

Context, Structural Variability and Distinctiveness of California Towhee (*Pipilo crissalis*) Vocal Duets

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Abstract

Avian vocal duets occur when paired birds produce temporally and structurally coordinated vocalizations. Duets are given by members of many species from taxonomically distinct lineages and show great variety in form that often reflects function. By describing the structure of vocal duets we can learn about the diversity of communication signals present in nature and also gain insight into the evolution and operation of those signals. This study quantified the usage patterns and acoustic structure of California towhee duet vocalizations, and tested the distinctiveness of duets among different pairs. California towhee duets consist of a 'squeal' vocalization that is highly unlike the species-typical call note or male advertisement song. California towhees duet an average of three times per hour during the breeding season, and all duets are accompanied by an approach response that brings duetting partners into close spatial proximity. Males and females produce duet contributions with the same syllabic structure. Individual birds produce highly variable squeal vocalizations that are distinctive enough to signal identity. California towhee duet characteristics indicate that the squeal vocalization has evolved separately from other vocal traits in this species and was promoted by natural selection as a duet-specific vocalization. Duet usage patterns and structure suggest that these communication signals function in a cooperative context.

Introduction

Paired birds produce vocal duets by coordinating sound production to produce a temporally and acoustically organized signal (Thorpe 1972; Farabough 1982). Existing definitions, however, allow a variety of different signals to be labeled 'duets'. Duet structures vary widely, and may consist of highly coordinated songs (like the duet of the plain wren; Mann et al. 2003) or simple overlapped calls (like the duet of the Carolina wren; Shuler 1965) (Farabough 1982). Duets are usually produced by mated pairs, but may also be produced by unmated male–female pairs (Rogers 2005) or by other associating individuals, such as male–male pairs of manakins displaying to attract females (Trainer et al. 2002). As duets have evolved independently in many distinct

avian lineages, and as natural selection shapes form and function simultaneously, it is likely that this variety in duet structure reflects variety in duet function (Darwin 1859; Hall 2004; Benedict 2008). By examining duet structure we can gain insight into duet function and also learn something about the apparently vast diversity of coordinated avian vocal signals (Wright & Dahlin 2007).

Multiple hypotheses explain the function of avian vocal duets and virtually all are supported by research into different species (for a review, see Hall 2004). Individuals may use duets to signal commitment to the partnership or to coordinate pair-based activities, such as breeding and territory maintenance (Dilger 1953; Wickler 1980; Hall 2000). Additionally, duets may carry information for individuals outside the pair bond. Duets are

used by some species during joint resource defense and for mate-guarding (Seibt & Wickler 1977; Sonnenschein & Reyer 1983). Several different aspects of duet structure may inform our understanding of function. For example, sex-specific duetting traits are predicted under hypotheses that posit conflict between the paired male and female. When mate-guarding, duetting birds indicate their sex and the mated status of their partner to extra-pair individuals. In some species where males guard mates, duets are initiated by females and males sing over female song to signal the female's mated status (Levin 1996). Thus, in mate-guarding situations, acoustically sex-specific duet vocalizations would facilitate duet function. In line with this expectation, several species that use duets to guard mates show duet elements that vary acoustically by sex (Levin 1996; Grafe & Bitz 2004; but see Seddon & Tobias 2006).

In addition to structural characteristics, the number and type of duet and solo songs given by individual birds should differ under hypotheses of conflict and cooperation between mates. Under a mate-guarding hypothesis, where partners are in conflict, unmated birds are expected to advertize for mates by singing their duet contribution frequently as a solo song. In contrast, if duets are used only in cooperative situations they need not be composed of the primary advertizement song of the species.

Like most avian vocalizations, duets often convey information about individual identity (Wiley & Wiley 1977; Hall 2000). The fact that duets are performed by fixed pairs in the majority of bird species suggests that nearly all duet contributions are individually distinct, as individuals must recognize the vocalizations of their mates in order to appropriately respond and create duets (Hall 2004). Playback experiments have shown that some birds recognize the duets of neighboring pairs (Wiley & Wiley 1977; Hall 2000). Individual or pair recognition is expected to be valuable because it allows partners and neighbors to interact appropriately (Catchpole & Slater 1995). Such interactions may occur in multiple contexts, but neighbor recognition would be particularly valuable under territory defense hypotheses that posit cooperation between mates.

In this paper, we quantify California towhee (*Pipilo crissalis*) duet characteristics, the rate of duet production, associated behaviors and duet acoustic structure. We examine duet structural variability in order to assess the acoustic distinctiveness of duets from different pairs and the potential for individual recognition.

Materials and Methods

Study Species

California towhees are oscine passerine birds that live year-round in the western part of the United States of America and Baja Mexico (Kunzmann et al. 2002). The California towhee 'squeal duet' or 'mate-call' was first described thoroughly by Quaintance (1941), who recognized that the vocalization was given exclusively by mated pairs. Quaintance (1941) described the general form of the squeal vocalization, but lacked the technology to provide a quantitative description of duet structure and variation among individuals. He noted that the squeal vocalization was almost always given in the context of a duet, when two birds were present, and was only occasionally produced by a lone bird as a 'solo' squeal. Marshall (1964) provided spectrograms of California towhee duets and observed that congeners produce similar vocalizations. Both authors observed that duets in this species are acoustically unlike the typical male advertizement song and call notes given by both sexes. They also noted that duets are often accompanied by a stereotyped behavior, where the duetting birds approach each other while vocalizing and may perform ritualized head and wing movements. Quaintance (1941) and Marshall (1964) suggested that the main function of the California towhee duet is to reinforce the bond between members of a pair.

Study Site

Research was conducted between Jun. to Jul. 2002 and Mar. to Jul. 2003–2006 at the Hastings Natural History Reservation, Carmel Valley, California. The study area comprised roughly 60 ha surrounding two creek drainages. Local habitat was predominantly oak woodland and chaparral, with areas of oak forest over dense understory vegetation (Griffin 1990).

Vocalization Use

Adult California towhees were trapped in potter traps baited with cracked corn. Upon first capture, we collected 50 μ l of blood sample, assessed the presence/absence of a brood patch (females only) or cloacal protruberance (males only), and banded each bird with a unique combination of three colored and one USFWS (United States Fish and Wildlife Service) metal leg bands to allow for visual identification of individuals. Sex was later confirmed using molecular

methods following Griffiths et al. (1998). Throughout the course of the study, individuals were resighted opportunistically. Thirty-six individuals were intensively observed during focal animal watches including 218 h of observation time between 31 May 2003 and 19 Apr. 2006. Watches began between 6:00 and 10:00 hours, depending on temperature and sunrise, and paired birds were observed on successive days.

During focal-animal watches, observers noted the location, habitat, behavior and vocalizations of the focal California towhee every 2 min. All interactions with conspecifics, including vocal duets, were noted. Researchers observing duets took natural history notes and sometimes measured duet loudness with a portable sound level meter (Radio Shack Model: 33-2055, Radio Shack, Fort Worth, Texas, USA). Duets and solo squeals were distinguished by ear, a task that is relatively easy when observing birds directly (but not when examining spectrograms) by aurally assessing the location of sound production. When both birds were visible, observers also watched for movements of the bill and body. Any squeal vocalization given by a single bird, not overlapped temporally by a squeal vocalization from another bird was considered a solo. Any squeal vocalizations given by two birds that overlapped temporally were considered duets.

California towhee squeal vocalization event frequencies were calculated for 17 pairs. Squeal duet frequencies per pair were calculated as the total number of squeal duets observed over the total observation time per pair. Overall squeal duet vocalization frequencies are averages of pair frequencies. Solo squeal frequencies per individual were calculated as the number of solo squeals observed over the total observation time for that individual. Overall solo squeal frequencies are calculated as averages of individual frequencies. We also calculated song frequency for mated and unmated males as the number of observation intervals during which a male was observed singing over the total number of observation intervals for all males in each category. Mean rates of solo squeal vocalizations from males and females were compared using a two-tailed Student's *t*-test.

Acoustic Structure

Vocalization structure descriptions and analyses are based on audio files recorded from the population between 23 May 2003 and 19 May 2006. Results come from over 400 h of recording time, and qualitative descriptions are based on observation of over 30 pairs. All recordings were made with a Sennheiser MKH70 long shotgun microphone (Sennheiser,

Wedemark, Germany) attached to either a Sony TC-D5ProII cassette recorder (Sony, Tokyo, Japan) or a Marantz PMD670 compact flash digital recorder (Marantz, Sagami-hara, Japan). Cassette recordings were captured at a sampling rate of 22 kHz and converted to digital files using the program SYRINX (<http://syrinxpc.com>). Digital recordings were made in mono at a sample frequency of 48 kHz and a bit-depth of 16, and were transferred directly to a Dell PC for storage and analysis. Vocalizations were converted to spectrograms using Raven sound analysis software (Version 1.2; Cornell Laboratory of Ornithology, New York, USA) for characterization of spectral properties.

To describe squeal vocalization properties we identified three syllable types ('squeaks', 'downsweeps' and 'squeals') and one of us (JM) measured the following variables on-screen with cursors relevant to the entire vocalization: number of squeak syllables, number of downsweep syllables, number of squeal syllables, total time (s), and total frequency range (Hz). We also measured the following variables for the first squeak syllable, the first downsweep syllable and the first squeal syllable (referred to as, e.g. an 'introductory squeak'): lowest frequency (Hz), highest frequency (Hz), time (s), frequency range (Hz) and maximum frequency (Hz). Measurements of squeal vocalizations were taken from Hanning-type spectrograms with a grid size of 5.38 Hz, and a DFT size of 512 samples. Reported population averages for the above variables were calculated as the average of individual averages for solo squeals and the average of pair averages for duets. Pair values for each variable were calculated for 90 duets from eight pairs with over six recorded duets each (11 ± 7 per pair). Male and female contributions to each duet are visible when they partially overlap temporally, but do not have evident sex-specific structural characteristics (see below). Thus, all measurements were performed on complete duets rather than on sex-specific contributions.

We tested the distinctiveness of squeal vocalizations in three ways. First, we included all of the above variables, untransformed, in two principal component analyses (PCAs). One PCA assessed individual (or sex-specific) differences in solo squeal vocalizations, using 14 solos from a paired male and female. The other PCA assessed differences among pairs using 57 duets from eight pairs. Differences between individuals and pairs were tested for statistical significance using analyses of variance and independent, two-tailed Student's *t*-tests on principal components. Sample sizes for these tests reflect the low frequency at which squeal vocalizations are produced in the population.

To test for differences between pairs we included the same 20 variables from all 57 duets in a discriminate function analysis (DFA). This analysis assessed whether or not all duets from each pair are classifiable as members of a single group unique to that pair. Because sample sizes varied among pairs, we subjected this DFA to chance correction (Titus et al. 1984). We also performed a DFA on the 14 solo squeals from a paired male and female in order to determine if we could accurately assign each squeal to an individual.

Our third test of duet distinctiveness examined the similarity of the introductory squeak notes across and within pairs. Mates frequently join duets after hearing only squeak notes from the initiating partner, so we hypothesized that these syllables are likely to contain signatures of identity. To test the distinctiveness of squeak syllables, we used the software program SOUND ANALYSIS PRO (Tchernichovski et al. 2000) to calculate similarity values for comparisons of pairs of squeak syllables. This program uses a multi-taper spectral analysis method and has been shown to be highly effective at classifying bird sounds to particular populations (analogous to individuals in our study) (Baker & Logue 2003). This analysis included 60 duets from nine pairs. Before performing similarity analyses, the first squeak syllable was cropped from each duet, leaving no lead-in or follow time and saved as a separate sound file. Using the program RAVEN, frequencies below 6 kHz and above 10 kHz were filtered out to remove potential confounding effects of background noise. In a minority of files, obvious remaining background sounds were also selectively removed. We then performed similarity comparisons on the 60 squeak note sound files, creating a table with (60 × 60) 3600 result values. This matrix was tested for correlations with a matrix of pair identity using a Mantel test (Mantel 1967) implemented using the software package POPTOOLS (Hood 2000). All other statistical analyses were performed using JMP, Version 5 (SAS Institute Inc., Cary, NC, USA). Reported values are mean ± standard deviation unless otherwise noted. Statistical test results and details not provided in the Results section of this paper are available upon request from the authors.

Results

Vocalization Descriptions

Recordings and focal animal watches confirmed that both male and female California towhees produce

squeal vocalizations and call notes, but only males produce the species-typical advertisement song. Nearly all male songs that we heard during focal animal watches were given by four unmated males, which sang during 47% of observation intervals. In contrast, mated males sang during only 0.09% of observation intervals. Both males and females called regularly. Call notes and song syllables are structurally similar to each other, but are very different from squeal vocalizations (Fig. 1).

California towhee squeal vocalizations have a relatively broad frequency range, and usually include harmonics above the fundamental frequency (Table 1, Figs 1d,e and 2). Squeal vocalizations consist of three primary syllabic types. 'Squeal' syllables always occur at the end of the vocalization and may be preceded by syllable types that we call 'squeaks' and 'downsweeps' (Fig. 1d,e). When included in a squeal vocalization, squeak syllables are always the first syllables to occur, followed by downsweep syllables and then by squeal syllables. Aside from syllable order, complete squeal vocalizations are highly variable in their composition. Both solo squeal vocalizations and squeal duets may include all three typical syllable types in varying numbers (Table 1). Figure 1d,e illustrates California towhee solo squeal vocalizations that include all three syllable types in their typical order.

Squeak syllables are relatively smooth notes, close to pure tones, that may appear flat, gently arc shaped or with a slight downward slope on spectrograms. Squeal vocalizations included anywhere from 0 to 12 squeak notes, with a population median of 3. Downsweep syllables often begin in the frequency range of squeaks and then descend rapidly to frequencies below 4000 Hz. On a spectrogram, they

Table 1: Properties of California towhee squeal vocalizations recorded at the Hastings Natural History Reservation, Carmel Valley, California 2004–2006. Values reported are means of the average trait values of eight pairs (standard deviations)

Vocalization	Duration (s)	Low frequency (Hz)	High frequency (Hz)	Frequency range (Hz)	Number per vocalization
Complete squeal	2.78 (1.35)	1451 (827)	8810 (978)	7326 (1283)	N/A
Squeak syllable	0.25 (0.11)	6311 (1020)	8580 (872)	2290 (1031)	2.91 (2.01)
Downsweep syllable	0.29 (0.12)	3310 (1158)	7866 (4879)	4175 (1167)	1.60 (1.29)
Squeal syllable	0.24 (0.13)	2170 (1025)	6315 (1096)	4146 (1206)	6.74 (4.98)

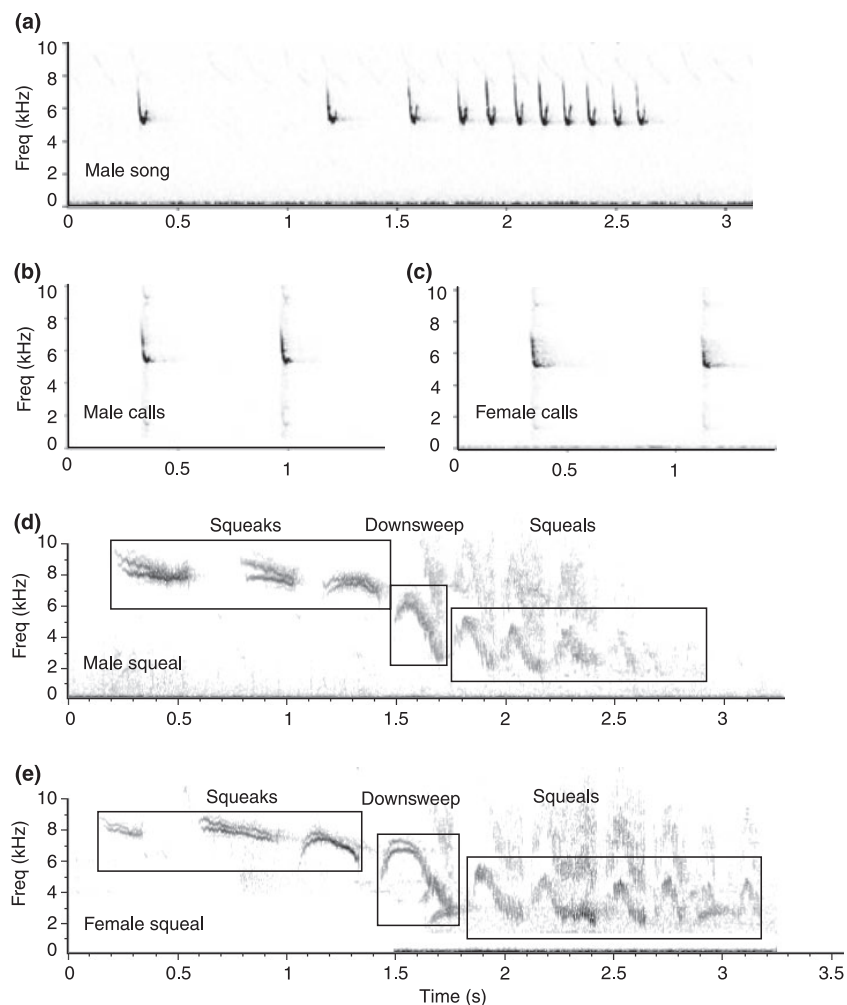


Fig. 1: Examples of California towhee vocalizations recorded at the Hastings Natural History Reservation, Carmel Valley California. Vocalization types include: (a) male advertisement song; (b) calls from a male; (c) calls from a female; (d) a solo squal vocalization from a male; and (e) a solo squal vocalization from a female. Three distinct syllable types termed 'squeaks', 'downsweeps' and 'squeals' are labeled in (d) and (e).

appear as fairly smooth descending slashes across a wide frequency range. Squal vocalizations recorded from the study population contained between 0 and 8 downsweep syllables, with a median of only 1. Squal syllables are trills containing a series of very brief descending notes (each one lasting approximately 0.02 s) that together form a squal-like noise. Squal vocalizations contained between 0 and 31 distinct squal syllables, separated by pauses. In many vocalizations, downsweeps grade seamlessly into squeals, and the two sounds may appear as part of a single, temporally continuous syllable (Fig. 1d,e). Squal vocalization properties and syllable properties are summarized in Table 1.

Duets are always composed of the squal vocalization, but do not have perfectly consistent structure or timing. Birds vary the number of each syllable type in duets and also timing with which they respond to the squeals of their partners (Table 1). Duet contributions from two partners are always

overlapping but not identical or simultaneous (Fig. 2).

Vocalization Use

Paired birds produced all duets with their partners and unmated birds were never heard to squal. The majority of squal vocalizations produced by focal animals during observations were used in duets, rather than solos. In 218 h of observation time, 95% of all squal vocalizations observed were given as part of duets. Population-wide vocalization rates were 3.0 ± 2.29 duets per hour per pair and 0.28 ± 0.40 solos per hour per individual. Males produced solo squeals at a rate of 0.38 ± 0.54 per hour, while females produced 0.19 ± 0.20 per hour. These rates are not statistically distinguishable ($t_{28} = 1.30$, $p = 0.21$). Additional observations indicate that California towhees duet throughout the year, but rates presented here apply only to the

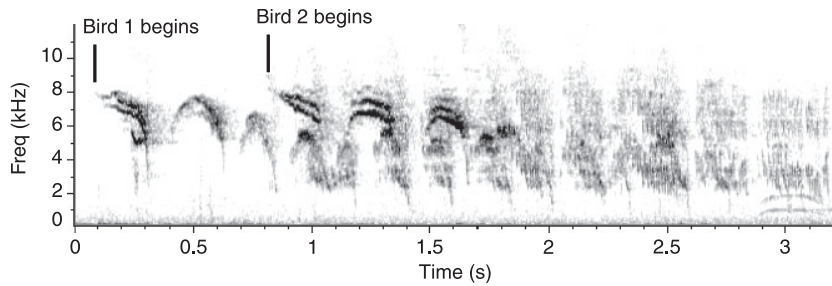


Fig. 2: Squeal duet produced by a mated pair of California towhees at the Hastings Natural History Reservation, Carmel Valley California. The duetting partners overlap their vocal contributions as indicated.

spring breeding season between 15 Mar. and 25 Jul. between 6:00 and 12:00 hours.

Squeal duets were performed at a range of volumes, sometimes as loud as 55–60 dB (measured at a distance of 5 m), and sometimes so softly as to be almost inaudible to a person at a distance of 5 m. Focal subjects duetted as infrequently as once in a 2-h observation period and as frequently as 15 times in an hour of observation. Duets were sometimes produced in relatively rapid succession, up to a maximum of five times in a minute. All duets occurred between mated pairs of California towhees. In a few instances, individuals appeared to direct squeal vocalizations at chicks, but this always occurred in dense vegetation where a mate may have been present.

Both males and females initiated duets and both sexes joined duets as the second partner to vocalize. Male and female squeal vocalizations were similar enough that they were indistinguishable to human listeners. Male and female behaviors were also apparently identical while duetting. Observers were only able to differentiate male and female birds performing duets based on band combinations.

Squeal duets were always associated with a stereotyped approach behavior between mates. Birds began vocal duets in a variety of locations, sometimes separated by distances of over 10 m and visual obstructions, but never concluded duets until the two pair members were positioned right next to each other (always within 1 m) and were in visual contact. Not only birds positioned close together but birds positioned far apart also began squeal duets regularly. Duets between spatially separated birds were sometimes initiated by a stationary individual which was joined by its mate, and sometimes initiated by a mobile individual approaching its stationary mate. Duets were sometimes produced by mated birds while mutually approaching each other. Partners approached each other rapidly after beginning duets, as is evidenced by the fact that duets lasted less than 3 s on average, and never more than 8 s.

Once positioned close together, pairs sometimes faced each other and performed a series of movements that included crouching, bobbing their heads up and down and opening their wings slightly. Individuals were never observed to perform this behavior when not duetting, although they did perform similar behaviors during aggressive contests and copulation solicitations.

Vocalization Distinctiveness

Recordings of solo squeal vocalizations indicate that both males and females produce all syllable types, with the same overall structure (Fig. 1d,e). Six solo squeals from a female California towhee and eight solo squeals from its mate suggest that male and female duet contributions have very similar characteristics; each of the 14 solo squeals contained all three syllable types, and among them the range of values for the female and the male overlapped across all 20 measured acoustic properties. Nevertheless, the squeal vocalizations of individual birds may be distinguishable to listeners. Principal components analysis provided six principal components with eigenvalues above 1. Principal component values from the two individuals overlapped heavily, but did provide information about identity. A Student's *t*-test indicated that mean values for the two individuals were distinguishable across PC-2, which accounts for 17% of the variance among the variables ($t_{12} = -2.30$, $p = 0.041$). Our second measure of individuality, the DFA, assigned all 14 squeals to the correct individual.

Spectral analysis of recorded duets indicated that both sexes perform all three syllable types with the same overall structure when duetting. Similar to individuals, pairs produced duets that varied greatly across all measured properties, including syllable number, temporal duration and frequency characteristics. Principal components analysis of 57 duets containing all syllable types from eight pairs (7.1 ± 3.8 per pair) generated seven principal components with

eigenvalues above 1, all of which indicated little pair distinctiveness. An analysis of variance for PC-1 did find that some pairs had significantly different means ($F_{7,56} = 2.76$, $p = 0.017$), but the ranges of PC-1 values overlapped for all pairs. Student's *t*-tests indicated that no single pair had a mean distinct from all other pair mean values. Similarly, an analysis of variance for principal component 2 (PC-2) found that some pairs had significantly different mean values ($F_{7,56} = 3.40$, $p = 0.005$), but Student's *t*-tests again revealed that no single pair had a mean distinct from all other pair mean values.

Discriminant function analysis classified 91% of duets to the correct pair. For five pairs all duets were classified correctly, and the remaining three pairs had either one or two of their duets misclassified to the wrong pair. Although sample sizes varied by pair, chance correction indicated that this result was due to a good model fit ($K = 0.90$).

Similarity analyses performed on 60 duets from nine pairs (6.7 ± 2.2 per pair) indicated that squeak syllables had over a 96% similarity to themselves, supporting the use of this technique. The average similarity value of within-pair squeak syllable comparisons was 70.4% ($n = 371$) and the average similarity value of between-pair squeak syllable comparisons was 67.9% ($n = 3121$). A Mantel test indicated that squeak note similarity correlated with comparison type, reflecting greater similarity for within-pair comparisons than for between-pair comparisons ($r = 0.051$, $p = 0.015$).

Discussion

Most California towhee squeal vocalizations occur when paired birds vocalize simultaneously, a pattern which led earlier researchers to label this sound a 'duet' or 'mate-call' (Quaintance 1941; Marshall 1964). Solo squeals are produced by male and female California towhees, and are rare compared with duets. Solo squeals necessarily result from the second partner failing to join a potential duet. The rarity of solo squeals indicates that partners of both sexes respond to the vast majority (roughly 95%) of squeal vocalizations from their mates. Thus, this vocalization is contextually most important as a duet.

The squeal vocalization is acoustically unlike other California towhee vocalizations (Marshall 1964). It has multiple syllabic elements, but does not have the melodic quality of a typical bird song and is clearly different from the male song that functions to attract mates (Quaintance 1938). Our observa-

tions confirmed that mated males virtually never sing and unmated males never squeal. Among other species, duets may be composed of songs that are regularly sung as solos, and mates form duets in response to a minority of the songs initiated (Mann et al. 2003; Logue 2007). Among such species, duetting may be an extension of typical singing behavior, but among California towhees both the usage patterns and the unique acoustic structure of the squeal vocalization suggest that it likely evolved within the context of duets. The lack of solo squeal vocalizations from unmated birds as well as the difference between the male advertisement song and the acoustic structure of duets both suggest that this vocalization does not function to attract potential mates and therefore has not evolved in a mate-guarding context.

California towhees duet approximately three times per hour during the breeding season, and do not duet repeatedly in long bouts. This pattern of squeal vocalization usage is markedly different than that of some other duetting species in which pairs may duet 30–50 times per hour and individuals produce duet initiation phrases over 200 times per hour (Mann et al. 2003; Gill et al. 2005). The relative scarcity of California towhee duets suggests that the duet is not a generalized broadcast signal which birds repeatedly send out to any potential listener. Instead, duets likely convey a directed message and duetting birds do not benefit from repeating that message indefinitely. Observations suggest that duets help mates to locate each other, a function that would not require duet repetitions once achieved. All California towhee duets are associated with a stereotyped approach behavior, such that no duet ends until the partners are in close spatial proximity. This approach behavior suggests cooperation between mates, rather than conflict which might cause partners to move away from each other.

Male and female California towhees produce similar squeal vocalizations made up of three-syllable types that occur in a set order. Beyond that basic framework all individuals vary the syllabic number, duration and frequency of duet elements. Solo squeal vocalization analyses were limited because solo squeals are rare and therefore hard to record in large numbers; however, analyses of solo squeals from one male and its female mate give some idea of individual squeal properties. Solo squeal vocalizations from the two birds were highly variable and overlapped across all measured characters, but did carry enough information to indicate identity. Among California towhees, it is unclear whether these vocal differences

are purely individual- or are sex-based. The duets of many other species have markedly different male and female parts, and even when males and females produce similarly structured duet contributions, researchers have found that individuals give vocalizations with non-overlapping acoustic traits (Mann et al. 2003; Rogers 2005; Seddon & Tobias 2006; Wright & Dahlin 2007). The similarity of California towhee duetting behavior and vocalization properties from males and females is remarkable and should limit, but not necessarily exclude, sex recognition based purely on squeal vocalizations. The similarity of male and female squeals may indicate that the important signal content of duets is not the sex of each bird, but the fact that two paired individuals are present and the identity of those individuals. This information would be most valuable under hypotheses that suggest cooperative functions of duetting, such as resource defense or signaling partner location and commitment (Hall 2004).

As with solo squeals, there is great within-pair variability in duet characteristics. Nevertheless, analyses of both entire duets and just the introductory squeal indicated that these vocalizations provide information about identity. Because duets are always performed by mates on their own territory, location may also provide clues about duetter identity. Separate analysis of duet contributions by individual birds would provide more information on this topic, but unfortunately it is impossible to separate male and female duet contributions in audio recordings or spectrograms. Nevertheless, if individuals produce distinctive squeal vocalizations, then differences between pairs should be measurable. Experimental tests of squeal recognition using vocalization playbacks would also be highly informative but difficult, if not impossible, to do among California towhees where male and female duet contributions cannot be separated. In the absence of such experimental tests, vocalization measurement data provide the best possible information about the potential for individual or pair recognition. California towhees are one of the few species to be studied in depth where males and females produce the same duet vocalization type. By examining this unique sound we add to the existing understanding of the diversity of avian vocal duets.

The duets of California towhees show far less pair distinctiveness than do duets of other species in which acoustic properties and even phrasing may vary considerably between pairs (Mann et al. 2003; Logue 2006; Seddon & Tobias 2006). It is unclear why squeal vocalizations are so highly variable, but

possible that plasticity in duet production may better allow pairs to adapt their vocalizations to a variety of situations. For example, as the duet is always associated with a physical approach behavior, duets will vary in duration according to the amount of time it takes for the pair to approach each other. Changes in syllable number and length therefore, might reflect the distance between birds at the start of the duet. Observations incorporating contextual information with duet structure would be highly informative in helping to make sense of this structural diversity.

California towhee duet structure provides insight into potential function. Acoustic mate-guarding hypotheses propose that duets are formed when a bird sings over the song of its mate in order to indicate their paired status to potential sexual competitors (Sonnenschein & Reyer 1983; Levin 1996). The fact that both male and female California towhees initiate duets indicates that duetting does not reflect mate guarding by a single sex. Duets might be used by both sexes to guard mates, and in that case males and females would benefit by producing sex-specific duet contributions. The lack of sex specificity in California towhee squeal vocalizations argues against the mate-guarding hypothesis, as does the low frequency of solo-squeal production. Rather, the similarity of male and female duetting behavior is suggestive of a cooperative function for duets. Cooperative functions may include joint resource defense, coordinating breeding behavior or signaling commitment to the partnership (Dilger 1953; Seibt & Wickler 1977; Wickler 1980; Hall 2000). Squeal vocalizations contain enough information to indicate the location, paired status, and identity of a vocalizing bird. The observed acoustic indicators of identity allow for functional roles dependent upon individual differences. For example, duets may indicate individual quality by signaling identity to a familiar conspecific (Smith 1994). More importantly, duet recognition should assist with maintenance of appropriate pair behaviors and territorial boundaries, increasing the relevance of the cooperative functional hypotheses discussed here.

Relative to the majority of avian duets, which tend to be antiphonal, composed of distinct male and female 'songs' and performed in repeated bouts, California towhee vocal duets are unusual (Thorpe 1972; Farabaugh 1982). Their structure is simple but highly variable and entirely unique within the species' repertoire. Results reported here add to the growing described diversity of coordinated animal signals, and provide evidence that duets are used cooperatively by California towhees.

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