

Duet Response Songs and Territorial Defense in the Gray-breasted Wood Wren (*Henicorhina leucostica*: Troglodytidae)

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ABSTRACT

Bird song serves a wide variety of functions. Avian duetting is one form of bird song that is especially common in the tropics but whose function is still not well understood. The Joint Territorial Defense and Acoustic Mate Guarding hypotheses explain duetting as either a cooperative form of song, in which a pair is working together to accomplish a common goal, or conflicting form of song, in which each bird in a pair is singing for individual motives. Under Joint Territorial Defense theory, pairs sing duets to better defend their territories. The Acoustic Mate Guarding theory predicts that pairs sing duets because one bird in the pair joins its mate's song to prevent solo singing and thus repel stranger birds of the same sex that pose a threat to their partnership. This study presented conspecific playbacks of solo and duet songs to the territories of paired Gray-breasted Wood-wrens (*Henicorhina leucostica*) in Monteverde, Costa Rica to determine the purpose of duet response songs. There was a higher likelihood of response to duet playbacks than to solo playbacks in the form of song or physical approach. There were ten out of 15 song responses to duets and only three out of 15 song responses to solos. Approaches to speaker were observed ten out of 15 times for duets and only two out of 15 times for solos. Also, for the pairs that responded to both playback types, the song characteristic measurements of high, maximum and delta frequencies in the response songs were significantly lower for duet playbacks than for solo playbacks. Both results support Joint Territory Defense over Acoustic Mate Guarding as the primary function of response duetting.

RESUMEN

Las canciones cumplen una amplia variedad de funciones. Los duetos de aves es una forma de cantos de aves que es común en los trópicos, pero que su función es no muy bien entendida. Las hipótesis de Defensa Territorial Conjunta y Protección Acústica de Pareja explican los duetos como una forma de canto cooperativa, en la cual el par trabaja en conjunto para cumplir una meta en común, o conflictiva, en la cual cada miembro del par canta por motivos individuales. Bajo la teoría de Defensa Territorial Conjunta, los pares cantan en dueto para defender mejor sus territorios. La Protección Acústica de Pareja predice que los pares cantan en dueto porque un individuo en el par se une al canto de la pareja para prevenir cantos solitarios y así repeler individuos del mismo sexo. En este estudio se presentaron playbacks de conespecíficos cantando en solitario y en dueto en territorios de *Henicorhina leucosticta* en Monteverde, Costa Rica para determinar el propósito de los cantos de respuesta. Hubo una mayor probabilidad de respuesta a cantos en dueto que solitarios en la forma de aproximación física. Hubieron 10 de 15 respuestas a duetos y solo tres de 15 a cantos solitarios. Además, los pares que responden a ambos tipos de playbacks, las medidas características del canto como frecuencia alta, máxima y delta fueron significativamente menores para duetos que cantos solitarios. Ambos resultados apoyan la teoría de defensa de territorio sobre la de protección acústica de pareja como función primaria de la respuesta al dueto.

INTRODUCTION

The functions of bird songs vary with song quality, intensity, context and motivation (Morton, 1977). Among the different types of songs are solos, in which a single bird sings, and duets, for which two birds sing simultaneously to produce a unique sound. Duetting is especially common in the tropics in birds that exhibit year round territoriality and permanent pair bonds (Morton 1996; Hall 2004). The functional significance of duet song is still controversial despite numerous previous experiments on the subject (Hall 2004). Two primary hypotheses for the function of duetting behavior in birds are Joint Territory Defense (JTD) and Acoustic Mate Guarding (AMG) (Gill 2005; Hall 2004; Lougue and Gammon 2004).

The use of song to establish and defend territories is a well-known bird behavior that is common in bird species that maintain year round territories (Dewolfe 1989). The Joint Territorial Defense theory suggests that birds duet to enhance their territorial defense. In other words, the quality of a duet may be more effective at defending territories (Hall 2004). Duet songs may be more complex, louder, longer or have some other component that dissuades interlopers. It is very possible that the duet is more effective at defense simply because two birds represent a stronger force than one bird and so are more intimidating to intruders. This theory has gained increasing experimental evidence from past experiments that have found that duets are a more effective means of defense than a song by an individual (Hall 2004; Langmore 1998).

The Acoustic Mate Guarding hypothesis postulates that the primary purpose for duet song is for sexual competition and assumes that the male and female bird within a pair sing as a result of individual motivation rather than as a result of a cooperative effort to accomplish a shared goal (Levin 1996). Levin (1996) argued that that joint territory defense was not the primary reason behind duet song in bay wrens because paired birds were equally likely to lose their territories than unpaired birds. She also found that partnerships between pairs are not as long lasting as previously thought and that new pairs do not invest time into learning new coordinated duets (Levin 1996). She then proposed that AMG was a better explanation for duetting behavior. Under this model, partners may sing to attract new mates causing its original mate to sing as well to form a duet and repel rival birds of the same sex. It then follows that individuals should join more of their partners' songs in the presence of same-sex outsiders (Hall 2004; Levin 1996). Multiple studies have found that the female component of duet songs is much more prevalent during female territory intrusions, possibly implicating that their contribution to the duet song is a result of competition for mates between females (Langmore 1998). Similar results have been found with the male component of duet song. A study on male boubous found that they joined a higher proportion of their partners' songs to form duets during male solo playbacks than during male initiated duet playbacks (Grafe and Bitz 2003 in Hall 2004). Acoustic Mate Guarding is a function of sexual competition and is a way to ensure reproductive success (Hall 2004).

There are several assumptions behind these models. First, there must be individual variation in song so that it can act as a form of communication that signals the identity, indicates the quality, or conveys the intent of the singer (Gil and Gahr 2002;

Lovell and Lein 2005; Ryan et al. 1985). The songs that the birds use allow for territorial defense and mate guarding because they are costly to produce and therefore can act as honest indicators of the quality of the singer (Gil and Gahr 2002). For example, song quality such as pitch, measured as acoustic frequency (in hertz), is dependent on physical constraints of the bird and so provides cues about the condition of the singer (Price et al. 2005). Numerous previous studies have found that the frequencies of bird songs are correlated with body size so that a lower produced frequency typically corresponds with a larger bird while a higher produced song frequency is usually characteristic of a smaller bird (Hardouin et al. 2007; Lambrechts 1996; Price et al 2005; Ryan et al.1985). As a result of this, birds often try to reach lower frequencies during vocal competition so that they can be perceived as larger and more of a threat, though only to a point constrained by body size (Price et al. 2005).

This study seeks to determine the function of duet song in Gray-breasted Wood-wrens (*Henicorhina leucostica*) as either a means of Joint Territorial Defense or Acoustic Mate Guarding by presenting conspecific playbacks of solo and duet songs to paired birds in their respective territories. The form of response (solo or duet) and the level of aggression of the response (characterized by likelihood of response song, likelihood of approach to speakers and frequency of response song) to simulated territory intrusion by solo and duet playbacks are recorded in this experiment to help choose one model over the other. Several predictions can be made about the behavior of the birds in response to playbacks under both models. Cooperative behavior is associated with the JTD model in that the two individuals collaborate for a more efficient defense of their shared territory. Therefore, under the JTD model, pairs are expected to respond to both treatments of solo and duet playbacks with duet response songs. The level of threat to the territories should be higher for duet playbacks assuming that two birds are more intimidating than one (Hall 2004). It can then be expected that the level of aggression from the resident pair should be higher as well in response to duet playbacks. The AMG hypothesis assumes the motivation behind each bird's component in the duet song is for the benefit of the individual rather than the pair. Based on the idea of AMG, it can then be predicted that the form of response to a solo playback could be a solo or a duet song. This is because the song of an individual bird would pose a threat to losing a mate and so the bird in the pair that is the same sex as the intruder would want to sing in response to that sexual competition. This response could take the form of either a solo or a duet depending on whether the other member in the pair also responded to the playback, which likely perceives as a signal of courtship. The level of aggression expected in response is one of the primary behaviors that can distinguish AMG from JTD (Levin 1996). The AMG model predicts a higher level of aggression in response to the solo playback than in response to the duet playback because a solitary bird should pose more of a threat to the partnership than to the territory (Hall 2004).

MATERIALS AND METHODS

Species and Study Site

I performed a series of playback experiments on 15 pairs of Gray-breasted Wood-wrens (*Henicorhina leucostica*) in Monteverde, Costa Rica. The Gray-breasted Wood-wren is a very vocal species of tropical bird that lives in the understory of highland forests and can

be found as low as 1100 m on the Pacific slope of Costa Rica. This bird is socially monogamous and lives in male and female pairs. While the breeding season *H. leucostica* is March through June, they still maintain and defend stable, year round territories. *H. leucostica* has been known to sing individually as well as participate in duetting (Stiles and Skutch 1989).

Ten of the 15 bird pairs tested in this experiment resided in territories located in the forest behind the Biology Station along the trails leading up to the continental divide. The other five pairs had territories located along the trails in the Monteverde Cloud Forest Reserve. I conducted experimentation from October 23rd through November 18th 2009 primarily between the hours of 0700 and 1100 because *H. leucostica* is typically most active in the morning.

Data Collection

In order to first find the territories, I walked along the trails at the Biology Station and the Reserve and located the territories by either seeing a bird pair or hearing their song. I then marked the territories with flagging tape and returned to the marked territory the next day to affirm that the birds were still there and that the location represented a stable territory. The playbacks used for the experiment were obtained from xeno-canto.org, a website that has recorded bird songs from all over the Americas. I chose the clearest sounding recordings of a solo, which was recorded in Panama, and duet, which was recorded in Costa Rica, from *H. leucostica*. I then used Raven Interactive Sound Analysis Software to improve the quality of the sound and to arrange the playback so that it consisted of alternating bouts of 30 seconds of song then 30 seconds of silence with three song bouts in total. This playback pattern was meant to emulate the calls of wild *H. leucostica* that sing in bouts interspersed with periods of silence.

To conduct playback experiments, I went to each territory and placed speakers attached to an ipod containing the playbacks in the middle of the territory. I initiated the playback and started observing and recording the reaction of birds in the territory at the same time. Recording was done with an ipod microphone attached to a separate ipod. At the start of the playback, I started a timer to record the time until a bird approached the speaker. Approaches were defined by either a bird flying over the speaker or moving in the foliage near it. I continued recording for six minutes after the start of the playback even though the playback ended after 2.5 minutes. This was to ensure that a response song was recorded, even if it was delayed and did not occur immediately after playback. Each territory was presented with solo and duet playbacks in this manner with at least a day between treatments.

The response songs were then analyzed in Raven to determine the frequency characteristics of each song. The low, high, delta and maximum frequencies were determined for response song bouts that did not overlap with the playback. The delta frequency is the range of song frequency and the max frequency is the frequency of the note that was produced with the most energy, or highest volume, in a song bout. The frequency values for usable song bouts were then used for statistical analysis.

RESULTS

The results show that there was a higher likelihood of response for duet playbacks than solo playbacks (See Figure 1). Chi-square tests showed that there was significantly more song responses ($\chi^2=6.65$, $p=.001$, $df=1$) and number of times a bird approached the speaker ($\chi^2=8.89$, $p=.003$, $df=1$) for duet playback trials than for solo playback trials. Additionally, it was observed that the majority of the song responses by the sampled pairs were duets. All ten of the songs recorded in response to duet playbacks were duets. Of the three response songs in the solo playback trials, there was only one solo response song and that pair also responded with a duet in the same trial.

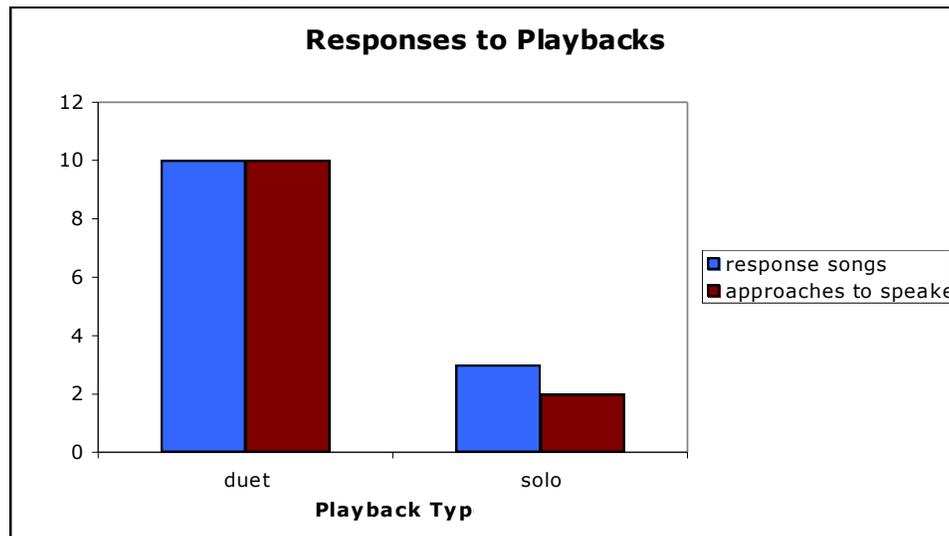


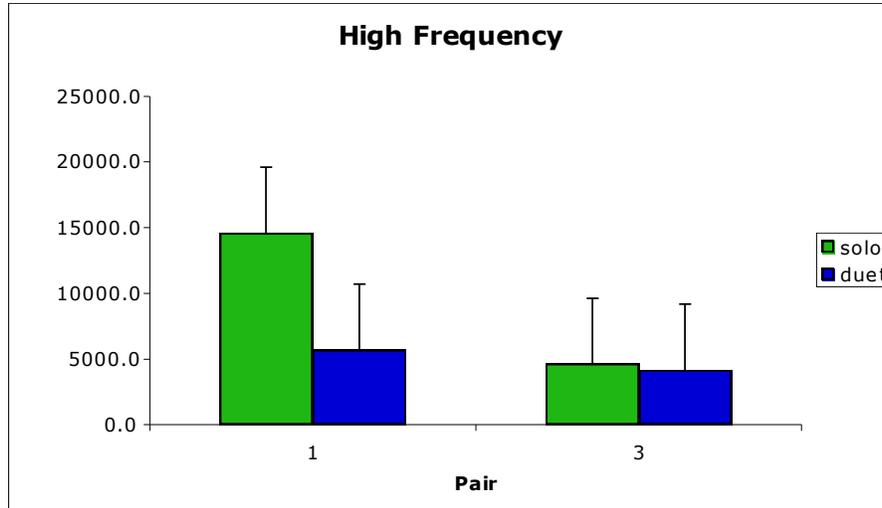
FIGURE 1. There was a higher occurrence of response to duet playbacks than to solo playbacks for both number of response songs and approaches to speaker. Duet playbacks elicited ten response songs out of 15 trials while solo playbacks only elicited three in the same number of trials. Similarly, there were ten out of 15 approaches to the speaker following duet playbacks while there were only two approaches out of 15 following solo playbacks.

Analysis of the low, high, delta and max frequencies of each of the pairs' songs in response to playbacks showed that there is significant variation in song between the pairs sampled. Each pair's song was differentiable from other pairs based on the frequencies of their song bouts ($F_{40, 214.2}=3.50$, $p< 0.0001$).

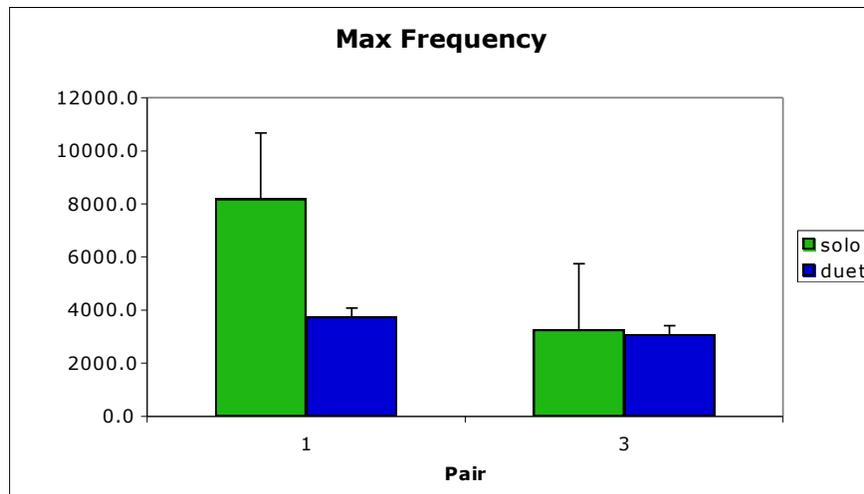
Two of the 15 pairs in the experiment responded with a song to both treatment playbacks. Pairs from territories 1 and 3 responded to both treatments and their respective frequencies showed that the two playbacks produced different responses. First, a Multivariate Analysis of Variance test showed that the two pairs' song bouts differed significantly from each other ($F_{4,21}=2.96$, $p<.0001$, $n=21$). The characteristics of these song bouts were analyzed to determine if there was a difference in song response to a duet playback versus a solo playback. Figure 2 shows that the pairs responded to the different treatments with significantly lower high, delta, and max frequencies in response

to duets ($F_{4,21}=1.39$, $p=.0008$). Both pairs did not differ from one another in their responses to solo and duet calls, meaning that they both had lower frequencies for duet playbacks and higher frequencies for solo playbacks. This is shown by a lack of significance in an additional Multivariate Analysis of Variance test ($F_{4,21}=.353$, $p=.156$).

(a)



(b)



(c)

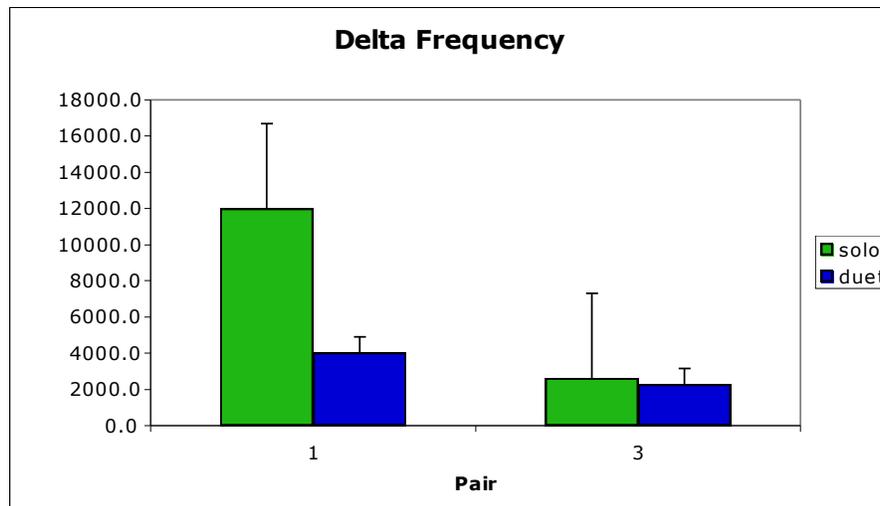


FIGURE 2. Song bouts in response to duet playbacks had lower average frequency measurements for the two bird pairs that sang in response to both duet and solo playbacks. The average high frequency (a) and max frequency (b) of response song bouts were both significantly lower in duet trials. The delta frequencies (c) were also significantly lower for duet trials, indicating a narrower range of song frequency. Pair 1 showed more dramatic differences in response to solo and duet playbacks, while pair 3 exhibited more similar responses to the two treatments.

DISCUSSION

This study examined the functional significance of response songs to solo and duet conspecific playbacks that were presented in the respective territories of *H. leucostica* pairs. There was a clear difference in the responses to each type of playback, suggesting that the presence of a solo and duet song within a territory represent different stimuli to the resident pair. Duet playbacks elicited more response from bird pairs for two measures of reaction that were observed during experimentation. More pairs sang, approached the speaker, or did both in response to duet playbacks than in response to solo playbacks. The higher likelihood of response to duet playbacks shows that duets receive a more aggressive response, indicating that they might signify a greater threat to the resident pair. This supports JTD because two birds may be more likely to usurp a pair from their territory and so would cause a more aggressive reaction from the resident pair. This can also serve as evidence against AMG because, under that model, a duet would pose less of a threat to the resident pair and so would incite less of a reaction than a solo playback.

Analysis of the songs recorded from the different pairs showed that there is significant variation in song characteristics between each of the pairs. Each pair sang unique songs based on the low, high, delta and max frequencies of their song bouts. This finding is essential to studies about the function of bird song. Variation in song allows

for the potential functions of song to include aspects of communication such as a means of individual recognition or a signal of the intent and quality of the singer (Gil and Gahr 2002; Lovell and Lein 2005; Morton 1977; Price et al. 2005; Ryan et al. 1985). This study focused on the ability for song to indicate the motivation and quality of the singer as it relates to the defense of a territory. Variation in songs signals that there is variation in bird quality and thus enables songs to defend territories instead of physical contests.

Of the 15 pairs sampled in the experiment, two pairs responded with a song to both playback types, allowing for comparison of song characteristics. Comparison of song frequencies for responses to solo and duet playbacks show that both the high and max frequencies were lower in response to duet playbacks. By comparing delta frequencies, it was also found that the frequency ranges of response songs were narrower in response to duet playbacks. This lowering of frequencies could further support the idea that duets present a greater threat to the resident bird. Past studies have shown that birds tend to lower the frequency of their songs in response to greater perceived threat. A study on Montezuma Oropendolas (*Psarocolius montezuma*) found that the males sing at lower frequencies during vocal competition with other males, than when they are singing alone (Price et al. 2005). Another study on *H. leucostica* pairs in the Monteverde area found that there was a decrease in maximum frequency and a narrowing of frequency ranges in song bouts following instigation by playback (Fandel 2009). This difference between spontaneous song and song in response to a simulated intrusion demonstrates that *H. leucostica* also uses lower song frequencies in response to threat. Although a sample size of only two pairs is undoubtedly low, the fact that both pairs responded the same way to the two different trials could suggest that the solo and duet playbacks constitute consistent signals that could elicit predictable reactions from all individuals in the species.

Almost all of the response songs to both playback types were duets, providing some evidence for both theories. The duet responses to both duet and solo playbacks support the JTD theory because a duet could be more effective at defending a territory against a single intruder as well as paired intruders. However, recent studies have also found that duet responses to solo intrusions, such as what was observed during this experiment, can also support the AMG hypothesis. Levin's study on bay wrens found that a primary function of a duet is to advertise the presence of the mate to same-sex competitors. It then follows that a solo playback representing a single intruder would cause the member of the same sex in the resident pair to join in its mate's song, creating a duet (Levin 1996).

Despite Levin's conclusions, this study still presents stronger evidence for JTD because there was also a higher level of aggression directed toward duet playbacks shown by lower frequencies of response songs and higher likelihoods of song and approach. In a study by Logue and Gammon (2004) it was also found that simulated territory intrusion evokes heightened levels of duet song as well as other associated measures of aggression such as flights and approaches to speaker in Black-Bellied Wrens (*Thryothorus fasciatoventris*). Similar results of increased duet activity in response to territory intrusions have been shown by multiple past studies on a wide range of bird species such as Striped-backed Wrens (*Campylorhynchus nuchalis*), Usambiro Barbets (*Trachyphonus usambiro*), Slate-colored Boubous (*Laniarus fenebris*), Striped Kingfishers (*Halcyon cehlicuti*) and Magpie Larks (*Grallina cyanoleuca*) (Logue and Gammon 2004).

The behavior observed in the bird pairs in this experiment suggests that JTD is the primary driver for duet response songs in Gray-breasted Wood-wrens. The AMG hypothesis did not sufficiently explain the reactions of the birds to solo and duet playbacks. Evidence against the AMG hypothesis has also been found in other studies about different bird species such as Australian Magpie Larks (*Grallina cyanoleuca*) and Buff-Breasted Wrens (*Thryothorus leucotis*) that examined duetting and its effects on extrapair paternity and male behavior during female fertile periods, respectively (Gill et al. 2005; Hall and Magrath 2000). However, past studies on the role of duetting are by no means unanimous in their conclusions and there is a high probability that the various hypotheses regarding its function are not mutually exclusive within one species or that not all bird species duet for the same reasons. Future studies involving a larger sample size could further help to support one hypothesis over another. Also, conducting this experiment during breeding season, which is March through June for *H. leucostica*, could further help to understand the use of duetting and its possible causes. Because sexual competition is more prevalent during breeding season, it is it could be hypothesized that Acoustic Mate Guarding may take on a more important role in the function of duetting during that time.

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