

California towhee vocal duets are multi-functional signals for multiple receivers

Lauryn Benedict¹⁾

(Museum of Vertebrate Zoology and Department of Integrative Biology, 3101 Valley Life Sciences Building, University of California, Berkeley, CA 94720, USA)

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Summary

Avian vocal duets provide a model system for studying the evolution and production of complex signals which require input from multiple individuals. Duets serve a variety of communication functions in diverse species. To explore the function of duetting in California towhees (*Pipilo crissalis*) I collected behavioural data from a marked population, conducted sound playback experiments, and removed males from established pairs to observe the behaviour of new partners. Results indicate that California towhees use duets during extra-pair communication with conspecifics and during intra-pair communication between duetting partners. During the breeding season duetting frequency peaked during the chick-rearing period and was low during periods of high female fertility. Playbacks provoked similar levels of aggressive response from male and female territory holders. Mated pairs duetted in response to simulated intrusion by conspecific males, females and pairs. California towhee duets briefly increased in frequency after pairing, and showed no evidence of change due to learning. Duets facilitate spatial and behavioural coordination by mates, which should allow them to more effectively perform behaviours related to mutual reproductive success. No single existing hypothesis adequately explains vocal duetting among California towhees. Instead, duets function in multiple contexts and provide multiple potential benefits.

Keywords: acoustic signals, birdsong, California towhee, pair-bond, *Pipilo crissalis*, vocal duets.

Introduction

Communication between individuals organizes interactions, shapes mating patterns and is in many ways vital to animal social behaviour. Understand-

¹⁾ Corresponding author's e-mail address: LB43@berkeley.edu

ing the operation of animal communication signals, therefore, helps us to understand how sociality evolves and is maintained. Like other traits, communication systems are shaped by natural selection, and complex communication mechanisms exemplify natural selection's power in crafting precise, sophisticated systems. One fascinating, highly specialized type of communication is duetting, where two animals coordinate sound production in a stereotyped manner (Farabaugh, 1982). Duets are observed widely in nature among animal groups including birds, mammals, amphibians and insects (Lilly & Miller, 1961; Thorpe, 1972; Mitani, 1985; Tobias et al., 1998; Bailey, 2003). The close coordination of vocal timing and structure seen in duets, combined with the likely costs of these conspicuous signals, suggests that duets are subject to strong selective pressures (Hall, 2004).

Among birds duets are relatively rare, occurring in less than 8% of species, the majority of which live in tropical or sub-tropical latitudes (Farabaugh, 1982; Benedict, 2008a; Hall, 2009). Despite this, duetting behaviour has evolved many times and has been described in 50 avian families (Hall, 2009). Duets are known to serve varied functions among, and even within, avian species (Hall, 2009). This diversity is perhaps not surprising given the many independent evolutionary origins of the trait (Thorpe, 1972). In the studies reported here, I examined a population of California Towhees (*Pipilo crissalis*) to simultaneously test multiple hypotheses regarding duet function. This study is the first to comprehensively test duet function in an Emberizid species and one of the first to examine duetting in temperate North America (McElroy & Ritchison, 1996). The hypotheses tested in this study are not mutually exclusive, and in fact, may all be relevant to a single species. Experiments and observations were designed to test both the extra-pair and intra-pair communication function of California towhee duets and to assess the potential for signal multi-functionality.

The earliest description of a California towhee vocal duet comes from Charles Quaintance (1941), who concluded that the 'squeal' duet vocalization was a communication signal between mates that functioned to reinforce the pair-bond. Other early researchers studying avian vocal duetting also concluded that duets function to strengthen the pair-bond, but failed to specify the mechanism by which duets accomplish this goal (Marshall, 1964; Diamond & Terborgh, 1968; Baptista, 1978). In fact, this general functional umbrella referred to as 'pair-bonding' includes a variety of different hypotheses for the function of avian duets (Tables 1 and 2).

Table 1. Hypothesis for the function of avian vocal duets tested in this study.

Hypothesis	Abbreviation	Description
1.	MG	Duets function in Mate Guarding
2.	RD	Duetting enhances joint Resource Defense
3.	RS	Duetting ensures Reproductive Synchrony
4.	MC	Duetting helps mates to Maintain Contact
5.	SI	Duets signal individual Investment by indicating attentiveness to the partner
6.	LI	Duetting requires a Learning Investment costly enough to ensure commitment

Table 2. Predictions generated under the six hypotheses for the function of avian vocal duets, with indications of how each prediction supports (+) or counters (–) each hypothesis.

Prediction	Duet signal recipient					
	Intruder		Mate			
	MG	RD	RS	MC	SI	LI
Duets always occur with aggressive behaviours	+	+	–	–	–	–
Males and females are aggressive to and duet towards all conspecific intruders		+				
Males and females are aggressive only to same-sex conspecific intruders	+	–				
Duetting frequency increases with female fertility	+		+			
Duets occur more frequently while partners are visually separated	+			+	+	+
Duet vocalizations show consistent individual variation				+	+	+
Duet coordination improves with pair-bond duration						+
Duets of high quality pairs are better coordinated than duets of low quality pairs					+	+
Newly formed pairs invest more time in duetting than experienced pairs					+	+

Pair-bonds may be maintained via extra-pair duet communication if the duet is a signal directed towards rival conspecifics, or through intra-pair duet communication if the duetters are also the signal recipients. Extra-pair communication functions for duets include acoustic mate guarding, where

duetting partners have different interests, and joint resource defense, where partners gain the same benefits (reviewed in Hall, 2004, 2009). Duets associated with mate-guarding have been observed in a variety of species. Males may use duets to guard female mates, females may use duets to guard male mates, or males and females may mutually mate guard with duets (Sonnenschein & Reyer, 1983; Levin, 1996b; Seddon et al., 2002; Seddon & Tobias, 2006; Rogers et al., 2007). In other species, however, mate guarding does not seem to be a primary function of duetting behaviour. In species including black-bellied wrens (*Thryothorus fasciatoventris*) and Australian magpie larks (*Grallina cyanoleuca*), duets appear to function mainly as a resource defense signal (Hall, 2000; Logue & Gammon, 2004). In some systems duets function both in acoustic mate guarding and in resource defense (Grafe & Bitz, 2004; Marshall-Ball et al., 2006).

Duets may function as intra-pair communication signals if they ensure reproductive synchrony, maintain contact between mates, signal commitment, or ensure commitment by requiring a learning investment (Cobb, 1897; Dilger, 1953; Thorpe, 1972; Wickler, 1980; Smith, 1994; reviewed in Hall, 2004, 2009). Dilger (1953) first proposed that duets synchronize avian physiological rhythms and ensure breeding success based on his observations of crimson-breasted barbets (*Megalaema haemacephala*). More recently, researchers have proposed that duets function to coordinate breeding by pairs and larger social groups (Sonnenschein & Reyer, 1983).

Pairs may use duets to maintain contact when mates are visually or spatially separated, particularly if they live in areas of dense vegetation (Cobb, 1897; Thorpe, 1972; Logue, 2007). Under this hypothesis, duets should occur when partners have been out of visual contact for prolonged periods of time, and partner vocalizations should be individual enough to signal identity. In a number of species, including California towhees, individuals of both sexes produce highly distinctive individual duet contributions that likely signal identity (Logue, 2006; Mays et al., 2006; Seddon & Tobias, 2006; Benedict & McEntee, 2009).

In any interaction, a duet is created when a second bird responds to a vocalization from the duet initiator. If duet responders signal investment in the partnership by being more attentive, then successful pairs should have more highly coordinated duets than other pairs (Smith, 1994). Many species of duetting birds do display pair-specific duet properties that might indicate

variability in attentiveness (Levin, 1996a; Hall, 2000; Grafe et al., 2003; Seddon & Tobias, 2006).

Duets may also function to maintain pair-bonds if they require a learning investment, such that mate-switching would be costly due to an inability to coordinate duets and elicit commitment from a new mate (Wickler, 1980). Thus far, there is mixed evidence that duetting species must learn to duet with new partners, and invest time in doing so (Wickler & Seibt, 1980; Arrowood, 1988; Levin, 1996a; Whittingham et al., 1997).

To examine the communication function of duetting in California towhees I used a combination of observational and experimental techniques to test predictions generated under the hypotheses discussed above (Tables 1 and 2). This paper includes results based on 3 studies: (1) behavioural observation of a marked population, (2) sound playback experiments and (3) male-removal experiments that allowed me to compare the vocalizations of experienced and inexperienced pairs. I discuss the relevance of my results to both the local study system and to other species that produce complex communication signals.

Material and methods

Research was conducted on a color-banded population of California towhees at the Hastings Natural History Reservation in Monterey County, CA, USA (for more details see Benedict, 2008b; Benedict & McEntee, 2009).

Study species

California towhees perform a relatively simple set of vocalizations including calls from both sexes and songs produced almost exclusively by unmated males (Quaintance, 1938; Benedict & McEntee, 2009). California towhee pairs produce squeal duets which consist of multiple elements that are acoustically unlike song or call notes, produced by both birds simultaneously in an overlapping fashion (Figure 1) (Quaintance, 1941; Marshall, 1964; Benedict & McEntee, 2009). Birds rarely produce solo squeals, which necessarily result when the second partner fails to vocalize, and may be considered duet initiation phrases (Benedict & McEntee, 2009). Males and females produce the same duet vocalization type, both sexes initiate duets, and

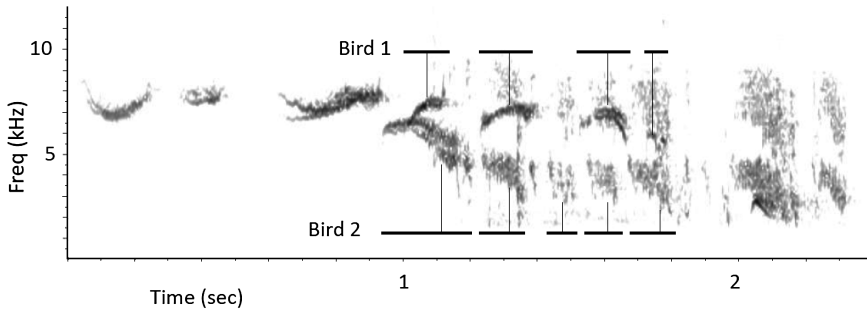


Figure 1. Spectrogram of a California towhee (*Pipilo crissalis*) duet recorded at the Hastings Reservation, Carmel Valley, CA, USA on April 2, 2005. Labels indicate the contributions of the two partners where the vocalizations overlap. The lower-pitched (3–6 kHz) vocalizations of bird 2 provide the ‘squeal’ sound.

both sexes perform similar behaviours when duetting, making it impossible for human observers to distinguish the sexes by duetting behaviour alone (Benedict & McEntee, 2009). Squeal vocalizations do carry enough information to acoustically indicate pair identity to conspecifics (Benedict & McEntee, 2009).

Population observations

I conducted focal observations designed to measure duet frequency during different stages of the breeding season. Pairs were identified based on shared occupancy of a single territory and affiliative behaviours, including care of young. During two hour focal observation periods researchers recorded the animal’s position, instantaneous activity (i.e., foraging, preening, in flight) and instantaneous vocalizations every two minutes. Researchers noted all duets and social interactions, including copulation events and aggressive encounters.

Watches began 2–3 h after sunrise, and the two members of a pair were observed on successive days. Nests were located through visual searches and nesting progress was tracked through the end of July each year. Observers performed focal watches during the ‘Pre-breeding’ period, the ‘Nest-building’ and egg laying period, during the early stages of ‘Incubation’ (days 2–6), during the first half of the ‘Chick rearing’ period (days 3–7), and during the period in which ‘Fledglings’ remained with their parents (1–2 weeks post-fledging). I considered nest-building by a female to signal fertility (Birkhead & Møller, 1992). After clutch completion females

were no longer considered fertile. All females observed soliciting copulation and pairs observed copulating ($N = 3$) did so while building nests, 1–12 days before clutch initiation. Between 15 March and 25 July of 2003–2005 researchers observed 18 California towhees representing nine pairs. Pre-breeding watches were conducted on an additional 8 pairs in 2006.

Researchers watched most pairs twice during each breeding stage (4 h total) in each year, but total observation time varied because birds sometimes moved out of sight during watches. Not all pairs were observed in every breeding period because of nest predation and late nest finding. Data reported here include only pairs with more than an hour of observation for a given period. I derived rates of duetting for each pair during each period by dividing the total number of duets over the total observation time per period. Since calling and singing behaviour can be continuous for long periods of time, I calculated rates of calling and singing as the number of 2-min observation intervals at which calling or singing was recorded over the total number of observation intervals. Overall vocalization rates represent an average of the pair averages. I used Wilcoxon rank sum tests to compare vocalization rates (duetting and calling) between different breeding periods. Unless otherwise stated, values presented are means \pm standard deviations. Statistical analyses were performed using JMP, Version 6 (SAS Institute, Cary, NC).

Aggressive events included fights, chases, a wing-flutter display behaviour that resembles copulation solicitation by females, and a challenge behaviour where one individual confronts another with a small twig or piece of grass in its bill (Tvrđik, 1977). I considered aggressive displays and duets that occurred within two minutes of each other to be related. To calculate the number of aggressive behaviours expected to co-occur randomly with duets, I used observed population data to calculate the probability of a duet occurring within any two-minute interval and multiplied that probability by the number of two-minute intervals that included aggressive encounters. Expected and observed numbers of duets paired with aggressive encounters were compared using a χ^2 test.

Playback experiments

I conducted playback experiments on 16 pairs with known territories between 4 May and 11 June 2004. Playback experiments assessed the extra-pair function of duets by testing the responses of California towhees to simulated

territorial intrusion by solo birds of both sexes and paired birds performing duets. Territory boundaries for subjects were estimated based on point locations recorded during focal observations and resighting efforts during which birds were followed opportunistically to track movement around the area. Experimental pairs were resighted an average of 13 times (range 7–32) between 15 March 2004 and the initiation of playbacks. Clutch completion dates for experimental subjects ranged from 23 April to 16 June.

Territorial pairs heard four different playback vocalization types presented one per day over four successive days. Playbacks took place between 16:00 and 18:00, a time when avian evening activity generally begins to increase and California towhees can often be seen foraging in open areas on their territories (Catchpole & Slater, 1995; LB, unpubl. data). I randomized playback presentation order and time across subjects; post-hoc chi-squared analysis showed no effect of presentation order on approach response ($\chi^2_{63} = 1.85$, $p = 0.60$). The four vocalization types used in playback presentations were: (1) male California towhee calls, (2) female California towhee calls, (3) California towhee duets and (4) spotted towhee (*Pipilo maculatus*) song. Male and female calls were used in playbacks to ensure equality of simulated intrusion by the two sexes. California towhee call notes are individually distinctive and may be used to signal sex and identity (Benedict, 2007). Spotted towhees co-exist with California towhees on the study site and do not maintain interspecific territories (Davis, 1957), so their songs should be recognizable but non-threatening signals to experimental pairs.

All playback stimuli were recorded on the study site with a Sennheiser shotgun microphone and a Sony TC-D5ProII cassette recorder. Recordings were captured at a sampling rate of 22 kHz and converted to digital files using the program Syrinx (available online at <http://syrinxpc.com>) and a Dell PC. I selected the best quality recordings of each type, recorded as naturally produced vocalizations (i.e., not response to playback) to use as playback tracks. Recordings were presented to pairs located at least 200 m and one intervening territory away from the recording site. Five different playback tracks were used in both the duet and male call presentations. Four different playback tracks were used in the female call and spotted towhee song presentations. In total, resident pairs heard playback vocalizations recorded from four different individuals (one calling male, one calling female and a different duetting pair). I randomized playback tracks across subjects; post-hoc

chi-square analysis showed no significant effect of conspecific track identity on approach response ($\chi^2_{47} = 14.0, p = 0.37$).

Playback trials included three minutes of silent pre-playback observation, three minutes of playback, and three minutes of silent post-playback observation. Playback tracks were designed to represent natural vocalization rates while also equalizing the total time of vocalization across treatments. Playbacks were broadcast from a single Radio Shack amplified speaker (catalog No. 277-1008C) connected to a portable Panasonic compact disc player. Speakers were placed at a height of approximately one meter in vegetation at the center of each territory, a location designed to maximize perceived threat. All playback sound levels reflected natural levels recorded in the field with a portable sound level meter (Radio Shack Model 33-2055).

Two observers recorded the following categorical response variables for each focal bird relative to the playback speaker position: visual confirmation of presence on the territory, approach to within 10 m, calling during playback and duetting during playback. Observers also recorded the following continuous response variables for each focal bird relative to the playback speaker position: distance of closest approach and time spent within 10 m of the speaker. Individuals not observed during trials were assigned a 30 m distance of closest approach.

I used Cochran–Mantel–Haenszel tests, blocked by trial, to compare approach responses during pre-playback control periods with approach responses during playback. Use of this test provides maximum power for comparing more than two variables within a chi-squared test format (Zar, 1999). I also used Cochran–Mantel–Haenszel tests, blocked by pair to compare categorical responses to conspecific vocalizations with responses to control spotted towhee vocalizations. Fisher exact tests were used to compare male and female categorical responses to each playback type. I assessed California towhee minimum distance of approach and time of approach responses to duet and solo (call) playbacks using Wilcoxon signed-rank tests. The use of chi-squared statistics with categorical response variables allowed for accurate analysis of power for non-significant results. Post-hoc statistical power estimates were generated for categorical variables with G*Power (Erdfelder et al., 1996) using Cohen's (1988) effect size conventions for small (0.1) medium (0.3) and large (0.5) effects.

Removal experiments

I conducted mate-separation experiments on ten pairs of California towhees between 29 March and 26 April 2005, and between 6 April and 27 April 2006. Mate separation experiments were designed to test the intra-pair duet function hypotheses that duets signal quality or ensure commitment by requiring a learning investment. I removed males from all pairs because previous observations suggested an abundance of unpaired males in the population, as well as a tendency for females who lost mates to remain on their exiting territories (LB, unpubl. data). All pairs from which males were removed had bred together in at least one previous season, and were considered successful, experienced partners. Prior to removing males, researchers performed focal animal watches on all 10 experienced pairs to determine baseline rates of behaviours and vocalizations. Removed males were captured and transported off the study site, and none were observed to return. For nine pairs, removals were conducted before the initiation of nesting behaviour. One established pair had a nest into which the female laid a third egg on the day her mate was removed. I removed the nest simultaneously with the male to encourage re-pairing by the female.

Pairs were observed for 6.8 ± 0.91 h prior to male removal. When females re-paired, new (post-removal) pairs were observed during focal animal watches during each of the first three mornings after re-pairing ($N = 9$) (designated as days 1, 2 and 3 post re-pairing). New pairs were watched twice between days 4 and 11 ($N = 8$), and at least twice every two weeks following that period until 10 June each year ($N = 6$). Focal observation pair sample sizes and number of watches decreased over time because of variability in female behaviour. Birds observed on days 4–46 did not have similar breeding cycles, and initiated breeding behaviour at different times. Therefore, data from new pairs taken more than 3 days after re-pairing are combined over longer time intervals and include multiple breeding behaviours. We observed each pair twice while incubating, rearing chicks, and caring for fledglings, and averaged data across breeding behaviours within the appropriate time windows. New pairs were observed for 11.3 ± 5.50 h following pairing.

Pair and individual rates of duetting and solo squeals were calculated as described above. Solo squeal rates of males and females were compared with a Wilcoxon rank sum test. Vocalization rate comparisons of the same pairs

in different time periods (i.e., 'experienced' or 'days 1–3 post re-pairing') were made using Wilcoxon signed rank tests, since sample sizes were small and data were not normally distributed. To maximize power, all statistical tests were performed on paired samples consisting of a female with her experienced mate versus a female with her new mate.

While conducting focal animal watches, and opportunistically at other times, researchers recorded vocalizations from focal pairs of California towhees both before and after re-pairing. All recordings were made with a Sennheiser long shotgun microphone and a Marantz PMD670 compact flash digital recorder. Digital recordings were made in mono at a sample frequency of 48 kHz and a bit rate of 768 kbps/ch, 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, Ithaca, NY, USA), and measurements of squeal properties were taken from Hanning type spectrograms with a grid size of 46.9 Hz and a DFT size of 1024 samples.

Measurements reported here are taken from 45 duets recorded from experienced pairs ($N = 4.5 \pm 2.2$ per pair), and 128 duets from new pairs ($N = 14.2 \pm 11.0$ per pair). All population averages for vocalization structure variables were calculated as the average of pair averages across indicated time periods. I compared experienced pair duet properties with new pair duet properties using Wilcoxon signed rank tests on the following 11 variables: number of each syllable type (squeaks, downsweeps and squeals), lag time until the second bird joins the duet, a syllable type coordination measure (calculated as the total squeak time, plus the total downsweep time, plus the total squeal time divided by the total duet time), duet lowest frequency (Hz), highest frequency (Hz), total time (s), total frequency range (Hz), frequency with maximum power (Hz) and time at which the maximum power occurred (s). Among new pairs, I assessed changes in duet structure over time using first and second order regression of the above 11 variables by day, post re-pairing. I used ANOVAs to test the fit of the regression lines. Regressions were based on an average of daily pair averages for each day post-pairing. Male and female California towhee duet contributions cannot be distinguished, so all measurements are based on complete duets rather than individual parts. All comparisons are paired such that the female did not change from the old to the new pair. Thus, changes to the duet vocalization post re-pairing would reflect a different male squeal contribution, and/or a change in female squeal properties.

Results

Population observations

Observations confirmed that duets were always performed by mated pairs, and that every duet was accompanied by an approach behaviour. Partners sometimes initiated duets when visually or spatially separated, but never ended duets until they were located within 1–2 m of each other.

Duets were frequently audible from neighbouring territories, making them potential extra-pair communication signals. Observers could hear duets from as many as three pairs (including the focal pair) simultaneously during a watch. Focal watches also confirmed that California towhees pair duets with aggressive or defensive behaviours. Territory holders involved in aggressive encounters were generally observed to duet after one or both of them had chased, fought with, or confronted a rival. Focal pairs were observed to duet when they encountered both lone male and lone female intruders. Territory-holders of both sexes chased and fought with intruders of both sexes, indicating a lack of sex-specific defensive behaviours. In total, California towhees were observed in 102 separate aggressive encounters. Of these aggressive encounters, 57 (55.9%) were accompanied by duets from either the winning or losing pair, and another 5 (4.9%) aggressive encounters were accompanied by solo squeal vocalizations. The co-occurrence of duets and aggressive behaviour is significantly higher than would be expected by chance ($\chi^2_2 = 49.1$, $p < 0.001$). In addition to chases, fights and displays, pairs of California towhees were observed 28 times to engage in bouts of counter-duetting, where two pairs would duet alternately, in response to each other, at territory boundaries. If these counter-duetting bouts are considered aggressive interactions, then California towhees produced squeal vocalizations in 69.2% of contest situations. Despite the frequent use of duets in contest situations, 93% of observed duets were not performed in the presence of extra-pair conspecifics, and appeared to be intra-pair communication signals.

Combined across all breeding periods, pairs produced an average of 2.9 ± 2.3 duets/h. California towhees duetted significantly more often during the incubation and chick rearing periods than they did prior to breeding or while building nests (pre-breeding vs. incubation: $\chi^2_1 = 9.33$, $p = 0.0022$, pre-breeding vs. chick rearing: $\chi^2_1 = 6.55$, $p = 0.011$, nest building vs. incubation: $\chi^2_1 = 5.49$, $p = 0.019$, nest-building vs. chick rearing:

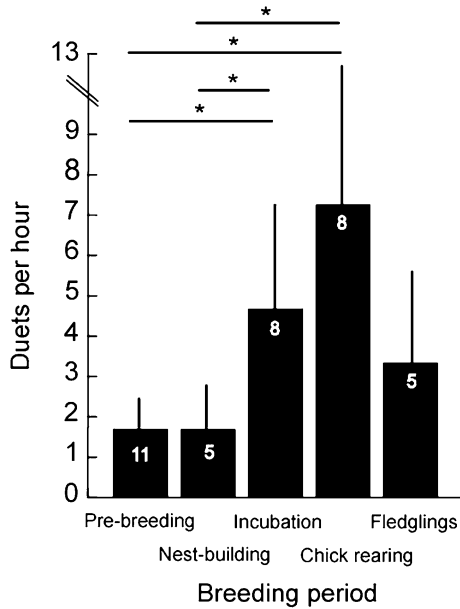


Figure 2. Observed rates of duetting by California towhees. Bars represent average pair rates of duetting \pm SD during pre-breeding, nest-building, incubation, chick-rearing, and raising fledglings. Asterisks indicate significant differences between groups (Wilcoxon rank sum tests, * $p < 0.05$). Numbers in bars indicate sample sizes.

$\chi^2_1 = 4.82$, $p = 0.028$) (Figure 2). Rates of duetting were statistically indistinguishable during all other period comparisons. All pairs observed in every breeding period showed substantial (167–1444%) increases in duet frequency from the nest-building to chick-rearing periods. Observations indicated that birds continue to duet year-round, but rates of duetting during the non-breeding season were not quantified. Rates of calling and singing did not differ statistically between the nest-building phase, when focal pairs vocalized during an average of 21% of observation periods, and the chick rearing phase, when focal pairs vocalized during an average of 29% of observation periods ($\chi^2_1 = 0.488$, $p = 0.51$).

Playback experiments

All three types of conspecific playback elicited approach responses at rates significantly higher than rates of approach during the pre-playback control period according to Cochran–Mantel–Haenszel tests (playback of male calls: $\chi^2_1 = 8.0$, $p < 0.005$; female calls: $\chi^2_1 = 6.0$, $p < 0.05$; duets:

$\chi_1^2 = 9.0$, $p < 0.005$; spotted towhee: $\chi_1^2 = 1.0$, $p = 0.32$). Pairs never duetted during the pre-playback control periods, but 9 of 16 pairs duetted in response to conspecific playback. Comparisons with heterospecific controls also validated the use of playback techniques. Territory holders approached playback speakers significantly more during conspecific than heterospecific playbacks ($\chi_1^2 = 12.9$, $p < 0.005$). Territory holders never duetted in response to spotted towhee song, but duetted in response to California towhee song during 27% of trials ($\chi_1^2 = 5.83$, $p < 0.05$). California towhees called at statistically indistinguishable rates in response to conspecific and heterospecific playback ($\chi_1^2 = 2.27$, $p = 0.13$), suggesting that calling was not a response to simulated intrusion by other conspecifics.

For each conspecific playback type there was no significant association between sex and tendency to approach (response to male calls: $p = 0.72$, $N = 32$, $1 - \beta_{(\text{small,medium,large})} = 0.76, 0.93, 0.99$. Response to female calls: $p = 1.0$, $N = 32$, $1 - \beta_{(\text{small,medium,large})} = 1.0, 1.0, 1.0$. Response to duets: $p = 0.29$, $N = 32$, $1 - \beta_{(\text{small,medium,large})} = 0.36, 0.74, 0.97$). Across all trials, males approached speakers broadcasting male calls, female calls and duets at statistically indistinguishable rates ($\chi_2^2 = 1.1$, $p = 0.58$, $1 - \beta_{(\text{small,medium,large})} = 0.62, 0.91, 0.99$), displayed minimum distances from the speaker that did not differ by playback type ($\chi_2^2 = 1.94$, $p = 0.38$), and spent indistinguishable amounts of time within 10m of the speaker across playback types ($\chi_2^2 = 1.27$, $p = 0.53$) (Figure 3). Females also approached speakers broadcasting male calls, female calls and duets at statistically indistinguishable rates ($\chi_2^2 = 0.05$, $p = 0.78$, $1 - \beta_{(\text{small,medium,large})} = 0.55, 0.88, 0.99$), displayed minimum distances from the speaker that did not differ by playback type ($\chi_2^2 = 1.40$, $p = 0.50$), and spent indistinguishable amounts of time within 10 m of the speaker across playback types ($\chi_2^2 = 1.60$, $p = 0.45$) (Figure 3).

When the sexes are combined, pairs showed stronger responses to duet playback than solo playback. Members of focal pairs spent 246.9 ± 85 s within 10 m of speakers playing duets and 153.4 ± 80.4 s within 10 m of speakers playing calls ($\chi_1^2 = 5.73$, $p = 0.017$).

Territory holders duetted in 71% of the 17 trials where duets were possible (because both members of the pair responded) and performed duets in response to all three types of conspecific playback. Pairs approaching the speaker duetted in response to 5 of 6 (83%) male call playbacks, 3 of 6 (50%) female call playbacks and 4 of 5 (80%) duet playbacks. These

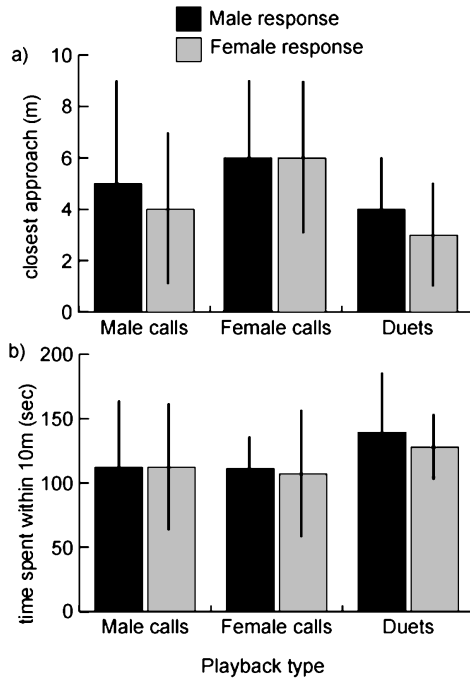


Figure 3. Two measures of sex-specific aggressive response to playback of three types of conspecific vocalizations by California towhees: (a) average distance \pm SD of closest approach to the playback speaker and (b) average amount of time \pm SD spent within 10 m of the speaker during 180 s of playback.

rates of response did not differ significantly (Fisher's exact test between response to female calls and response to male calls (most extreme difference): $p = 0.55$, $N = 10$, $1 - \beta_{(\text{small,medium,large})} = 0.55, 0.62, 0.73$).

Removal experiments

After male removals, resident females were not observed to produce squeals when occupying a territory alone. When a new potential mate arrived, females resumed squealing within a single day. Of the 10 females, 5 re-paired within a single day, 9 had new mates within one week, and one never re-paired.

On days 1–3 following re-pairing, new pairs produced an increasing number of duets and a very high number of solo squeals (Figure 4). New pair solo rates dropped after day 2 and then fluctuated, but remained higher than



Figure 4. Rates of duetting, solo squeal production and calling for 10 females and their mates prior to and following male removal experiments. Pre-removal values are from experienced pairs, and other values are from newly-formed pairs following the removal of experienced males. All vocalization rates are population averages of pair rates over the designated time periods. Data are from 172 h of observation of California towhees at the Hastings Natural History Reservation, Carmel Valley, CA, USA.

experienced pair rates for up to 46 days (Figure 4). After day 3, population duet rates decreased to levels very similar to pre-removal values (Figure 4). Rates of calling by new California towhee pairs were significantly higher than those observed among experienced pairs, peaking on day 1 and remaining elevated through the remainder of the breeding season (Figure 4). Members of experienced pairs called during $9.3 \pm 4.7\%$ of all observation intervals, and members of new pairs called during $24.8 \pm 11.7\%$ of all observation intervals.

Pre and post re-pairing comparisons of duet properties representing investment in duetting are detailed in Table 3. Prior to and following male removals, males and females produced solo squeals at statistically indistinguishable rates (experienced pairs: $\chi_1^2 = 1.42$, $p = 0.23$, new pairs: $\chi_1^2 = 0.34$, $p = 0.56$). Although solo squeal production did not differ by sex, it did differ among experienced and new pairs, indicating that new partners failed to respond to duet initiation phrases more often than experienced partners (Table 3). Duet frequency also increased following the formation of new pairs, and duets tended to be longer among new pairs (Table 3).

Table 3. Measures of investment (mean \pm SD) in duetting by experienced, pre-removal pairs and newly-formed post-removal pairs of California towhees during the three days following pair formation.

	Solos/h	Duets/h	Duet duration (s)
Experienced pairs	0.30 \pm 0.37	1.20 \pm 0.73	3.22 \pm 0.52
New pairs	1.71 \pm 1.17	2.14 \pm 0.78	3.57 \pm 0.73
<i>p</i> -value*	0.006	0.049	0.037

*1-tailed Wilcoxon signed-rank tests.

Table 4. Measures of duet coordination (mean \pm SD) by experienced, pre-removal pairs and newly-formed post-removal pairs of California towhees during the three days following pair formation.

	Syllable coordination	Time lag to second bird (s)	Frequency range (Hz)
Experienced pairs	1.10 \pm 0.086	0.66 \pm 0.48	6901.72 \pm 770.05
New pairs	1.20 \pm 0.14	0.66 \pm 0.30	6954.42 \pm 354.44
<i>p</i> -value*	0.082	0.213	0.5

*1-tailed Wilcoxon signed-rank tests.

Pre and post re-pairing comparisons of duet properties representing duet coordination are detailed in Table 4. Measures of temporal duet coordination — including the time lag between duet initiation and response by the duetting partner, and a measure of syllable coordination — did not differ between experienced pairs and pairs that had been together for less than 4 days (Table 4). Similarly, a measure of structural coordination, frequency range, was statistically indistinguishable between experienced and new pairs (Table 4). Comparisons of other measured duet structural characteristics indicated no significant differences between the duets of experienced and new pairs (2-tailed Wilcoxon signed rank tests on 6 structural variables: all $p > 0.359$).

Duet properties did not change over time among new pairs following pair formation. Linear regressions performed on 11 duet measurements indicated no significant relationships between duet properties and pair-bond duration (for all 11 regression ANOVAs: $F_{1,18} < 1.57$, $p > 0.23$). R^2 values indicated that pair-bond duration over the first two months of a partnership explained less than 9% of the variance in each duet characteristic. Second

order regressions using a quadratic fit also found no significant patterns (for all 11 regression ANOVAs: $F_{1,18} < 0.80$, $p > 0.47$).

Discussion

California towhees produce vocal duets with multiple potential functions that have signal content for extra-pair and within-pair receivers (Table 5). Extra-pair functionality is indicated by the finding that California towhee duets are significantly associated with aggressive encounters. This finding could suggest either a mate-guarding function or a joint resource defence function for duets, but additional results provided evidence against the hypothesis that California towhees use duets to guard mates (Table 5). Pairs duet relatively infrequently when the female is fertile. Furthermore, during both observations and playback experiments, California towhees did not display elevated levels of intrasexual aggression. Instead, during experimental manipulations, both sexes responded equally aggressively towards playback of male, female and duet vocalizations. Power values suggest that medium or large effects of playback type would be highly detectable, but tested birds displayed no response bias according to the sex of the simulated intruder. Mate-guarding and strong sex-biased aggression has been found in a number of duetting species, but is apparently not typical of California towhees (Levin, 1996b; Seddon et al., 2002; Seddon & Tobias, 2006; Rogers et al., 2007). The lack of sex-specific aggression and mate-guarding via duets is perhaps surprising, given that males regularly lose paternity to extra-pair individuals and that duets are accompanied by an approach behaviour which could assist with mate-guarding (Benedict, 2008b).

All tested predictions of the joint resource defence hypothesis were supported by this study (Table 5). In natural and experimental settings, pairs were observed to defend cooperatively against and duet in response to conspecific intruders. California towhees showed a tendency to approach speakers simulating intrusion by pairs more persistently than those simulating intrusion by lone birds, indicating that paired intruders were seen as a substantial threat. During playback experiments, pairs produced duets in the majority of agonistic situations during which both mates were present and duets were possible. Rates of calling did not change in response to playback. Duets were the only vocal signals that increased significantly in frequency

Table 5. Major results of this study with indications of how they provide support for (+) or evidence countering (–) six hypotheses for the function of vocal duets in California towhees.

Result	Duet signal recipient					
	Intruder		Mate			
	MG	RD	RS	MC	SI	LI
Duets sometimes occur with aggressive behaviours	+	+				
Males and females are equally aggressive to and duet towards all conspecific intruders	–	+				
Duetting frequency is low during the period of female fertility	–		–			
Duetting frequency is high during the period of chick rearing		+			+	
Duets may begin while partners are visually separated and are always accompanied by an approach behaviour	+			+	+	+
Duet vocalizations show consistent individual variation				+	+	+
Duet coordination does not improve with pair-bond duration						–
Duets of high quality pairs are not better coordinated than duets of low quality pairs					–	–
Newly formed pairs invest more time in duetting than experienced pairs					+	+

For abbreviations of hypothesis, see Table 1.

during simulated conspecific intrusion, indicating an important functional role for duets during such encounters.

A high rate of duetting while raising chicks is also consistent with the hypothesis that duets facilitate resource defence. Raising offspring is a demanding task that requires energy derived from resources including food, water, and cover (Williams, 1966; Kunzmann et al., 2002). Duets given during this period may serve to defend these valuable resources. They may also help parents to signal investment in the partnership and coordinate parental care duties during this critical time. Several avian species use duets to defend local resources, but even within the generally cooperative context of joint resource defence, there exist variations in duet behaviour and potential signal content. In particular, many duetting species show increased levels of intra-sexual aggression while jointly defending resources (Grafe & Bitz, 2004; Marshall-Ball et al., 2006). In some species the sexes differ in their levels of aggression and vocal behaviour when defending resources (Logue

& Gammon, 2004; Rogers et al., 2006). Among California towhees, males and females show apparently identical behaviour when duetting and respond equally to intruders of both sexes, suggesting little conflict between mates when duetting during extra-pair communication contexts.

The majority of California towhee duets were given when the duetting partners were the only obvious signal recipients. This and the fact that all duets were accompanied by an approach behaviour strongly suggest that the vocalization sometimes functions as an intra-pair communication signal. My experiments found no support for the hypothesis that California towhees use duets to synchronize reproductive behaviour, since the rate of duetting is low prior to egg-laying and increases following that time (Table 5). I did, however find support for other intra-pair communication hypotheses.

Maintaining contact seems to be an important duet function in this species (Table 5). In order to help pairs maintain contact, squeal vocalizations used in duets must carry information about identity. A previous study showed that squeal vocalizations do carry enough information to indicate identity (Benedict & McEntee, 2009). Observations reported here confirmed that birds only duetted with their mates, even when duets were initiated while the pair was visually separated. Thus, California towhees must be able to recognize the introductory notes of their partners' squeals quickly so that they can respond appropriately. The hypothesis that mates use duets to maintain contact also predicts that duets should occur more often when mates are visually and/or spatially separated. California towhees in this study initiated duets when mates were separated or close together and always ended duets side by side. Duets certainly facilitate contact between mates, but they do not function, as envisioned and observed for other species, strictly as an alternative to visual contact or physical proximity (Thorpe, 1972; Mays et al., 2006). Other simple vocalizations, including calls would be sufficient to indicate partner locations (Benedict, 2007). Duets convey more information than just location, they also are used to coordinate partner approach. Duets in California Towhees and other species are signals that help partners to organize their spatial locations in advantageous ways (Logue, 2007; Mennill & Vehrencamp, 2008).

In a critical test of the learning investment hypothesis, I found that California towhee pair duet properties do not change over time (Table 5) (Wickler, 1980). Although other predictions of this hypothesis were supported, the lack of learning provides a strong reason to reject the applicability of this

hypothesis to this species (Table 5). In one avian species, duet coordination does relate to pair-bond duration, with longer partnerships producing more threatening duets, but this pattern may or may not be due to learning (Hall & Magrath, 2007). In general, studies have failed to find evidence that vocal duets require learning in birds, but studies of primates have supported the hypothesis that duet learning ensures commitment (Arrowood, 1988; Levin, 1996a; Geissmann, 1999).

I found no evidence that experienced pairs produced better coordinated duets than new pairs. Long-established pairs with breeding experience were expected to be of higher quality than newly formed pairs, many of which included males that had previously been unable to attract a mate. The result that experienced and new pairs produced duets with indistinguishable temporal properties counters the hypothesis that California towhees use duet timing to signal quality via attentiveness (Smith, 1994). This result provides evidence against the signalling investment hypothesis as originally envisioned (Table 5). It is likely, however, that because duets are given when partners are variable distances apart, timing may be more affected by partner location than it is by partner quality. If so, then lack of support for this prediction does not rule out the idea that duets may be used by California towhees to signal investment in a partnership.

Regardless of temporal coordination, just the presence of a duet response may be a strong signal of attentiveness and investment. California towhees combined solo squeals to form duets more reliably as they established pair-bonds. The rate of solo squeals increased immediately after pairing while duet rates increased more slowly, indicating that after day two individuals were responding more often to their partners' squeal vocalizations to create duets. Newly formed pairs of California towhees also invested more time in individual duets, producing slightly longer vocalizations. The high rate of squeal production just after pairing indicates a potentially important role for duets in the pair-formation process, a result that has mixed support from other species (Arrowood, 1988; Whittingham et al., 1997). Such a pattern of improvement in duet coordination over time likely reflects individual motivation, rather than ability. California towhees may increase duet rates after re-pairing as a signal of investment, a duet function that is also supported by other lines of evidence in this study (Table 5) (Smith, 1994). The gradual increase in response to solo duet-initiation phrases during the first few days post-pairing is predicted by models in which cooperation develops as mates

incrementally increase investment in a partnership (Hall, 2004; Roberts & Sherratt, 1998).

In sum, California towhees pair vocal duets with a mutual approach response, duet during aggressive encounters, increase rates of duetting when raising offspring, and increase investment in duetting following pair formation. Results suggest that no one existing hypothesis provides a complete or satisfactory explanation regarding the benefits of duetting in this species (Table 5). Instead, duetting occurs in multiple contexts and may provide partners with different benefits at different times (Table 5). Duets may also provide multiple benefits simultaneously, all of which are associated with pair-based activities. Duetting species, both avian and mammalian, are more likely than other species to exhibit long-term pair-bonds, providing a real reason to look for potential connections between this vocal behaviour and the mating system (Farabaugh, 1982; Haimoff, 1986; Malacarne et al., 1991; Benedict, 2008a). Mates should improve their ability to perform critical pair-based behaviours, such as resource defense and offspring production if they can coordinate individual activities. Among monogamous species, behavioural coordination between mated pairs is known to correlate with duetting (Geissmann & Orgeldinger, 2000). Improved behavioural coordination is also known to increase fitness (Spoon et al., 2006; van De Pol, 2006). This evidence suggests that duets which function to improve pair coordination may have the effect of increasing reproductive success, making them an important target for the action of natural selection.

California towhee duets are used in a variety of contexts and may serve multiple functions by communicating information to a variety of receivers. All of these functions, however, result from the fact that when individuals respond to their partners' squeals they indicate the existence of coordinated action between the two mates. California towhee duets are used to assist with joint resource defence, mate localization and coordination of investment by paired birds. Observations of other species indicate that duets are often found in conjunction with a physical approach response, so the hypothesis that animals use duets to coordinate pair activities may have broad applicability (Wolf, 1977; Baptista, 1978). In all species, partners that increase reproductive success by effectively coordinating their behaviours may be said to have a strong pair-bond, so many of the discrete hypotheses tested here could be considered aspects of pair-bonding. In fact, classic explanations claiming that duets function to strengthen the pair-bond may have been on the right

track by not narrowing their focus to assume that duets provide a single benefit in a single context (Quaintance, 1941; Marshall, 1964; Thorpe, 1972). Like many communication signals, avian vocal duets are context-dependent, multi-functional, and best understood by taking a comprehensive view of species-specific social behaviour.

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