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A review of acoustic playback techniques for studying avian vocal duets

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ABSTRACT. Playback experiments involve the broadcast of natural or synthetic sound stimuli and provide a powerful tool for studying acoustic communication in birds. Playback is a valuable technique for exploring vocal duetting behavior because it allows investigators to test predictions of the various hypotheses for duet function. Here, we adopt a methodological perspective by considering various challenges specific to studying duetting behavior, and highlighting the utility of different playback designs for testing duet function. Single-speaker playback experiments allow investigators to determine how duetting birds react to different stimuli, but do not simulate duets in a spatially realistic manner. Multi-speaker playback experiments are superior to single-speaker designs because duet stimuli are broadcast with spatial realism and unique and additional predictions can be generated for testing duet function. In particular, multi-speaker playback allows investigators to evaluate how birds respond to male versus female duet contributions separately, based on reactions to the different loudspeakers. Interactive playback allows investigators to ask questions about the time- and pattern-specific singing behavior of birds, and to understand how singing strategies correspond to physical behavior during vocal interactions. Although logistically challenging, interactive playback provides a powerful tool for examining specific elements of duets (such as the degree of coordination) and may permit greater insight into their functions from an operational perspective. Interactive playback designs where the investigator simulates half of a duet may be used to describe and investigate the function of pair-specific and population-wide duet codes. Regardless of experimental design, all playback experiments should be based on a sound understanding of the natural duetting behavior of the species of interest, and should aim to produce realistic and carefully controlled duet simulations. Future studies that couple playback techniques with other experimental procedures, such as Acoustic Location System recordings for monitoring the position of birds in dense vegetation or multimodal techniques that combine acoustic with visual stimuli, are expected to provide an even better understanding of these highly complex vocal displays.

RESUMEN. **Una revisión de las técnicas de la reproducción de sonidos grabados para el estudio de las duetas vocales de las aves**

Los experimentos de reproducción de sonidos grabados involucran el uso de sonido natural o sintético y proveen una herramienta poderosa para el estudio de la comunicación acústica de las aves. La reproducción de sonidos grabados es una técnica valiosa para explorar las duetas vocales porque permite probar las predicciones de varios hipótesis sobre la función de duetas. Aquí, adoptamos una perspectiva metodológica, considerando los varios retos específicos al estudio del comportamiento de duetas y resaltando la utilidad de diferentes diseños de reproducción de sonidos grabados para probar la función de las duetas. Experimentos de reproducción de sonidos grabados hechas con un parlante permiten una determinación de como las aves que realizan duetas reaccionan a diferentes estímulos, pero no simulan las duetas de una manera espacialmente realística. Experimentos de reproducción de sonidos grabados hechas con múltiples parlantes son superiores a diseños con un solo parlante porque transmiten el sonido de una manera espacialmente realística y generan predicciones únicas y adicionales para probar la función de la dueta. En particular, la reproducción de sonidos grabados con múltiples parlantes permite una evaluación de cómo las aves responden a las contribuciones del macho y de la hembra separadamente, basado en sus reacciones a los diferentes parlantes. La reproducción de sonidos grabados interactiva permite hacer preguntas temporalmente especificas y en relación a patrones especificas sobre el comportamiento de canto. También permite entender como las estrategias de canto corresponden al comportamiento físico durante las interacciones vocales. Aunque es un reto logístico, la reproducción de sonidos grabados interactiva provee una herramienta poderosa para examinar elementos específicos de las duetas (como el grado de coordinación) y podría permitir un mayor conocimiento sobre sus funciones de una perspectiva operacional. Los diseños de la reproducción de sonidos grabados interactivas, en la cual el investigador simula la mitad de una dueta, podrían ser usadas para describir e investigar la función de los códigos de dueta específicos a una pareja y a una población. Sin importar el tipo de diseño experimental, todos los experimentos de reproducción de sonidos grabados deberían ser basadas en una buena comprensión del

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comportamiento natural de las duetas en la especie de interés, y deberían tener la meta de producir simulaciones de duetas realísticas y cuidadosamente controladas. Se espera que los estudios futuros cuales combinan técnicas de la reproducción de sonidos grabados con otros procedimientos experimentales, como grabaciones del Sistema de Ubicación Acústica para monitorear la posición de aves en vegetación densa, o técnicas multimodales que combinan estímulos acústicos con estímulos visuales, provean un mejor entendimiento de estos despliegues vocales altamente complejos.

Key words: behavior, bird song, communication, duets, interactive playback, multi-speaker playback

Playback experiments provide ornithologists and behavioral ecologists with a useful tool for exploring the ecology and evolution of acoustic communication in birds (McGregor 2000). Over the past 50 years, the number of studies involving playback experiments has increased dramatically with the development of portable recorders that allow investigators to record birds in the field (Falls 1992, Eekhout et al. 2006), and sophisticated software programs that facilitate editing and manipulating digitized sounds for broadcast. Additionally, inexpensive playback devices and portable loudspeakers have become more accessible, providing researchers with the equipment needed to design and conduct playback studies.

A recent resurgence of interest in the ecology and function of vocal duets, combined with increasingly sophisticated playback techniques, provides opportunities for studying avian duetting behavior. Duets occur when two individuals—usually the male and female of a mated pair—vocalize together in a highly coordinated fashion (Farabaugh 1982, Hall 2004, 2009). These acoustic displays are among the most complex coordinated signals in the animal kingdom (Mann et al. 2003, 2006). For several reasons, we still have only a basic understanding of duetting behavior despite several decades of research. Most duetting birds are found in tropical and south-temperate ecosystems, whereas most scientists studying bird song are associated with research institutions in north-temperate areas (Stutchbury and Morton 2001). In addition, most duetting species are found in densely vegetated habitats where they are difficult to observe (Mennill and Vehrencamp 2008). Furthermore, duets consist of the vocalizations of more than one bird and, therefore, are inherently challenging to study; the behavior of two individuals must be monitored simultaneously, and individuals may interact with their duet partner at the same time they are interacting with other conspecifics. Compared to male solo song, few investigators have studied duetting behavior using playback experiments. However, recent studies have revealed that such experiments can provide important insight into the proximate and ultimate bases of duetting behavior.

A number of hypotheses have been proposed concerning the possible functions of avian duets (Farabaugh 1982, Hall 2004, 2009). Playback is a valuable technique for exploring vocal duetting behavior because it allows investigators to test predictions of the various hypotheses for duet function (Table 1). Specifically, playback experiments can be used to examine the joint resource-defense hypothesis (Seibt and Wickler 1977), the mate-guarding hypothesis (Stokes and Williams 1968), the paternity-guarding hypothesis (Sonnenschein and Reyer 1983), the signaling-quality hypothesis (Smith 1994), the identity hypothesis (Farabaugh 1982, Logue and Gammon 2004), and the pair-bond maintenance hypothesis (Armstrong 1963, Hall 2004, 2009). Other important hypotheses concerning the function of duets cannot be readily tested using playback experiments, including the contact-maintenance hypothesis, the reproductive-synchrony hypothesis, and the signaling-commitment hypothesis (Hall 2004).

In this paper, we adopt a methodological perspective and discuss playback as an experimental tool for studying the form and function of avian duets. Although we focus on duets where the participants are the male and female of a mated pair, playback can also be used to explore other types of duets, such as the male–male duets of *Chiroxiphia* manakins (Trainer and McDonald 1995). We discuss different playback techniques and highlight the utility of each technique for exploring duet function. Additionally, we consider various design features and challenges that are specific to studying duetting behavior, and emphasize opportunities for future studies. We hope to stimulate further research and provide a resource for investigators

Table 1. Predictions for behavioral responses of duetting species to single-speaker and multi-speaker playback.

Hypothesis for duet function	Predictions for responses to single-speaker playback	Additional predictions for responses to multi-speaker playback[a]
Joint resource defense	• Simulated territorial intrusion should elicit duets from subjects. • Playback of duets should elicit a stronger territorial response than playback of solos. • The focal male and female should be equally likely to answer their partners' songs in response to playback of solo songs of male and female strangers.	• Equivalent responses to both male and female speaker for both the focal male and female.
Mate guarding	• Resident birds should be more responsive to same-sex playback stimuli than duet playback stimuli.	• Strong response to same-sex speaker for both male and female subjects.
Paternity guarding	• When playback simulates a male intruder, the resident male should be more responsive to his partner if she is fertile.	• Strong response to male speaker for male subject, particularly during reproductive season.
Signaling quality	• Highly coordinated duets should elicit stronger responses from subjects than weakly coordinated duets.	• No reason to expect different responses to male versus female speaker.
Identity	• Simulated territorial intrusion should increase duet responsiveness in both sexes. • During solo playback, initiation rates should be high during opposite-sex playback so mates can locate each other. • Responsiveness should be high during same-sex playback.	• Duet initiation rates should be highest when a subject is near the opposite-sex speaker. • Duet responsiveness should be highest when a subject is near the same-sex speaker.
Pair-bond maintenance	• Playback of solos should increase duetting rates from opposite-sex subject.	• No reason to expect different responses to male versus female speaker.

[a]For multi-speaker playback, the predictions of single-speaker playback also apply.

designing playback experiments to study duetting behavior.

PLAYBACK METHODS: NON-INTERACTIVE DESIGN

Playback techniques can be categorized as non-interactive or interactive depending on the way that stimuli are presented (Smith 1996). Non-interactive playback involves broadcasting stimuli that do not vary with respect to the timing or patterning of the behavior of focal animals. Prior to the advent of digital sound storage, non-interactive playback was the standard design because analog playback equipment did not facilitate rapid choice of multiple stimuli or fine control over the timing of sound playback (Dabelsteen 1992). Thus, most published single-speaker and multi-speaker playback studies fall under this category of experimental design. Today, digital sound storage and innovative software tools facilitate interactive playback whereby an investigator manipulates the timing or type of stimulus, based on the behavior of the focal bird(s) (reviewed by Dabelsteen and McGregor 1996, Smith 1996).

Non-interactive playback—sometimes referred to as fixed-stimulus, loop playback, or tape-loop playback—is a powerful tool for understanding animal communication. This technique has been instrumental in improving our understanding of the role of song in territory defense and mate attraction in temperate songbirds (Catchpole and Slater 2008). In a non-interactive design, the investigator does not alter the pattern or timing of the stimulus based on the focal animal's behavioral response.

Non-interactive playback experiments allow investigators to determine how birds react to different types of stimuli, and can also provide information about the identity and location of responding individuals. A non-interactive design offers many advantages. First, it is the easiest type of playback to perform with respect to both stimulus preparation and trial execution. Non-interactive stimuli are prepared in advance and the investigator does not need to alter the stimulus in the field, freeing the investigator to make detailed behavioral observations during the playback trials. Second, because all test subjects receive the same stimulus type and pattern, non-interactive experiments lend themselves to easy replication, with the experimenter having tight control over stimulus type and levels of output.

Playback experiments using non-interactive-stimuli may broadcast sounds to focal birds through a single speaker or multiple speakers. Below, we distinguish between these two designs and discuss their utility in investigating avian duets. For both single-speaker and multi-speaker designs, we review studies that have examined different hypotheses for duet function and summarize these results in Table 2.

Non-interactive playback using a single speaker. Much of what is known about the functions of avian duets stems from non-interactive playback experiments where the duet stimulus representing the voices of two individuals is simulated using a single speaker. Until recently, this design was the sole type used to study duets, and the primary design for most playback studies. Thus, much of our understanding of the functions of these complex displays stems from the findings of these experiments.

Non-interactive, single-channel stimuli are relatively easy to prepare. Single-channel recordings are obtained from focal birds in the field or from sound libraries, targeting recordings with a high signal-to-noise ratio and little interference from other sounds. Recordings can be digitally manipulated to ensure that the stimuli are prepared at an appropriate amplitude (using the amplification function of the software) and an appropriate duration (possibly by repeating sections of the original recording or truncating the recording, always with the goal of creating realistic stimuli). As with multi-speaker and interactive designs, manipulations of time, frequency, and amplitude characteristics can provide innovative tests of duet function. Regardless of the nature of the stimulus presented, investigators need to avoid pseudoreplication (McGregor et al. 1992, McGregor 2000, Kroodsma et al. 2001).

Hypothesis testing with non-interactive, single-speaker playback. Single-speaker playback experiments facilitate testing of some hypotheses for duet function. First and foremost, such experiments have provided compelling support for the joint resource-defense hypothesis. Single-speaker playback experiments have demonstrated that duets function in territory defense in Barbary Shrikes (*Laniarius barbarous*, Payne 1970), Stripe-backed Wrens (*Campylorhynchus nuchalis*, Wiley and Wiley 1977), Bay Wrens (*Thryothorus nigricapillus*, Levin 1996a), Magpie-larks (*Grallina cyanoleuca*, Hall 2000, Mulder et al. 2003), Warbling Antbirds (*Hypocnemis cantator*, Seddon and Tobias 2006), Purple-crowned Fairy-wrens (*Malurus coronatus*, Hall and Peters 2008), Stripe-headed Sparrows (*Aimophila ruficauda*, Illes and Yunes-Jimenez 2009), and Barred Owls (*Strix varia*, Odom and Mennill 2010). In each of these studies, resident pairs responded to playback of duets with increased vocal output (see Table 1 for predictions for each hypothesis). Plain Wrens (*Thryothorus modestus*, Marshall-Ball and Slater 2004, Marshall-Ball et al. 2006) also use duets in territory defense, although the level of threat perceived differs significantly with mated status; unpaired Plain Wrens were more threatened by playback of duets than solos.

Single-speaker playback experiments of three duetting species have generated different results, suggesting that joint resource defense is not a universal function of vocal duets. In Tawny Owls (*Strix aluco*, Appleby et al. 1999), White-bellied Antbirds (*Myrmeciza longipes*, Fedy and Stutchbury 2005), and Rufous-naped Wrens (*Campylorhynchus rufinucha*, Bradley and Mennill 2009a), territorial pairs responded with equal levels of aggression regardless of whether solo or duet stimuli were presented. Warbling Antbirds (Seddon and Tobias 2006) responded more strongly to same-sex solo stimuli than to duet stimuli, suggesting that solo songs are more

Table 2. Playback studies that support or refute hypotheses for duet function, categorized by experimental design.

Experimental design	Hypothesis for duet function	Species
Non-interactive:		
Single-speaker playback	Joint resource defense	Support:
		Barbary Shrikes (Payne 1970), Stripe-backed Wrens (Wiley and Wiley 1977), Bay Wrens (Levin 1996a), Magpie-larks (Hall 2000, Mulder et al. 2003), Plain Wrens (Marshall-Ball and Slater 2004, Marshall-Ball et al. 2006), Warbling Antbirds (Seddon and Tobias 2006), Purple-crowned Fairy-wrens (Hall and Peters 2008), Stripe-headed Sparrows (Illes and Yunes-Jimenez 2009), Barred Owls (Odom and Mennill 2010)
		Refute:
		Tawny Owls (Appleby et al. 1999), White-bellied Antbirds (Fedy and Stutchbury 2005), Warbling Antbirds (Seddon and Tobias 2006), Rufous-naped Wrens (Bradley and Mennill 2009a)
	Mate guarding	Support:
		Bay Wrens (Levin 1996a), Subdesert Mesites (Seddon et al. 2002), Magpie-larks (Mulder et al. 2003), Plain Wrens (Marshall-Ball et al. 2006), Warbling Antbirds (Seddon and Tobias 2006, Tobias and Seddon 2009), Stripe-breasted Sparrows (Illes and Yunes-Jimenez 2009)
		Refute:
		White-bellied Antbirds (Fedy and Stutchbury 2005)
	Paternity guarding	Refute:
		Plain Wrens (Marshall-Ball et al. 2006)
	Pair-bond maintenance	Support:
		Purple-crowned Fairy-wrens (Hall and Peters 2008)
Multi-speaker playback	Joint resource defense	Support:
		Magpie-larks (Rogers et al. 2004, Hall and Magrath 2007), Black-bellied Wrens (Logue and Gammon 2004), Rufous-and-white Wrens (Mennill 2006, Mennill and Vehrencamp 2008), North Island Kokakos (Molles and Waas 2006)
		Refute:
		Eastern Whipbirds (Rogers et al. 2006)
	Mate guarding	Support:
		Rufous-and-white Wrens (Mennill 2006, Mennill and Vehrencamp 2008), Eastern Whipbirds (Rogers et al. 2006, Rogers et al. 2007)
	Identity	Support:
		Black-bellied Wrens (Logue and Gammon 2004)
		Refute:
		Eastern Whipbirds (Rogers et al. 2007)
	Signaling quality	Support:
		Black-bellied Wrens (Logue et al. 2008), Magpie Larks (Hall and Magrath 2007)
Interactive:		
Single-speaker playback	Joint resource defense	Support:
		Tropical Boubous (Grafe and Bitz 2004b)
	Mate guarding	Support:
		Tropical Boubous (Grafe and Bitz 2004b)

important than duets for territory defense in this species. However, in both species of antbirds, duetting behavior is driven solely by females responding to the songs of their mate. Because duetting is female-driven in these species, it may not be as likely to function in cooperative resource defense as in species where both sexes contribute to duet production. Additionally, because many birds in the family *Thamnophilidae* (the typical Antbirds) forage opportunistically near ephemeral ant swarms, territory defense may not be as critical as for birds that defend stable territories or resources.

The results of studies using single-speaker playback experiments suggest that duets may also serve a mate-guarding function, although empirical support has not been unanimous. In Subdesert Mesites (*Monias benschi*) and Plain Wrens, pairs use duets to mutually guard their mate, responding to playback of same-sex solo songs with greater intensity than playback of duets (Seddon et al. 2002, Marshall-Ball et al. 2006). In Bay Wrens, only males perform duets in a mate-guarding context (possibly indicating paternity guarding; Levin 1996a), whereas only female Warbling Antbirds and Stripe-breasted Sparrows perform duets in a mate-guarding context (Seddon and Tobias 2006, Illes and Yunes-Jimenez 2009, Tobias and Seddon 2009). In response to playback, in each of these three species, the individual apparently guarding their mate responded with greater song output to same-sex stimuli than duet stimuli (Table 1). The use of duets in mate guarding likely varies across species, possibly with variation in the probability of divorce or extra-pair mating. More detailed studies of divorce and extra-pair mating in tropical birds are needed (Macedo et al. 2008) and will provide context for interpreting playback results.

Few investigators have used single-speaker playback experiments to examine the paternity-guarding and pair-bond maintenance hypotheses. A key prediction of the paternity-guarding hypothesis for duet function (Sonnenschein and Reyer 1983) is that males should be the most responsive to their partner's songs during her fertile period (Hall 2004). Several investigators have used non-playback, longitudinal studies of duetting behavior to test this hypothesis (e.g., Gill et al. 2005, Hall 2006, Topp and Mennill 2008), but only one study has involved the use of playback experiments. A study of Plain Wrens (Marshall-Ball et al. 2006) revealed that males were no more likely to answer their partner's songs in response to a simulated intrusion during their mate's fertile period than when she was not fertile, suggesting that duets do not function as a paternity guard in this species.

The pair-bond maintenance hypothesis (Armstrong 1963) has been examined using playback experiments in a single duetting species. Hall and Peters (2008) used the amount of time pairs of Purple-crowned Fairy Wrens spent close together as a proxy for "pair-bond strength." Pairs that spent more time together (within 2 m) during simulated territorial intrusions also duetted more (Hall and Peters 2008), suggesting that pairs used duets to maintain the pair-bond.

Most playback experiments investigating duet function were conducted during the focal birds' breeding season, a time when territorial and mate-guarding behaviors are heightened, and simulated territorial intrusions may be most likely to elicit both (Hall 2004). Given the difficulty of distinguishing between predictions of the multiple hypotheses for duetting, the timing of playback with respect to breeding is an important factor to consider when designing experiments. Some functions of duets are expected to be important year-round (e.g., resource defense and pair-bond maintenance), whereas others may be important during some breeding stages, but not others (e.g., paternity guarding).

In summary, many single-speaker playback studies provide support for the cooperative territory-defense hypothesis for the function of duets, and mixed support for the mate-guarding, paternity-guarding, and pair-bond maintenance hypotheses. However, without careful attention to the behavior of both members of a focal pair, and determining whether they respond differently to male and female playback stimuli, the possibility that pair members have independent or conflicting strategies for responding to duet playback cannot be ruled out. To better examine and understand the respective responses of both members of focal pairs and to improve our understanding of the functions of avian duets, multi-speaker playback experiments may be needed.

Non-interactive playback using multiple speakers. Using multiple speakers during playback experiments—also referred to as

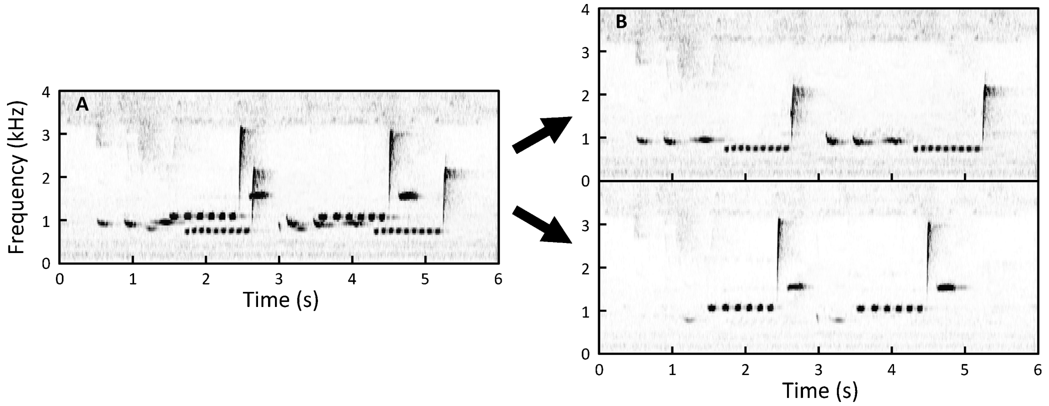

Fig. 1. Creation of a two-channel duet stimulus from a single-channel recording for use in multi-speaker playback. A good-quality stimulus sound is chosen from a field recording (A). The female components are filtered from one version of the sound file to leave only the male contribution, which is copied into one channel of a stereo sound file (B, top); the male components are filtered from another version to leave only the female contribution, which is copied into the other channel of a stereo sound file (B, bottom). Each sex's contribution can be normalized in amplitude, to remove differences in broadcast volume. When broadcast through a stereo playback apparatus, the male and female contributions will be presented through the separate speakers.

dual-speaker playback, stereo duet playback, or multi-speaker duet playback—can provide a much more realistic experimental approach for simulating acoustic signals originating from two point sources (Langmore 2002, Logue and Gammon 2004, Mennill and Ratcliffe 2004a, Rogers et al. 2004). In contrast to single-speaker playback, a two-speaker design allows for male and female duet components to be separated and presented as a two-channel signal with male and female contributions broadcast through separate speakers (Fig. 1). This simple difference in design is important for two reasons. First, birds appear to be highly adept at locating the source of acoustic stimuli (Stutchbury and Morton 2001; see Naguib 1996 for a review of song ranging and playback design) and, as a result, multi-speaker playback may be critical for simulating duets that, by definition, originate from two point sources. Second, duetting has been traditionally viewed as a cooperative display between pair members to maintain territory tenure and pair-bonds. However, this view is now being re-evaluated in light of evidence that males and females may have different agendas when performing duets (Farabaugh 1982, Levin 1996a, Hall 2004). Multi-speaker playback allows an investigator to test the intrasexual communication functions of duetting by comparing the responses of focal pairs to the male and female duet components (e.g., physical approach to the two speakers), a comparison not possible with single-speaker playback.

Evidence from single-speaker and multi-speaker playback experiments reveal that duetting birds can readily distinguish between these two designs and, in some cases, exhibit different responses to stimuli presented through a single speaker versus multiple speakers. For example, a two-speaker playback study of Magpie-larks revealed that duets presented in stereo elicited significantly more flights toward the speakers by focal birds (Rogers et al. 2004). Similarly, Kokakos (*Callaeas cinerea*) responded to stereo duet stimuli by approaching speakers more quickly than they did to duets broadcast from a single speaker (Molles and Waas 2006). These results demonstrate, for the first time in the duetting literature, that spatially realistic stimuli influence the intensity of response of the playback subjects (measured in flights towards speakers). Investigators should recognize that multiple speakers provide a larger "target" for playback subjects to approach than would a single speaker, and this difference should be considered when comparing the responses of birds to single versus multi-speaker stimuli.

Two characteristics of duetting species and their duets should be considered when designing multi-speaker experiments. First, careful attention should be given to whether one individual is capable of producing both parts of a duet and, second, the proximity of pair members during naturally occurring duets should be known in advance of designing the playback to inform decisions about placement of speakers. For species where pair members routinely perform duets at some distance from each other, such as Black-headed Gonoleks (*Laniarius erythrogaster*, Thorpe 1963) and Rufous-and-white Wrens (*Thryothorus rufalbus*, Mennill and Vehrencamp 2008), a dual-speaker design is likely essential for the playback simulation to be realistic. This design may be less important when studying species where pair members routinely perform duets in close proximity, such as Tropical Boubous (*Laniarius aethiopicus*, Grafe and Bitz 2004a), Magpie Larks (Tingay 1974), and Rufous-naped Wrens (Bradley and Mennill 2009a). In species where individuals can perform both parts of a duet, dual-speaker design may be critical; duet stimuli broadcast through a single speaker may simulate one individual producing both parts of a duet, whereas the same stimulus broadcast through separate channels of a multi-speaker apparatus necessarily simulates two individuals (Rogers et al. 2004). For example, male Eastern Whipbirds (*Psophodes olivaceus*; Watson 1969, Rogers 2005) and Kokakos (Molles et al. 2006) can produce both the male and female duet components. Thus, duets of these species broadcast through a single speaker probably simulate the song of a single individual, whereas the same sound broadcast as a stereo stimulus would simulate a pair performing a duet. This ambiguity leads to difficulty in interpreting the results of single-speaker playback experiments.

Sound manipulation software, such as Audition (Adobe, San Jose, CA), facilitates easy preparation of stereo stimuli for multi-speaker playback by allowing investigators to copy sounds separately into the left or right channel. Preparing stereo stimuli comes with some unique challenges. Recordings must be available where male and female duet components do not overlap in both time and frequency characteristics so they can be separated into different channels (e.g., Fig. 1). If such a recording is unavailable, recordings of male and female solo songs could be combined to create a two-channel duet stimulus, although this should only be done when careful analysis reveals that males and females contribute the same types of vocalizations to solos and duets. The amplitude of the two channels must also be considered. In several studies (Logue and Gammon 2004, Rogers et al. 2004, Mennill 2006), the male and female duet components were normalized to the same amplitude so that responses to the two loudspeakers would not be influenced by differences in amplitude. This works well for duetting species where males and females produce songs at similar amplitudes. For species where the duet contributions of males and females consistently differ in amplitude, normalizing the two channels may create an unnatural stimulus.

Hypothesis testing with non-interactive, multi-speaker playback. To date, multi-speaker playback experiments have been used to study the function of duets in five species of birds. As with studies using single-speaker playback, the results of multi-speaker studies tend to support the resource-defense and mate-guarding hypotheses. Multi-speaker playback experiments have revealed that duets function in cooperative territory defense in Rufous-and-white Wrens (Mennill 2006, Mennill and Vehrencamp 2008), Magpie-larks (Rogers et al. 2004, Hall and Magrath 2007), Black-bellied Wrens (*Thryothorus fasciatoventris*, Logue and Gammon 2004), and North Island Kokakos (*C. cinereus wilsoni*, Molles and Waas 2006). In each of these studies, pairs engaged in more duets during multi-speaker playback of duets than they did prior to playback. Rogers et al. (2006) found that duet rates of Eastern Whipbirds increased during playback of duets, but that patterns of song type use by males and females differed. Male whipbirds matched the song types of conspecific males during playback, whereas females preferentially matched the songs of their mate rather than matching the female component of the duet stimulus (Rogers et al. 2006). This difference in behavior suggests that male and female whipbirds have different and possibly conflicting strategies for mate and territory defense, possibly resulting from the female-biased population sex ratio (Rogers et al. 2006, 2007).

The results of studies of female Eastern Whipbirds (Rogers et al. 2006, 2007) and Rufous-and-white Wrens (males only: Mennill 2006; both sexes: Mennill and Vehrencamp 2008) provide support for the mate-guarding hypothesis, with multi-speaker playback experiments indicating that birds use duets to advertise the mated status of their partner. In each of these studies, birds exhibited greater responses to speakers broadcasting same-sex stimuli.

Few investigators have examined the remaining hypotheses using multi-speaker playback experiments. Studies testing the identity hypothesis have provided conflicting results. Male Black-bellied Wrens were more likely to initiate duets during opposite-sex playback, whereas both males and females responded to their partner's songs more often when in close proximity to each other, possibly to provide information about location and individual identity (Logue and Gammon 2004). In contrast, female Eastern Whipbirds did not initiate duets more often during opposite-sex playback, suggesting that female whipbirds do not duet with their partner to provide information about their identity (Rogers et al. 2007).

Several studies have provided support for the signaling-quality hypothesis. In response to multi-speaker playback, Logue et al. (2008) found that male and female Black-bellied Wrens tightly coordinated their duets and prematurely terminated duets that were not well coordinated, suggesting that coordinated duets signal a high-quality, territorial pair. Similarly, Hall and Magrath (2007) found that paired Magpie-larks responded more aggressively to multi-speaker playback of precisely coordinated duets than to playback of uncoordinated duets, suggesting that coordination between pair members is directly related to the perceived threat of display. Additional studies are needed to test these hypotheses and clarify possible functions of duetting behavior.

Multi-speaker duet playback offers many research possibilities that have not yet been explored. For example, dual-speaker designs with different degrees of coordination between male and female duet stimuli would be useful in understanding the relative importance of the coordination of male versus female contributions. Multi-speaker designs involving more than two loudspeakers may offer additional insight. For example, a four-speaker playback design could be used to simulate two duetting pairs that differ only in their degree of duet coordination, or that differ in their adherence to a duet code (defined below); the relative responses of a resident territorial pair could elucidate the signal function of coordination or code adherence.

Playback involving non-interactive stimuli, whether it involves one speaker or multiple speakers, is the most straightforward playback design, and can be useful in improving our understanding of duetting behavior. However, non-interactive designs have limitations. Non-interactive experiments allow investigators to compare the effects of different types of acoustic stimuli in eliciting a behavioral response, but cannot easily elucidate the value or information encoded in the timing and patterning of signal production (Smith 1996). Additionally, because stimulus presentation is fixed, it cannot accurately mimic birds producing multiple vocalization types over time or vocalizations that vary with respect to the behavior of conspecific individuals (Mennill and Ratcliffe 2000). Consequently, non-interactive playback design may not be appropriate for investigating complex dyadic interchanges between senders and receivers, whether between the members of a duetting pair or during counter-duetting exchanges between rival territorial pairs. As an alternative, investigators should consider the use of interactive designs.

PLAYBACK METHODS: INTERACTIVE DESIGN

Interactive playback differs from non-interactive playback because the investigator manipulates the broadcast stimulus based on the subject's behavior (McGregor 2000). As a result, the focal birds—not the investigator—drive interactions with the simulated intruders. Several studies of non-duetting birds have demonstrated that an interactive design can be important for presenting relevant and meaningful stimuli when studying bird vocalizations (e.g., Nielsen and Vehrencamp 1995, Smith 1996, Otter et al. 1999). In some species, behavioral or motivational information conveyed by a signal may only have value when presented interactively (Dabelsteen and McGregor 1996). Indeed, studies of non-duetting songbirds have demonstrated that interactive playback elicits more intense responses than similar stimuli presented in a non-interactive manner (Mennill and Ratcliffe 2004b). Interactive playback is a relatively new technique in the study of bird song. As an experimental tool, it has become more popular because of the availability of user-friendly software (e.g., Syrinx-PC, J. Burt, Seattle, WA; Mennill and Ratcliffe 2000) that permits rapid changes in the timing and patterning of stimuli from a portable device (for a detailed discussion of interactive playback, see Dabelsteen and McGregor 1996).

Interactive playback experiments may provide more detailed information about duet function because they allow precise manipulation of the playback stimuli (Grafe and Bitz 2004a). The flexible nature of the design allows investigators to determine how individuals link their vocal responses to the stimuli presented and examine short-term interactions in signaling behavior (Dabelsteen and McGregor 1996). With interactive playback, investigators can better interpret or understand the information encoded within the timing and patterning of the acoustic signals themselves (Smith 1996). Two features of signaling behavior that may vary during an interaction are a bird's use of song types from its repertoire of songs, known as pattern-specific responses, and when each song is used, known as time-specific responses (Todt and Naguib 2000). Interactive playback experiments allow investigators to manipulate these parameters during simulated interactions with birds.

A prerequisite for using an interactive design to study avian duetting behavior is that the investigator must have a reasonably comprehensive understanding of the vocalizations of the focal species, either with respect to the interplay of male and female signals within duets or the way that pairs use duets when counter-duetting with other pairs. For most duetting species, especially those in the tropics, these features have yet to be described in detail. Interactive playback will become an even more valuable tool as the number long-term studies of color-banded populations of duetting birds increases, providing details about these features of the birds' duetting behavior.

Hypothesis testing with interactive playback. Some duetting species combine song types from their repertoire non-randomly with song types of their mate (see Logue 2006 for a list of species). This non-random association of song types is known as a duet code (Logue 2006), and analyses suggest that these codes are pair-specific in some species (Levin 1996b, Logue and Gammon 2004, Logue 2006). Interactive playback could be used to simulate the voice of one member of a duetting pair to stimulate an interactive response from their mate (a technique referred to as the karaoke protocol; Logue, pers. comm.). This technique, which we call interactive duet playback, could be used to determine how stable duet codes are over time and across partners, to evaluate the likelihood of an individual adhering to rules that govern the code, or to describe the code itself. Logue (2007) studied the duet codes of Black-bellied Wrens and used interactive playback to simulate the duet contributions of males to determine how strictly females adhere to their pair-specific duet code. Although the stimuli presented by Logue (2007) were given in a predetermined order, the experiment was interactive in the sense that if the focal female became unresponsive or lost interest, duet stimuli would be broadcast to re-engage the subject. This technique can also be used at the start of an interactive experiment, and is often referred to as priming the subject (Smith 1996). Logue (2006) found that female Black-bellied Wrens adhere strictly to a duet code, with each female singing only one song type in response to each male song type presented. This clever experimental design should be used to study duet codes in other duetting species.

There is much room for creativity in interactive designs to imitate half of a duet when engaging territorial birds in playback encounters. For example, interactive designs where the experimenter simulates a pair of birds that duet type match or overlap the duets of a pair of territorial subjects would help elucidate the dynamics of counter-duetting exchanges. Although it would necessarily be a challenging design, such experiments should be coupled with a multi-speaker approach to simulate the vocalizations of a pair of intruding birds with spatial realism.

In some duetting species, instead of having a pair-specific duet code, there is a population-wide tendency to non-randomly combine certain types of songs, producing what is referred to as a duet type (Grafe and Bitz 2004a). For example, Tropical Boubous have a repertoire of 12 duet types that are shared throughout a population. Grafe and Bitz (2004a) conducted an interactive playback study where each of a focal bird's vocalizations was followed immediately by playback of a solo song, and found that joint territorial defense and mutual mate guarding are important functions of Tropical Boubou duets. Grafe and Bitz (2004b) also interactively examined one specific duet type that birds appeared to sing only after the interactive experiments had ended. When the focal birds were engaged in an interactive encounter, pairs who had "won" the encounter sang one specific duet type significantly more often after the conclusion of the playback session. Tropical Boubous appear to use this specific duet type as a post-conflict victory display (Grafe and Bitz 2004b). This study provides evidence that different duet types may encode different information, and that interactive playback experiments have the potential to elucidate the information content encoded within these complex signals.

Interactive playback can also be used to examine the functional significance of small-scale temporal variations that occur within and between duet bouts. Interactive playback allows an investigator to have tight control over inter-song intervals and the sequence of songs presented. By simulating one member of the duetting pair, interactive playback could be used to assess the responses of individuals to varying reaction times of their partner (e.g., coordinated or uncoordinated, or fast or slow). It is important to note that bouts of singing likely provide information that cannot be provided by a single song unit (Smith 1996). This is indeed the case for many temperate species where males that have their songs overlapped behave differently than males that do not (e.g., Todt and Naguib 2000). For species with structurally simple duets, such as those of some suboscines, e.g., Barred Antshrikes (*Thamnophilus doliatus*, pers. obs.) and Cocos Flycatchers (*Nesotriccus ridgewayi,* Kroodsma et al. 1987) as well as a parrot (Yellow-naped Amazon, *Amazona auropalliata*; Wright and Dahlin 2007), the rhythmic sequence of songs may provide information about the intentions of the singers. Interactive experiments that vary the degree of overlap of duet components would be illustrative. For example, by playing a song in response to the vocalizations of a focal bird, investigators could manipulate the extent of overlap of the focal bird's vocalizations with those of their duet partner.

Although interactive playback has much potential for use in studying avian duets, the complexity of this technique may, in some cases, be limiting. Perhaps the greatest limitation is our general lack of knowledge of duetting species, particularly in the tropics where duetting is especially prevalent, but where most species have not been studied in detail. Without a well-developed understanding of the vocalizations, which individuals exchange signals (e.g., within the territorial pair, between territorial neighbors, or with conspecific intruders), and their motivation for communicating, interactive playback experiments are difficult to conduct and results difficult to interpret (Smith 1996). Other challenges include the need for investigators to identify acoustic signals, select an appropriate stimulus, and play it back in a timely manner, often under challenging field conditions (Dabelsteen and McGregor 1996). For species with highly coordinated duets, where partners may coordinate duet elements at a scale of milliseconds (e.g., Plain Wrens; Mann et al. 2003), we are not aware of any playback technique that would allow an investigator to respond with satisfactory control over stimulus timing. However, the required reaction times would be much less demanding in species where duets are more loosely coordinated. Finally, although interactive playback can simulate the early phases of territorial intrusion, it cannot simulate physical confrontation (Smith 1996). This may not be relevant for species where duetting birds routinely sing at some distance from one another without close physical approach. However, this limitation should be considered when studying species that duet in close proximity to one another, or those that occupy small territories. Investigators must also be cautious when using interactive playback because simulating highly aggressive interactive encounters with territorial birds can potentially influence their behavior, including changing patterns of extra-pair paternity (Mennill et al. 2002).

Beyond interactive and multi-speaker techniques, experimental playback designs are likely to become increasingly sophisticated with new technology. Given that many duetting birds live in dense tropical habitat where tracking individuals is logistically challenging, combining playback with acoustic spatial monitoring (e.g., Mennill et al. 2006, Mennill and Vehrencamp 2008) or other passive monitoring systems may enhance our ability to understand animal responses to playback. In the future, acoustic playbacks could be combined with other multimodal playback techniques, including models (e.g., Wiebe 2004), mechanical robots (e.g., Patricelli et al. 2006), and video stimuli (Evans and Marler 1991, but see Cuthill et al. 2000). Multimodal playback techniques have been used to study other aspects of animal behavior, and so materials and methods are available in the literature. To our knowledge, multimodal playback techniques have not been used to examine duet function. However, the combination of visual and acoustic stimuli would represent an important advancement in the study of duetting behavior. Indeed, given that many duets are accompanied by specific body postures and movements, such as the bowing and tail-fanning duet displays of Rufous-naped Wrens (Bradley and Mennill 2009b) and the intricate cartwheel displays of Long-tailed Manakins (Trainer and McDonald 1995), visual stimuli may be an especially revealing complement to acoustic playback.

CONCLUSIONS AND FUTURE DIRECTIONS

Playback experiments with duetting birds can be categorized on the basis of whether stimuli are presented in an interactive or non-interactive fashion, and whether stimuli are broadcast from a single speaker or multiple speakers. Single and multi-speaker playback designs can be used to simulate duets and evaluate how birds respond to different stimuli. The use of multi-speaker playback is superior to single-speaker playback for studying vocal duets because it simulates duets with spatial realism, and also generates unique and additional predictions for testing duet function. Interactive playback allows investigators to ask questions about how a bird's selection of songs and timing of songs correspond with its physical behavior as it interacts with the simulated bird(s). Although little used to date, interactive playback provides an important tool for exploring the interactions of males and females during duets, and the exchanges of duets between rival pairs.

Despite increasing attention to the many hypotheses for the functions of duets, much remains to be learned about the behavioral significance of duetting. Carefully designed playback experiments will help clarify the relative importance of the many hypotheses for duet function (Table 1). To date, the cumulative results of playback experiments point to the importance of the joint resource-defense hypothesis (Table 2). Other hypotheses, such as the mate-guarding, paternity-guarding, pair-bond maintenance, identity, and signaling-quality hypotheses, need to be more thoroughly investigated if we are to gain a comprehensive understanding of duet function.

Historically, playback experiments have been used to study the singing behavior of temperate species, where typically only males sing. Among tropical birds, duets involving singing by both males and females are more common (Farabaugh 1982). Although avian duets share some functions with male solo song, they are not analogous, and therefore creative experimental designs should be used to explore the functions of duets. We recommend that future studies of duetting birds employ multi-speaker designs, with speakers placed at a realistic distance for the species being studied. Increasingly realistic stimulus presentations and experimental designs will provide us with a better understanding of the functional significance of these complex and coordinated acoustic displays.

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