

Context, Structural Variability and Discriminability of California Towhees (*Pipilo crissalis*) Vocal Duets

Lauren Beddard & Ja P. McEwen

Department of Psychology, University of Cambridge, Cambridge CB2 3RQ, UK

✉

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

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

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

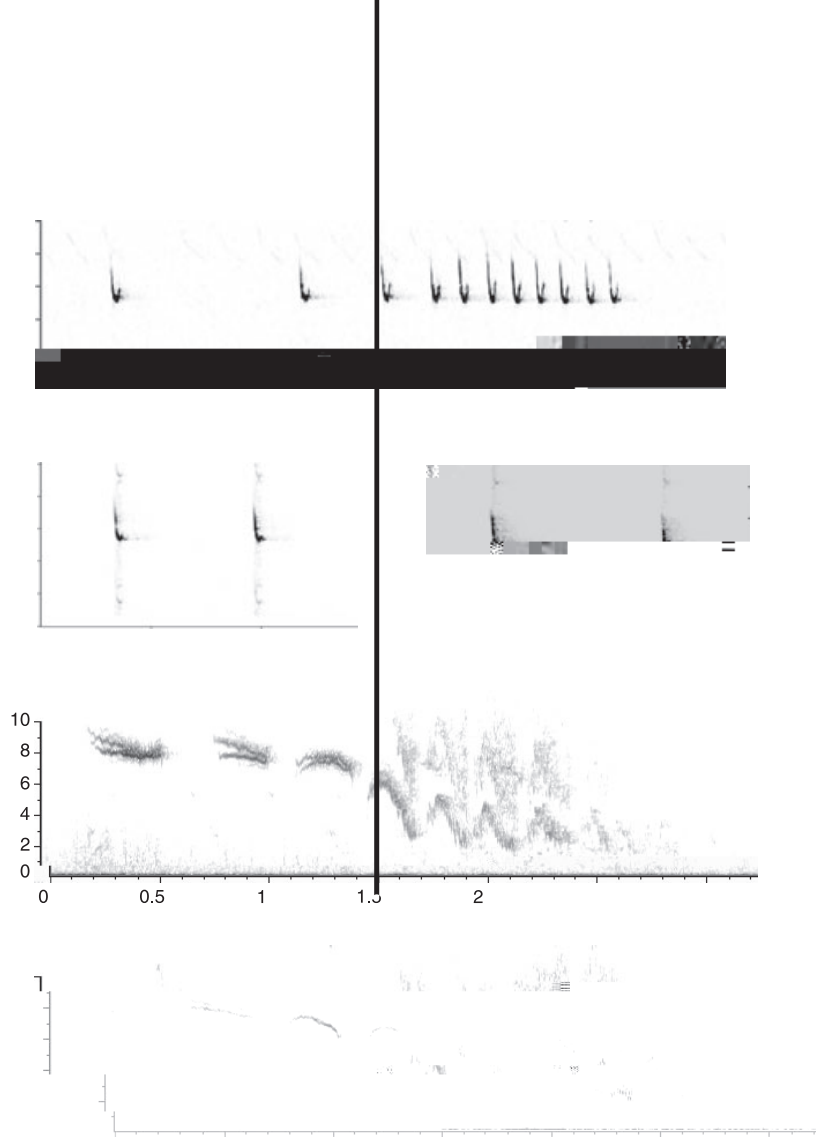
Vocalization structure descriptions and analyses are based on audio files recorded from the population between 23 May 2003 and 19 May 2006. Results come from over 400 h of recording time, and qualitative descriptions are based on observation of over 30 pairs. All recordings were made with a Sennheiser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

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



appear as fairly smooth descending slashes across a wide frequency range. Squeal vocalizations recorded from the study population contained between 0 and 8 downsweep syllables, with a median of only 1. Squeal syllables are trills containing a series of very brief descending notes (each one lasting approximately 0.02 s) that together form a squeal-like noise. Squeal vocalizations contained between 0 and 31 distinct squeal 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). Squeal vocalization properties and syllable properties are summarized in Table 1.

Duets are always composed of the squeal 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 squeal. The majority of squeal vocalizations produced by focal animals during observations were used in duets, rather than solos. In 218 h of observation time, 95% of all squeal 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

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

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

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,

Acknowledgments

We thank Wendy Fair and Sarah Knutie for their assistance with data collection. Thanks are due to Walter Koenig, Eileen Lacey, Craig Moritz, Justin Brashares and an anonymous reviewer for feedback on earlier versions of this manuscript. Rauri Bowie advised us during manuscript preparation. Tim Krein provided software support. This research was funded by the National Science Foundation (Doctoral Dissertation Improvement Grant no. 0407974), an American Ornithologists' Union AOU Student Research Award, Sigma Xi Grants-in-Aid of Research from both the Berkeley and national chapters of Sigma Xi, a Robert and Nancy Beim Graduate Field Research Award, the UCB Department of Integrative Biology, a Museum of Vertebrate Zoology Koford Grant in Aid of Research, and a Museum of Vertebrate Zoology Alexander Fellowship.

References

- Baker, M. C. & Logue, D. M. 2003: Population differentiation in a complex bird sound: a comparison of three bioacoustical analysis procedures. *Ethology* **10**, 225—244.
- Benedict, L. 2008: Occurrence and life history characteristics of duetting in North American passerines. *J. Avian Biol.* , 57—65.
- Catchpole, C. K. & Slater, P. J. B. 1995: *Bird Song: Biological Themes and Variations*. Cambridge Univ. Press, Cambridge.
- Darwin, C. 1859: *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life*. John Murray, London.
- Dilger, W. C. 1953: Duetting in the crimson-breasted barbet. *Condor* **55**, 220—221.

- slate-coloured boubou (*Laniarus funebris*). *Z. Tierpsychol.* **1**, 112—140.
- Tchernichovski, O., Nottebohm, F., Ho, E., Pesaran, B. & Mitra, P. P. 2000: A procedure for an automated measurement of song similarity. *Anim. Behav.* **4**, 1167—1176.
- Thorpe, W. H. 1972: The biological significance of duetting and antiphonal song. *Acta Neurobiol. Exp.* **4**, 517—528.
- Titus, K. B., Mosher, J. A. & Williams, B. K. 1984: Chance-corrected classification for use in discriminant analysis: ecological applications. *Am. Midl. Nat.* **111**, 1—7.
- Trainer, J. M., McDonald, D. B. & Learn, W. A. 2002: The development of coordinated singing in cooperatively displaying long-tailed manakins. *Behav. Ecol.* **1**, 65—69.
- Wickler, W. 1980: Vocal duetting and the pair bond. I. Coyness and partner commitment, a hypothesis. *Z. Tierpsychol.* **4**, 201—209.
- Wiley, R. H. & Wiley, M. S. 1977: Recognition of neighbours' duets by stripe-backed wrens *Campylorhynchus nuchalis*. *Behaviour* **4**, 10—34.
- Wright, T. F. & Dahlin, C. R. 2007: Pair duets in the yellow-naped amazon (*Amazona auropalliata*): phonology and syntax. *Behaviour* **1**, 207—228.