to possess a family signature, rather than a group signature, and call similarity in males appears to extend to even distant relatives (Price 1998), suggesting that the calls are also learned socially from related males, although this has not been demonstrated experimentally. Note that high similarity of calls between distant relatives would tend to decrease the utility of a family signature in kin discrimination compared with signatures that vary in similarity with the actual degree of relatedness. A signature system of the latter kind was found in another cooperatively breeding bird, the bell miners (*Manorina melanophrys*), where similarity of provisioning calls between 2 birds was found to depend on the measured coefficient of relatedness of the 2 birds (McDonald and Wright 2011). It is important to note, however, that it is not clear if the provisioning calls in bell miners are learned or genetically determined.

An interesting feature of the previous studies of vocal kin recognition reviewed above is that all of these species namely the stripe-backed wrens (Rabenold et al. 1990), long-tailed tits (Hatchwell et al. 2002), and bell miners (Conrad et al. 1998) show low levels of EPP (or extragroup paternity), such that social relationships are good indicators of genetic relationships. As noted above in 2 of these species, there is evidence that signatures used in kin recognition are learned. From the receiver's perspective, a strong positive relationship between social and genetic parentage increases the strength of selection on a learned kin signature by increasing indirect fitness benefits of using this signature to direct helping behavior. Such learned signatures will become unreliable, however, as the number of offspring unrelated to the parents increases either due to EPP or brood parasitism.

Here, we investigate vocal kin recognition in western bluebirds, *Sialia mexicana*. Western bluebirds live in a complex society composed of both kin and nonkin, and they show moderate levels (~20% of offspring) of EPP, which translates to the social relationship being equal to the true relatedness only 64% of the time (Dickinson and Akre 1998; Ferree and Dickinson 2011). Kinship plays an important role in shaping western bluebird society in our study population (Dickinson et al. 1996, 2009; Dickinson and

Weathers 1999). In their first winter, sons often delay dispersal from their natal territory, spending the winter in their natal groups, whereas most daughters disperse in fall and join other groups for the winter (Kraaijeveld and Dickinson 2001). Most first-winter males pair with unrelated females joining their winter groups and settle onto nearby breeding territories in spring. During the breeding season, the majority of adults attempt to breed independently with relatively few sons staying home to help. Helping usually arises when males lose a nest or mate and redirect their efforts to help at a parent's or brother's nest; occasionally sons become simultaneous breeder-helpers feeding young both at their parents' nest and their own nest within a single day (Dickinson et al. 1996). Additionally, relatives sometimes enter each other's territories to assist in territory defense against conspecifics or to respond to playback of recorded screams (Stern 2012). Although these behaviors suggest that kin recognition occurs in western bluebirds, the mechanisms of recognition could rely extensively on spatial cues, vocal cues, or both.

As a first step in determining whether western bluebirds use a spatially independent mechanism of kin recognition, we investigated vocal signals of western bluebirds and their possible role in kin recognition. In this paper, we describe a playback experiment designed to determine if western bluebirds can recognize kin from their vocalizations. We presented western bluebirds with songs recorded from living male relatives and nonrelatives, matched for nest-box distance. To control for spatial cues, we presented the playback of kin and nonkin songs from the same location on consecutive days. Given the kin-biased prosocial behavior shown by western bluebirds, we predicted that subjects would be less aggressive toward male relatives compared with male nonrelatives, when we simulated their singing near the subject's nest-box.

METHODS

Study site and subjects

We studied a nest-box population of western bluebirds on Hasting Natural History Reservation and the adjoining Oak Ridge Ranch in upper Carmel Valley, which is located in the outer coast range of central California. Nestlings and immigrant adults have been routinely banded with a USFWS metal band and a unique combination of 3 color bands since 1983 (see Dickinson et al. 1996 for details on the study population). Nesting activities were monitored so that for each nesting attempt the first egg date and hatching date were known (with the exception of breeding attempts at natural cavities, which were checked less frequently).

Western bluebirds live in kin-structured neighborhoods resulting from male philopatry in which sons show a high incidence of local dispersal. In the year of this study, 2012, our subjects were 13 males on the study area that had at least 1 male relative based on the social pedigree (see Table 1). With one exception, all of the relationships were established based on banding of nestlings. The one exception was a case where a younger male banded as adult (as determined by molt limit, Shizuka and Dickinson 2005) was a helper in both 2011 and 2012 at the nest of an older male. We assumed that this was a father-son pair because all previous cases of younger males helping at nests of older males of known relationship involved a father and son (Dickinson et al. 1996). Further, all helping between same-aged males involved brothers, which, similar to a father and son, will have an average relatedness coefficient of 0.5.

Territories of all the males were mapped through observation of the pair for at least 1 h (in most cases 2 h). These observations were then entered into an ArcGIS 10 (ESRI, Inc.) database that also

Table 1
List of subjects and stimulus birds

Bird ID			Distance (m)		Age			<i>r</i>	Relation to the kin stimulus bird
Focal	Kin	Nonkin	Kin	Nonkin	Focal	Kin	Nonkin		
6683	6754	6779	949	834	3	3	3	0.25	Nephew
6567	6683	6997	785	978	4	3	2	0.5	Father
6939	6617	6970	141	66	2	4	2	0.25	Half-brother/younger
6970	6685	6848	65	103	2	4	3	0.5	Son
6568	6567	6834	1245	944	4	4	3	0.5	Full brother/same nest
6681	6567	6620	838	595	3	4	4	0.5	Son
6838	6848	6617	73	114	4	3	4	0.5	Presumed father
6754	6681	6348	1245	1203	3	3	6	0.5	Full brother/younger
6595	6348	6939	427	436	4	6	2	0.5	Son
6617	6939	6620	141	270	4	2	4	0.25	Half-brother/older
6848	6838	6685	67	161	3	4	4	0.5	Presumed son
6685	6970	6595	65	313	4	2	4	0.5	Father
6348	6595	6683	426	405	6	4	3	0.5	Father
Averages			497	494		3.53	3.38		

Distances are between nest-boxes of the focal subject and kin and nonkin stimulus bird. There was no significant difference between the nest-box distances of kin and nonkin stimulus birds (paired *t*-test; *t* = 0.07; *P* = 0.93). Age also did not differ between kin and nonkin stimulus birds (paired *t*-test; *t* = 0.29; *P* = 0.77). “*r*” refers to relatedness.

contained nest-box locations. Because we wanted to ask whether bluebirds can discriminate kin versus nonkin, we had to control for any “Dear Enemy” effect, which depends on whether or not the stimulus bird was a neighbor (Temeles 1994), and other potential effects of proximity on learning and social behavior. Therefore, we matched the stimulus birds in kin and nonkin categories using their nest-box distances as determined from ArcGIS 10 (Table 1).

Trials were conducted between 22 May and 7 June 2012 during the nestling feeding period for each subject. We conducted the 2 trials (kin and nonkin playback) on subsequent days for a given subject (responder). The design was balanced so that in half the trials the kin playback was presented on the first day, and in the other half the nonkin playback was presented on the first day. The trials were conducted during the first 3 days of the nestling period, with the exception of 1 subject nesting in a natural cavity for which the trials were carried out on the 6th and 7th day of nestling period, estimated based on nestling growth. The rationale to carry out the playbacks in the early stages of nesting cycle was to ensure that both playback locations within the territory (5 m from the nest-box) and stage in nesting cycle were standardized across males.

Stimuli

We recorded males that later became stimulus birds in this experiment using Marantz PMD 660 solid-state digital recorders and either Sennheiser ME66 or ME 88 (Sennheiser GmbH) shotgun microphones. Western bluebirds sing most vigorously during the 20–30 min before dawn and immediately after dawn, and we recorded individual males in this time period in April and May 2012. The identity of the recorded bird was ascertained through the location of singing when the bird sang near his nest-box and, less commonly, by radio tracking or visual identification (if the bird was still vocalizing when it was light enough to see bands). Radio tracking was employed for 3 birds where close proximity to other territories or overly large territories made recording without radios ambiguous or difficult. Radio-tagged birds were fitted with Holohil BD-2 tags (Holohil, Inc.) using a loop harness (Rappole and Tipton 1991) and followed using a Communication Specialist R-1000 receiver and a Yagi antenna. Each tag weighed 0.9 g with harness.

The accuracy of our methods for identifying birds recorded in the dark was established via observation of 8 radiotracked pairs in 1996–1997, which demonstrated that early morning forays off the territory were uncommon (Dickinson J, unpublished data). The recordings were annotated and processed using Syrinx (www.syrinxpc.com, John Burt, Seattle, WA).

Our predawn recordings served as the source for the stimuli in the kin recognition experiment. Western bluebirds have 2 types of simple vocalizations they use in predawn singing: “pew” notes and “chuck” notes (Figure 1). The “pew” note consists of single or double (rarely triple) downward frequency sweeps, and each male has a repertoire of 5–9 pew notes that he repeats in succession with immediate variety (i.e., consecutive notes are different from each other). The stream of pews is punctuated every 3–4 pew notes by the chuck notes. These notes consist of harsh and short click-like elements usually coming as doublets, although sometimes singly or in triplets and very rarely in quadruplets. Both chucks and pews are readily used intermittently in daytime calling as well, although usually not in as steady a stream as in the predawn chorus. During the day, singing in the predawn manner is restricted to periods of intense interactions such as observed when an intruder male ventures onto a pair’s territory or, more rarely, when a female leaves a territory to check out nearby nest-boxes.

A total of 16 males were used as stimulus birds. Most stimulus birds were used as both kin and nonkin stimulus in different trials with 2 exceptions where 1 bird was used as kin stimulus twice and 1 bird was used as nonkin stimulus twice (Table 1). These exceptions were necessary to control for distance of the stimulus bird. For each stimulus male, we made stimulus tapes of 11 s that consisted of 9 or 10 pew notes and 1 or 2 chuck notes for a total of 11 notes total (the average number of chucks in both conditions was 1.61). The rate of 1 note per second approximates the rate of singing during the predawn chorus. To eliminate low-frequency noise, the stimulus tapes were processed using the hand-filter tool in Syrinx, which allows filtering of a custom selection in the spectrograms. The trials were carried out in a double-blind fashion, which was achieved by having a person not involved in the experiment (Walter D. Koenig) randomize (and equalize) the trial order and rename the stimulus files so as to preclude identifying which condition was which during the playback experiments.

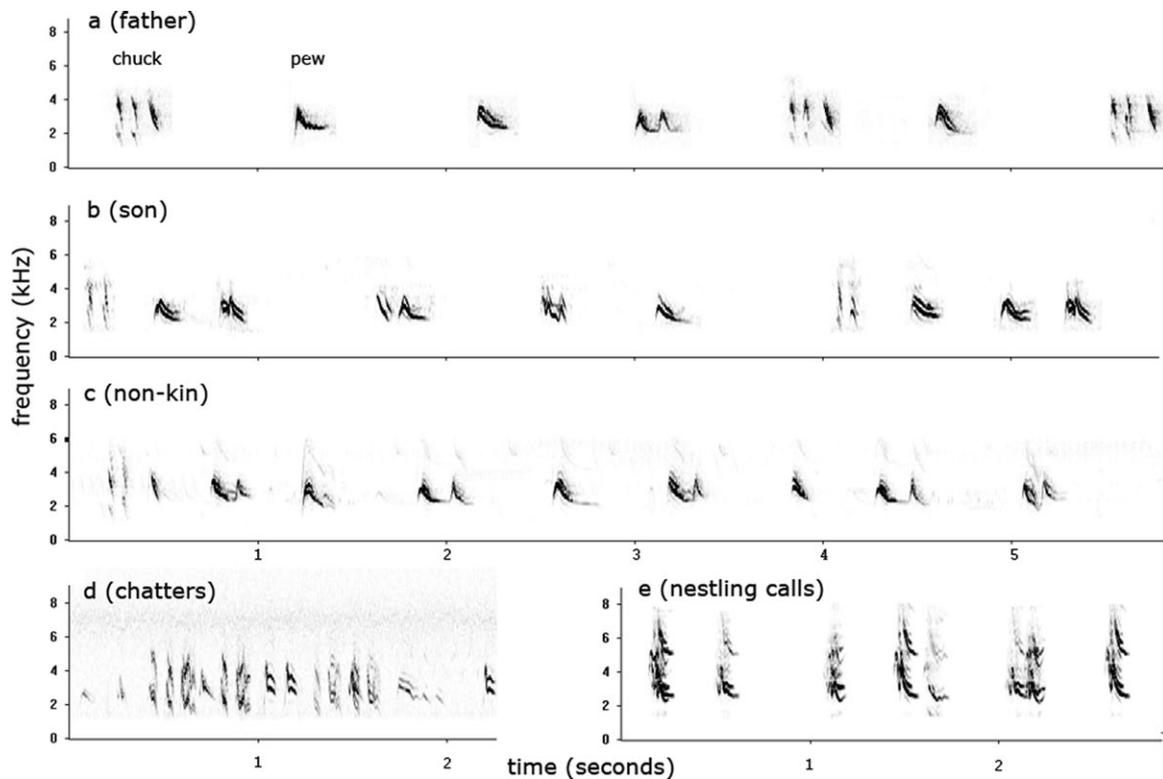


Figure 1

Examples of western bluebird vocalizations: dawn song from (a) father, (b) son, (c) another male not related to either (a) or (b), (d) burst of chatter calls, and (e) begging calls of a single nestling, recorded on day 15.

Procedure

Before each trial, we placed the speaker 5 m from the active nest-box (or in 1 case, the trunk of the tree holding the natural cavity) by hanging it from a branch marked with flagging tape. We also measured and marked with flagging tape 5 and 10 m distances from the speaker to facilitate distance estimation during the trial. The speaker (iMainGoX, Portable Sound Laboratories, Inc.) was connected via a 25-m cable to an iPod (Apple, Inc.), which was used to control the playback from a distance. After the equipment and flagging tapes were setup, 2 or 3 observers settled and tried to locate and identify the focal male and his mate using binoculars and spotting scopes. One observer was focused on the male and also recorded the trial using the same recording equipment as above. The other observer focused on the female. The third observer, when present, attempted to identify the bands on any intruders that came onto the focal territory during the trial. The observers sat close enough to each other to be within earshot. In some trials (3 nonkin trials and 2 kin trials), a third bluebird was seen. In all but 1 trial, we were able to identify the third bird from his bands as a male relative that was also a neighbor. In the one exception, the third bird (also a male) appeared to come in from the direction of a neighbor who was a relative but we could not read the bands of this male and thus were unable to determine whether the bird was in fact a relative or not.

Once the male and the female were both located and identified by their band combinations, we obtained a baseline activity level during a 5 min preplayback observation period. After the preplayback period, we started the 5 min playback period during which time the stimulus tape was played in loop for 5 min. The playback period was followed by a 5 min post playback period. The same behaviors were observed during each of the periods.

Response measures and data analysis

For measures of male aggression, we noted the number of male flights, the distance of the male to the speaker for each flight, and chatter calls. The first 2 measures are common measures used in playback experiments to quantify aggression (e.g., Kroodsma 1976; Searcy et al. 1982; Akçay et al. 2011). Chatter calls (Figure 1d) are distinctive bursts of notes that are given by both males and females. Although chatter calls probably serve multiple functions in western bluebird signaling, we have observed during our banding efforts and in pilot experiments that rates of chatter calls by males increase dramatically during experimental intrusions with a live decoy. It would seem that chatters either function in mate guarding and/or aggression. Therefore, we predict that in our experiment, rates of chatter calls, along with the rest of the aggressive behaviors, will increase in response to nonkin playback compared with kin playback.

As our final response measure, we noted flights of the female and whether the male followed the female in her flight within 2 s. These close follows are indicative of mate guarding (Dickinson and Leonard 1996). Although we carried out the experiment during the nestling period, when the female is presumed to be non-fertile, nest failure and immediate re-nesting are common in this population, and an intruding male might still present a threat to paternity should the current nest fail or be depredated later on. Again, we expected nonkin males to be perceived as a higher threat to paternity. Note that because in most trials there were too few (<10) female flights during the trial to calculate the proportion of these that the male followed, we used number of close follows instead of calculating proportion of female flights that the male followed.

We converted number of flights, chatters, and close follows into rates per minute. We then subtracted the rates during the pretrial period from the rates during the playback to get a change in activity level in response to playback. Similarly, we subtracted the proportion of time spent within 5 m during pretrial period from the proportion of time spent within 5 m during playback. Following recent trends in statistical approaches (Nakagawa 2004; Nakagawa and Cuthill 2007), we report the effect size \pm standard error of the mean for all comparisons. We also report nonparametric significance tests. We calculated effect sizes and carried out statistical tests on the difference scores for all the response variables. Finally, for completeness, we also report the posttrial response measures, although we did not carry out statistical tests on these (Table 2).

RESULTS

As expected, the change in response measures between the pretrial and playback periods was more pronounced in the nonkin condition compared with the kin condition. Subjects increased their rate of flights significantly more in the nonkin treatment compared with the kin treatment (Cohen's $d \pm$ SE: 0.62 ± 0.39 ; $z = 2.27$, $P = 0.02$) and gave more chatters ($d = 0.93 \pm 0.34$; $z = 2.31$, $P = 0.01$; Figure 2a) in response to nonkin playback compared with kin playback. Males did not significantly increase their time spent within 5 m of the speaker in response to nonkin playback compared with kin playback ($d = 0.28 \pm 0.25$; $z = 0.52$, $P = 0.60$). Finally, despite a numerical trend, males did not follow their mates significantly more in response to nonkin playback compared with kin playback ($d = 0.77 \pm 0.46$; $z = 1.35$, $P = 0.18$; Figure 2b). Postplayback behaviors were intermediate to the behaviors observed during the playback and pretrial period.

DISCUSSION

We found that western bluebirds responded differently to kin versus nonkin playback. Specifically, males increased their rates of aggressive chatters and flights in the nonkin treatment compared with the kin treatment. Males also tended to follow their mates more closely during the nonkin playback, although the effect size, while large, did not achieve significance. Because we controlled for distance of the stimulus bird, the different response strengths cannot be due to a "Dear Enemy" or other proximity effect. These results suggest that western bluebirds are able to recognize their relatives from vocalizations alone.

This study adds to the growing list of studies that show vocal kin discrimination in cooperatively breeding birds (Price 1999; Hatchwell et al. 2001; Sharp et al. 2005; McDonald and Wright 2011). In all of these species, researchers have found that vocalizations serving as kin recognition cues contain a family signature so that vocalizations of relatives are more similar to each other than to vocalizations of nonrelatives. Furthermore, in one of these species, the long-tailed tits, cross-fostering experiments demonstrated that these vocalizations are learned from parents (Sharp et al. 2005).

Although the present experiment shows that western bluebirds can recognize relatives using their songs, we do not yet know if these songs contain a family signature, and whether the songs are learned or genetically acquired. Previous studies in cooperatively breeding species (above) as well as the fact that song is almost always learned from conspecifics in songbirds (Beecher and Brenowitz 2005) suggest that song is likely to be learned in western bluebirds as well. From the receiver's perspective, learning signatures from a parent is an effective way to acquire family signatures,

Table 2
Means (SD) of each response measure in pretrial, playback, and posttrial periods

	Means (SD)		
	Pretrial	Playback	Posttrial
Flights			
Kin	0.89 (0.41)	2.82 (3.01)	1.35 (1.39)
Nonkin	0.62 (0.45)	4.30 (3.86)	2.19 (2.36)
Time spent within 5 m			
Kin	0.13 (0.20)	0.38 (0.35)	0.20 (0.30)
Nonkin	0.08 (0.13)	0.43 (0.37)	0.33 (0.36)
Chatters			
Kin	0.02 (0.06)	0.34 (0.39)	0.23 (0.39)
Nonkin	0.01 (0.05)	1.57 (1.86)	0.49 (0.58)
Male follows			
Kin	0.01 (0.05)	0.04 (0.08)	0.05 (0.12)
Nonkin	0 (0)	0.26 (0.36)	0.02 (0.07)

The analyses reported in the text were carried out on the difference scores between pretrial and playback periods.

so long as social association is reliably correlated with genetic kinship, that is, if extrapair parentage and brood parasitism are low or nonexistent. Subsequently, one might predict that low levels of EPP should lead to social learning of kin signatures. This last point has been repeatedly emphasized in recent literature (Sharp et al. 2005; Komdeur et al. 2008).

Western bluebirds, unlike the species mentioned above, do show significant levels of EPP although extrapair offspring do not behave as if they have information regarding their extrapair status and are as likely to help as are genetic offspring of both parents (Dickinson and Akre 1998). Significant levels of EPP would mean that a socially learned signal would be a less reliable signal of kinship and that other ways of kin recognition, like self-referent phenotype matching, may be expected to evolve (Hauber and Sherman 2001). However, signatures indicating the true genetic makeup of an individual are only expected to evolve when they are beneficial to individuals that bear them (Beecher 1991). When one considers this fact, social learning of signatures, if anything, is expected to be selected for even more strongly where significant levels of EPP exist, especially in an altricial species like the western bluebird where males provide significant parental care. In a scenario in which an extrapair offspring is being raised by an unrelated father, it would be disadvantageous for offspring to signal their status as nonkin to the parent (Beecher 1991). More generally, learning of signatures is expected to evolve readily in situations where senders stand to benefit from copying the vocal signatures of individuals within their social groups, so long as the benefits of social group membership is higher than recognition of true kin.

A case in point is a recent study in splendid fairy-wrens, *Malurus splendens*, a cooperatively breeding songbird with high levels of EPP (~40% of offspring; Webster et al. 2004). In this study, Greig et al. (2012) asked whether songs of sons that are extrapair offspring would match that of their social fathers or their genetic fathers and found that extrapair sons actually acquired their social father's song. Given that almost half the sons are extrapair offspring, learning songs from the social father would render vocal signatures unreliable for kin recognition from the receiver's perspective. From the sender's perspective, however, acquiring songs socially from the social father may function in insuring group membership for the unrelated sender, which could have positive fitness consequences (Beecher 1991; Greig et al. 2012).

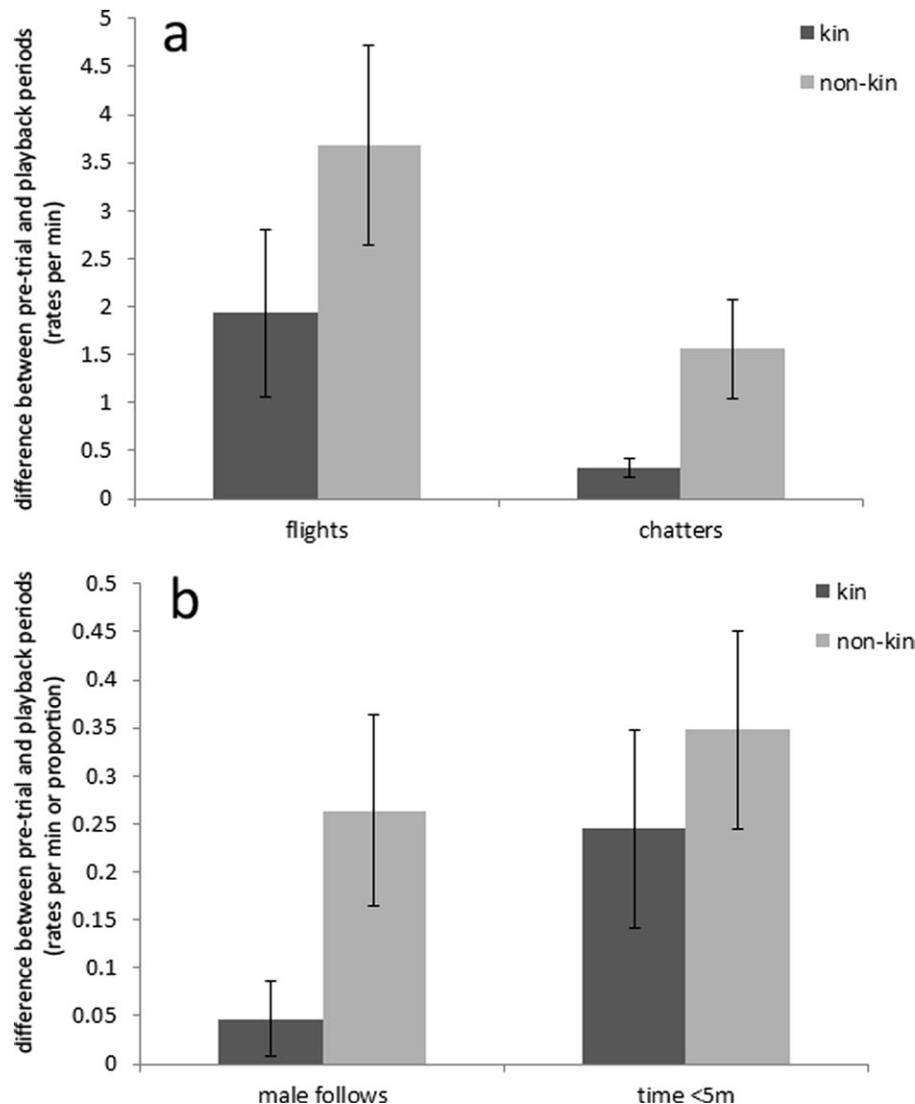


Figure 2

(a) Difference between pretrial and playback periods in rates of flights and chatters. (b) Difference between the pretrial and playback in rates of male “follows” and proportion of time spent within 5 m. Error bars are 1 SE.

We are currently investigating the development of vocalizations in western bluebirds by tracking vocal development of a cohort of males that were recorded the first time as nestlings in 2012. A prior study—albeit with a small sample size—has found evidence of a family signature in the calls of nestlings in our bluebird population (Monk et al. 1997), although western bluebird parents do not seem to use these family signatures in making feeding decisions toward the end of the nestling period as evidenced by an experiment where nestlings were swapped between nests (Leonard et al. 1995). Nestling calls are most similar in acoustic structure to the pew notes (see Figure 1) and although we do not know if these indeed develop into the pew calls later on, it is possible that nestling calls are learned from the parents while in the nest, much like in the long-tailed tit case.

It is worth noting that although the above discussion focused on acquiring family and/or group signatures through learning, it is also possible that western bluebird song is individually distinctive. Some relatives do not seem to have songs that are acoustically similar to each other (see, for instance, the example in Figure 1

of a father–son pair and an unrelated male). In the absence of a signature of kinship, the kin recognition demonstrated in this experiment would have to rely on recognizing individuals first and subsequently categorizing them as kin versus nonkin, which would preclude recognition of unfamiliar kin. Although social fathers and sons always have prior experience with each other and brothers that differ in age may interact in winter family groups (Kraaijeveld and Dickinson 2001), it is possible in our population to gather samples from brothers whose life span do not overlap and conduct playbacks of older brothers’ vocalizations to younger brothers that have had no prior experience with them, definitively separating prior experience from kinship.

Whatever the developmental mechanism, the present study demonstrates that vocalizations are indeed used in kin recognition in western bluebirds and that they are likely used in an interesting and meaningful context (mate guarding and assessment of threat to paternity). These findings, therefore, represent the first step investigating the function and development of vocalizations and their use in mediating interactions with neighboring kin and nonkin in kin

neighborhoods, opening up an interesting avenue of research into the ways in which birds navigate social relationships in the complex societies of exploded kin groups.

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