DISSERTATION

DUET STRUCTURE AND THE ADAPTIVE SIGNIFICANCE OF COORDINATED SINGING IN THE BLACK-BELLIED WREN

Submitted by

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WE HEREBY RECOMMEND THAT THE DISSERTATION PREPARED UNDER OUR SUPERVISION BY DAVID M. LOGUE ENTITLED "DUET STRUCTURE AND THE ADAPTIVE SIGNIFICANCE OF COORDINATED SINGING IN THE BLACK-BELLIED WREN" BE ACCEPTED AS FULFILLING IN PART REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY.

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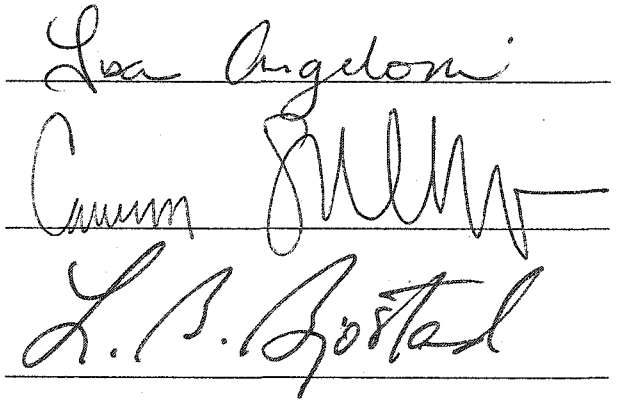

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ABSTRACT OF DISSERTATION

DUET STRUCTURE AND THE ADAPTIVE SIGNIFICANCE OF COORDINATED SINGING IN THE BLACK-BELLIED WREN

In a diverse array of bird species, mated pairs coordinate their songs to form vocal duets. I investigated duet structure and the adaptive significance of duet participation in free-living black-bellied wrens *(Thryothorus fasciatoventris)*. Both sexes sign repertoires of sexually diphonic songs which they combine to create vocal duets. Pairs duet at elevated levels during border disputes, territory intrusions, territory expansion, mate switching, and nest building, and in response to duet song from conspecifics and buff-breasted wrens *(T. leucotis)*.

I used a series of playback experiments to test the functions of duet participation during agonistic encounters, and to examine the roles of the sexes in territory defense. Males initiated more songs during opposite-sex playback than during same-sex playback and both sexes were more likely to answer their mate's songs when the mate was physically closer. These patterns support the hypothesis that duetting during territorial encounters allows males to identify and locate their mates. Males with dependant juveniles were found to defend inter-sexually, but other birds exhibited a same-sex bias in territory defense. This result is consistent with a model that assumes birds act to maximize their own fitness.

Unique 'duet codes' that link the male song-type that a female hears to the song type that she sings in response could provide a mechanism for mate recognition through duet song. I tested for duet codes by inducing females to answer playback of male songs. I found that females abided strictly by duet codes. Different females use different codes, which do not change over time or after re-mating. There is some evidence that codes are learned.

Throughout this study, I recorded and played back sounds with MiniDisc (MD) digital audio recorders. I compared the performance of MD recorders with that of professional grade cassette recorders and found that MD recordings exceed cassette recordings in several measures of found fidelity. I also found that MD recorders introduce acoustic artifact in certain recordings. Nevertheless, these units are appropriate for most field recording and playback applications, and afford numerous advantages over audio cassette recorders.

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Thank you, birds. Thank you, forest. I'll try to repay you.

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Chapter I: Vocal signaling in the black-bellied wren

INTRODUCTION

For over 100 years, researchers have studied bird song as a model of animal communication (Baker 2001). The majority of this work has focused on temperate breeding species, leaving vocal communication in tropical species largely open to speculation (Stutchbury & Morton 2001). Yet tropical resident birds exhibit diverse territorial and breeding systems, many of which are rare or absent among their temperate breeding counterparts. As a consequence, much of what is known about vocal communication from studies of temperate birds may not apply generally to tropical species.

Duet singing, in which two mated birds sing together, is primarily a tropical phenomenon (Farabaugh 1982). Though duet singing has attracted much scientific interest (reviewed in Farabaugh 1982, Hall 2004), we know little about the basic vocal behavior of duetting species. In the present report, I use quantitative and qualitative methods to describe the vocal natural history of the black-bellied wren (*Thryothorus fasciatoventris*). Specifically, I describe the structure of their calls, songs, and duets, examine patterns of song initiation and song answering over annual and diel time scales, and describe the contexts in which pairs duet at elevated levels.

The vocal behavior of the genus *Thryothorus* has garnered much attention, making it a model genus for the study of duetting. There are reports on singing behavior in the Carolina wren (*T. ludovicianus,* Morton 1987), sinaloa wren (*T. sinaloa*, Brown &

Lemon 1979), happy wren (*T. felix*, Brown & Lemon 1979), rufous-and-white wren (*T. rufalbus*, Farabaugh 1983), buff-breasted wren (*T. leucotis*, Farabaugh 1983), bay wren (*T. nigricapilus*, Levin 1988, 1996a, 1996b), banded wren (*T. pleurostictus*, Molles & Vehrencamp 1999), and plain wren (*T. modestus zeledoni*, Mann et al. 2003). Other than the sinaloa wren and the banded wren, all of these species sing duets. I incorporate findings from these studies with those from the present study to draw attention to common behavioral patterns within the genus, and to suggest avenues for additional research.

METHODS

Species

As is typical of duetting species (Farabaugh 1982), black-bellied wrens are socially monogamous, and mated birds share an all-purpose territory throughout the year. Territories are characterized by semi-deciduous second growth or edge forest, with an abundance of tangled vines, and one or more patches of large herbaceous monocots (e.g. *Heliconiaceae*, *Saccharum spontaneum*). The study population breeds asynchronously, nesting throughout much of the late-April to mid-December tropical wet season (personal observation), though details of the breeding cycle are not known.

Both sexes participate in building a globular nest near the ground (usually in a patch of tall monocots) and both sexes feed the nestlings and juveniles for several weeks after fledging (personal observation). These insectivorous birds spend much of their time in the canopy and sub-canopy, searching for food in vine tangles and dead leaves. Though pairs often forage together, they also forage separately, sometimes spending

several hours over 100m apart (unpublished data). Black-bellied wrens are sexually monochromatic, but size dimorphic, with male weight exceeding female weight by an average of 26% (Chapter II). In Chapter III of this volume, I report that females consistently answer each male song type with a single song type of their own. I call this association a duet code, and suggest that males use the code to identify their mates.

Data collection

Two experienced field biologists (D.E. Gammon and W.P. Veber) and I made all recordings and observations during three field seasons, in Gamboa, Republic of Panama. We used body size and vocalizations to sex birds. Dissection and genetic testing (Chapter II) have confirmed that these indicators are accurate predictors of sex. All birds discussed in this chapter were fitted with unique combinations of colored leg bands. I identified birds as juveniles based on their close associations with their siblings and parents, their *pi-zeet* vocalizations, and their gray (rather than white) throats.

During the 2001 season, recordings were made with a Radio Shack omnidirectional microphone (product number 33-3014) mounted in a 45 cm aluminium parabolic reflector and a Marantz tape recorder (PMD 222). During the 2002 season, recordings were made with a Sennheiser omnidirectional microphone (ME62) mounted in a 60 cm Telinga Pro-universal parabola and a Sony MiniDisc recorder (MZ-R700). During the 2003 season, recordings were made with a Sennheiser omnidirectional microphone (ME62), mounted in 45cm aluminum parabolic reflector and a Sony MiniDisc recorder (MZ-N1).

I define 'notes' as vocal units that appear as continuous traces on a spectrogram. One to several notes constitute 'calls,' which are not included in duets, other than as

introductory contributions. 'Songs,' comprise two or more notes and can be sung either as solos or as part of a duet. 'Duet trains' or 'duets' are defined as continuous bouts of alternating vocalizations from a male and a female (Brown & Lemon 1979). All vocalizations included in duets are 'duet contributions.' Every duet can be classified as either a 'male-initiated duet' (MID) or a 'female initiated duet' (FID). Song 'initiation' describes singing that does not immediately follow a song from the mate. I define song 'answering' as singing immediately after the mate has initiated. According to this definition, each duet train has one initiation and one answer, regardless of the number of duet contributions. To 'terminate' a duet is to deliver the final contribution (measured at the beginning of the contribution) in a duet train.

Data

Time series data were obtained by following pairs of birds for a predetermined duration in the early morning. Most pairs were followed for the first three hours after the onset of singing, but in 2002, two pairs were followed for an entire day. One pair was followed for four days in 2001, six pairs were followed for one day each in 2002, and three pairs were followed for four days each in 2003. I conducted observations from May-August (wet season) in 2001 and 2002, and from January-April (dry season into early wet season) in 2003. During these observation periods, I noted all vocalizations, male song switches (2001and 2002 only), and duet train structures (i.e. the order of male and female duet contributions). These data were used for analyses of duet properties, and seasonal and temporal patterns of vocalization.

I gathered data on vocalizations and duet train structures from 20 pairs during the five-minute "pretrial period" from a 2002 playback experiment (Chapter II), and from a

similar pilot experiment in 2001. While these observation periods were predetermined, they were biased toward periods of high vocal activity because the experimenters began the pre-trial observations only after detecting vocal activity. These data were used for analyses of duet properties.

During the study, I cataloged examples of all song-types given by each bird. The known song repertoires of five mated pairs of birds were isolated for intensive analysis. Each song-type and duet type from these pairs was saved as a wave file (digitized at 44,100Hz) in either MultiSpeech (Kay Elemetrics Corp., Model 3700, Version 2.3, Lincoln Park, NJ) or Syrinx (John Burt, http://syrinxpc.com/). Three of the pairs lived in forest edges at the western border of Parque Nacional Soberania. The other two pairs lived in a second growth forest fragment known as the Gamboa Woods. The two sites are separated by 1.5km. I used these recordings to characterize vocalization types, and for repertoire estimations. Error terms represent standard deviations.

Song

This analysis describes the degree of sexual diphonism in black-bellied wren song. One example of each known song-type from each of the five males and five females was viewed as a spectrogram (1024pt, Blackman window) in Syrinx. I recorded the maximum and minimum fundamental frequencies, and counted the number of notes in each song-type. I used the maximum and minimum frequencies to derive the central frequency of each song according to the formula $(F_{max}-F_{min})/2+F_{min}$. I then constructed mixed ANOVA models in SPSS to test for sex differences in the central frequency and the number of notes in the songs, with the random effects of individuals nested within sex.

I classified and named all known song-types from five pairs. Individuals may include or omit an introductory note within a bout of song, so song-types were not separated based on the inclusion/omission of a single introductory note. Songs were lumped as a single type if they were judged to be 80% similar.

Many of these recordings were made during song playback. Female black-bellied wrens are known to choose song-types based on the male song-type they hear (Chapter III), and both sexes may be more likely to match a song-type that is played back than to sing a non-matching song-type. As a consequence, song sampling is not random, and these data are not suitable for the inclusion in a collector's curve.

Duet structure

I recorded the sequence (measured from the beginning of the contribution) of male and female contributions in all duets from the time series and pre-trial datasets. Chi-squared test were used to determine whether one sex initiated duets more often, and whether duet termination was independent of duet initiation in each season.

The distribution of duet train lengths (number of contributions) was found to be non-normal, necessitating non-parametric analysis. I used Mann-Whitney U-tests to compare train lengths over the two seasons and to separately test the effects of initiating and terminating sex on the length of the duet train. I counted the number of duets in which the sexes strictly alternated contributions (e.g. MFMFMF). I describe associations between male and female duet-contribution mechanism by which they are generated elsewhere (Chapter III).

Seasonal patterns

I compared wet season and dry season frequencies of song initiation and song answering in the first three hours after the initiation of vocal activity for both sexes. I also compared each sex's 'answer rate' (Levin 1988) across seasons. The answer rate is defined as the number of songs answered by the focal individual divided by the number of songs initiated by the mate. In cases where I observed a pair on more than one day, I used the average values over all days. Student T-tests were used to compare wet and dry season means for each of the three response variables for the two sexes.

Diel Patterns

I examined the same data set at a finer scale to reveal diel singing patterns of song use during the morning. I divided initiations, answers, and answer rate into 20 minute bins, and averaged bin values across all pairs for each season. I omitted the wet season data from 2001 because it lacked the necessary temporal resolution for this analysis. Two pairs were observed continuously for an entire day during the wet season. I examined the rate of male song initiation over this period (there was little other vocal activity later in the day).

RESULTS

Calls

Both males and females emit amplitude modulated, broadband *chirrs* (Figure 1.1*a-f*). These vocalizations are quiet relative to other vocalizations. Adults produce a drawn-out *rattle* when a human approaches the nest or fledglings, the sound of which is similar to that produced by drawing a plectrum across the teeth of a comb. Birds tend to be bold while *rattling*, often allowing observers to approach within a few meters.

Male black-bellied wrens produce calls known by the onomatopoetic device, *cream-o-wheat* (F.O. Chapelle, cited in Ridgely & Gwynne, 1989; Figure 1.1*a-c*). These tonal calls consist of 2-4 notes (average= 2.73±0.67, N=66) and always end with a rapid decrease and then increase in frequency, producing a V-shaped note or pair of notes on a spectrogram. Often, males chirr immediately before a *cream-o-wheat* call (Figure 1.1*a-c*). Males issue *cream-o-wheat* calls at a high rate while foraging with juveniles. Playback of this call is attractive to juveniles; a fact that can be exploited to lure young birds into a mist net. Each male has several variants of the cream-o-wheat call. At least some of these are identical to the final several notes of male songs. While females sometimes answer cream-o-wheat calls to form duets (Figure 1.1*g*), males never answer female song with this call. Interestingly, the call used to initiate a duet is often identical to the end of the song the male will use in the duet.

Females produce a loud one- or two-note call that I term the *bell call* because the main note produces a bell-shaped trace on a spectrogram (Figure 1.1*d-f*). All bell calls rise and then fall in pitch. This call often initiates duets (Figure 1.1*h*), but like the cream-o-wheat call, it is never used to answer the mate's song. In another parallel to the cream-o-wheat call, *bell calls* are often immediately preceded by *chirrs*.

During the post-fledging period, juveniles forage with their parents while emitting broadband doublets, usually given in series and known by the onomatopoeic device, *pi-zeet* (Owings & Morton 1998; Figure 1.1*i*). Adult females also give *pi-zeet* calls while attending to juveniles, and I once observed a male to emit a low-pitched, *pi-zeet*-like call when a new female (with whom he would develop a pair bond) came onto his territory (Figure 1.1*j*). Both sexes occasionally give distress calls when caught in a mist net or

handled. Typically these are repeated, broadband calls that sound like *rhah-rhah-rhah* (Figure 1.1*k*), but one adult female issued high-pitched tonal warbles (Figure 1.1*l*).

Song

Both sexes of black-bellied wren emit loud tonal vocalizations that are comparable to male song in temperate passerines. Song consists of slow whistled notes, and lacks buzzes, trills, or rattles (Figures 1.2&1.3). Compared to female songs, male songs include more notes (Male: 6.0±1.0 notes, Female: 3.1±0.6 notes; nested ANOVA $F_{1,9.4}$=296.9, P<0.001) and center around a lower frequency (Male: 1.52±0.15kHz, Female: 2.63±0.32kHz; nested ANOVA $F_{1,7.6}$=294.6, P<0.001). The frequency ranges of male and female song (average ranges: male: 0.79±0.08-2.25±0.3kHz; female: 1.25±0.2-4.01±0.6Hz) fall in a 'notch' between low-frequency noise generated by wind and high frequency noise generated by calling cicadas (Homoptera, Cicadidae; Figure 1.4). Male and female differ in timbre; male songs sound mellow and rich whereas female songs sound thin and sharp. All male songs end with a note or pair of notes that decreases and then increases in frequency (Figure 1.2), and all female songs end with a note that increases and then decreases in frequency (Figure 1.3).

Males sometimes rapidly repeat one song-type 2-5 times. These multiple song utterances usually follow long periods without vocalizations. On three occasions, males have been observed to emit rapidly repeated songs that include high-pitched, female-like notes (Figure 1.5). In all three cases, the males were responding to duet playback and were not accompanied by their mates. I call these songs 'duet' solos (after Grafe et al. in press).

I recorded 55 song-types from the five males. Known male repertoires averaged 20.8±3.3 song-types (range: 16-24). I found new male song types throughout the recording catalogue, suggesting that males may have many more song types than I recorded.

The known repertoires of the five females include 31 song-types. I recorded an average of 13.0±2.2 song-types per female (range: 10-16). Two females (repertoire sizes 10 and 16) sang no new songs in the third year of sampling, and one sang only one new song during that time. I therefore suspect that my samples of female repertoires are nearly complete. I spent equal time observing the male and female of a given pair, but consistently recorded more song-types from males than females.

Duet structure

The sexes strictly alternate contributions in 84.3% (285/338) of duets. The amount of overlap between duet contributions is highly variable between duets. Both sexes may begin their contribution before their mate has finished its contribution, or they may wait to begin until their mate has sung its entire contribution. Some duets are clearly 'in-phase,' but others are out of phase, with substantial variation in the relative timing of duet contributions.

During counter-singing contests, or when subjected to song playback, black-bellied wrens sometimes type-match one or both contributions of the neighbor or stimulus duet. It is not clear whether type-matching occurs more or less often than would be predicted by chance alone, nor is it clear if this behavior is associated with a particular context.

I recorded a juvenile female imitating her mother's song-type to answer her social father's song (Figure 1.6). Shortly after this observation was made, the juvenile moved to a neighboring territory and sang duets with the resident male.

Seasonal Patterns

The tropical seasons exert strong effects on the vocal behavior of both sexes. Males initiated many more songs during the wet season versus the dry season (Table 1.2), but female song initiation rate was not affected by season. The mean number of male answers was slightly greater during the dry season, but the difference was not statistically significant. Females answered the songs of their mates more often during the wet season. Male answer rates were higher during the dry season, but female answer rates were not affected by season. In summary, during the wet season males initiate more songs but answer songs at a lower rate, and females answer more songs.

During the wet season males initiate many more duets than females (248 MID's, 52 FID's; χ^2 =128.05, df=1, p<0.001), but this pattern is reversed in the dry season (11 MID's, 27 FID's; χ^2=6.7, df=1, p=0.009). Initiation and termination are not independent in either season (wet: χ^2=5.41, df=1, p=0.02; dry: χ^2=7.17, df=1, p=0.007). Specifically the non-initiating individual is more likely to terminate a duet than would be expected by chance in both seasons (Table 1.1).

Duet trains are shorter during the wet season (wet: 3.9±2.6 contributions, dry: 7.4±1.9 contributions, Mann-Whitney Test, N=300,38, U=1435.5, P<0.001). In both seasons, the sex of the individual initiating and terminating the duet have no effect on train length (Mann-Whitney Test, all P>0.1).

Diel patterns

During the wet season, males initiate song at a high rate in the early morning (Figure 1.7*a*). During this 'dawn chorus,' four of the seven males in this study switched frequently between a few song-types, while the other three males did not switch song-types during early morning singing (Figure 1.8). In the later morning, all males switched song-types at a low rate (Figure 1.8). Males answer few of their mates' songs during the dawn chorus and as a consequence, the FID rate peaks in the late morning (Figure 1.7*a*). In contrast, male song initiation exhibits no clear peak during the dry season (Figure 1.7*b*). During the dry season, male song answering peaks at dawn and decreases throughout the morning (Figure 1.7*b*).

Both of the males that were observed for an entire day initiated few songs after the first four hours of daylight (Figure 1.9). They were particularly quiet through the intense heat and subsequent heavy rain that typify the wet season afternoon. Both males initiated song at slightly elevated levels in the hour prior to sunset.

During the wet season, female song initiation does not adhere to a clear temporal pattern, but female song answering increases throughout the early morning, peaking about two hours after sunrise (Figure 1.7*c*). This pattern disappears in the dry season (Figure 1.7*d*).

Context of duet song

Black-bellied wrens engage in duets during the course of normal foraging and in a variety of special circumstances. The commonest of these is in response to duet song from neighboring pairs. In elevated contests, neighboring pairs engage in lengthy bouts of counter-duetting with all four birds singing near the shared border. In one case, paired

birds BS & BR had been radio tagged for 2 weeks, and their territory thoroughly mapped, when they challenged a neighboring solo male on his own territory. Over the course of two hours, BS & BR sang 26 MID's and 15 FID's. The solo male repeatedly matched male BS's song-type, prompting female BR to answer him on 9 occasions. Each time this happened, male BS interupted the duets and BR took up singing with him. The paired birds drove the solo male east and then north, to capture a patch of *Saccharum spontaneum* (a preferred nesting habitat).

Vocal duets from congeneric buff-breasted wrens stimulate black-bellied wrens to sing duets, and the converse is true as well. I have observed two buff-breasted wrens (presumably a mated pair) cooperatively attack an adult black-bellied wren.

On two occasions, I observed a female black-bellied wren to leave her mate and pair with a neighboring solo male. In both cases, all three birds vocalized profusely, and in both cases, the female answered male songs from both males. Pairs also duet at elevated levels during the early stages of nest-building. This pattern has been observed in three pairs, and I have never observed a pair to begin nest-building without also duetting at a high rate.

DISCUSSION

Calls

The structure of the *chirr* and *rattle* calls produced by both sexes suggest homology with similar vocalizations given by other *Thryothorus* species (Skutch 1960, Stiles & Skutch 1989). Compared to the whistled song notes, these calls include a wide range of frequencies, and are relatively quiet. These properties render the active space of these calls small relative to that of the wren's tonal vocalizations. When birds are close

together, however, these broad-band signals should be highly localizable, and may be sufficiently complex and stereotyped for the receiver to reliably identify the sender.

Cream-o-wheat calls are clearly involved in father-fledgling communication, but the function of this call in the absence of juveniles is not clear. Interestingly, male bay wrens and male plain wrens also issue a vocalization type that females answer, but that males never use within duet trains (Levin 1988, Mann et al. 2003). The system appears to be most derived in the plain wren, in which each variant of the introductory male vocalization (called an "I-phrase") elicits a particular female song-type ("A-phrase"), which elicits a particular male song-type ("B-phrase;" Mann et al. 2003). The coding of I- to A-phrases and A- to B-phrases varies from pair to pair, much like the coding between male and female song in the black-bellied wren (Chapter III). The *bell* call of the female black-bellied wren often stimulates male song, and is often preceded by a *chirr* vocalization, suggesting that it may be functionally similar to the male *cream-o-wheat* call. This is the only female call known to initiate duet song in a *Thryothorus* wren. It is not known why either sex would use these tonal call types rather than song, nor is it known whether answering calls is functionally equivalent to answering songs.

The juvenile *pi-zeet* call is well adapted to maintain contact between parents and juveniles. It covers a broad range of frequencies, allowing easy localization, but is not loud enough to inform distant predators or neighbors of the juveniles' presence. The *pi-zeet* calls of fledged juvenile Carolina wrens are similar in structure and function to those of juvenile black-bellied wrens (Owings & Morton 1998, p123).

Song

There is mounting evidence that environment influences the evolution of signal structure (Endler & Théry 1996, Slabbekoorn & Smith 2002). The black-bellied wrens' slow, whistled songs are well suited for transmition in this species' acoustically complex environment. Songs with these characteristics maintain their structure better than fast, frequency rich sounds when subjected to the global attenuation, reverberation, and frequency dependant attenuation that characterize dense forest (reviewed in Bradbury & Vehrencamp 1998). Further, the birds avoid two major sources of noise masking by singing at higher frequencies than wind-generated noise and lower frequencies than cicada-generated noise.

Male songs are longer, contain more notes and exhibit more inter-individual variation than do female songs. With their spectral and temporal simplicity and low inter-individual variation, female songs probably do not convey identity. Rather, females communicate their identity to their mates over long-distances by answering their mates' song according to an individually unique duet code (Chapter III). The happy wren is the only other duetting *Thryothorus* species in which females are known to sing simpler songs than males (Brown & Lemon 1979).

The songs and tonal calls of black-bellied wrens are not only sexually diphonic, they are opposites. The terminal note(s) of all male songs descends and then increases in pitch, while the terminal note of all female songs increases and then decreases in pitch. This finding recalls Darwin's (1872) Principle of Antithesis, which states that signals communicating opposite "states of mind" tend to exhibit opposite structure. All duetting

birds studied to date sing sexually diphonic duet contributions, but no other species is known to sing sexually antithetical songs.

Males issue two to five songs in rapid succession after periods of low vocal activity. Such vocalizations may represent male attempts to locate their mates. By repeating a song several times, they would allow the mate time to respond with the appropriate song-type. Indeed, females have been observed to answer their mates after the second and third repeat. This hypothesis predicts that males will tend to be out of contact with their mates when issuing repeated song. I intend to use data from an ongoing radio-telemetry study to test this hypothesis. Multiple song utterances have been reported in male happy wrens (Brown & Lemon 1979), and are known to occur rarely in male buff-breasted wrens (Farabaugh 1983).

The simplest explanation for male 'duet' solos is that duet song is more likely to deter potential intruders than male solo song. When a male's mate fails to show up during a singing contest, the male can use duet solos to bluff a strong defensive presence. Evidence for this hypothesis includes the female-like structure of certain notes in duet solos, their duet-like rapidly-succession delivery, and their apparent restriction to situations in which lone males hear duet songs. A speaker-replacement experiment could test the premise that duets are more effective than solo songs at preventing intrusion: an important question that has not been subjected to direct testing. In such a study, the experimenter would remove the resident birds from a territory, position speakers broadcasting various one of three song classes (male solo, female solo, duet) within the territory, and measure the time until birds claimed the territory (design after Krebs et al. 1978).

Male repertoires are probably larger than female repertoires in this species. Among duetting Thryothorus, repertoire inequity has been reported in two other species, while the sexes are known to have roughly equal repertoire sizes in three other species (Table 1.3). In theory, equal repertoire sizes would be necessary for perfect coding in species where both sexes use a duet code and all song types are used in duets.

Duet structure

Most (84.3%) duets consist of strictly alternating contributions from the sexes. This pattern is consistent with a dynamic duet structure in which each contribution from one pair member influences the subsequent choice of contribution from the other member (Souček & Vencl 1975, Mann et al. 2003, Chapter III). Interdependence of contribution types is virtually ubiquitous among duetting passerines (Chapter III, this volume). Selection to hear the mate's song-type and quickly reply with the appropriate song-type may drive the evolution of temporal coordination in duetting species. This hypothesis presents an alternative to the prevailing viewpoint that temporal song coordination is the driving force behind duet evolution while song-type use is a secondarily evolved feature (Hall 2004). A comparative study mapping non-random combination of duet contributions and the degree of temporal coordination of song onto a phylogeny would shed light on this critical question.

The degree of temporal overlap of duet contributions varies from no overlap to nearly complete overlap. Farabaugh (1983) categorized *Thryothorus* duets as either 'antiphonal,' 'partially overlapping,' or 'overlapping' based on the degree of temporal overlap in duet contributions. She categorized black-bellied wren duets as 'overlapping,'

but according to the current, more extensive data, they should be considered 'partially overlapping.'

Song-type matching has been described in several duetting species (reviewed in Hall 2004), and may function to direct a signal at the matched pair or to signal a heightened probability of escalation, much like song-matching among certain non-duetting passerines (e.g. Vehrencamp 2001). During interactive playback experiments, banded wrens (which do not duet) approach the playback speaker more quickly in response to matched song versus non-matched song (Molles & Vehrencamp 2001). Type matching behavior takes on a special significance if, as I have argued, mates recognize one another on the basis of song-type (Chapters II, III). Under this framework, matching could mask the identity of the song-matcher, providing a strategic advantage during escalated conflicts.

The recordings of a female juvenile singing sub-song in response to songs from her social father suggest that juveniles learn duet codes, as well as song-types, from the parents (Chapter III, this volume). Juvenile buff-breasted wrens and bay wrens are also known to join the duets of their parents (Farabaugh 1983, Levin 1988). A careful field or laboratory study of this phenomenon would greatly clarify the role of learning in duet ontogeny.

Previous authors have categorized *Thryothorus* species according to the structure of their duets (Brown & Lemon 1979, Farabaugh 1983). Such categorizations are useful because they draw attention to broad trends in singing behavior, and encourage discussion of functional correlates to duet structure. Until the phylogeny of this group is understood, however, our ability to relate the observed patterns to ecological factors will

be limited. I found it useful to arrange species along a continuum of vocal behavior, rather than into discrete categories (Table 1.3). At the one extreme are species with highly overlapping duet contributions, a strong male-biased skew in repertoire size, and long duet contributions that are combined at random. At the other extreme are species with highly antiphonal duets, equal repertoire size in males and females, and short duet contributions that are combined according to sophisticated rules. Covariance in these characters suggests an underlying trend toward a more derived style of duetting.

Seasonal patterns

I found that the tropical seasons exert strong effects on vocalization rates. Males, but not females initiate song at a much higher rate during the wet season versus the dry season, even though birds maintain territories and pair bonds throughout the year. Though female answer rates tend to decrease during the wet season, the very high male initiation rate results in over 18 times as many MID's during wet season mornings versus dry season mornings, a pattern that could be due to a relaxation of male territoriality during the dry season. This hypothesis, however, is at odds with the finding that song playback during the dry season provokes high levels of sustained agonistic behavior from both sexes (pers. obs.). Alternatively, high rates of male song may function to attract extra-pair females that might copulate with the territorial male. Current evidence, though limited, suggests that extra-pair fertilizations are uncommon among year-round territorial birds with low breeding synchrony (Stutchbury & Morton 2001). Stutchbury and Morton (1995, Stutchbury 1998) hypothesize that when breeding is asynchronous, as in the black-bellied wren, males do not simultaneously advertise their quality, thus females are unable to choose high quality males for extra-pair copulations, resulting in high levels of sexual

fidelity. Female black-bellied wrens, however, can hear many males singing at high rates throughout their breeding cycle and female bay wrens are known to make extra-territorial forays during their fertile period (Levin 1988). Paternity analyses and radio tracking studies would improve our understanding of seasonal patterns of male song in the tropics.

Unlike many duetting species in which one sex always leads a duet, black-bellied wrens sing both MID's and FID's, making this an excellent species for the study of sex-roles in duetting. Males lead most duets during the wet season, and females lead most duets during the dry season. The majority of duets (62%) are terminated by the non-initiating bird. This pattern is consistent with the hypothesis that one function of song initiation is to provoke answering in order to locate the mate. Having received a sufficient number of answers to locate and identify the mate, an initiating bird ceases to repeat his contribution, resulting in the non-initiator terminating the duet. Dry season duets are substantially longer than wet season duets. This variation may be attributable to the absence of breeding-related duets in the dry season, or the increase in territorial activity during the wet season. In any case, this pattern draws attention to the paucity of work on duet train length. I know of no studies addressing the function of persistence in responding to the mate (the behavior responsible for long duet trains), nor of any addressing the response to playback of duet trains of different length.

The finding that male answer rates were significantly lower in the wet (breeding) season versus the dry season, and the total number of male answers issued showed a non-significant trend in the same direction, suggests that guarding paternity is not an important reason for song answering by male black-bellied wrens. These results agree with those from several other studies, showing no increase in male answering during the

female fertile period (reviewed in Hall 2004). The strong seasonal effects reported here emphasize the importance of explicitly considering season when designing studies of vocal behavior in tropical birds.

Diel patterns

During the wet season, males' exhibited a pronounced dawn chorus. During this period, the seven males studied were observed to assume two different strategies. Four males rapidly switched between a few song-types, resulting in high-switching, low diversity singing (Molles & Vehrencamp 1999). Three of the males sang only a single song-type. An investigation is under way attempting to link early morning singing mode with breeding cycle. Female answer rates peak after the peak in male-song initiation, and male answer rates peak later still.

Context of duet song

Black-bellied wren pairs duet during territory defense and during offensive campaigns to gain additional territory. Virtually all studies of duetting birds have linked duet song to agonistic contests (reviewed in Chapter III), but this is the first report of duetting during territory expansion. The observed offensive campaign was against a solo male and was characterized by high levels of initiation and answering by both sexes. This behavior differs markedly from that observed during natural and simulated solo male intrusions. When defending against solo males, paired males do not initiate song at a high level, and females do not approach closely or answer song at a high level (Chapter II). This suggests that territory defense and territory expansion should be considered separately in year-round territorial species. Indeed, from a cost-benefit perspective, these

two scenarios are quite different, and may be expected to provoke different levels of cooperation.

The duet songs of buff-breasted wrens provoke black-bellied wrens to duet, and a pair of the former species has been observed to attack an individual of the latter. Taken together, these facts suggest that duetting in this context communicates the presence of both pair members, reducing the likelihood of escalation. Like territory expansion, interspecific defense is a context in which mated birds are expected to have similar interests, and therefore one in which duet singing functions as a cooperative defensive display.

Table 1.1 The number of occurrences of duets separated by initiating sex, terminating sex, and season.

	Male initiated	Female initiated
Wet Season		
Male terminated	95	29
Female terminated	153	23
Dry Season		
Male terminated	3	20
Female terminated	8	7

Table 1.2 The number of initiations and answers, and the answer rate for each sex in the three hours after the initiation of vocal activity. Error terms are standard deviations.

	Song Initiations		Answers		Answer Rate	
	Male	Female	Male	Female	Male	Female
Wet season	307.3±92.9	5.4±6.9	1.6±3.4	13.7±11.8	0.21±0.25	0.046±0.035
Dry Season	5.3±6.2	3.3±2.9	2.1±1.8	0.75±0.66	0.63±0.05	0.15±0.19
T	8.6	0.7	0.27	2.9	3.2	0.93
Df	6.1	7.9	7.1	6.1	3.5	2.1
P	<0.001	0.53	0.80	0.027	0.039	0.45

Table 1.3 Duetting styles of seven Thryothorus wrens arranged along a continuum of covarying factors.

Species	Overlapping or antiphonal	Repertoire size (m/f)	Song length (m/f)	Song-type coordination	Source
*T. ludovicianus**	overlapping	32/1	long/ chatter	none	Morton 1987, Shuler 1964
T. rufalbus	overlapping	14/6	long / long	random	Farabaugh 1983
T. felix	some overlapping	>29/?	medium / short	?	Brown & Lemon 1979
T. fasciatoventris	some overlapping	>20.8/13	medium / short	female duet code	This chapter, Chapter III
T. nigricapillus	antiphonal	16.0/15.2	short / short	male duet code	Levin 1988
T. leucotis	antiphonal	13.0/11.7	very short / very short	coordinated (coding sex not known)	Farabaugh 1983
T. modestus	antiphonal	~20/~20	very short / very short	male and female code	Mann et al. 2003

* Duets in this species consist of female chatter over male songs

Figure 1.1 The call repertoire of the black-bellied wren. These three male *cream-o-wheat* calls (*a-c*) are preceded by *chirr's*, as are the three female *bell* calls (*d-f*) depicted below them. Both of these call types are sometimes answered by the mate to form duets (*g-h*). Juveniles emit *pi-zeet* calls to maintain contact with their parents (*i*), but the function of the adult male *pi-zeet* (*j*) is not known. Black-bellied wrens emit both broad-band (*k*) and tonal (*l*) distress calls when handled. Female duet contributions in *g* and *h* are represented in white with black lining.

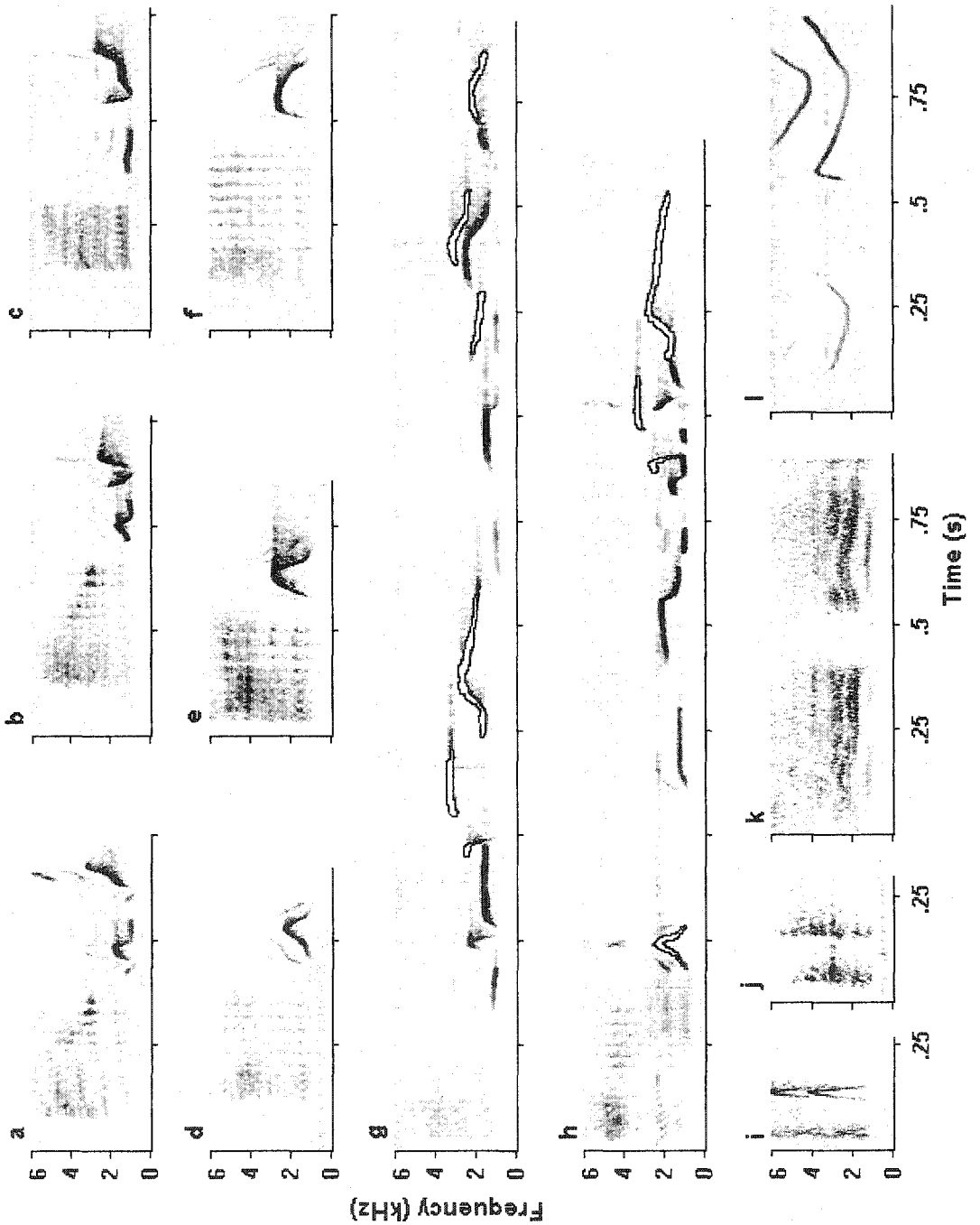


Figure 1.2 Spectrograms of male song-types *28*, *3*, and *4* from males F, AX, and AB. There is noticeable variation between different males' renditions of each song-type.

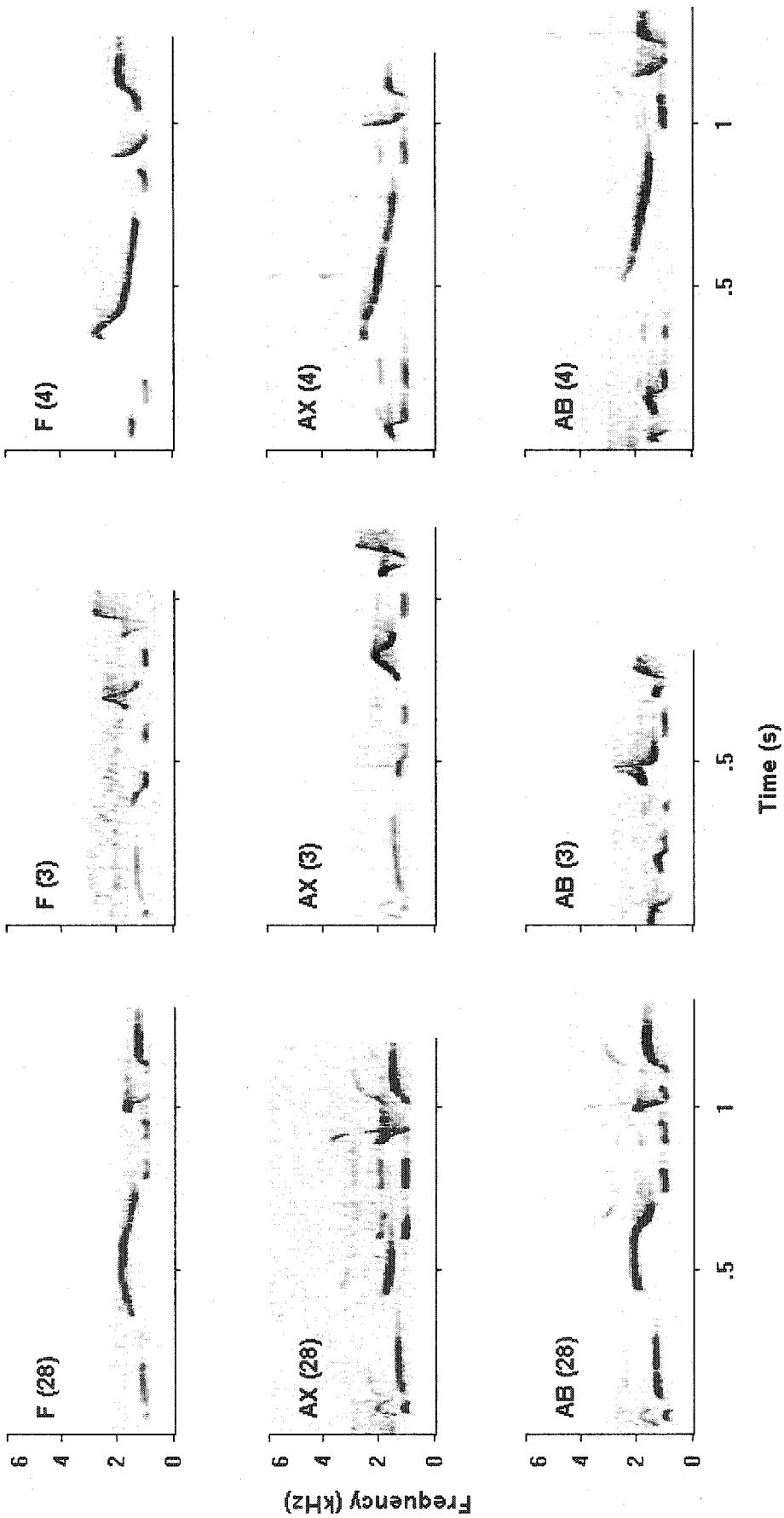


Figure 1.3 Spectrograms of female song-types *s*, *p*, and *f* from females AB, R, and BI. Different females' renditions of a given song-type can be virtually identical.

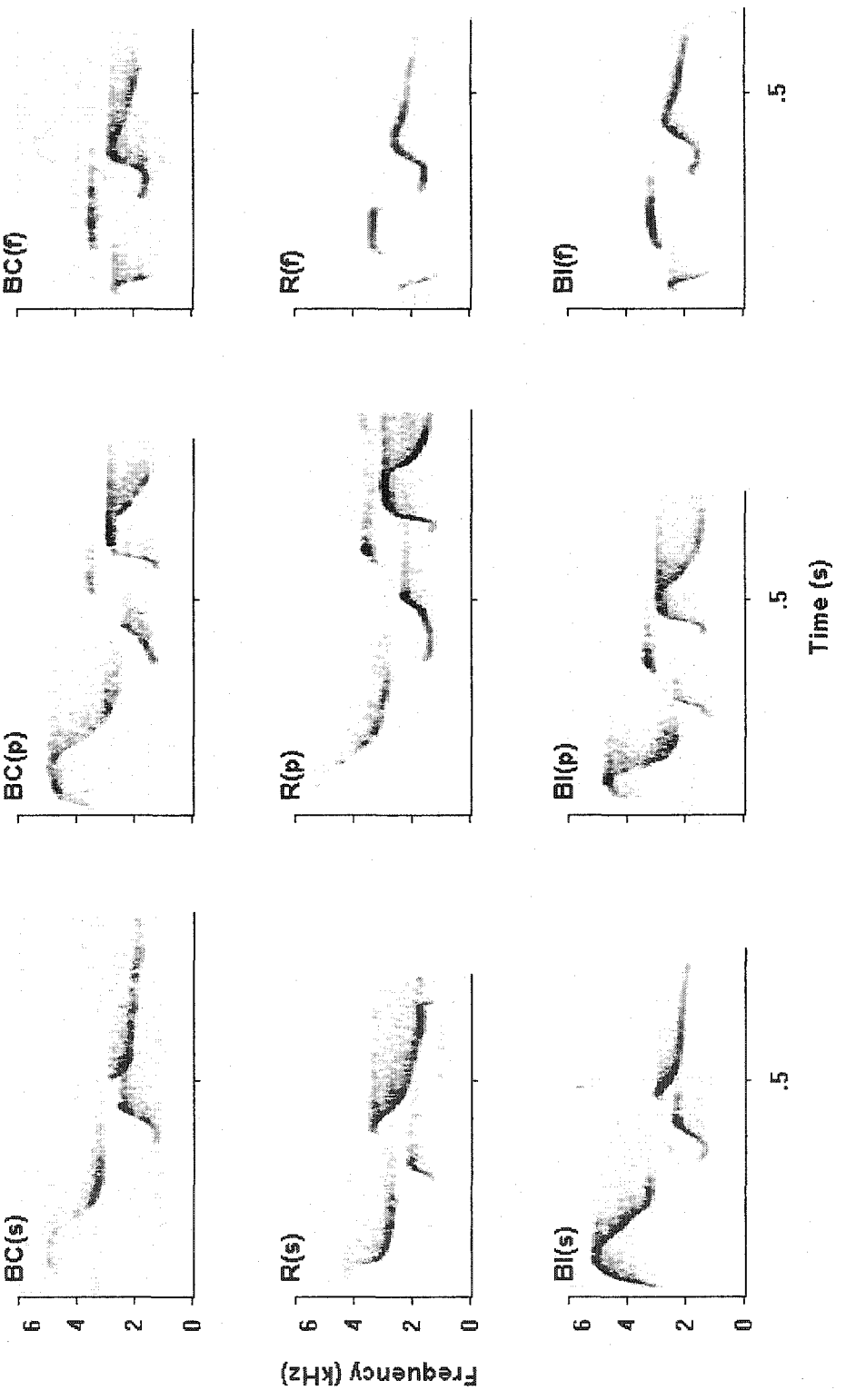


Figure 1.4 Spectrogram showing a black-bellied wren duet over a noisy background. Their vocalizations fall within a relatively quiet frequency band. The low frequency noise is wind-generated; high frequency noise is caused by cicadas. Female duet contributions are represented in white with black lining.

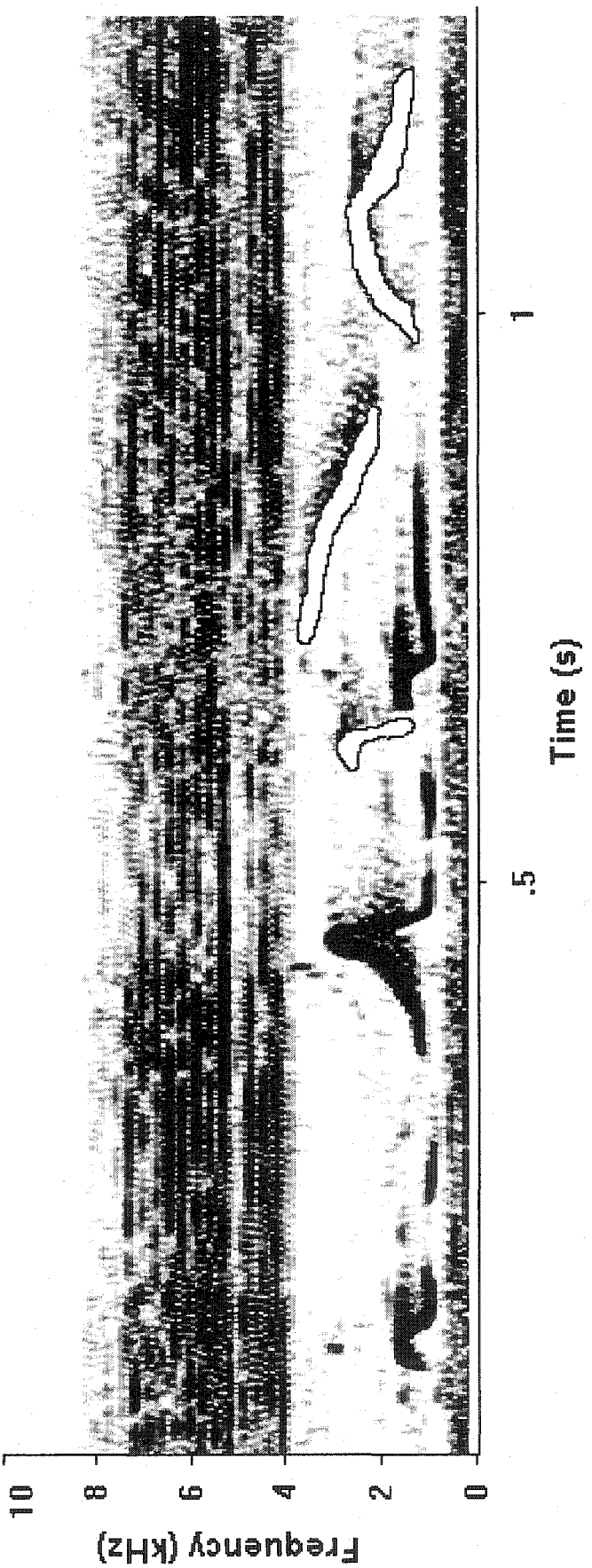


Figure 1.5 A false duet issued in response to duet playback. The note indicated by the arrow is a female note type (see Figure 1.3*BI(p)*).

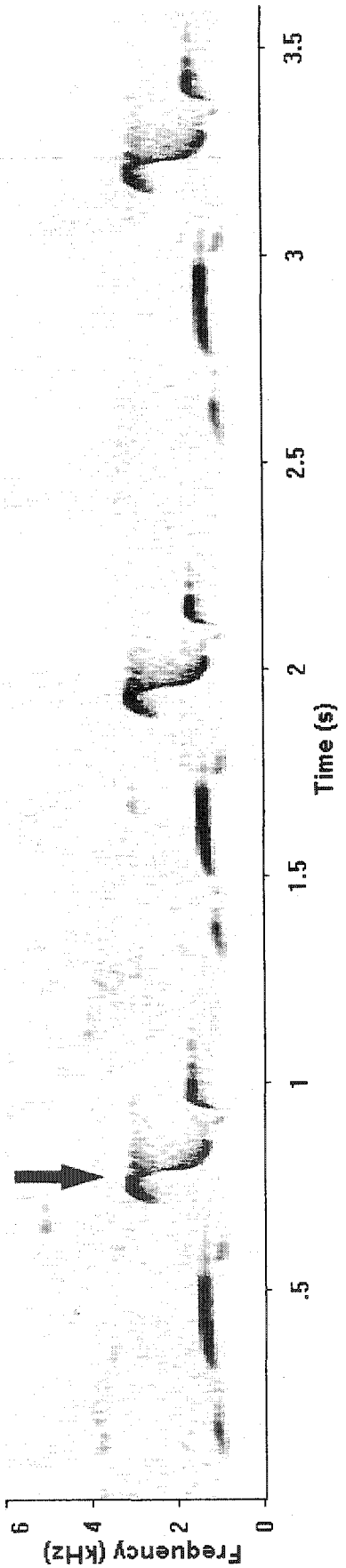


Figure 1.6 This sequence begins with an adult male (am) and an adult female (af) singing a brief male initiated duet. Within one second, their daughter, a juvenile female (jf) begins singing quiet, warbled imitations of the adult female's contribution. When the male sings again, the juvenile female answers him with sub-song that includes some of the elements of the adult female's song. The two trills in the background are a white-bellied antbird (*Myrmeciza longipes*) duet.

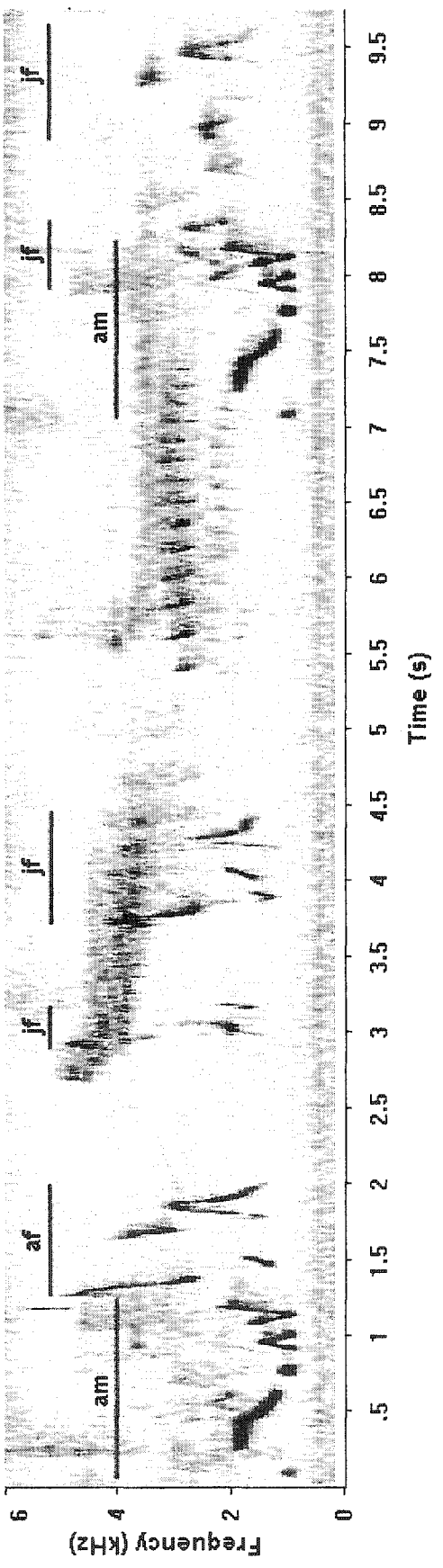


Figure 1.7 The mean number of songs initiated (bars) and answered (lines) by males (*a*&*b*) and females(*c*&*d*) in the two tropical seasons.

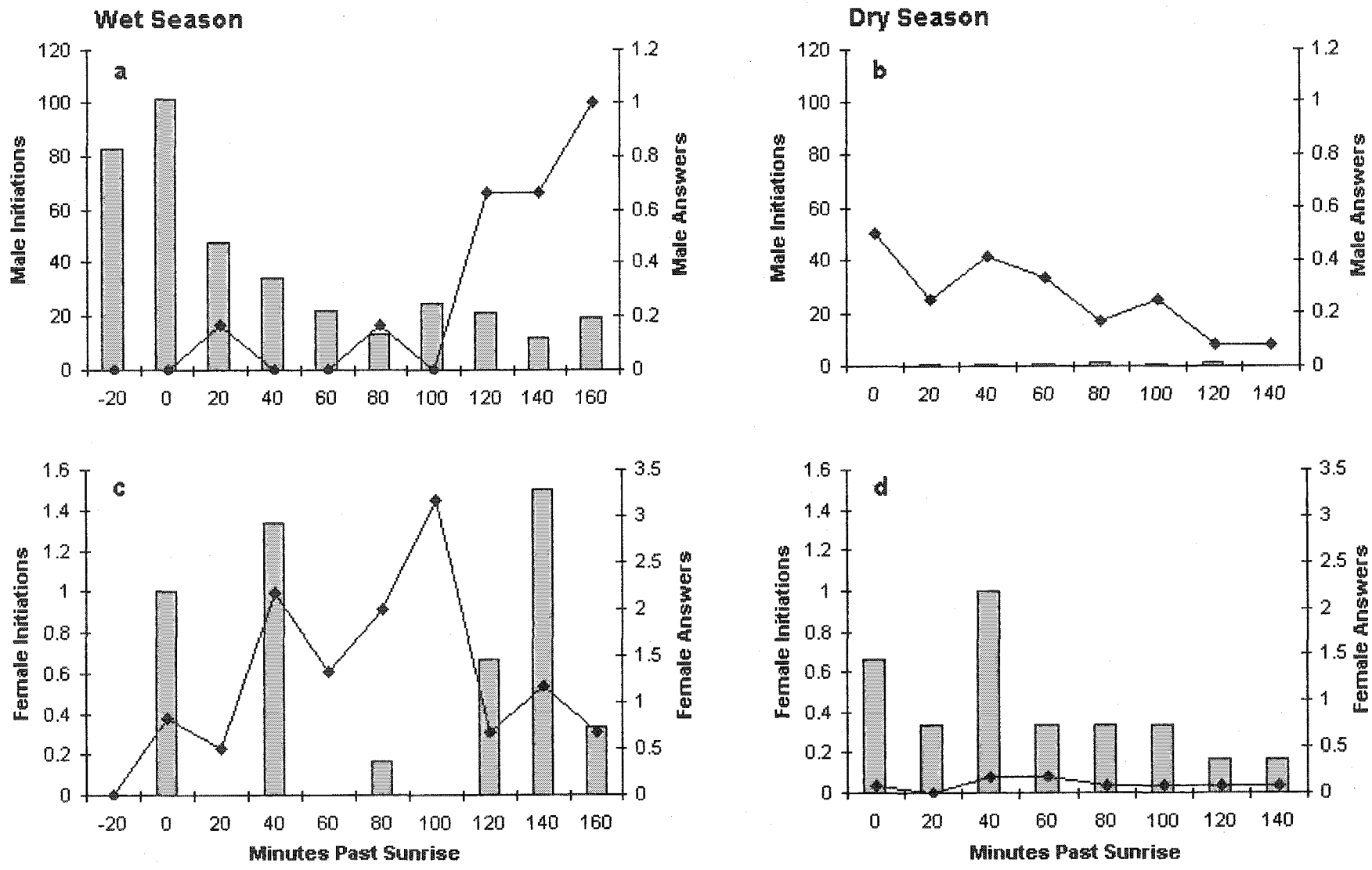


Figure 1.8 Examples of song-type use by males over the first two hours of morning singing during the wet season. Male F sang in repeat mode throughout the morning, beginning with a long bout of a single song-type. Male W sang with an intermediate degree of switching in the early morning. He then switched to repeat mode singing. Male AB began the morning by switching song-types nearly every song. He maintained this pattern for nearly an hour, eventually switching to repeat mode like the other males. Arrows represent the one-hour mark.

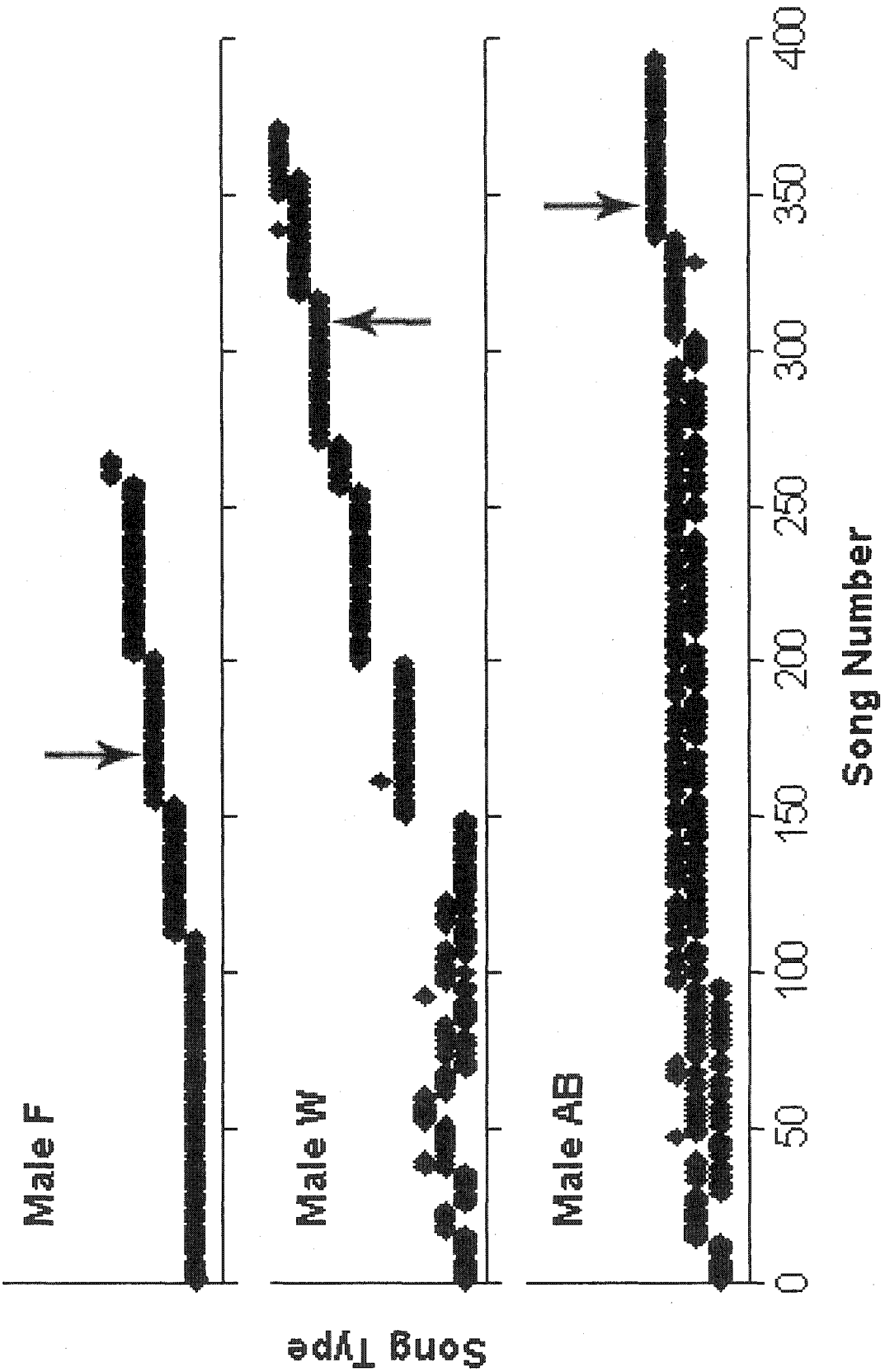
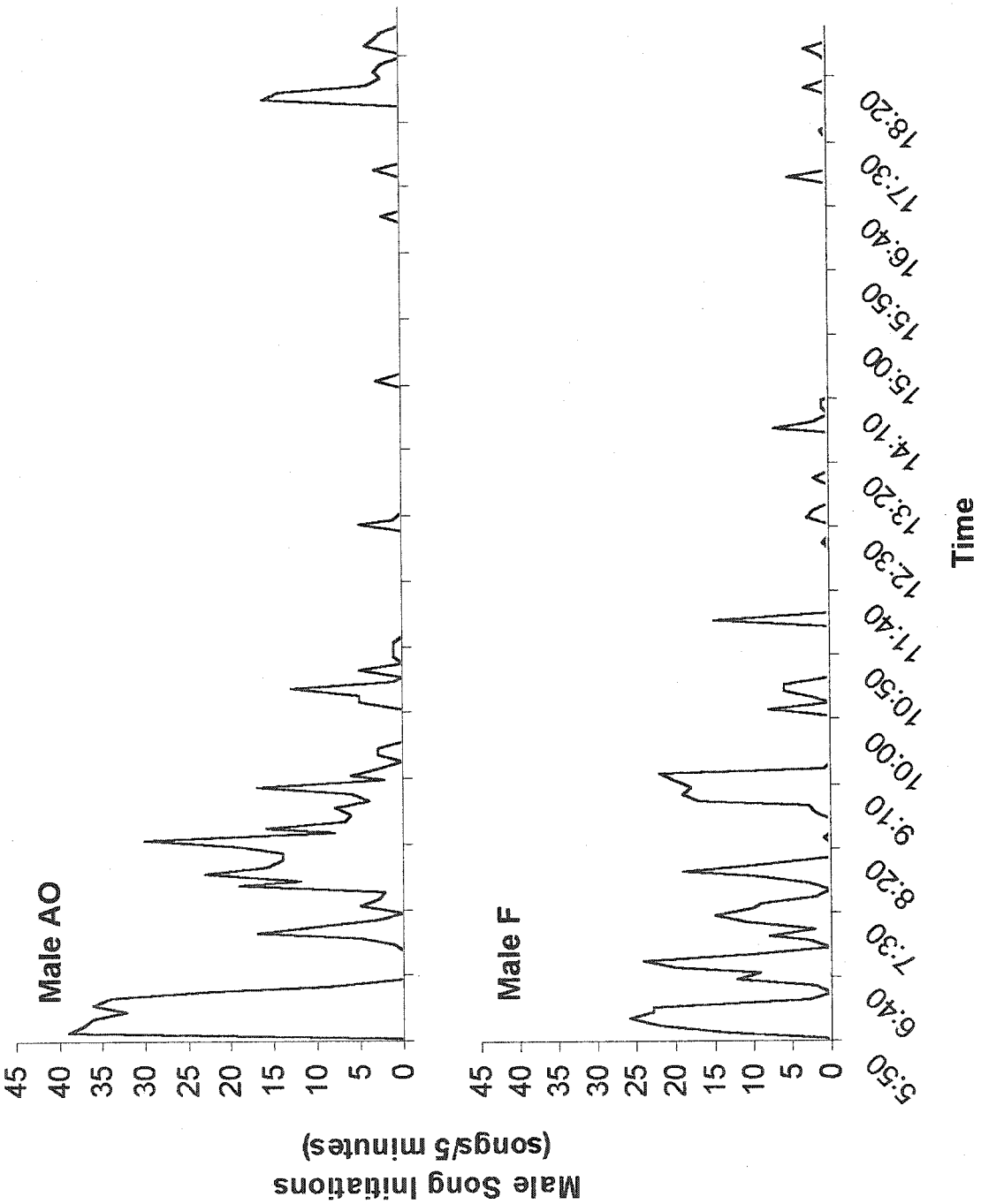


Figure 1.9 Rates of male song initiation from two males during the wet season. Both males sing at high rates at dawn, and sing in bursts throughout the morning. Song levels are low in the afternoon, when heat and rain are most intense. Both of these males sang at slightly elevated levels before dusk.



Chapter II: Duet song and sex roles during territory defense in the black-bellied wren

INTRODUCTION

Avian vocal duetting is especially common in species in which a mated male and female defend a shared territory throughout the year (Farabaugh 1982). Though the adaptive significance of this behavior varies among species, sexes (Levin 1996b), and contexts (Sonnenschein & Reyer 1983), simulated territory intrusion evokes heightened levels of duet song in many species of year-round territorial birds. Pairs of robin chats (*Cossypha heuglini*) duet when presented with conspecific mounts and playback (Hultsch & Todt 1984). Female bay wrens (*Thryothorus nigricapillus*) initiate song more often and are more likely to form duets by answering their mates during conspecific versus heterospecific playback (Levin 1996b). Magpie-lark (*Grallina cyanoleuca*) pairs coordinate a higher proportion of their songs to form duets during conspecific playback versus prior to playback (Hall 2000). Similar results have been found for stripe-backed wrens (*Campylorhynchus nuchalis*, Wiley & Wiley 1976), usambiro barbets (*Trachyphonus usambiro*), slate-colored boubous (*Laniarus funebris*), and striped kingfishers (*Halcyon chelicuti,* Wickler 1976). In all of these experiments, an elevated level of duet song during playback was associated with other measures of agonistic response (e.g. flights, approach to speaker).

Clearly pairs duet more during simulated territorial intrusions, but what is the adaptive significance of coordinated song to individual birds? One obstacle to answering this question is our poor understanding of territory defense in year-round territorial birds

(see Hall 2000, Table 5 for a review of duetting and joint territorial defense). Several studies have reported a strong same-sex bias in territorial defense (Greenberg & Gradwohl 1983; Freed 1987; Levin 1996b; Morton & Derrickson 1996; Hall 2000; Bard et al. 2002; Seddon et al. 2002). The evidence presented in such studies typically shows that birds respond more strongly to intra-sexual versus inter-sexual solo song playback. All of these studies, however, also revealed that mated birds respond physically (e.g. by approaching the speaker) to opposite-sex playbacks. It has been suggested that this apparent inter-sexual territory defense represents inter-sexual protection against infanticide (Freed 1987) or a means of mate retention when unattended individuals are likely to advertise for a new mate (Morton & Derrickson 1996).

I developed a simple model that predicts the conditions under which inter-sexual territory defense should occur. The model assumes strict social monogamy; either an intruder is rebuffed or it replaces the same sex territory holder. Consider the case in which a solo female intrudes upon a mated pair's territory. The paired male will have a lifetime fitness of V_1 if he keeps his current mate and a fitness of V_2 if the intruder becomes his mate. If the male does not attempt to drive the intruding female from his territory there is a probability p that she will achieve residence on the territory and become his mate. I assume that if he does help to defend the territory against the intruder he will retain his current mate. Finally, defending the territory against the intruding female imposes a cost C to the male. With these assumptions I can generate a simple model that predicts that a mated male will optimize his fitness by defending his territory against intruding females when

$$V_1 - C > p\,V_2 + (1-p)\,V_1$$

The left side of the inequality represents the fitness payoff of the male if he defends the territory against the intruding female. The right side of the inequality represents his average fitness payoff if he does not defend; the average payoff if the male does not defend will depend on both V_1 and V_2 since either female could potentially occupy the territory after the conflict. The above inequality can be simplified to yield:

$$V_1 - V_2 > C/p$$

This model suggests that a male should defend his territory against an intruding female given the conditions that (a) the male assesses that his fitness with the current mate would exceed his fitness with the intruder and (b) the cost of inter-sexual territory defense is sufficiently low. Of course, one could apply the model to a mated female during a solo male intrusion to make predictions about inter-sexual territorial defense by females.

For species in which one sex is larger than the other, it is reasonable to expect that the larger sex will pay lower costs for inter-sexual territoriality than the smaller sex. Therefore, all else being equal, the model predicts that in species where one sex is larger, the larger sex is most likely to practice inter-sexual territoriality. The model also predicts increased inter-sexual territoriality when retention of the current mate stands to provide high fitness benefits. This is likely to be the case during the period of nestling and juvenile care if stepparents do not aid in raising the young (as in female black-bellied wrens, unpublished data) or if they commit infanticide (as in male house wrens, *Troglodytes aedon*, Freed 1987).

The model does not address mate following during opposite sex playback as a means of mate retention, though in some cases it may provide a simpler explanation for

the observed pattern of inter-sexual approach to the playback speaker. In the interest of keeping the model simple, I do not consider the cost represented by an injury to the mate who has defended alone. Including such a cost would increase the conditions under which inter-sexual defense is less costly than the alternative. The model applies equally well to a pair of intruders, rather than a single intruder, if we bear in mind that the cost (C) to the focal individual is likely to be greater if it also has to defend against a same-sex intruder. Until now, it has been impossible to address the question of inter-sexual territoriality during simulated pair intrusions since traditional duet playbacks broadcast both male and female duet contributions from a single speaker. I developed a method of broadcasting duet recordings from two sources in order to more realistically simulate a duetting pair.

I conducted song playback experiments on free-living black-bellied wrens, *Thryothorus fasciatoventris*, to address the following questions: (1) How and why do these birds initiate song and answer their partner's songs to form duets during territorial intrusions? and (2) Does either sex exhibit inter-sexual territorial defense?

Male black-bellied wrens are substantially larger than females (all N's >21; $\overline{X}_{mass}$: M=28.0g, F=22.3g; $\overline{X}_{tarsus}$: M=26.7mm, F=24.0mm; $\overline{X}_{wing}$: M=67.7mm, F=63.5mm). Unmated males regularly obtain and hold solo territories. I have no evidence that females naturally acquire or maintain solo territories, nor do I have evidence that older offspring help in the rearing of younger offspring. Social monogamy is the only known mating system in this species.

METHODS

Study population

I performed a series of field playback experiments on 16 pairs of free-living black-bellied wrens near Gamboa, Republic of Panama. Experiments were conducted from May 15 through August 15, 2002, a period that corresponds with the tropical wet season and the approximate middle of the black-bellied wren's breeding season. Four of the pairs lived in the Gamboa Woods, a small (~37 hectare) wood lot surrounded by residential areas on three sides. The remaining 12 pairs lived near railroad tracks that run parallel to the Panama Canal, on its south side. Creation of the railroad generated swaths of second growth and edge forest on both sides of the tracks. Black-bellied wrens are partial to such regenerating and edge habitats (Ridgely & Gwynne 1989). Both study sites were characterized by mixed level forests with dense undergrowth and high densities of tangled woody vines, a preferred foraging substrate.

Prior to the study, permits for conducting song playback experiments and for banding birds were obtained from the Colorado State University Animal Care and Use Committee and from Autoridad Nacional del Ambiente in Panama. Of the 32 birds used in this study, 12 males and eight females were uniquely color banded prior to the onset of experimental manipulation. I banded the remaining four males and five of the remaining eight females prior to the end of the study. Over three field seasons of field observations, I never observed pairs to move together to a new territory. I have observed five instances in which females left (or died) and were quickly replaced, but these were followed by greatly heightened levels of spontaneous duet song. Despite frequent observation periods (at least twice weekly), I did not encounter any drastic changes in the level of spontaneous duet song, so it was unlikely that I misidentified individual birds.

I observed dependent juveniles on 6 of the 16 territories during the 2002 season. The presence of juveniles was unambiguous because males emitted loud 'cream-o-wheat' (F.O. Chapelle cited in Ridgely & Gwynne 1989) calls almost continuously while attending to dependent juveniles (Chapter I). Also, the presence of juveniles is readily apparent from their distinctive *pi-zeet* calls and their grey (rather than white) throat feathers (Ridgely & Gwynne 1989; Stiles & Skutch 1989). During the study, I sexed the birds by morphology and song. Subsequent amplification and visualization of the sex chromosome linked CHD gene with 1237L and 1272H primers (Kahn et al. 1998) from ten of the birds (seven males and three females) confirmed that those individuals were correctly sexed.

Stimuli

All of the recorded vocalizations used as playbacks were obtained from May-August of 2001 and 2002 from free-living birds near Gamboa, Republic of Panama. Songs used as stimuli were recorded during or shortly after stimulating the birds with song playback. During the 2001 season, recordings were made with a Radio Shack omnidirectional microphone (product number 33-3014) mounted in a 45 cm aluminum parabolic reflector and a Marantz tape recorder (PMD 222). During the 2002 season, the recordings used as playback stimuli were made with a Sennheiser omnidirectional microphone (ME62) mounted in a 60 cm Telinga Pro-universal parabola and a Sony Minidisc recorder (MZ-R700). True pitch for the recordings was verified using a tuning fork.

Using the program Real Time Spectrogram (Kay Elemetrics, version 2.3), I digitized the recorded songs at a sampling rate of 44,100 Hz and visually examined sonograms for quality. When choosing recordings, I attempted to maximize signal to

noise ratios and minimize reverberation. I employed Syrinx (John Burt, http://syrinxpc.com/) and Canary's (Charif et al. 1995) cursor defined filters to remove low frequency noise. Filters were never used to remove high frequency noise because I did not want to delete the high frequency harmonics, which have been shown to contribute to sound source localization in this genus (Naguib 1995). After filtration I adjusted the amplitude of the signals so that the maximum amplitude of each signal was the same.

Because my access to computers changed throughout the course of this study, I used both Canary (which runs on a Macintosh platform) and Syrinx (PC) to create stereo duet stimuli. I believe that stimuli made with the two programs are indistinguishable. In this report I describe how to create stimuli using Canary, though the process is similar to the one that I employed using Syrinx.

To overcome the limitations inherent in the use of a single sound source to simulate a paired intrusion (see Introduction), I converted all duet recordings into stereo stimuli (Figure 2.1). This allowed me to broadcast the male and female contributions through separate speakers. Both male initiated duets (MID's) and female initiated duets (FID's) were converted into stereo stimuli. All duet stimuli consisted of three contributions with mates alternating contributions (MFM or FMF). I used Canary to display two identical sonograms of the high-pass filtered recordings. Using the cursor delimited filter; I erased all of the male contributions from one of the copies and all of the female contributions from the other copy. Subsequently, I set the sonogram's clipping levels to the lowest settings that maintained a legible signal. By examining the adjusted sonogram and listening to the signal I determined that the filtering had eliminated the

unwanted signals. I then copied the two files and pasted them into the two channels of a blank stereo recording, maintaining the original temporal relationships among the three contributions. For each duet stimulus, a coin flip determined which channel would carry the female contribution(s) and which the male's.

I am confident that I correctly distinguished male contributions from female contributions when creating stereo stimuli. Male and female contributions differ in timbre and pattern of frequency modulation, so the experienced listener can accurately assign syllables to one or the other sex (Chapter I). Further, duet contributions are identical to solo songs and males typically repeat a song type alone several times before incorporating that song into a duet. Because a given male song type is highly stereotyped I could compare the solo songs just given to the duet songs to identify ambiguous syllables.

All solo songs used in playbacks were high pass filtered in the same manner as the duets. After filtration, duet and solo stimuli were standardized for amplitude and recorded onto Minidisc (Chapter IV). Each Minidisc track contained a single stimulus followed by enough blank space to bring the track to 30 s. I played stereo stimuli through a pair of identical 5 w speakers (Saul Mineroff Electronics, SME-AFS). The speakers were placed face-up on the ground, 8 m apart. They were connected to a single minidisc player via a cord composed of a single male stereo plug leading into two male mono plugs. Solo song playbacks were set up similarly, but required only one speaker and a standard connecting cord.

Playback Trials

I ran stereo duet playback trials from May 29 through July19, 2002, and solo playback trials from June 29 through August 7, 2002. I lack complete data on the black-bellied wren's breeding season, but I observed nests and young juveniles on territories throughout the course of this investigation. All trials began between 0600 and 0830 hours. I avoided playing birds their own vocalizations or the vocalizations of a neighbor, and no stimuli were used in more than one trial. Before each experiment (duet playback or solo playback) I randomly determined which stimulus type a pair would receive first.

A pilot study had shown that black-bellied wrens do not consistently respond to playback if the broadcast speaker is placed haphazardly within the territory with respect to the focal birds, so I employed the following system for placing the speakers. I approached a territory on which I wanted to run a trial and listened for black-bellied wren vocalizations. When a bird (usually the male) was located, I set up the playback speakers at least 15 m inside the territory and 20-30 m away from the bird. I chose areas with sufficient visibility to allow for distance estimates and sufficient vegetation to provide numerous perch sites at varied distances from the speaker(s). In the event that I did not detect one of the birds (usually the female, since I had located the male in order to place the speaker) during the playback, I repeated the trial on another day. If I observed only one bird on the second trial, only the first trial was counted (N=2).

Each trial was preceded by five minutes of observation without stimulus (hereafter the "pretrial period"). During this period I attempted to record the same response variables that I recorded during the playback (see below). Each of the two observers recorded the focal birds' vocalizations as well as his observations throughout

the pretrial and trial periods. My collaborator (D.E. Gammon) made recordings with a Sennheiser omnidirectional microphone (ME62) mounted in a Telinga Pro-universal parabola and connected to a Sony Minidisc recorder (MZ-R700). I recorded using a Sennheiser short shotgun microphone (ME-66) and a Marantz cassette recorder (PMD 222). If, during the pretrial observation period I determined that one or both of the birds were involved in territorial countersinging or nest building, I postponed the trial until the behavior ceased. At the end of the five-minute pretrial period, I began the playback stimulus. We matched playback intensity to the intensity of the vocalizations given by focal birds. The minidisc was set on "one-track repeat" mode so that the stimulus was repeated every 30 s for 5 min. I recorded the following responses for each of the two focal birds: vocalizations, distance(s) from the male and/or female speaker, and distance to the mate. Distance measures were estimated using the 8 m speaker cable as a reference. I updated distances after each change in location ≥1 m.

Each observer made observations on the bird that was closest to him at the time. Care was taken to communicate the location and sex of the animal under observation (when known) to the other observer. Occasionally one of us was able to see both of the birds, and the other could not see either bird. When this happened, the observer with the better vantage point recorded observations for both birds.

Data Compilation

Each trial generated two recordings, which were used to fill in a time line with the events that transpired. I first analyzed the Minidisc recording because this format includes a run time display that can be used to assign a time to each event. The data from the tape recording were then added onto the time line. When our distance estimates

differed, the data from the observer with the better vantage point was used. In the event that it was not clear which observer had a better vantage point, the distances were averaged.

I used the time line to score the following response variables for each bird: song initiations, answers to the mate's songs, closest approach to each speaker, and the distance between the mated birds (hereafter referred to as the inter-bird distance or IBD). We were only rarely able to measure the IBD during the pretrial period; therefore I do not use these data in comparisons of pretrial versus trial behavior. Vocal initiations included all tonal vocalizations that did not immediately follow a vocalization by the focal bird's mate. An answer was any vocalization that immediately followed a mate's vocalization, thus forming a duet. Only one answer was scored for each duet.

The closest approach to the speaker was defined as the minimum distance between the *perched* bird and the speaker. I used the time line to determine the average IBD. I did not want the birds' locations prior to playback to bias this measure, so I did not include the first two minutes of the playback period when calculating average IBD's.

I was interested in the frequencies with which the sexes answered their mates to form duets. I derived answer rates by dividing the number of times an individual answered its mate by the number of initiations by the mate (after Levin 1996b). Derivation of answer rate required that the focal bird's mate initiated a song to which it could respond. Failing this requirement, I logged a missing value.

Statistical Analysis

Most response variables required transformation prior to analysis with parametric statistics. Arcsine transformations were used for percentage data and ln(X+1)

transformations were used for variables possessing large extreme values. All statistical analyses were conducted with Minitab (2000) software. I adhere to the standard alpha level of 0.05, but because sample sizes were small I report p-values where $0.05 < P < 0.10$ as "marginally significant."

I compared male and female behavior prior to playbacks using ANOVA models blocking for the identity of the pair. Two-tailed paired T-tests were used to compare closest approach (as measured from the nearer speaker for stereo duet playbacks), initiation, and answer rate during pre-trial and trial periods.

I used one-tailed paired T-tests to test the hypothesis that birds would approach the same-sex speaker more closely than the opposite-sex speaker during stereo duet playback trials. One-tailed statistical tests were appropriate in this instance because all previous song playback studies have documented a stronger approach to same-sex playback than to opposite-sex playback (see Introduction). Approach distances to the two speakers during stereo duet playbacks were not independent of one another. The paired T-test overcame this problem by subtracting the distance to the opposite-sex speaker from the distance to the same-sex speaker, generating a single variable that described the magnitude and direction of approach bias.

After careful consideration, I chose to conduct univariate, rather than multivariate, comparisons of behavior among treatment types. Some of the measures are correlated with one another, but this does not detract from the suitability of univariate analysis as long as the different measures are understood to represent "different aspects of the response elicited by playback" (McGregor 1992).

Closest approach, number of songs initiated, and answer rate were used as dependent variables for ANOVA models. I constructed ANOVA models using stimulus type, presence of dependent offspring, and an interaction term as treatment factors. If the interaction term was found not to have a significant effect ($P>0.10$) it was dropped from the model. For the sake of clarity, I report these statistics only in those cases where the presence of offspring was found to have a significant effect. If the presence of juveniles was not found to have a significant effect on the results, data were pooled with respect to presence of offspring. In these cases I used two-way ANOVA's to test for treatment effects while blocking for individual identity.

I used multiple regression to explore answer rates in relation to IBD and average distances to the speakers. I did not use a model selection algorithm (e.g. stepwise model selection) because the various spatial variables were non-independent and it was my aim to determine the usefulness of each spatial variable in predicting answer rates while holding all other spatial variables constant.

Since I conducted all of the duet playback experiments prior to beginning solo playback experiments, it was not possible to control for the effects of order of presentation when comparing the birds' responses to duet versus solo playbacks. Accordingly, I did not analyze the data in this manner. During the FID trial on the mated pair F and BG, the male (F) remained over 40m away from the speaker, and his pattern of song suggested that he did not hear the playback. Data from this trial were omitted from all analyses.

RESULTS

Pooling over all pretrial observations, males initiated song at a much higher rate than females ($\overline{X}$ ±SE: males: 2.46±0.32 song initiations/min; females: 0.06±0.04 song initiations/min, ANOVA blocking for pair: $F_{1,93}$=150, P<0.001). Males were marginally more likely to answer their mates to form duets, answering 47.8% of their mates' songs, compared to an answer rate of 16.3% for females (ANOVA blocking for pair: $F_{1,37}$=3.81, P=0.059).

Comparisons to Pretrial Behavior

Birds of both sexes responded strongly to both duet and solo playbacks (summarized in Tables 2.1 & 2.2). Males approached the speaker more closely during all trial types than during control periods (paired T-tests: all P≤0.01). Compared to pretrial levels, male song initiation rates were marginally lower during male song (MS) playback ($\overline{X}$ ±SE: Pre: 14.4±3.0 songs; MS: 5.3±1.3 songs, paired T-test: T_{12}=2.07, P=0.063; Figure 2.2*a*), and marginally higher during female song (FS) playback ($\overline{X}$ ±SE: Pre: 13.6±4.0 songs; FS: 22.1±4.4 songs, paired T-test: T_{12}=-1.882, P=0.087; Figure 2.2*a*) but were not affected by either duet playback. I was not able to compare male answer rates during the pretrial periods with those during the trials because females rarely initiated song prior to playback.

I detected significant reductions in female distance to the speaker during both FS and FID trials (paired T-tests: all P<0.01), but not in MS or MID trials. My failure to detect female approach during MID trials may represent type II error, since missing values reduced my usable sample size to 6, and those samples show a non-significant trend toward reduced distance (paired T-test: T_5=-1.93, P=0.11). Female song initiation rates increased during MS, MID, and FID trials (paired T-tests: all P<0.005; Figure 2.2*b*),

but did not change in response to FS playback (paired T-test: T_{11}=-1.67, P=0.12; Figure 2.2*b*). Females answered the songs of their mates at a significantly higher rate during FS and FID trials (paired T-tests: all P<0.05), but not during MS or MID trials (paired T-tests: all P>0.5). In summary, both males and females responded to all treatment types with a significant change in one or more of the three measured variables.

Response to Stereo Duet Playback

Male response

During both MID and FID trials, males did not approach the male speaker more closely than the female speaker (closest approach by males over all duet playbacks: $\overline{X}$ ±SE: male speaker: 7.0±0.63 m; female speaker: 6.5±0.61 m, one-tailed paired T-tests: MID: T_{16}=-0.02, P=0.49; FID: T_{15}=0.78, P=0.78; Figure 2.3*a*). I detected no difference in the males' closest overall approach to a speaker during MID versus FID playbacks (two-way ANOVA blocking for pair: $F_{1,14}$=1.78, P=0.20). Male initiation rates (two-way ANOVA blocking for pair: $F_{1,14}$=2.37, P=0.15) and answer rates (two-way ANOVA blocking for pair: $F_{1,11}$=1.31, P=0.28) were also unaffected by duet playback treatment type. Taken together, these measures suggest that male response to duet playback is independent of the sex that initiates the stimulus duet.

Female response

During playback of MID's, females did not approach the female speaker significantly more closely than the male speaker ($\overline{X}$ ±SE: male speaker: 7.2±1.1 m; female speaker: 6.7±1.1 m, one-tailed paired T-test: T_{17}=0.57, P=0.29), though the trend was in that direction. During FID playback they approached the female speaker more closely than the male speaker ($\overline{X}$ ±SE: male speaker: 8.5±0.77 m; female speaker:

7.0±1.2 m, one-tailed paired T-test: T_{15}=2.50, P=0.013). The level of bias was not significantly different between treatment types (two-way ANOVA blocking for pair: $F_{1,14}$=0.60, P=0.45), so I pooled over both playback types and found that females approached the female speaker more closely than the male speaker (one-tailed paired T-test: T_{31}=1.85, P=0.037), especially during trials when the female approached both speakers closely (Figure 2.3*b*). Duet type did not affect the females' approach to the speaker (two-way ANOVA blocking for pair: $F_{1,14}$=0.85, P=0.37), song initiation rate (two-way ANOVA blocking for pair: $F_{1,14}$=0.46, P=0.51), or answer rate (two-way ANOVA blocking for pair: $F_{1,10}$=0.39, P=0.54). Like males, females responded to stereo duet playbacks without regard to the sex that initiated the stimulus.

Answer Rate and IBD

I discovered strong negative relationships between the distance separating pair members and the rate at which mate's songs were answered for both sexes, even when simultaneously accounting for both average and closest distance to both of the playback speakers (multiple regression: male: b_{Yj}=-0.54, T_{IBD}=-3.78, P=0.001; female: b_{Yj}=-0.48, T_{IBD}=-3.50, P=0.002; Figure 2.4). Table 2.1 summarizes the results of the stereo duet playbacks.

Response to Solo Song Playback

Male response

The effect of treatment type (MS vs. FS) on males' approach to the speaker depended on whether the male had dependant juveniles on his territory ($\overline{X}$ ±SE: MS w/juv: 12.7±3.8 m; MS no juv: 8.2±0.94 m; FS w/juv: 4.3±0.78 m; FS no juv: 9.9±2.4 m, two-way factorial ANOVA: playback type $F_{1,20}$=5.07, P=0.036, juveniles $F_{1,20}$=0.58, P=0.45, playback type*juveniles $F_{1,20}$=1.18, P=0.016). Specifically, males without

juveniles approached equally close during both treatments, while those with juveniles approached closer during FS versus MS (Figure 2.5*a*). Males initiated song at higher levels during FS versus MS playback ($\overline{X}$ ±SE: MS: 5.3±1.3 songs; FS: 22.1±4.4 songs, two-way ANOVA blocking for pair: $F_{1,11}$=7.96, P=0.017; see also Figure 2.2*a*). Male answer rate was not affected by treatment ($\overline{X}$ ±SE: MS: 0.80±0.12; FS: 0.61±0.18, two-way ANOVA blocking for pair: $F_{1,5}$=0.80, P=0.41; Figure 2.6*a*), but because of several missing values I do not have strong confidence in this result.

Female response

Unlike the males', the females' closest approach was not affected by the presence of juveniles ($\overline{X}$ ±SE: MS w/juv: 14.3±3.2 m; MS no juv: 13.9±1.9 m; FS w/juv: 6.8±2.3 m; FS no juv: 7.9±2.1 m, two-way factorial ANOVA: playback type $F_{1,20}$=9.63, P=0.006, juveniles $F_{1,20}$=0.02, P=0.88, playback type*juveniles $F_{1,20}$=0.17, P=0.68 Figure 2.5*b*). Regardless of the presence of juveniles, females approached the speaker more closely during FS playbacks than during MS playbacks ($\overline{X}$ ±SE: MS: 14.0±1.5 m; FS: 7.5±1.5 m, two-way ANOVA blocking for pair: $F_{1,11}$=17.29, P=0.002; Figure 2.5*b*). Female song initiation rates were unaffected by treatment ($\overline{X}$ ±SE: MS: 2.4±1.0 songs; FS: 2.2±0.86 songs, two-way ANOVA blocking for pair: $F_{1,11}$=0.001, P=0.978; see also Figure 2.2*b*). Females answered their mates at a marginally higher rate during FS trials ($\overline{X}$ ±SE: MS: 0.27±0.09; FS: 0.49±0.08, two-way ANOVA blocking for pair: $F_{1,10}$=4.54, P=0.059; Figure 2.6*b*). Because of the high male initiation rate during FS trials, the doubling of the female answer rate resulted in a dramatic increase in the number of answered male songs (i.e. MID's) during FS versus MS playbacks ($\overline{X}$ ±SE: MS: 1.5±0.54 MID's; FS: 8.5±1.83 MID's). See Table 2.2 for a summary of results from the solo song playbacks.

DISCUSSION

My study addressed the questions (1) How and why do male and female black-bellied wrens initiate song and answer their partner's songs during territorial intrusions? and (2) Does either sex exhibit inter-sexual territory defense?

Males generally initiated songs at a high rate regardless of whether or not a stimulus was playing. Specifically, male song initiation rate was indistinguishable from pretrial levels during duet and female solo playback and marginally lower than pretrial levels during male solo playback (Figure 2.2*a*). Males also initiated song at a higher level during opposite-sex versus same-sex playback. Female song initiation rate was indistinguishable from pretrial levels during female solo playbacks, but increased during duet and male solo playbacks (Figure 2.2*b*).

I did not detect a difference in male answer rate across playback types or between the playback and pretrial periods, but recall that the usable sample was quite small, and male answer rates were consistently high ($\overline{X}$ >60% for all playback types). Females generally answered at a lower rate than males, but their answer rates increased during duet trials and increased marginally during female song trials. Relative to male song playback, female song playback provoked females to answer at a marginally higher level (Figure 2.6*b*). Birds of both sexes were more likely to answer their mates' songs as the distance between them decreased (Figure 2.4).

Having described how black-bellied wrens duet during simulated territorial intrusions, I now consider why they do so. The acoustic mate-guarding hypothesis (Sonnenschein & Reyer 1983; see Smith 1994 for a variation of this hypothesis) has received considerable attention in recent years. The acoustic mate-guarding hypothesis

states that song answering serves to counter the mate-attracting properties of the mate's song. Levin (1996b) suggested that a higher answer rate during same-sex versus opposite-sex playbacks would be evidence of acoustic mate guarding by the answering sex. Though I found that females answer at a higher rate during same-sex playbacks versus opposite sex playbacks, I believe an alternative explanation can explain this and other behavior not accounted for by the acoustic mate-guarding hypothesis.

I propose that birds engage in duets during agonistic encounters in order to prevent intra-pair aggression (Farabaugh 1982), an idea I term the 'identity hypothesis.' This hypothesis is similar to the 'contact maintenance hypothesis,' an old idea (Skutch 1960 p118; Thorpe 1973) that has received little attention in the last twenty years. The contact maintenance hypothesis states that pairs use duet songs to coordinate their foraging and other non-agonistic activities. The identity hypothesis extends this hypothesis by stating that individuals use duet songs to identify and localize their mates during both agonistic and non-agonistic activities. The identity hypothesis builds on well-established work showing that birds can recognize individuals on the basis of song alone (reviewed in Stoddard, 1996) and can localize singing conspecifics (e.g. Morton 1982, Naguib 1995).

Suppose that a territorial male sees a conspecific but does not know whether that individual is an intruder or his own mate. If the male sings, and the territorial female answers in a way that communicates her identity and location, she can prevent the male from directing his aggression at her by mistake. Reversing the sexes yields an equally plausible scenario. Several predictions of this hypothesis were supported by the data gathered in the present study and by previous duetting studies.

Mate identification may explain why many species duet at high levels during song playback (see Introduction). According to this interpretation, birds initiate song to stimulate their mates to answer and they answer to prevent aggression from the mate. This framework generates several predictions. Initiation rates should be high (but not necessarily exceeding pretrial levels) for both sexes during duet playbacks regardless of whether playback is an MID or FID. During solo playback, initiation rates should be high during opposite-sex playback so that mates can locate each other, and answer rates should be high during same-sex playback. All of these predictions were upheld in the present study. Further, an individual's answer rate should be positively correlated with the risk of misdirected attack. This may explain why the IBD was negatively correlated with answer rate in both sexes. Another prediction of the identity hypothesis is that a bird that fails to duet may come into physical conflict with its own mate during a territorial intrusion. Owings and Morton (1998) report that a captive male Carolina wren (*T. ludovicianus*) will attack and kill its mate unless the mate answers the male's song. I observed a similar incident during a single-speaker duet playback to a pair of free-living black-bellied wrens. Both birds were perched near the playback speaker when the male peered at his mate, flew up, seized her by the bill, and wrestled her to the ground. The female freed herself and immediately initiated a duet. After that point, neither bird directed aggression toward its mate.

While promoting the identity hypothesis I have often faced the question, 'why would certain species use coordinated song for identification while others achieve the same result using simple calls?' I believe that certain ecological conditions and evolutionary trajectories might favor identification via coordinated song over individually

distinctive calls. Large IBD's and densely vegetated territories tend to distort quiet, broad-band calls more than loud whistled songs. As a simple alternative, birds might use individually distinctive songs, but among song-learning species (e.g. Oscine Passerines) this type of identifier could be easily copied by another bird, making it evolutionarily unstable. A simple 'duet code,' unique to each mated pair, in which initiating song types are linked to answering song types, would be highly effective in allowing the pair to identify each other reliably. Though an intruder might be able to bluff a few answers, the song initiator could use several different song types in sequence to update the probability that any individual is his mate.

The most compelling evidence that certain species duet for mate identification is that a great number of duetting species use duet codes rather than combining duet contributions at random. Buff-breasted wrens (*T. leucotis*, Farabaugh 1983), bay wrens (Levin 1996a), eastern whipbirds (*Psophodes olivaceus*, Watson 1969), bell shrikes (*Laniarius aethiopicus*, Thorpe 1973), white-crested laughing thrushes (*Garrulax leucolophus*, Souček & Vencl 1975), african drongos (*Dicrurus adsimilis*, Wickler 1976), and slate-colored boubou shrikes (*Laniarius funebris*, Wickler 1976) all exhibit non-random song-type associations and / or pair-specificity in duets. Female black-bellied wrens adhere strictly to individually unique duet codes (Chapter III).

The model that I developed in the introduction section suggests that inter-sexual territorial defense could arise under realistic conditions. The model made the novel predictions that males are more likely than females to exhibit inter-sexual territory defense and that birds engaged in a parenting effort are more likely to defend inter-sexually than those that are not. Both predictions of the model were upheld in this study.

In accordance with the first prediction, stereo duet playbacks revealed that females, but not males, approached the same-sex stimulus more closely than the opposite-sex stimulus (Figure 2.3). Solo song playbacks revealed a similar trend, with females approaching solo female song more closely than male song, while males approached both types of solo song. Additionally, during female song playback males with dependent juveniles approached the speaker more closely than males without juveniles (Figure 2.5*a*). Given that black-bellied wren fledglings require a great deal of parental care and that replacement females do not aid in caring for the juveniles (unpublished data; see Freed 1987 for a detailed description of mate replacement in house wrens) it is unlikely that this strong male response was an attempt to encourage the intruding female to join him on the territory. It is much more plausible that fathers attempt to oust intruding females because it is in their best interest to retain their current mate. I did not find any evidence that the presence of juveniles encourages opposite-sex territoriality in females. Further, females did not approach the speaker during male song playback (Figure 2.5*b*), perhaps because size dimorphism in this species renders females incapable of defending the territory against males without incurring unacceptably high costs.

In conclusion, I wish to emphasize that intra-sex territoriality is generally stronger than inter-sexual territoriality. The results of these playback experiments, however, suggest that inter-sexual territorial defense occurs at non-trivial levels in this species. Its occurrence in males with juveniles is consistent with a model that predicts inter-sexual territory defense can be an optimal strategy in territorial, socially monogamous species. Understanding the roles of the sexes in territory defense promises to improve our understanding of the behavioral ecology of tropical birds in general.

Table 2.1 Summary of results of male-initiated duet (MID) and female-initiated duet (FID) playbacks

Comparison	Male subjects	Female subjects
Trial vs. pretrial		
Distance to speaker	Decreased	Decreased
Initiation rate	Unchanged (always high)	Increased
Answer rate	Not testable	Increased*
MID vs. FID		
Distance to speaker	No effect	No effect
Initiation rate	No effect	No effect
Answer rate	No effect	No effect
Pooled over treatments		
Speaker bias	No bias	Female speaker bias
Answer rate vs. IBD	Negative correlation	Negative correlation

"IBD" represents the distance separating a mated pair.
*Data between male- and female-initiated duet playback treatments were pooled.

Table 2.2 Summary of results of male song (MS) and female song (FS) playback

Comparison	Male subjects		Female subjects	
Trial vs. pretrial	MS	FS	MS	FS
Distance to speaker	Decreased	Decreased	Unchanged	Decreased
Initiation rate	Decreased*	Unchanged	Increased	Unchanged
Answer rate	Not testable	Not testable	Unchanged	Increased
MS vs. FS				
Distance to speaker	With juveniles: closer approach during FS		Closer during FS	
	Without juveniles: no effect			
Initiation rate	Higher during FS		No effect	
Answer rate	No effect		Higher during FS	

*Marginally significant result

Figure 2.1 An example of duet splitting using cursor delimited filters. (a) A high pass filtered three contribution duet is copied twice. This example shows a male initiated duet. (b) Cursor delimited filters are used to remove the female contribution from one copy, leaving only the male duet contributions. (c) The male contributions are then removed from the other copy, leaving only the female contribution. The split songs can now be pasted into the two channels of a stereo track and played through separate speakers without altering their temporal relationship (see text).

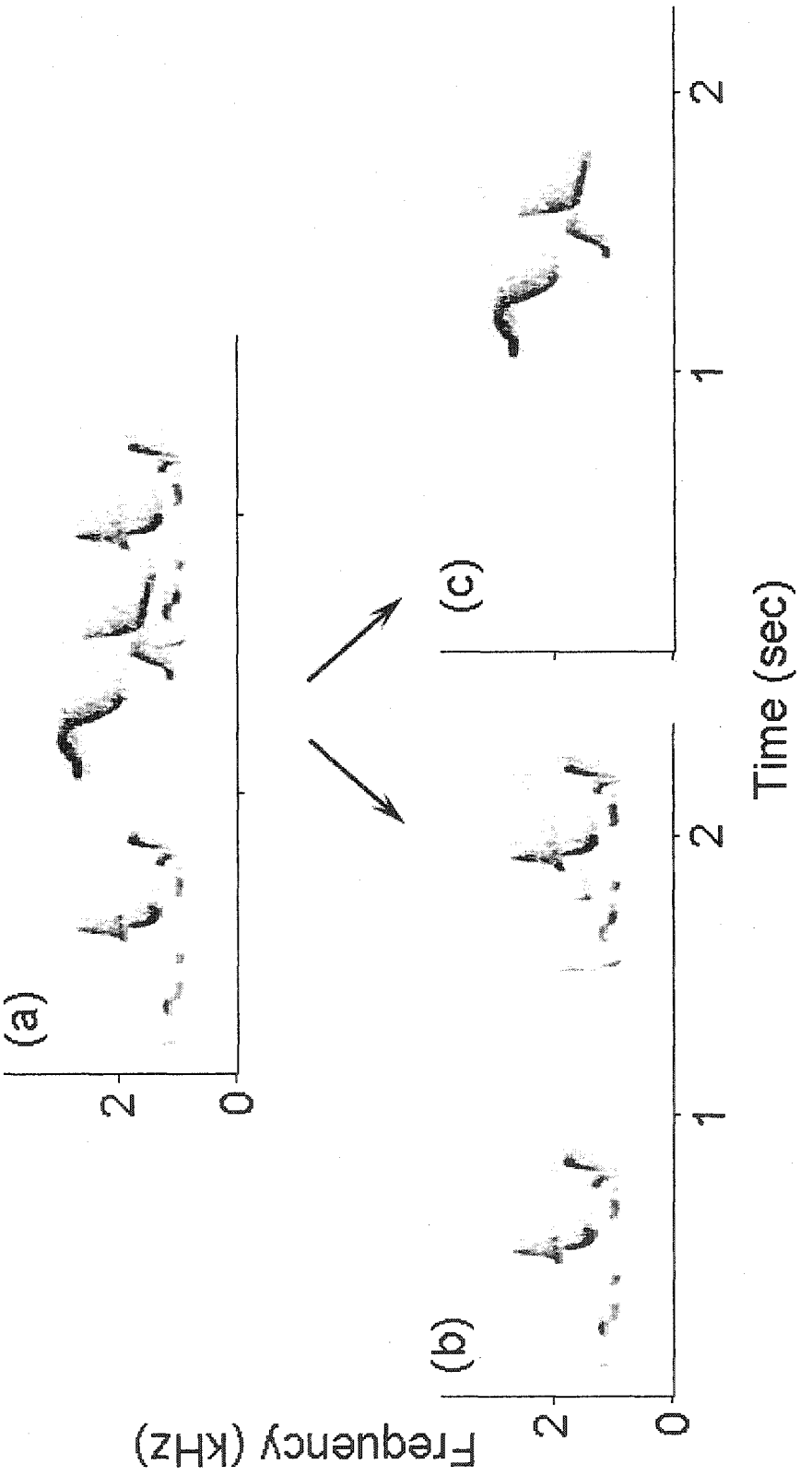


Figure 2.2 Boxplots showing variation in the amount of vocal initiations during both types of solo playback for (a) male and (b) female subjects (FS=female song, MS=male song). I subtracted the number of initiations during the pretrial period from the number of its initiations during the trial period to obtain input values for the boxplot. Medians (horizontal line within the box), quartiles (top and bottom of box), the 0.05 and 0.95 quantiles (tips of vertical whiskers), and extreme data points (asterisks) are shown for each boxplot. Males were more likely to initiate during playback of female than male song, but females gave approximately equal numbers of initiations to both male and female solo playback.

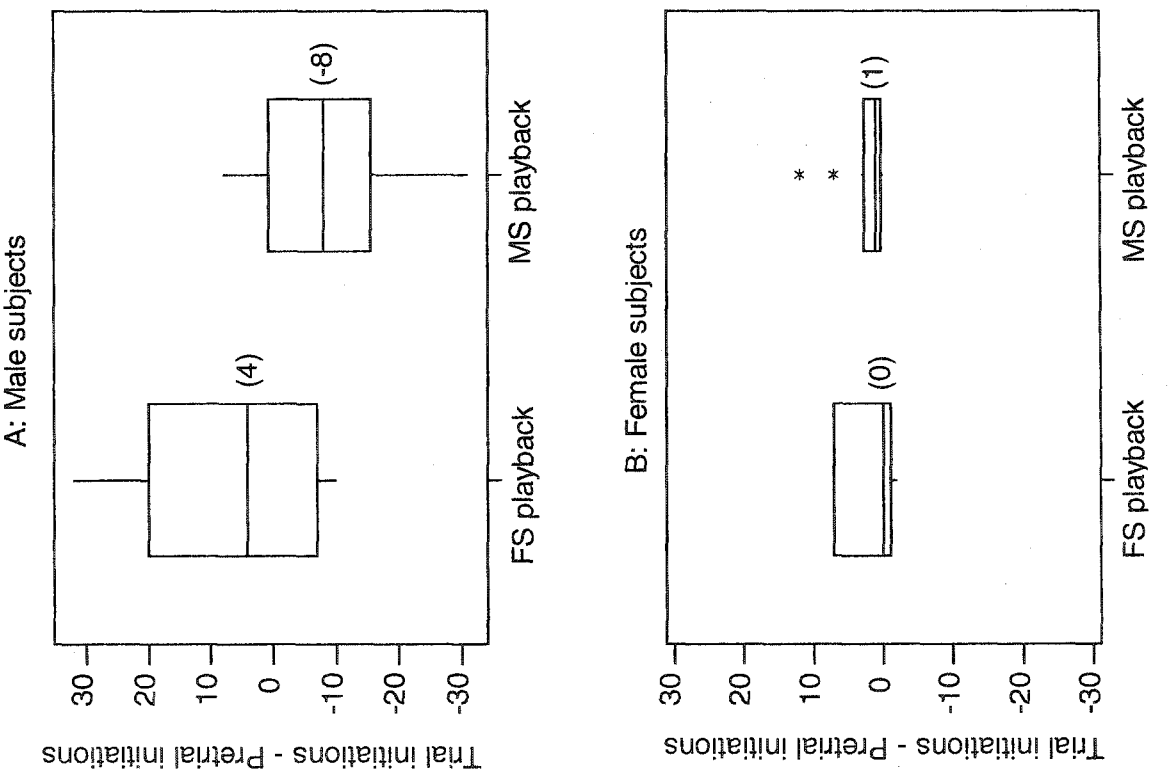


Figure 2.3 Histograms showing same-sex approach bias in (a) focal females but not in (b) focal males during both types of stereo duet playbacks. The x-axis represents the closest approach of an individual to the male speaker (in meters) minus the closest approach of the same individual to the female speaker. In four trials the focal female did not approach within 10m of either speaker; these trials are indicated in black.

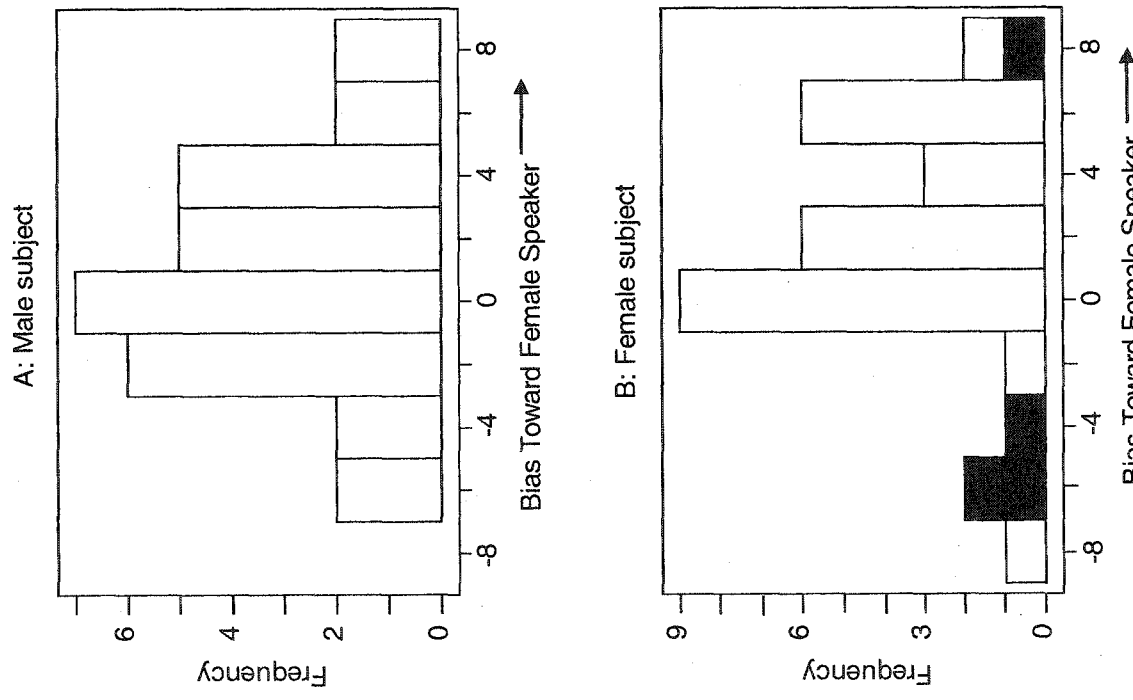


Figure 2.4 Both males (a) and females (b) answer their mates at a higher rate as the distance between mates decreases. Note that the figure shows a simple regression, but the relationship is still significant when distances between the birds and the speaker are included in the regression equations (see text). Data are from both MID and FID trials, so each bird is represented by two points.

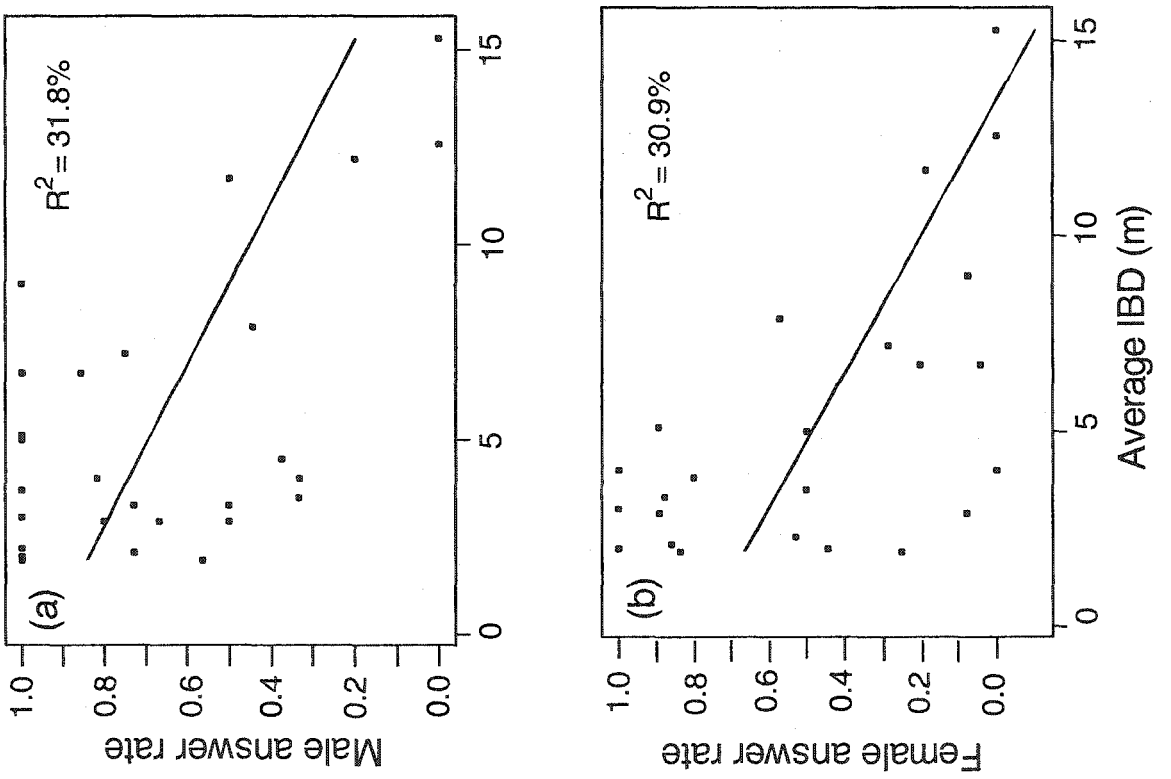


Figure 2.5 Interaction plot showing the closest approach to the speaker for (a) female and (b) male subjects with and without juveniles during male song (MS) and female song (FS) playbacks. Females came closer to the speaker during FS than MS playback, regardless of the presence of juveniles. Males, however, approached more closely during FS trials, but only if they had dependent juveniles.

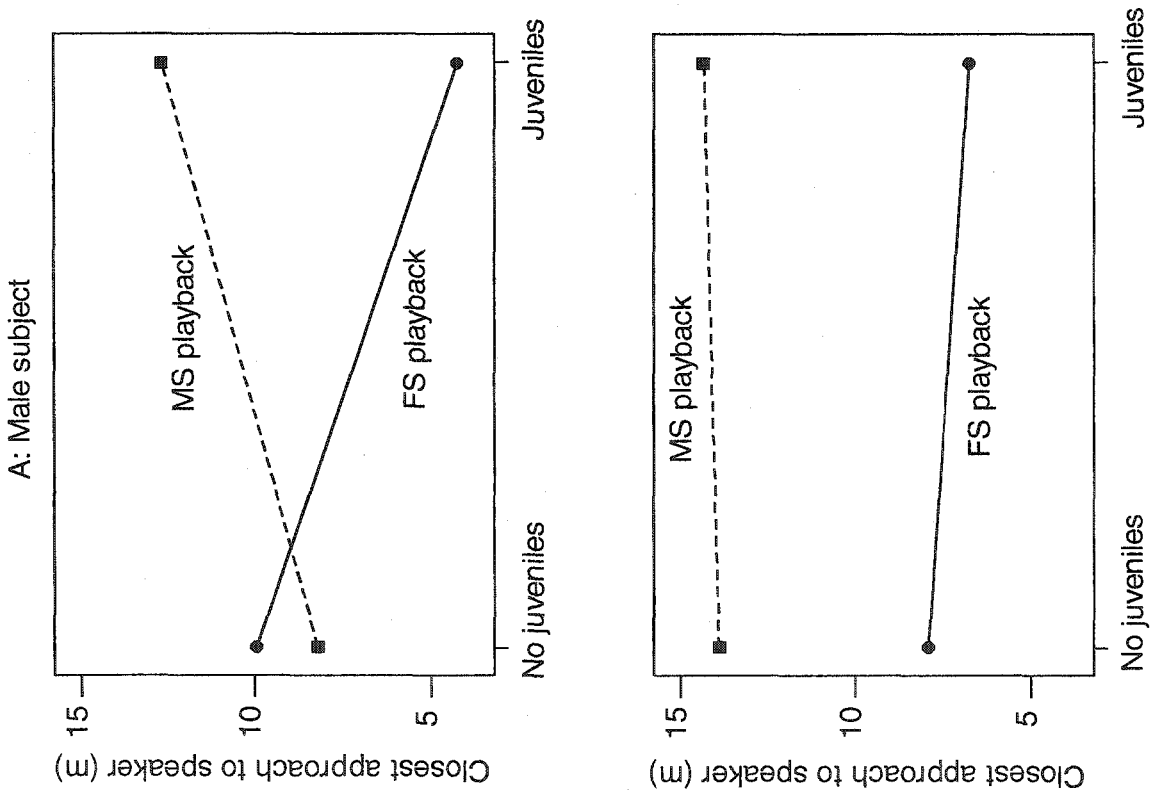
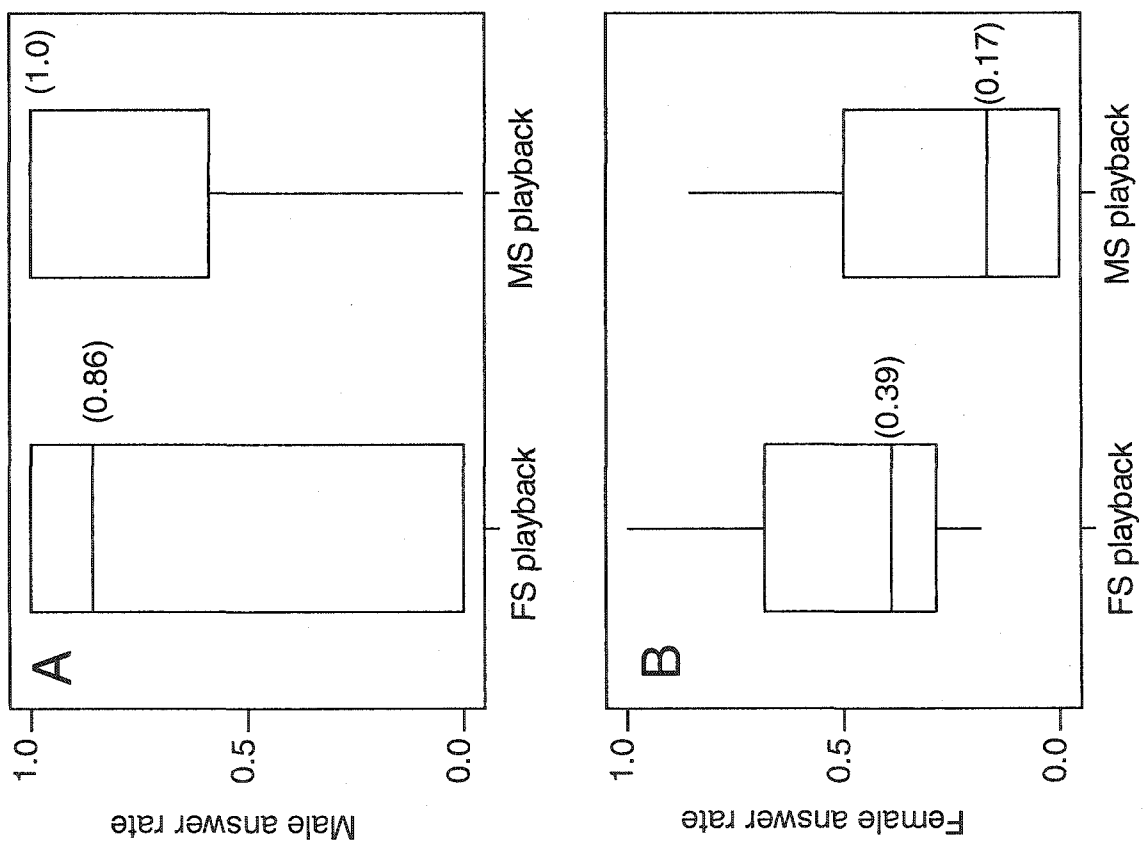


Figure 2.6 Boxplots showing variation in the rate of answering a mate to form a duet during both types of solo playback for (a) male and (b) female subjects (FS=female song, MS=male song). See Fig. 2 legend for boxplot symbols.



Chapter III: The duet code of the female black-bellied wren

INTRODUCTION

In over 200 species of birds, mated individuals coordinate their songs to form vocal duets (Farabaugh 1982). Male and female song types are combined non-randomly in the duets of plain wrens (*Thryothorus modestus zeledoni*, Mann et al. 2003), bay wrens (*T. nigricapillus,* Levin 1988), buff-breasted wrens (*T. leucotis,* Farabaugh 1983), tropical boubou (*Laniarius aethiopicus* Thorpe 1972, Grafe et al. in press), white-crested laughing thrushes (*Garrulax leucolophus* Souček and Vencl 1975), african drongos (*Dicrurus adsimilis,* Wickler 1976), slate-colored boubous (*Laniarius funebris,* Wickler 1976, Seibt and Wickler 2000), and Australian magpies (*Gymnorhina tibicen*, Brown and Farabaugh 1991). The above species represent five families (Payne 2000), suggesting repeated convergence on non-random song type association among duetting songbirds.

A duet code is a set of rules linking the song type an individual hears to the song type that individual uses to answer. In the parlance of Seibt and Wickler (2000), a duet code links auditory stimuli from the 'silent repertoire' with vocal responses from the 'overt repertoire.' Duet codes could provide a mechanistic explanation for the widespread phenomenon of non-random song type associations. Alternatively, non-random song type associations could be the result of both pair members choosing their song type on the basis of a common factor (e.g. location, motivation to fight). I tested for a duet code in female black-bellied wrens (*Thryothorus fasciatoventris*) with a 'karaoke'

experiment, in which female birds sing responses to pre-recorded stimuli of male songs (similar to experiments by Watson 1969, Thorpe 1972).

METHODS

Study Population

All recordings and experiments were conducted in and around Gamboa, Republic of Panama. All birds studied in 2001-2002 were fitted with unique combinations of colored leg bands. Three of the experimental pairs lived in a small (~37 ha) wood lot known as Gamboa Woods. The remaining eight pairs lived on the edge of the 22,000 ha Soberania National Park.

Black-bellied wrens exhibit a life history typical of duetting Passerines: they are socially monogamous and both sexes defend a shared territory throughout the year (Farabaugh 1982). While both sexes defend vigorously against same-sex intruders, males also respond aggressively toward playbacks of female song, especially when the male is involved in a breeding effort (Chapter II). Both sexes initiate song and both answer the songs of their mates. Duet contributions are indistinguishable from solo songs, and any given song type may be used either as a solo song or as a duet contribution. Black-bellied wrens are sexually monochromatic, but both the note timbre and the pattern of frequency modulation of the terminal note are sex-specific (unpublished data). Using genetic sexing (Chapter II), I confirmed these acoustic patterns were confirmed to be ubiquitous, so they were used for sexing birds in the wild.

Stimuli

Duets were recorded from twelve pairs of birds (hereafter 'original pairs') between May and August of 2001 and 2002. Most of the recordings used in this

experiment were obtained during playback experiments or capture attempts. Recordings from 2001 (stimuli for one 'intact' trial and two 'new female' trials) were made with a Radio Shack omnidirectional microphone (product number 33-3014) mounted in a 45 cm aluminum parabolic reflector and a Marantz cassette recorder (PMD 222). Recordings from 2002 (all other stimuli) were made with a Sennheiser omnidirectional microphone (ME62) mounted in a 60 cm Telinga Pro-universal parabola and a Sony Minidisc recorder (MZ-R700).

I used Syrinx (John Burt, http:www.syrinxpc.com/index.html) to generate spectrograms of the duet recordings. For each pair of birds, I noted which female duet contributions answered particular male duet contributions. Among well coordinated duets, there was only one response type for each male song type. These song type combinations were labeled 'expected' combinations.

One high quality recording of each original male song type was used for playback stimuli. If the best version of a male song type was given in a duet, I employed Syrinx's cursor-delimited filter to isolate the male contribution. This filter was also used to eliminate noise below the lowest frequency in the male song. Each male song type was transferred to its own track on a Sony Minidisc (MZ-N1). Using this method, I generated 2-7 male song stimuli for each trial (=3.6 stimuli/trial).

The stimulus set played to each pair contained seven repeats of each male song stimulus. Playing the same stimulus song several times could be considered pseudo-replication (Kroodsma 1989). This design is justified, however, because (a) for a given male, the variation between song types far exceeds the variation within a song type, (b) only high quality stimuli elicit answering, limiting the availability of suitable stimuli, and

(c) nearly half (22/47) of the stimuli were recorded as solo songs; these test directly whether male song type, as opposed to some unmeasured factor, was the variable affecting female response type. Females seldom answer a song type the first time that it is played in a bout, so after randomizing the stimulus order, I re-arranged songs to include more doublets and triplets of each song type. In nature, males sing the same song type 20-200 times before switching types (unpublished data), so this scheme is more realistic than random presentation.

Playbacks of stranger duets were used to simulate a territorial intrusion and thus stimulate the resident female to answer male song stimuli at a high rate. I used seven high quality, high-pass filtered recordings of stranger duets composed of 3-11 contributions. These were recorded to Minidisc for use in the field. A subset of these same seven stimuli was used on each experimental pair.

The karaoke protocol

I conducted the karaoke experiment from March 11-April 24, 2003. None of the pairs used in experiments had nests or dependent juveniles. Experimental pairs were divided into three categories. 'Intact' (IT) pairs contained both members of the original pairs. 'New female' (NF) pairs contained the original male and a new female. 'New male' (NM) pairs contained a new male and the original female. I was careful to observe the leg bands of all of the birds used in experiments at the time of trial. Absence of leg bands on three females was taken as evidence that they were new to the territory, because the prior territorial females were banded, and here is no evidence of band loss in this species. Female AJ was tested as both IT and NF, and female AN was tested as both NF

and NM. In each case the male song types used were different in the treatments, and the trials were conducted on different days.

The playback apparatus consisted of one Sony Minidisc player, two 5 w speakers (Saul Mineroff Electronics, SME-AFS), and cables attached to each speaker. The speakers were placed face up on the ground, 10-16m apart within the territory of the focal pair. I sat between the speakers holding the Minidisc player and the free ends of both cables. My assistant recorded the entire trial, including commentary, using a Sennheiser omnidirectional microphone (ME62), a Sony Minidisc recorder, and a parabolic reflector.

I began each trial by playing stranger duets from the speaker that was farthest from the focal female. This phase of the trial lasted until the female approached the playback area and began duetting with her mate. Once this occurred, I switched to the speaker nearer the female and played male song stimuli in the predetermined order. If the female failed to respond to several male song stimuli in a row, I switched back to duet stimuli from the more distant speaker for a few repetitions. The trial was ended after I played all of the male song stimuli. I occasionally played stimuli too many or too few times. These errors were spread evenly over the experimental groups and appear to have no bearing on the results.

Data analysis

Note shape, timing of notes, and relative frequency (pitch) of notes were consistent among renditions both within and between females and were therefore used to define female song types. The hypothesis that females use a duet code would be rejected if each female's answers were random with respect to male song-type. To test for this, I let the first song type that a female used to answer a particular male song type count as

the "correct" answer for that female for that stimulus. Subsequent answers to that song type were counted as "consistent" if they were the same as the correct answer or "inconsistent" if they were not. For the statistical analysis, I used only those songs that came as song type switches. This ensured the statistical independence of each data point. For example, I would count the answer in the female song sequence, "A, A, (stimulus)-B," but not in the sequence "A, B, (stimulus)-B." The binomial equation was then applied, using 1/(estimated repertoire size of each female) as the probability of a consistent answer given random song associations. Repertoire sizes were underestimated, introducing conservative error. The binomial equation provided the probability that random answering would elicit the observed number of consistent answers for each female. The product of these probabilities represents the probability of achieving the observed number of consistent answers if female black-bellied wrens choose their answers at random with respect to male song stimulus type.

An unpaired Wilcoxon test was used to compare the frequency of expected responses by IT females versus NF females. The NM group was too small to include in statistical analyses.

A randomization test (Manly 1997) was used to determine whether females in the NF group chose the same responses as the original females at a level exceeding chance. The original females' answers were derived from recordings (same as expected answers) and the NF female's answers were taken directly from the results of the karaoke trials. In the randomization test, songs were randomly drawn from each female's known repertoire and counted as hypothetical answers for each of the 19 male songs answered by both the original and NF females. Underestimation of female repertoire size represents a

conservative error. I did not have sufficient data to weight female song-types according to the frequency with which they were sung, so I assumed that females chose song types equiprobably. If females tend to answer many male song types (regardless of which song types they were) with the same female song type, this assumption would be violated, possibly resulting in a Type I error. The number of matched hypothetical choices among original-NF dyads (theoretically ranging from 0-N, where N is the number of dyads that share at least one song type) was scored in each of the 10,000 iterations of the randomization test. This generated a distribution of the expected number of matches given random coding within dyads. The observed number of NF females' expected answers was compared with this distribution to determine the realized probability of the observed pattern of code sharing given random coding within dyads.

RESULTS

Females answered 21.4% (89/415) of male song playbacks comprising 37 of 47 song types used as stimuli (= 2.85 song types answered per trial). These answers were clearly in response to the stimuli, though the delay between stimulus and response was often greater than in naturally occurring duets (Figure 3.1).

Females answered each stimulus type with only a single song type of their own (see discussion of 'double song' below). Of the females' 89 responses, 37 consisted of song switches and followed a prior answer of that particular stimulus type by that female, thus fitting my criteria for statistical consideration. The known repertoire of each female averaged 8.5 song types (min = 4, max =16). Females do not choose song types randomly with respect to male stimuli (Table 3.1; Binomial equation, product of probabilities across all females < 10-34).

Females in the IT and NM groups answered 100% of male songs as expected, while NF females answered only 26% of songs according to expectations (Table 3.2; unpaired Wilcoxon test of IT vs. NF: W=21, N=11, P=0.004). The NF females answered 5 of 19 song types with the expected song; a value matched or exceeded in only 4 of 10,000 iterations of the randomization test (Median of simulated distribution=2, Exact P=0.0008).

'Double song,' in which females consistently alternate between two song types to answer one male song (e.g. "♂-A-♂-B-♂-A") was observed in one of the original recordings and during two trials. Each double song was considered a single answer type. Two females (both in the NF group) each answered two distinct male song types with a single song type of their own.

DISCUSSION

Female black-bellied wrens adhere strictly to duet codes. Because the IT and NM females answered all male songs as expected, I may conclude that adult females do not change their codes over time or after re-mating. The low rate of expected answers from NF females confirms that codes differ among females.

The randomization test revealed that the codes of original and NF females were more similar to one another than would be predicted if coding were random. I can extrapolate this pattern to females in general if I make the assumption that the level of code sharing among original-NF dyads is representative of the level of code sharing among randomly chosen dyads in the population. I see two alternatives to random code generation: codes may be based on more-or-less innate rules pertaining to the structure of the songs, or females may learn their codes. The learning hypothesis is supported by the

findings that juvenile bay wrens (Levin et al. 1996) and slate-colored boubous (Wickler and Sonnenschein 1989) tend to learn their duet contributions from the same-sex parent and juvenile buff-breasted wrens (Farabaugh 1983) and black-bellied wrens (pers. obs.) emit sub-song while their parents duet. I could learn much from a direct study of duet code ontogeny.

It is not yet clear whether male black-bellied wrens use a duet code, but studies of other Thryothorus wrens suggest this is a possibility. In bay wrens, it appears that only males use a duet code (Levin 1988), and in plain wrens both sexes use a code to construct a duet with three sections (Mann et al. 2003). In rufous-and-white wrens (T. rufalbus), song types are combined at random (Farabaugh 1983), so neither sex uses a code. Ultimately, it may be possible to link the evolution of duet-coding in each sex with ecology, morphology, or life history. Such comparative work would compliment the growing body of literature on the adaptive significance of duetting.

Of the many hypotheses about why birds duet, three bear directly on the adaptive function of duet codes: females require males to learn their codes prior to copulation ("coyness," Wickler 1980), codes aid in neighbor recognition (Mann et al. 2003, Grafe et al. in press), and codes aid in mate recognition (Skutch 1960, Thorpe and North 1966, Chapter II). The coyness hypothesis states that newly paired females delay copulation until their mates learn to sing pair-specific duets with the appropriate temporal coordination or song type combinations. Both theoretical and empirical concerns have hindered the general acceptance of this hypothesis. First, it is not clear that coyness could be an evolutionary stable strategy for females. Serpell (1981) argues that waiting to copulate until the code is learned is probably no more costly to the males than waiting

to copulate without learning. Therefore, even if females demand investment prior to copulation, they would gain nothing by waiting for code-learning versus waiting without code-learning. Second, coyness fails to link the duet-code to the widespread elevated use of duet song during territorial conflicts (reviewed in Chapter II). Finally, removal and mate-exchange experiments on bay wrens resulted in no change in individual repertoires or duet precision (Levin 1996a), challenging key predictions of the coyness hypothesis.

Non-random, pair specific song type associations arising from duet codes may facilitate recognition by neighbors (Mann et al. 2003, Grafe et al. in press). Stripe-backed wrens (Campylorynchus nuchalis, Wiley and Wiley, 1977) and Australian magpie larks (Grallina cyanoleuca, Hall 2000) recognize the duets of their neighbours, which would support an argument for an inter-pair function of duet codes if neighbours identify pairs based on whole duets rather than identifying individual pair members based on individual duet contributions. This contingency could be tested by comparing responses to neighbor duets, stranger duets, and artificial duets made from neighbor songs that are not associated in accordance with the neighbor's code.

The identity hypothesis states that by answering according to a code, the responder communicates her identity to the initiator. The black-bellied wren is typical of duetting song birds, in that it is territorial throughout the year and socially monogamous (Farabaugh 1982). This natural history coincides with cooperative (intersexual) territory defense in a variety of avian taxa (e.g. Hultsch and Todt 1984, Appleby et al 1999, Hall 2000, Grafe and Bitz), including the black-bellied wren (Chapter II). Intersexual territory defense is problematic: both pair members stand to benefit by using song to communicate their presence to extra-pair birds (e.g. Langmore 1998), but both could pay

a high cost if their mate mistook their song for that of an extra-pair bird. By communicating identity through her choice of song type, a female can sing without provoking aggression from her mate. There are inherent advantages of this system over simple song recognition. Because of the complex acoustic environment of the habitat in which most duetters live (Farabaugh 1982), long distance signals must be acoustically simple (Bradbury and Vehrencamp 1998) such that inter-individual variation within a song type may not be sufficient for individual discrimination. Further, duet coding allows males to act as Bayesian updaters, "asking" for assurance of identification by switching to a new song type. According to this view, the duet code is an adaptation that allows increased cooperation in year-round territorial, socially monogamous songbirds.

Table 3.1 All females answered each male song type with only a single song type of their own

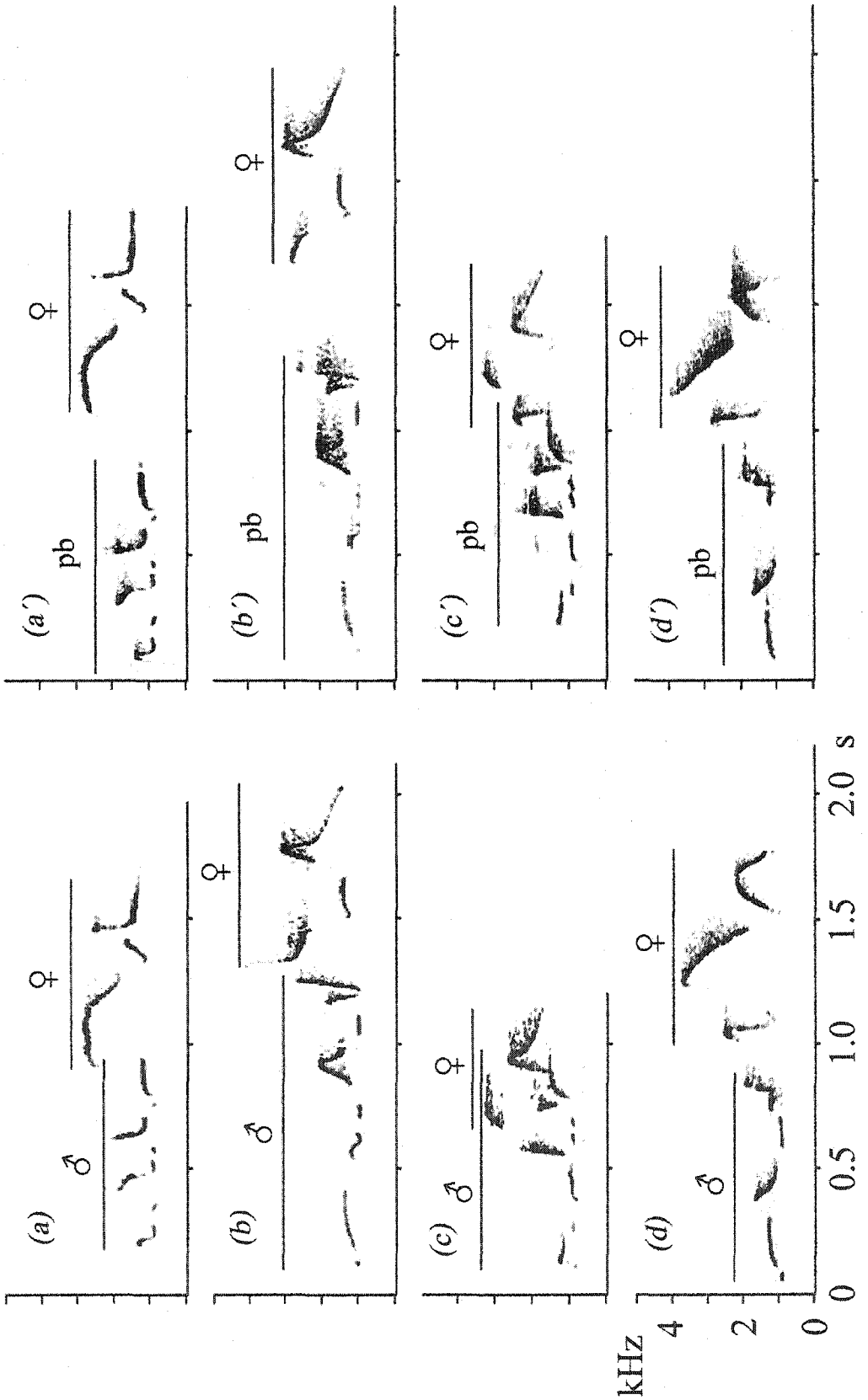
Female	known repertoire	consistent answers[a]	inconsistent answers	individual p(random)
AJ	11	2	0	0.0083
AG	5	1	0	0.20
BI	13	0	0	N/A
AD	5	1	0	0.20
R	11	6	0	5.6E-07
AN	16	6	0	6.0E-08
AS	7	2	0	0.020
EN	5	2	0	0.040
BM	4	9	0	3.8E-06
WM	8	0	0	N/A
BG	9	8	0	2.3E-08
			cumulative p(random)	8.0E-34

[a]Only answers that were songs switches and followed a prior answer to the same stimulus type contribute to this column (see text).

Table 3.2 Females in the 'intact' and 'new male' groups answered all male song types as expected, while females in the 'new female' group chose many unexpected answers

experimental group	female	male song types answered as expected	male song types not answered as expected	p(exp.)
Intact	AJ	2	0	1
	AG	3	0	1
	BI	2	0	1
	AD	1	0	1
	R	4	0	1
New Female	AJ	1	2	0.3
	AN	2	3	0.4
	AS	0	2	0
	EN	0	2	0
	BM	2	2	0.5
	WM	0	3	0
New Male	AN	3	0	1
	BG	3	0	1

Figure 3.1 Examples of naturally occurring duets (a-d) and their karaoke duet counterparts (a'-d'), from both IT pairs (a&b) and NF pairs (c&d). All of the karaoke duets shown here were counted as "expected answers." Male (♂), Female (♀), and playback (pb) contributions are labelled. The delayed onset of female song in some karaoke duets (a', b', and c') may result from females' inability to quickly track the high rate of male song switching employed in the protocol.



Chapter IV

Are minidisc recorders suitable for bioacoustics research?

INTRODUCTION

This paper addresses the suitability of MiniDisc (MD) digital audio recorders for bioacoustic research. MD technology was developed in the 1980s as a way to store long blocks of digitized sound on a compact, skip-free medium. This was accomplished through ATRAC compression, an audio coding system that compresses compact disc audio to approximately 1/5 of the original size by allocating different amounts of memory (and conversely, accepting different degrees of quantization noise) to each of 52 frequency sub-bands (http://www.minidisc.org, Tsutui et al. 1992). The allocation is based on human psychoacoustics with the most audible sub-bands recorded with the highest fidelity (Tsutui et al. 1992). ATRAC compression results in little or no loss in sound quality to human listeners (Tsutui et al. 1992).

Despite several practical advantages of MD recorders over cassette recorders (see Discussion), MD recorders are rarely used in bioacoustical research. The primary source of reluctance is undoubtedly the Cornell Laboratory of Ornithology's (hereafter CLO) published claim that MD recorders are 'unacceptable for natural sound recordings' (Macauley 2001, as of March 16, 2004). The CLO web page states that sounds containing rapid amplitude modulation (e.g., the trills produced by certain anurans and emberizid sparrows) are distorted through ATRAC compression in a manner that certain

animals, but not humans, may perceive. It goes on to say that ATRAC compression can mask quiet sounds when another louder sound occurs at a nearby frequency. Humans cannot perceive the lower amplitude sounds, but it is unknown if animals can hear them.

I chose to revisit the question of whether MD recorders are suitable for bioacoustical research because ATRAC technology has progressed substantially since the CLO tests. Furthermore, statements about the absolute quality of MD recordings may not be as useful as comparisons between MD recorders and their most widely used alternative, cassette recorders.

I used bioacoustical techniques to quantify and compare various types of distortion introduced by MD and cassette tape recordings. First, I tested all units for artifactual variations in pitch and power because all tape recorders are known to distort sound in these ways (Wickstrom 1982, Kroodsma et al. 1996, Jiang et al. 1998). Second, I compared the abilities of the two kinds of recorders to reproduce natural sounds accurately. Third, I tested the CLO claims that MDs distort trills and fail to reproduce low amplitude signals when a high amplitude signal occurs at a nearby frequency. Finally, I discuss the practical advantages and disadvantages of the two kinds of recorders and offer recommendations for their use. I focus on bird vocalizations since that is my area of expertise, although inferences may apply to other natural sounds.

METHODS

My basic methodology can be summarized in four steps: 1) synthesize or record a sound directly onto a computer, 2) transfer the sound to all the recording devices to be tested, 3) transfer the sound back to a computer, and 4) compare the re-recorded versions

of the sound to the original recordings by quantifying the loss of quality caused by each recording device.

Sound generation and recording

Synthetic sounds were designed to reveal various types of recording distortion. I used the programs Multi-Speech (Kay Elemetrics Corp., Model 3700, Version 2.3, Lincoln Park, NJ) and Goldwave (Version 4.26, http://www.goldwave.com/, St. Johns, Newfoundland) to synthesize three waveforms, (Figure 4.1*a- c*): (*a*) a sine wave at 2000 Hz, (*b*) a sine wave that increased in pitch linearly from 20-15,000 Hz in 10 sec with a 0.10 second-delayed echo at 1% of the signal volume, and (*c*) a white noise 'trill' with 10 notes each of durations 0.1, 0.05, and 0.03s. All synthetic sounds were generated at a sampling rate of 44,100 Hz and saved as wave files.

Natural sounds were recorded with a Sennheiser microphone (ME62) connected to the microphone input of a laptop computer (Gateway 450SX4 with ESS Allegro PC1 Audio sound card; the same machine was used for all sound transfer). The sounds were sampled at 44,100 Hz and saved as wave files using the program Syrinx (John Burt, http://syrinxpc.com/). I used four, high quality, unfiltered recordings: (Figure 4.1*d*) a 'jay' call from a blue jay (*Cyanocitta cristata*), (Figure 4.1*e*) a 'fee-bee' song from a black-capped chickadee (*Poecile atricapillus*, Gammon & Baker, *In Press*), and two short calls from a captive male nanday conure (*Aratinga nenday*) that I call a 'scream' and a 'grunt,' respectively (Figure 4.1*f&g*). Sounds *d* and *e* were recorded near Fort Collins, Colorado, with the aid of a 60 cm Telinga Pro-Universal parabola. Sounds *f* and *g* were

recorded in an anechoic chamber (interior dimensions 80 x 60 x 60 cm, Industrial Acoustics, Co.)

Sound transfer

All sounds *a-g* were transferred from the computer to five different recording devices: a new (unused) Marantz PMD-222 cassette recorder (NMAT), a two year old Marantz PMD-222 (OMAT), a 9 year old Sony TCM-5000EV cassette recorder (OSAT), a new (unused) Sony MZ-N10 MD recorder (NMD), and a one year old Sony MZ-N1 MD recorder (OMD). The OMD unit compresses sound with ATRAC Type-R, while the NMD unit uses ATRAC Type-S. Version appellations are based on both the microprocessor and the compression algorithm, and so can not be compared linearly (http://www.minidisc.org). Nevertheless, the newer machines are advanced relative to the machines tested by CLO, which used ATRAC Version 2 (http://www.minidisc.org). Other than the two new machines, I have no records of the amount of use of the recorders, although all had received regular use. All used recorders were cleaned thoroughly prior to these tests. The cassette recordings were made on new TDK Type II high bias cassette tapes, and the MD recordings were made on new Memorex minidiscs. A 60 cm Radio Shack cable ran from the 'headphone out' jack on the computer to the 'line in' jack on each device. Even though all of the recorders were set to 'automatic gain control,' it was necessary to adjust the computer's output levels to avoid clipping. For each cassette recorder, I played sound *a* (Figure 4.1*a*) and adjusted the computer's output level until the maximum volume registered by the VU meter on the cassette recorder was slightly below the red zone. MD meters are digital and I adjusted the output of the computer signal until each MD meter displayed a maximum of four bars (as

recommended by http://www.minidisc.org). Sounds were then recorded from the devices back to the computer. A 60 cm Radio Shack cable ran from the 'line out' jack of the device to the 'line in' jack on the computer. I played sound *a* and adjusted the volume on each device to the highest level possible without overloading Syrinx (as evidenced by red volume readings). Each sound was recorded to its own wave file at a sampling rate of 44,100 Hz.

Comparing original and re-recorded sounds

Pitch and amplitude fidelity

Sound *a* (sine 2000 Hz) was chosen for this analysis because the energy in this signal is concentrated near the frequency of peak sensitivity for the avian ear (e.g. Dooling et. al 1978). I used Syrinx to trim each version of sound *a* to 2s. I then used the 'Save Features' function in the program Sound Analysis (version 3.21), window size=512 points, FFT size=1024, all other settings at 'default;' Tchernichovski et al. 2000; Tchernichovski & Mitra 2001) to sample the peak frequency and power every 1.4ms. I ignored the first 10 samples and last two samples from each waveform, because some of these contained extreme values that I attribute to computer software trimming artifacts. I then calculated the mean and variance in pitch and power over the remaining 1428 samples from each version of the sound.

Reproduction of natural sounds

This analysis relied on two techniques for the comparison of complex sounds (Baker and Logue 2003) to test for overall recording fidelity: Sound Analysis's 'accuracy' measure and Canary's (Version 1.2, Charif et al. 1995) spectrogram cross-correlation (SPCC). Sound Analysis uses multi-taper spectral analysis to represent

sounds as sharply defined contours on a time-frequency display. The program divides the sounds into small segments and derives values of four biologically relevant features for each segment (Fee et al. 1998, Tchernichovski et al. 2000, Baker et al. 2003, Baker & Logue 2003). The four features are: Wiener entropy (randomness of sound), spectral continuity (the continuity of element contours over time), pitch (the fundamental frequency), and frequency modulation (the slope of the contour traces). I conducted pair-wise comparisons between original and re-recorded versions of sounds *d-g* (natural sounds) as well as comparisons of each original recording versus itself. I selected 'overall' comparison rather than 'chunks', because the former forces syllable order to be conserved. These analyses generated 'accuracy scores' representing the mean similarity (in terms of the four features) of the segments between the two sounds being compared. Accuracy scores range from 0-100, where 100 represents maximum similarity.

Using the SPCC function of Canary, I compared the re-recorded versions of sounds *d-g* to the original recordings. SPCC quantifies the similarity of two sounds by generating normalized spectrograms of the sounds. The two spectrograms are then compared in successive steps of overlap along the time axis. The similarity score that is reported represents the overlap of the two spectrograms that results in maximum correlation coefficient. I used batch processing to compare re-recordings with original recordings and to compare each original recording to itself (SPCC settings were: frame length 512 points, time grid resolution 2.9 ms with 75% overlap, FFT size 1024, Hamming window, and clipping level –80 dB). SPCC generates similarity scores ranging from 0-1, where 1 represents maximum similarity.

Masking of low amplitude sounds

I used Multi-Speech to generate FFT spectra (2048 pt) from the point on each version of sound *b* (slide with echo), where the high amplitude signal equals 2kHz. Syrinx was used to make spectrograms of each version of sound *b* (1024 point FFT size, Blackman window). Spectra and spectrograms were examined visually.

Temporal onset and offset

I visualized the waveforms of each version of sound *c* (accelerating white noise trill), in Syrinx. Upon finding artifactual noise in the MD recordings, I measured the duration of the artifacts in Syrinx using the onscreen cursors, which allowed a temporal resolution of 0.1ms. Any visible perturbation in sound pressure level preceding or following a trill element was included in the measure of artifact duration. I measured the amplitudes (RMS) of artifacts and their associated trill elements in Multi-Speech (window size=32 points). The difference between the trill elements and the artifacts (in dB), defines the signal to noise ratio (after Bradbury & Vehrencamp 1998, p. 35). I used SPSS 11.0 for Windows (SPSS Inc. 2001) to construct two-way factorial ANOVA models testing for the effects of the recording unit (NMD vs OMD) and the duration of the notes on the signal to noise ratio and the duration of the offset artifacts.

The results of this analysis prompted further questions about the effect of signal frequency (pitch) on the generation of artifacts. To test for a relationship between these factors, I used Multi-Speech to generate a sine wave 'trill' consisting of four 0.05s notes at each frequency 75, 150, 300, 600, 1200, 2400, 4800, 7200, and 9600Hz. This trill was recorded onto the NMD recorder, and transferred back to the computer. I employed the methods described above to measure the duration of the artifacts and the signal to noise ratio for each trill element.

RESULTS

Pitch and amplitude fidelity

The MD recorders reproduced the pitch of the sine wave accurately whereas the cassette recorders altered the mean pitch by 9-80Hz (Table 4.1). The MD recorders did not introduce any detectable variation in pitch over time, but the cassette recorders introduced substantial amounts of variation in pitch (Table 4.1). Additionally, the cassette recorders introduced more variation in power than did the MD recorders (Table 4.1).

Reproduction of natural sounds

When comparing original sounds against themselves, both Sound Analysis and SPCC delivered maximum or near maximum similarity scores (Table 4.2). According to both methods of analysis, the NMD unit reproduced all sounds with higher fidelity than any of the other units (Table 4.2). The OMD ranked second (in terms of mean similarity score) according to the Sound Analysis accuracy measures, but it ranked fourth (behind the OMAT and NMAT) according to the SPCC similarity measures. The OSAT delivered the poorest fidelity according to both methods of analysis.

Masking of low amplitude signals

The low amplitude signal in sound *b* (slide with echo) was clearly visible in both MD recordings, and was represented at appropriate amplitude relative to the high amplitude signal (Figure 4.2). In contrast, the low amplitude signal was masked by noise in many parts of the cassette tape recordings (Figure 4.2). To ensure that this result was not caused by inappropriate volume settings during sound transfer, I produced several recordings across a range of volume settings on both the computer and the NMAT

recorder. These recordings all contained substantial noise masking the low amplitude signal.

Temporal onset and offset

Examination of the white noise trill recordings revealed that both MD recorders introduced artifacts immediately before and after the trill elements (Figure 4.3). Artifacts were found with every note, included a broad range of frequencies, and were variable in amplitude and duration. The onset artifacts were generally <1 ms in duration. The duration of the offset artifacts was greater in the NMD machine versus the OMD machine ($\overline{X}$ ±SD: NMD: 8.9±1.6 ms; OMD: 5.6±2.7 ms), but artifact duration was not affected by the trill element duration (Two-way ANOVA; machine: $F_{1,54}$=31.23, P<0.001; note duration: $F_{2,54}$=0.045, P=0.96; interaction of machine X note duration: $F_{2,54}$=0.20, P=0.82). Onset artifacts were too brief to obtain accurate amplitude measures, but were clearly much quieter than trill elements (Figure 4.3). Offset artifacts were also lower in amplitude than trill elements. The signal to noise ratio varied between the two machines ($\overline{X}$ ±SD: NMD: 19.9±6.7 dB RMS; OMD: 15.14±4.7 dB RMS), but was not affected by the duration of the note (Two-way ANOVA; machine: $F_{1,54}$=9.69, P=0.003; note duration: $F_{2,54}$=0.36, P=0.70; interaction of machine X note duration: $F_{2,54}$=0.36, P=0.70).

Cassette recorders did not produce periodic artifacts, but they did produce a spurious increase in pressure after each syllable termination that decreased monotonically to the zero level (Figure 4.3). These monotonic declines appear as low frequency noise on a spectrogram.

The NMD recording of a trill composed of pure tones (sine waves) of varying frequency revealed that for tones <1200Hz, the offset artifacts approached a monotonic

return to the zero level, with little periodicity (Figure 4.3). These artifacts are similar to the offset artifact introduced by cassette recorders in response to white noise (compare Figure 4.3*b*&*d*). Artifacts following low pitched trill elements were longer and of greater relative amplitude than those following higher pitched tones (Figure 4.4). The 1200Hz tones were followed by semi-periodic artifacts (Figure 4.3*e*). Above 1200Hz, the artifacts were periodic, relatively short (average=8.0ms), and quiet (Figure 4.4; average signal to noise ratio=16.9dB RMS).

DISCUSSION

Both cassette recorders and MD recorders distort sounds in ways that may influence bioacoustic research. In most respects, MD recorders reproduce sounds as well as or better than professional grade cassette recorders. Compared to cassette recorders, MD recorders introduce less variation in amplitude and frequency, reproduce fundamental frequencies with greater accuracy, and add much less noise.

According to both measures of sound similarity, the NMD recorder reproduced all four natural sounds at higher fidelity than any of the other units. According to the similarity scores generated by Sound Analysis, the OMD recorder ranked second, outperforming all of the cassette tape recorders. Sound Analysis is highly effective at characterizing similarity among several frequency rich natural sounds like three of the four used in this study (Baker and Logue 2003). According to SPCC analysis, the OMD unit was outperformed by the two Marantz cassette recorders. With a small sample of recorders, it is impossible to determine whether this discrepancy between the two MD recorders is attributable to differential wear or to some other attribute of the machines, such as the ATRAC compression version (OMD: Type-R; NMD: Type-S).

I found mixed support for the claims regarding MD recording quality. On the one hand, I reject the claim that MD's fail to reproduce low amplitude signals when a high amplitude signal occurs at a nearby frequency (Macauley 2001). To the contrary, I found MD recorders to be effective at reproducing both signals, while cassette recordings obscured the quieter signal in noise. On the other hand, I found support for the CLO claim that MDs distort signals with rapid amplitude modulation. Specifically, I found that MD recorders generate artifactual variation in sound pressure levels following rapid signal offset. While the duration of the recorded signal appears to be unimportant in determining the duration or relative amplitude of these artifacts, the signal's frequency affects both measures. At low frequencies these artifacts are non-periodic, and thus unlikely to be perceived as a continuation of the signal by either researchers or test subjects. Cassette recorders introduce similar non-periodic artifacts at the rapid offset of sounds. Recordists should be aware that these non-periodic artifacts for both types of equipment appear on spectrograms as low frequency noise. The offset artifacts introduced by MD become shorter, quieter, and more periodic as the frequency of the signal increases. Because of their low amplitude, these artifacts are unlikely to affect researchers' ability to make fine scale temporal measurements, but they may be perceptible to animals in playback experiments. While cassette recorders also introduce artifacts at the rapid offset of a sound, these are non-periodic, and thus unlikely to be perceived as a continuation of the signal by either researchers or test subjects. Recordists should be aware, however that non-periodic artifacts such as those generated by cassette recorders (and MD recorders in response to low frequencies) appear on spectrograms as low frequency noise.

I have only limited knowledge of how animals may perceive recordings from MD and cassette recorders. Several types of distortion introduced by cassette recorders, but not MD recorders, are likely to be perceived by animals. For example, a number of songbird species (e.g., field sparrow, *Spizella pusilla*, Nelson 1988; white-throated sparrow, *Zonotrichia albicollis*, Hurly et al. 1990; Carolina chickadee, *Poecile carolinensis*, Lohr et al. 1991; veery, *Catharus fuscescens*, Weary et al. 1991; black-capped chickadee, Weisman and Ratcliffe 1989) perceive changes in absolute and relative pitch. I do not know whether animals can perceive the temporal artifacts introduced in MD playbacks, but in psychophysical experiments that use continuous sounds interrupted by silent gaps of variable duration, some birds (e.g. Dooling et al. 1978) and mammals (Giraudi et al. 1980) can detect gaps of substantially shorter durations than these artifacts.

Psychophysical experiments inform us of the capabilities of animals to distinguish among various features of sound signals. Often, such studies reveal capacity for fine-scale discriminations (e.g., Dooling 1982, Lohr & Dooling 1998, Dent et al. 2000), but these results must be considered in light of mitigating factors. For example, the well-known "just noticeable difference" (JND) between two sounds that can be revealed in psychophysical experimentation may tell us little about the "just meaningful difference" (JMD) to the animals themselves (Nelson & Marler 1990). In field recordings or playbacks of natural sounds, the environmental noise and degradation of the sound between source and receiver would likely overwhelm many of the fine-scale differences I have illustrated in my comparisons among recording devices. A study examining animal

perceptual discrimination capacities for the artifacts introduced by different recording devices could benefit the field of bioacoustics.

Minidisc recorders offer several practical advantages over cassette recorders. MD recorders are typically less expensive than cassette recorders. While most cassette recorders are relatively bulky and must be carried over the shoulder, most MD recorders can fit into a shirt pocket. Extreme temperatures and low battery power can alter tape speed and consequently pitch in cassette recordings, but they have no effect on MD recordings. Since the laser head used to read and write MD recordings does not actually touch the disc itself, there is less cleaning and maintenance involved, and MD signal quality does not degrade with many uses or in extreme temperatures. I have played a single MD stimulus thousands of times with no perceptible change in signal quality and have used MD to record and broadcast sounds in a variety of environmental conditions: from winter in Colorado to the wet season in Panama. Random access to discrete track allows for easy record keeping and quick access to sounds. Tracks can be labeled with alphanumeric characters and (in some models) an automatic time/date stamp. Higher end MD recorders can record to a buffer, allowing the recordist to capture sounds that occurred a few seconds before releasing the 'pause' button.

MD technology allows research techniques that are not available to cassette users. For example, one can record a sound stimulus followed by the desired duration of blank space, and set the machine on one-track-repeat mode to emulate a tape loop of any duration, and the signal never degrades. These units also work well in interactive playback experiments, wherein the experimenter controls the timing of the playback stimulus (e.g. the Karaoke experiment described in Chapter III). MDs record in stereo,

and so can be used for stereo playbacks (Chapter II). Unlike stereo cassette tapes, however, MD recorders do not 'cross-talk' from one channel onto the other. The sound editing features of MD recorders allow researchers to add or delete track marks at specific points during sound recordings, as well as move or delete the tracks themselves. Using these editing capabilities, I have recorded several seconds of birdsong, isolated a desired sequence, and created a novel stimulus while in the field. The entire process – from the bird singing until he hears its own song played back – takes less than two minutes.

Researchers who are interested in MD recorders should consider the practical limitations of these devices. In contrast with most professional grade cassette recorders, most MD recorders do not have a built-in speaker. MD recorders are digital, and thus moisture sensitive. However, I used MD recorders for eleven months of fieldwork in a Panamanian moist forest without significant moisture-related problems. One MD recorder (Sony MZ-R700), having spent several minutes underwater, was opened, dried under a fan, and regained full function.

In conclusion, researchers who require temporally precise recordings of signals undergoing rapid amplitude modulation might consider avoiding MD recorders. Those who need accurate reproduction of pitch with minimum introduction of noise, frequency modulation, and amplitude modulation may safely consider MD recorders and the novel research opportunities they afford. For much of the routine descriptive work in birdsong research, I see no compelling reason to avoid MD recorders.

Table 4.1 The arithmetic mean and variance of pitch and power over 2s of sine wave

Recorder		Pitch (Hz)	Power*
Original	Mean	1984	0.126
	Var	0	1.48E-09
NMD	Mean	1984	0.126
	Var	0	2.69E-09
OMD	Mean	1984	0.126
	Var	0	2.59E-09
NMAT	Mean	2064	0.126
	Var	1153	1.07E-05
OMAT	Mean	1993	0.126
	Var	715	1.4E-05
OSAT	Mean	2054	0.126
	Var	3408	2.09E-06

* Power measurements derived directly from uncalibrated signals are without acoustical units.

Table 4.2 Measures of similarity between re-recorded sounds and original recordings

Sound Analysis

	Scream	Blue Jay	Fee-Bee	Grunt	Average	Rank
Original	100	100	99.99	100	100	
NMD	97.38	94.35	99.30	96.82	96.96	1
OMD	96.88	93.60	98.48	91.09	95.01	2
NMAT	94.94	86.10	94.11	87.7	90.71	3
OMAT	85.82	93.06	95.98	84.63	89.87	4
OSAT	94.62	94.72	88.10	75.44	88.22	5

SPCC

	Scream	Blue Jay	Fee-Bee	Grunt	Average	
Original	1	1	1	1	1	
NMD	0.982	0.984	0.978	0.965	0.98	1
OMD	0.887	0.919	0.899	0.785	0.87	4
NMAT	0.91	0.868	0.818	0.942	0.88	3
OMAT	0.907	0.895	0.862	0.921	0.90	2
OSAT	0.878	0.885	0.845	0.751	0.84	5

Figure 4.1 Spectrogram of the three synthetic sounds (*a-c*) and four natural sounds (*d-g*) used to test recording fidelity. I generated (*a*) a sine wave at 2000Hz, (*b*) a sine wave that increases in pitch with an echo at 1% of the signal volume, and (*c*) an accelerating white noise 'trill.' I recorded (*d*) the 'jay' call of a blue jay, (*e*) a 'fee-bee' song from a black-capped chickadee, and (*f*) 'scream' and (*g*) 'grunt' calls from a nanday conure. All spectrograms use 1024 point FFT size, Blackman window. Note variation in time and frequency scales.

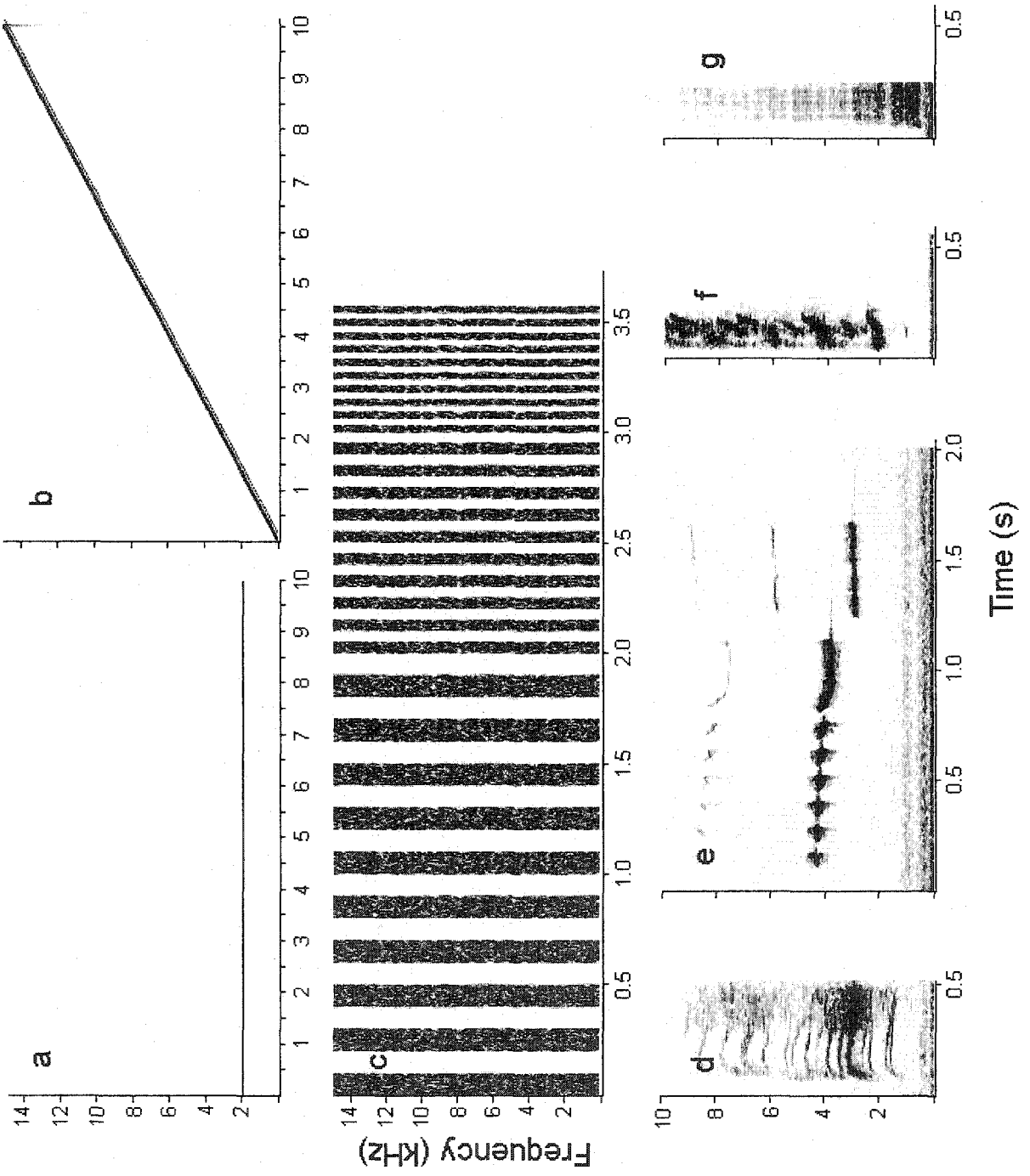


Figure 4.2 Spectrograms and associated FFT power spectra for three versions (Original, NMD and NMAT) of the 'slide with echo' sound showing how MiniDisc recorders preserve low amplitude signals when they are next to high amplitude signals of a similar frequency, while cassette recorders introduce noise that masks these low amplitude signals. Sounds were amplified equally before making spectrograms. Power spectra were created using 2048-point FFT's. Arrows for each spectrogram show where the associated power spectrum was taken, and arrows on each spectra show where the high and low amplitude signals should appear.

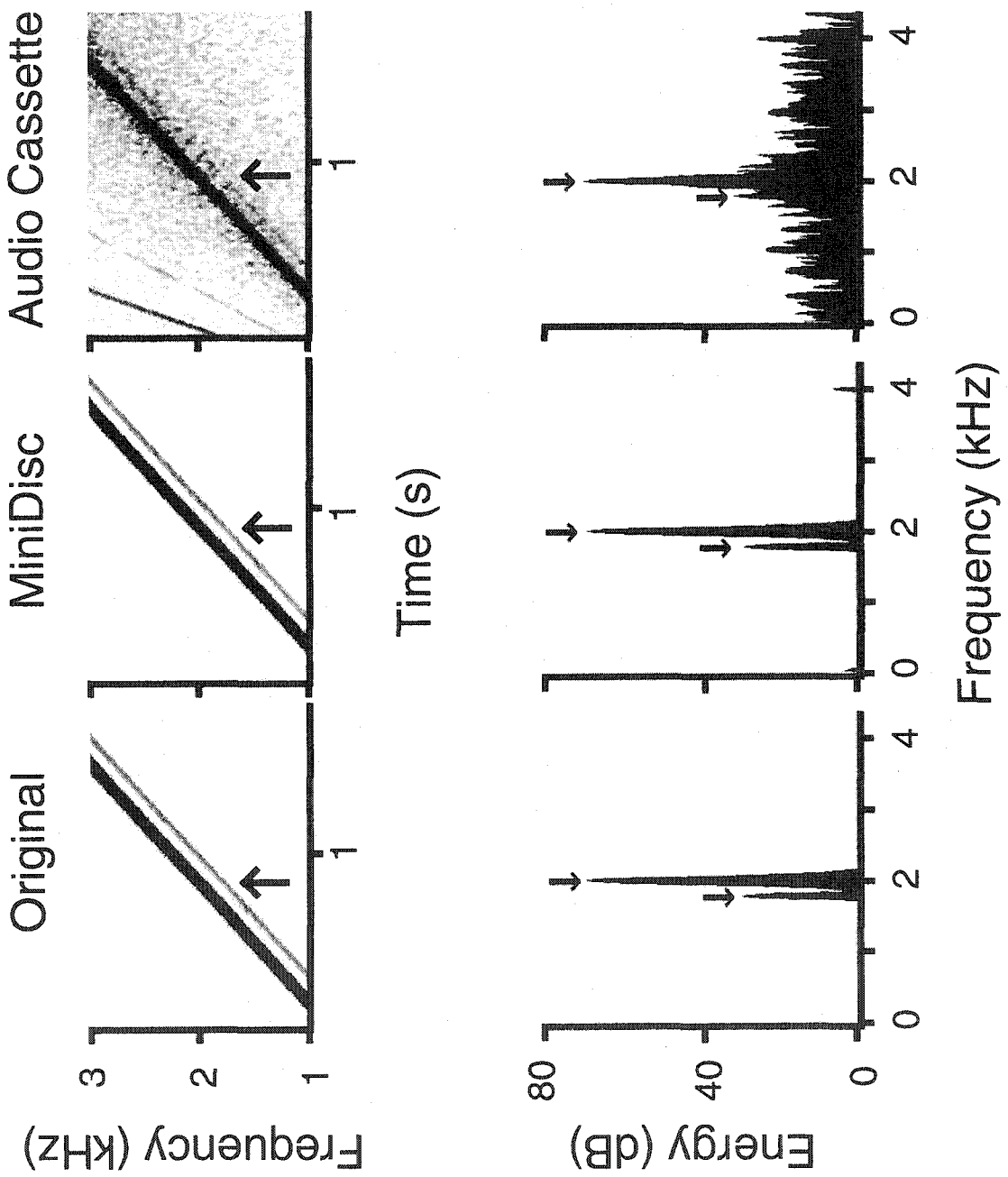


Figure 4.3 Oscillograms of single notes from white noise trills (a-c) and the tonal trill (d-f). In (a) the original version of the white noise trill, the sound begins and ends abruptly, whereas in (b) cassette recordings like this note from the NMAT, there is a non-periodic return to zero sound pressure after the end of the note. In (c) MD recordings, like this one from the NMD unit, periodic artifacts are introduced at the beginning and end of the note. The NMD recorder introduces non-periodic offset artifacts after low-pitched pure tones (d, 150Hz), semi-periodic artifacts after pure tones in the middle of the test range (e, 1200Hz), and periodic artifacts at the upper end of the test range (f, 9600Hz). The horizontal bars represent 0.05s, and the arrows point to artifacts introduced by the recording equipment.

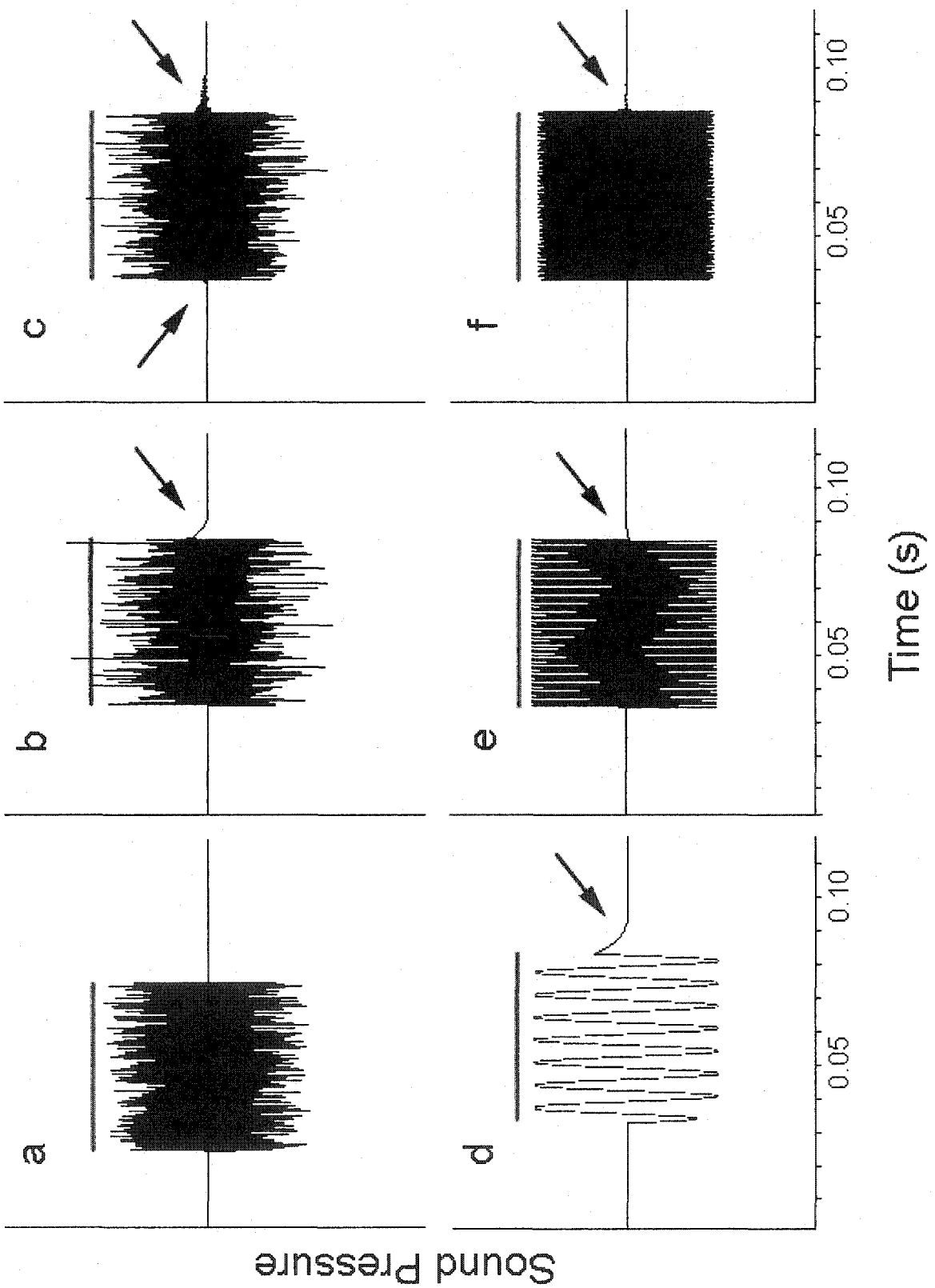
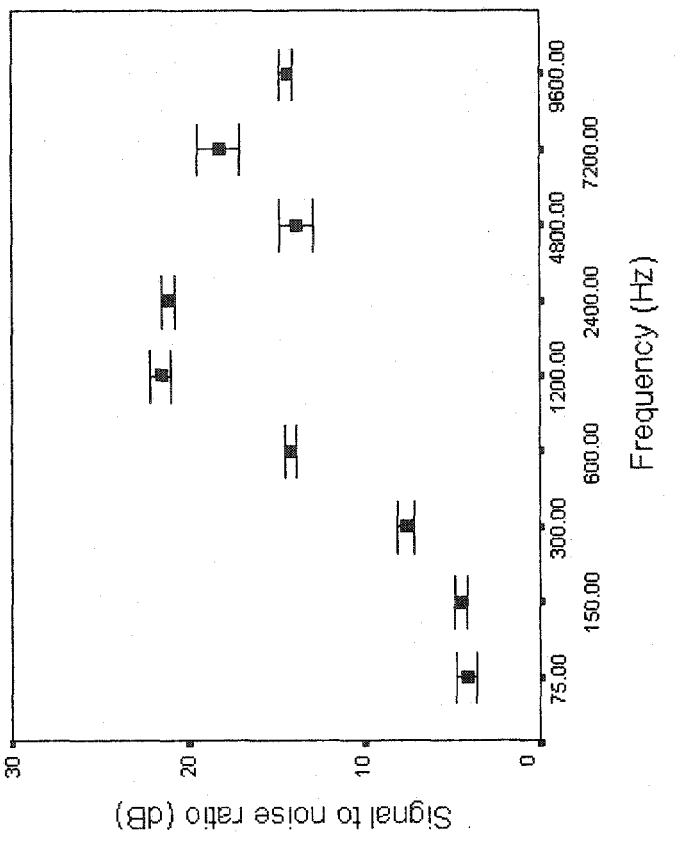
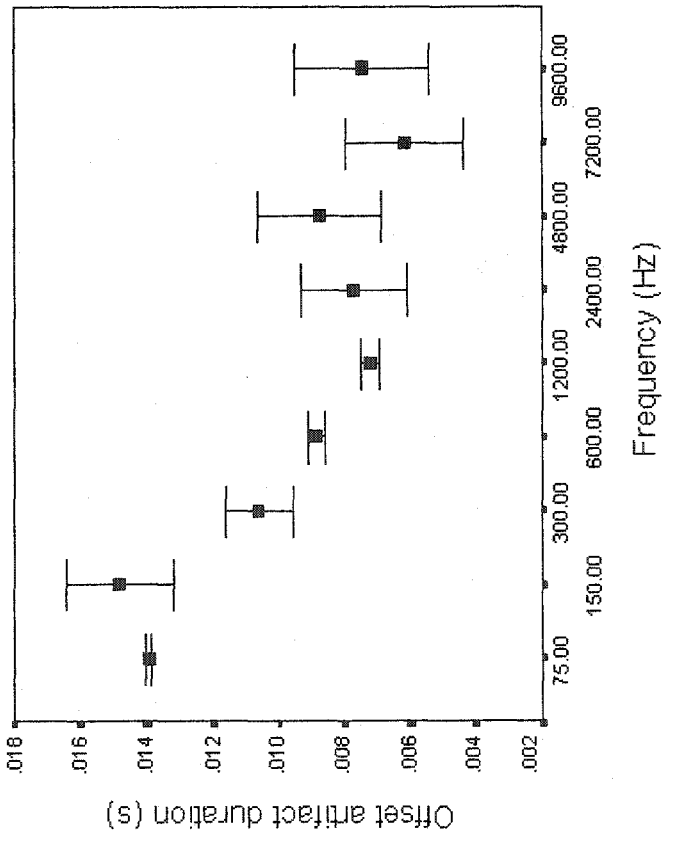


Figure 4.4 The amplitude and durations of offset artifacts introduced by the NMD recorder in response to tonal bursts of sound vary according to the frequency (pitch) of the signal. Boxes represent the mean measures from four tones at each frequency and error bars represent standard errors. The x-axis is in $\log_{10}$ scale. See text and Figure 4.3 for further characterization of artifacts.





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