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SINCRONIZACIÓN DE LOS DUETOS EN LAS AVES ENDÉMICAS
CANTORCHILUS SEMIBADIUS Y *PEZOPETES CAPITALIS* E HISTORIA
NATURAL DEL AVE DE ZONAS ALTAS, *P. CAPITALIS*

Tesis sometida a la consideración de la Comisión del Programa de
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Dedicatoria

*A la pareja de anillos rojos, sin su disposición y cercanía esto
no hubiera sido posible.*

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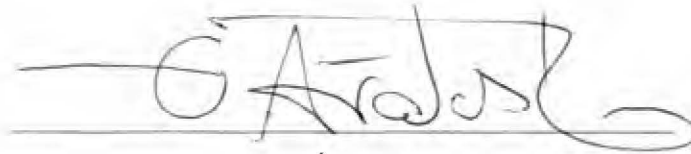
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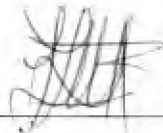
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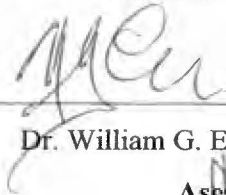
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Resumen

Los duetos se dan en casi el 5% de las especies de aves. Sus funciones pueden variar entre especies, sin embargo, en todos los casos la sincronía de los elementos cantados por cada sexo, parecen tener un papel importante dentro del dueto.

En este proyecto describo la estructura temporal de los duetos del soterré *Canthorchilus semibadius* y del xancuinclas, *Pezopetes capitalis*. Además, determiné el grado de sincronización temporal entre individuos en la pareja, y analicé si los individuos eran capaces de modificar su tiempo de canto y tiempo de espera, en respuestas a modificaciones de su pareja en estas mismas variables. Definí sincronización como la coordinación temporal de los elementos cantados por ambos individuos en un dueto. Estos duetos tuvieron elementos cantados de manera antifonal o presentaron traslape temporal entre las notas de ambos individuos.

El soterré *C. semibadius*, es un ave endémica de la costa del pacífico sur de Costa Rica y el oeste de Panamá, y presenta un dueto muy diverso. *P. capitalis* es un ave endémica de las zonas altas de Costa Rica y el oeste de Panamá, es común en el sotobosque del bosque montano. Es una especie monógama y territorial, que se reproduce a lo largo del año. Ambos sexos participan en la construcción del nido y el cuidado de los juveniles. El canto de dueto difiere del canto de la especie, el cual es solamente realizado por el macho, aunque éste puede cantar los elementos que usualmente usa en el dueto, de manera solitaria, sin la hembra.

Encontré que el grado de sincronización fue similar entre los sexos de ambas especies. Las parejas de *C. semibadius* cantaron sus duetos sincrónicamente, mientras que las de *P. capitalis* presentaron duetos sincrónicos o con elementos cantados de manera azarosa. El traslape se dio en ambas especies y fue frecuente (hasta 70% de las ocasiones en que un individuo cantó), además representó, en algunos casos, hasta el 65% del tiempo de canto de un individuo.

En ambas especies, los individuos fueron capaces de modificar sus tiempos de canto y de espera durante el dueto, en donde los individuos redujeron el tiempo de espera, antes de cantar un nuevo elemento, ante un incremento en el tiempo de canto de un elemento en su pareja. Especulo que estas modificaciones les permiten a las parejas probar la efectividad de sus compañeros, los cuales tendrán que ajustar sus respuestas temporales para mantener la sincronía.

En *P. capitalis*, encontré que las parejas tendían a modificar la frecuencia alta de sus elementos y el número de elementos cantados por unidad de tiempo, cuando eran provocados con una grabación de otras parejas. Además, ambos individuos en una pareja disminuyeron la frecuencia alta de sus elementos, conforme el dueto continuaba, en un patrón similar. Esto a pesar de que el segundo individuo (presumiblemente la hembra) comenzaba a cantar con el primero (macho) tiempo después de que él comenzara. Este patrón encontrado puede ser una posible evidencia de coordinación en frecuencia (Hz), lo cual no ha sido reportado antes en ninguna especie de ave.

El traslape durante duetos, es una interacción común entre individuos, la cual puede ser útil como una señal de coalición que produce una señal de amenaza contra competidores potenciales. En ambas especies, los duetos funcionan como una señal conjunta en la defensa del territorio. Sin embargo, es necesario realizar más estudios para determinar las posibles funciones de la coordinación en frecuencia encontrada en *P. capitalis*.

Abstract

Male-female duets occur in nearly 5% of bird species. Duetting has been widely studied, and its function vary between species, though in all cases temporal synchrony of the elements sang by each sex in the duet seems to play an important role.

I describe the temporal structure of duets of Riverside wrens, *Canthorchilus semibadius* and the large footed finch, *Pezopetes capitalis*, and determine the degree of temporal synchronization between mates in order to analyze whether duetters were able to modify their timing (singing time and the waiting time to respond to the partners elements). I considered synchronization the temporal coordination of the elements sung by both individuals in a duet. Pairs sung duets that were either antiphonal or presented temporal overlap between mates elements.

The Riverside wren *C. semibadius*, a species endemic to the Southern Pacific coast of Costa Rica and western Panama, presents highly diverse duetting. *P. capitalis* is an endemic species common in montane forest understory in the highlands of Costa Rica and western Panama. It is monogamous and territorial, and reproduces more than once a year during a non-synchronic reproductive season. Both sexes participate in nest construction and care for the offspring (usually one chick per breeding period). The acoustic repertoire of *P. capitalis* consists of two songs which differ in acoustical characteristics such as frequency range). The first song is a solo used by males, in two contexts: morning songs and territorial displays. The second song is a highly synchronize duet, sung by both sexes, though sometimes the male sings its part of the duet alone. The duet is sung when a pair reunited after a spatial separation, or more frequently as a territorial display.

The degree of synchronization was similar in both sexes of both species. Pairs of *C. semibadius* sung their duets synchronically, meanwhile pairs of *P. capitalis* sung their duet's elements randomly or synchronically. Overlapping was present in both species, with a frequency of 70% of the occasions a bird sung, and representing in some cases as much as 65% of the time a bird was singing.

In both species, individuals were able to modify their timing during duetting in response to changes in their partner's timing, where an individual reduced their silence intervals before sung a new element as a response to an increase in the duration of its partner's elements. I speculate this modifications allows them to test effectiveness of its mate, whom may have to adjust its own temporal responses to maintain synchronization.

In *P. capitalis*, I found that pairs tended to sung elements with a higher frequency and increased the number of elements sang per duration of duets, when they were provoked. Furthermore, both mates decreases their elements high frequency, as the duet continued, with a similar decrease pattern, despite females joined males later on the second section, which can be a possible evidence of frequency coordination on the second section of the duet, which have not been reported before for any species.

Overlapping during duets is a common interaction between individuals that might be useful as a coalition signal to produce a threatening signal that against competitors. Duets in both species serve as a joint defense of territory. Further studies are needed to determine the functions within a duet of the possible frequency coordination found on this species.

PREFACIO

La comunicación acústica en aves, por medio de vocalizaciones, tiene un papel importante para el reconocimiento entre especies diferentes y en la selección sexual (Handford y Loughheed 1991). Entre las funciones de estas vocalizaciones, encontradas para los cantos de machos, se han mencionado la competencia macho-macho para la defensa de un territorio y la atracción de pareja (Brenowitz *et al.* 1997, Gil y Gahr 2002, Ellers y Slabbekoorn 2003).

Durante muchos años el canto en aves se asoció exclusivamente a machos, esto debido a que un gran porcentaje de estudios en bioacústica fueron realizados en las regiones templadas, en donde en la mayoría de especies los cantos de cortejo son producidos principalmente por los machos (Levin 1996, Logue 2005). Sin embargo, en los trópicos existen muchas especies en donde las hembras también emiten cantos, los cuales poseen funciones diferentes a los cantos de los machos y pueden ser el producto de la selección tanto natural como sexual (Langmore 1998). Sin embargo, debe aclararse que el canto de las hembras, cuando ocurre, no representa una inversión en el papel de cada sexo, sino que cuando se presenta, tanto machos como hembras cantan (Farabaugh 1982), siendo usual que canten juntos formando duetos.

En aproximadamente de 400 especies de aves, que representan un 40% de las familias (Hall 2009), las parejas vocalizan con coordinación temporal para producir vocalizaciones más o menos estereotipadas conocidas como duetos (Logue 2007). Los duetos han surgido de manera independiente en varios grupos de aves poco relacionados filogenéticamente (Rogers *et al.* 2007), y son considerados como uno de los tipos de vocalizaciones más complejos dentro del reino animal (Mennill y Vehrencamp 2008).

Para que las vocalizaciones emitidas por dos individuos sean consideradas duetos, existen tres características principales que deben cumplir (Farabaugh 1982, Hall 2004). La primera característica está relacionada con la identidad de los individuos, pareja o grupo familiar (Farabaugh 1982, Hall 2004). No obstante existen excepciones, como los duetos ejecutados por machos, que pertenecen al mismo grupo familiar, en las especies de *Chiroxiphia* para atraer hembras (Hall 2004). Por lo tanto, cantos de respuesta entre machos territoriales vecinos, no son considerados como duetos (Farabaugh 1982).

La segunda característica se refiere al tipo de comportamiento que se presenta durante el dueto, ya que aunque pueden darse despliegues mutuos, principalmente visuales, solamente se consideran como duetos los despliegues acústicos (Farabaugh 1982; Hall 2004). Sin embargo, Farabaugh (1982) menciona que los duetos de muchas especies, son a menudo ejecutados junto con despliegues visuales coordinados.

La tercera característica de los duetos, se relaciona con la coordinación temporal de las vocalizaciones de las dos aves, en donde ambos individuos emiten vocalizaciones coordinadas, las cuales son vocalizadas siempre de manera no azarosa (Farabaugh 1982).

La contribución vocal de cada individuo al dueto y la coordinación con el otro individuo, puede ser un indicador de su calidad (Hall 2004). Por ejemplo, producir duetos coordinados podría funcionar como un parámetro para medir la calidad individual del compañero del dueto. Más aún, si se considera que la percepción y producción suficientemente rápida del sonido para producir duetos coordinados de manera precisa, están relacionados con la calidad de un individuo. Esto puede ser determinado por un desarrollo neural temprano, lo cual es análogo a la propuesta de que la habilidad de los machos de aprender repertorios puede permitir a las hembras evaluar la calidad del macho como determinada por un desarrollo temprano (Hall 2004).

Si la precisión con que un dueto es ejecutado es señal de calidad de los individuos, entonces, a mayor grado de coordinación de un individuo con su pareja, se esperaría que esto se relacione con ciertas medidas que reflejen la calidad individual. Ejemplos que reflejan medidas de la calidad individual son: el éxito reproductivo durante la vida del ave y su sobrevivencia, así como, la elección de pareja, divorcios y cópulas extras. Además, la precisión de los duetos podría funcionar como una señal de calidad hacia los intrusos, en el contexto de defensa de recursos (Hall 2004).

Los primeros estudios sobre los duetos comenzaron hace aproximadamente 100 años (Hall 2009). Desde entonces, varias funciones han sido propuestas para los duetos, ya que la diversidad existente entre las aves que los realizan y el tipo de dueto que ejecutan, es muy grande.

Los duetos posiblemente presenten varias funciones dentro de una especie en particular, y diferentes funciones entre diferentes especies (Hall 2004). Estas hipótesis no son excluyentes ni exclusivas para un solo grupo de aves. Además, pueden representar varios niveles de cooperación y conflicto entre los sexos, y ayudan a explicar el valor adaptativo de los duetos, tanto desde la perspectiva de la hembra como desde el macho (Bradley y Mennill 2009).

Las funciones de los duetos se pueden inferir utilizando tres aproximaciones (Vehrencamp *et al.* 2007): i) el contexto ambiental en el cual el emisor transmite sus señales, incluyendo sus características, como sexo, edad, condición y motivación, y las características externas, como depredadores y alimento, ii) las respuestas del receptor de la señal, incluyendo comportamientos de acercamiento/retirada, y iii) el comportamiento asociado al emisor, el cual puede o no ser dependiente de la respuesta del receptor.

Según Hall (2004), en la actualidad se reconocen cuatro hipótesis principales sobre la posible función de los duetos, ya sea desde el punto de vista del macho o de la hembra: i) para evitar ser usurpado de la posición en el territorio por un rival, ii) para prevenir que la pareja sea usurpada por un rival, iii) para estimular la colaboración para la defensa de un recurso, ya sea alimento y/o territorio o iv) para señalar el compromiso con la pareja. Para mi investigación, me basé en estas últimas dos funciones, ya que preliminarmente he observado son las que se presentan en mis especies de estudio *Cantorchilus semibadius* y *Pezopetes capitalis*.

Funciones estudiadas

1. Defensa conjunta de un recurso

Los duetos pueden funcionar como una señal de defensa cooperativa hacia otros individuos o parejas. En este caso, los duetos deben ser fácilmente localizables y la estructura de su vocalización debe permitir que el sonido viaje a mayores distancias para ser transmitidos a individuos externos. Además, ambos sexos deben participar en la defensa del territorio y la producción del dueto (Hall 2004).

Existe un debate sobre la función de los duetos durante estos encuentros territoriales. Sin embargo, se ha sugerido que los duetos facilitan la defensa contra

otras parejas que intenten usurpar una parte o todo el territorio comparado a cantar solo (Langmore 1998; Logue 2005; Hall 2009).

2. Señal de compromiso

Hall (2004), define el compromiso entre los miembros de una pareja como la voluntad que tengan los individuos para invertir o dedicar esfuerzo en diferentes actividades sociales, como por ejemplo el cuidado parental, la defensa del territorio u otros aspectos que involucren compañerismo. Este tipo de señales, son importantes cuando el beneficio que se obtiene depende del esfuerzo en conjunto de la pareja. Propone además, que entre especies los duetos deben ser más comunes cuando ambos sexos tienen roles similares, por ejemplo, si ambos invierten lo mismo en el cuidado parental, en la vigilancia contra depredadores, en la defensa territorial, entre otros.

Si los duetos representan una señal honesta bajo este contexto, sus medidas deberían estar relacionadas a la calidad de la pareja dentro de especies, como por ejemplo, que los individuos con parejas de mayor calidad canten más en duetos o de manera más precisa, y los duetos deberían estar asociados con niveles bajos de cópulas extra y divorcios (Hall 2004, 2009).

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Capítulo 1. Synchronization and variation of duets in the Riverside wren *Cantorchilus semibadius*, Costa Rica

Abstract

Male-female duets occur in nearly 5% of bird species. Understanding the role of a highly temporal coordination in avian duets is a challenge for bioacoustical aspects of ecology and evolution. I describe the temporal structure of duets of Riverside wrens, *Canthorchilus semibadius*, and determine the degree of temporal synchronization between mates in order to analyze whether duetters were able to modify their timing (singing time and the waiting time to respond to the partners elements). I considered synchronization the temporal coordination of the elements sung by both individuals in a duet. *C. semibadius* duets consist of intercalated elements of females and males, and are initiated by females elements. Pairs sung duets that were either antiphonal or presented temporal overlap between mates elements. The degree of synchronization was similar in both sexes of a pair. Females tended to overlap their partner's elements more frequently than males, but the overlapping time was higher in males than females, representing as much as 65% of the male's singing time. In a pair, both individuals were able to modify its waiting time in response to changes on its partner's singing time, most females and males were more prompt to decrease their waiting when their partner increased its waiting time, which I speculate allows them to test effectiveness of its mate, whom may have to adjust its own temporal responses.. Overlapping during duets is a common interaction between individuals that might be useful as a coalition signal to produce a threatening signal that against competitors.

Key words. Temporal coordination, overlapping, timing modifications, endemic bird.

Communication in animals is central for understanding the role of visual, chemical, and acoustical signals in social interactions such as mating and intraspecific competition (e.g. defense of resources) (Todt and Naguib 2000). Acoustic communication in birds has an important role in species recognition and mate choice (Farabaugh 1982, Handford and Loughheed 1991, Hall 2004). Bird song has often been associated with males in temperate regions, where most of the studies were conducted, and because in these regions courtship songs are produced primarily by males (Levin 1996; Langmore 1998; Logue 2005). Nevertheless, in nearly 450 bird species around the world, representing 40% of the families, females as well as males vocalize and the

two sexes show temporal coordination, producing stereotyped acoustic patterns known as duets (Farabaugh 1982, Logue 2007, Hall 2009).

Although duetting has been studied for over a century, its functions remain unclear (Hall 2009), in part because of the high variation in the duets structure and behavior of duetters, (Farabaugh 1982; Brenowitz and Arnold 1986; Langmore 1998; Bradley and Mennill 2009; Logue 2005; Logue 2007; Hall 2009; Mann *et al.* 2009). Five hypotheses have been proposed to explain the functions of avian duetting; all of them regard cooperation in many levels between partners as the main factor promoting mutual acoustic displays: 1) Joint resource defense that includes territory defense and food defense, 2) Mate guarding: partnership or pair bond, 3) Mate guarding: paternity, 4) Recognition and contact, and 5) Reproductive synchrony (Hall 2009). These hypotheses are not mutually exclusive, and it has often been proposed that duetting synchrony (time periodicity in elements sang by each bird) may serve different functions within duets. For instance, a female can test male capacity to synchronize with her own temporal variation and use this information as a honest signal of a male's general condition or of his vocal abilities, or duetting synchrony may indicate better territory defenders to their neighbors (Hall and Magrath 2007, Hall 2009). This array of hypothesis may imply that determining the specific causes of duetting would be a challenge, especially in a group as diverse as wrens.

Wrens have been subjected to a variety of ecological and behavioral studies which have documented dialects, vocal repertoires, and duetting (Levin 1996, Barker 2004, Cuthbert and Mennill 2007, Bradley and Mennill 2009, Mann *et al.* 2009). In this study I explore duets structure and synchrony of the Riverside wren *Cantorchilus semibadius*, a species endemic to the Southern Pacific coast of Costa Rica and western Panama (Skutch 2001), presents highly diverse duetting. The solo song and duet of this species are extremely variable, and both vocalizations have different elements that are modulated in time and frequency (Hz) (Stiles and Skutch 1989). Mann *et al.* (2009) described the duet of *C. semibadius* in a comparative study of the structures of duets across species of the genus *Cantorchilus*. However, the coordination between members of a duetting pair and the possible function of such coordination has not yet been studied.

This study has three main goals. First, to describe the acoustical and temporal structure of the vocalization produced by each sex in the duet of *C. semibadius*. Second, to determine the degree of temporal synchronization of each individual of the pair during duetting. Finally, I wanted to test if individuals were able to modify their timing during duetting due to temporal changes in their partners own timing. This is the first study that analyzes the temporal synchronization of male and females in the genus *Cantorchilus*. In addition, I discuss on the possible function of duetting synchronization in this species, as the functions proposed for bird's duets can not be generalized for all duetting species.

Materials and methods

Study Population.— Recordings and playbacks trials were done at three sites in Costa Rica from January 2010 to July 2012: Carara National Park (9°46' N, 84°36' W), Manuel Antonio (9°22' N, 84°8' W) and Golfito (8°39' N, 83°11' W), in territories that included forest edges near streams. These sites represent the northern, middle and southern pacific distribution of this species in Costa Rica.

I used a directional microphone Sennheiser ME66 at all sites and a solid state digital recorder Marantz PMD 620 for Golfito recordings in 2010 and a Marantz PMD 661 for the other three sites. All digital recordings were saved as uncompressed monoaural WAV files (24-bit and 48-bit, 44 kHz).

I recorded 14 pairs of the *C. semibadius* in their territories, 11 from Golfito, two from Carara, and one from Manuel Antonio. I recorded at least two duet songs per pair. I recorded all duets for each pair on the same day, and then walked at least 300 m before searching for the next territory, thus assuring I did not record the same pair more than once. In my analysis, I included three additional duets (LCH 042, LS1093, LS384), which I obtained from the Bioacoustic Lab, University of Costa Rica, that where recorded in the Osa area on 2009.

I used the same playback duet recording in all cases to elicit duets by simulating intrusions in their territories. I played this playback no more than three times per pair, after the first response to it.

Analysis of vocalizations.— I analyzed the recordings using Raven pro 1.4. (Bioacoustics Research Program 2011). I defined a duet as a vocalization with repeated sequence of elements sung by both members of a pair. I assigned these elements to the different individuals in the pair using two criteria: 1) I directed the microphone toward one of the individuals (there is no sexual dimorphism in plumage in this species), allowing me later to see a contrast in the spectrogram, so I was able to distinguish which elements were sung by each individual. and 2) in some duets, I observed that one individual did not sing in some units (Fig. 1b), allowing me to confirm that elements that I had previously classified using the other two criteria, were correctly assigned to an individual. I assigned sexes on the basis of a previous study which showed that females of this genus sing at higher frequencies than males (Mann *et al.* 2009),

I measured two main temporal variables for the duet: 1) time spent singing, hereafter "singing time", and 2) time spent waiting by one individual to respond to its partner, henceforth "waiting time". I measured the waiting time, from the time between the end of one individual's element until the beginning of its partner's next element (Fig. 2). When elements of the two sexes overlapped I measured the amount of time they overlapped; to differentiate this value from waiting times, I converted it to a negative value. I defined synchronization as the temporal coordination of the elements sung by both individuals in a duet, and measured it as described in the next paragraph. Temporal coordination could occur either if elements of both individuals overlap or if elements do not overlap, as long as elements sung by each bird occurred at regular intervals.

Statistical analysis.— Duets in the genus *Cantorchilus* are composed of repetitions of similar notes, which are emitted with apparently regular time intervals (periodicity). Given this periodical nature, it is possible to represent the elements of the duet with a sine function. To calculate the periodicity of the elements for one individual relative to the other individual in the duet of *C. semibadius* (reference individual), I used circular statistical calculations following the methods outlined in Zar (2010) and the modified equation (equation 1) used by Maynard *et al.* (2012). This equation includes triads of elements as the sampling unit (Fig. 3). The triads are composed by a sequence of elements in which the first (R_1) and third (R_2) element of the triad belongs to one bird

(e.g., female) and the second element (X) belongs to the second bird (e.g., male). Then the time between the beginning of R_1 and the beginning of X , and between the beginning of R_2 and the beginning of R_1 are measured and included in the equation A , which transform these time intervals to degrees.

$$\text{(Equation 1)} \quad A = \frac{360(X - R_1)}{R_2 - R_1}$$

For instance, if the element of the male is exactly halfway between the two elements of the female the value of A is 90° . I calculated a mean value of A for the female and male within each pair.

For each value of A , I calculated the sine and cosine to obtain the r-vector, which represents the periodicity between the time the elements of both individuals are emitted; r-vector varies from 0 to 1, where a value of 0 indicates absence of periodicity, meanwhile a value of 1 indicates that the elements in a duet were sung periodically. I then calculated the mean angle for each duet sang by every pair and used it in a second order sample parametric analysis (Zar 2010, page 645) to statistically test whether or not the time between elements of the duet are periodically for one or both duetting birds.

To determine the synchronization of both members of the mated pair, I considered only the variation in waiting times. I calculated the coefficient of variation (CV) for this variable for each sex, and considered individuals with lower CV values as more synchronized than ones with higher CV. Once I obtained a measure of synchronization for each sex, I calculated which sex was more coordinated by dividing the female's CV by the male's CV. This index combine with circular statistics results about the duet's dynamic (periodically or random sung elements), and behavior observations may function as an indication of each sex's role during duetting and the possible function of duets in this species.

To determine whether the index of synchronization was similar between sexes and between pairs, I conducted a paired T-test by each sex CV. Additionally, I tested for each pair, whether an individual was able to modify its timings in response to changes in its partner's timing, I analyzed if there was an association between the changes in the singing time of each individual and temporal changes in the waiting time of its partner (e.g. if an increase in the singing time of an individual was associated with an a increase

in the waiting time of its partner), using linear regression analyses. Circular statistics analysis were calculated using Microsoft Excel 2003. The rest of analyses were performed using R software (R Core Team 2012).

Results

Pairs of *C. semibadius* responded aggressively when provoked by a playback stimuli, both individuals stayed close to each other (less than 2 m apart) during duetting, and got close to the speaker moving constantly between responses. Duets were initiated by higher frequency elements (presumed to be the female) in all the recordings I analyzed. During duetting, pairs of the *C. semibadius* sang with or without overlapping their elements, and in both cases pairs synchronized their elements periodically. Hence r-vector showed that an individual in a duet tend to be relatively invariant in the periodicity of its elements relative to the elements of its partner (Table 1). All 17 mated pairs of *C. semibadius* synchronized the timing of most elements throughout the duet, synchrony (CV) for both individuals were similar ($t = -1.49$, $df = 16$, $p = 0.156$), for the female synchrony was 0.55, and for the male 0.48.

I found temporal overlapping in nine pairs. In four of these pairs, both the male and the female overlapped with the other member of the pair; in four pairs only the male overlapped with the female; and in one pair only the female temporally overlapped her mate's elements. When females overlapped their overlapping frequency was from 17% to 70 % of the occasions they were singing (i.e., number of elements within duets). Meanwhile males did it from 6.5% to 37.5% of the times.

When considering the time this overlapping represented in these pairs, I found that males temporally overlapped more than females; for females, the average overlapping time was 0.277 ± 0.122 s ($N = 5$; ranged from 20% to 44% of their total singing time). For males, the mean overlapping time per duet by every pair ($N = 8$) was 0.297 ± 0.254 s, which represented 1.5% to 65% (in five pairs this percentage was over 15%) of their total singing time. These results indicate that in pairs of *C. semibadius*, temporal overlapping is frequent.

In 11 out of 17 pairs, females modified their waiting times when their partners changed their singing times. The most common change was a decrease of the female's waiting time as the male's singing time increased; in just two pairs the female increased

her waiting time with an increase of her partner's singing time. Males, in contrast, tended to present little temporal modifications in their waiting times; in only 6 out of 17 pairs was there a statistical significant change in the way males responded to females changes in their singing time. In five pairs the males decreasing their waiting times as females increased their singing times; in only one pair the male presented the opposite response (Table 2). When I considered this responses in the waiting time per pair, I found three different scenarios: 1) singing time of an individual increased as waiting time of its mate increased, 2) singing time of one individual increased as with waiting time of the other decreased, and 3) both, singing and waiting time decreased in both sexes (Fig 4).

Discussion

The females of *C. semibadius* (or at least the individual with higher frequency elements) initiated all of the duets. Duets in this species are sometimes initiated by the male with a short series of elements (Mann *et al.* 2009), but these particular elements were absent in the majority of duets I analyzed, therefore I did not considered those elements as the beginning of duets in this species. My results differed from those of Mann *et al.* (2009), they found that *C. semibadius* males initiated duets in 67% of the occasions.

The bird that initiates the duet induces a response in its mate (in this species a response in a scale of milliseconds). Through this stimuli one bird could test the capacity of the other bird to synchronize its response. This individual could be testing effectiveness of its mate to adjust to its own temporal changes in the song elements (Smith 1994). Adjustments of this type are thought to be related with the neural capacity that allow a bird to have a rapid, adjusted vocal response.

Duetting synchronization in *C. semibadius* may be related with joint resource defense, as an indicative of this I always observed an active and restless behavior in both individuals, and a joint acoustical response from pairs when using a playback to simulate a territory intrusion. In *C. modestus zeledoni*, Marshall-Ball and collaborators (2006) found a similar behavior where pairs responded to duet playback stimuli by duetting, never with a solo song by the female or male, and they also perched to sing

close to the speaker. In this study they prove that duets resulted a more threatening signal to conspecifics than solo songs.

I found that both individuals in a duet were able to modify their timing in response to temporal changes in their partner's duetting. As Hall (2009) implies, the vocal perception and production of highly coordinated antiphonal duets involves fine-scale adjustments, on a scale of milliseconds, of the elements each mate contribute to the duet as well as matching of particular combinations of elements types. All these adjustments should be associate with an important investment of energy, as bird song involves multiple traits, such a sexual selection signals that in some cases must be costly to constitute a reliable indicator of an individual quality (Gil and Gahr 2002). These costs could be associated not only to metabolism, where data is not available yet, but also to the activities (i.e., foraging, defense against predators) that birds have to change or reduce in order to maintain or improve its singing characteristics.

Synchrony has been considered as an important parameter to avoid misdirected aggression when pairs are involved in territorial encounters by providing information about individual and sexual identity (Farabaugh 1982). Evidence supporting this possible function of synchrony has been observed during territorial counterduets of wrens (Carolina and some *Thryothorus* wrens), where females and male fight only individuals of their same sex (Farabaugh 1982). I did no test if synchrony in *C. semibadius* pairs was related to this function, however, it a possibility that can not be discharged and needs to be tested.

Other hypothesis for the function of synchrony were proposed by Hall and Magrath (2007) studying Australian magpie-larks (a non related species to wrens). They found that highly synchronized duets created a more threatening territorial response, for this they considered the song rate as a measure of how threatening a response could be (e.g., a increase in the song rate means a more threatening response to duets). They also proposed that on this species a synchronization (temporal coordination) serves as an honest signal of coalition quality when considering territorial displays; they reached this conclusion based on the work by Hagen and Bryant (2003) that stated that in humans coalition quality depends on ongoing motivation and ability to act collectively, Hall and Magrath (2007) considered coordination as the ongoing motivation's signal and coordination precision as an index of the capacity to act

collectively. Although this last function seems to be interesting, we have to be cautious because there is an extrapolation of findings that apply for a system communication in humans, where you can know the reasons behind certain behaviors, but not necessarily in avian communication systems.

Overlap between elements of duets occurs in a few species of *Thryothorus* (= *Cantorchilus*), but this is not apparently the rule (Mann *et al.* 2009). However, in the duets *C. semibadius* I analyzed, temporal overlapping was a common vocal behavior between female and male elements while duetting. My findings suggest that males overlap more frequently, in number of occasions and time, than females. Overlapping represented a large percentage of the time that both individuals spent singing during duetting. One possibility to explain this overlapping is the limitations of acoustic space, where the only chance for one individual responding to another one is to produce a song with overlapping elements (Todt and Naguib 2000, Naguib and Mennill 2010, Maynard *et al.* 2012). Also, it has been denoted that singing duets with overlapping elements can produce a more threatening signal than solo songs sang by one individual (Todt and Naguib 2000, Fitzimmons *et al.* 2008), which could be related to the hypothesis that duetting function for the joint defense of resources (Hall 2004).

Similar results regarding synchronization and timing per sex, were found by Fortune *et al.* (2011) studying the duets of Plain-tailed wrens (*Pheugopedius euophrys*). They found that contributions of males and females to the duet, include an alternated group of elements with a high degree of temporal coordination. They also found that during duets, males were more variable in the timing their elements with those of the female. In cases in which the male wrens failed to produce their elements, females continued singing and lengthened intervals between elements intervals during these omissions. I noted both patterns in *C. semibadius* pairs.

The only function of duetting on *C. semibadius* that can be assumed based on behavior observations and theoretical assumptions, is the joint defense of a resource, in this case territory. Further experiments are necessary to determine the role of synchronization, with or without overlapping, and the ability to modify the timing during duetting. Thus, understanding how and why birds coordinate their elements during duetting is essential to understand the evolution of duetting and its role in sexual selection, individual quality and resource defense.

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Table 1. Antiphonal duets in the *C. semibadius*. Circular statistical analysis revealed that duetting individuals sang their elements periodically, in this cases alternating their elements; r-vector varies from 0 to 1, where a value close to 0 would mean that a pair were timing their elements in the duets randomly, meanwhile a value of 1 would imply that the elements in a duet were sung periodically.

Pair code	F-value	DF	p	r- vector	Mean angle
1	4750.288	2/9	<0.001	0.970	150
2	14.837	2/19	<0.001	0.440	134
3	33235.343	2/12	<0.001	0.960	156
4	170.808	2/18	<0.001	0.707	174
5	14770.750	2/20	<0.001	0.964	167
6	658.238	2/58	<0.001	0.499	135
7	60.145	2/29	<0.001	0.432	178
8	456.320	2/8	<0.001	0.938	169
9	11.020	2/10	0.00296	0.749	176
10	7.379	2/8	0.0153	0.718	156
11	11.319	2/4	0.0225	0.733	171
12	25297.993	2/4	<0.001	0.995	170
13	11660.526	2/17	<0.001	0.937	164
14	10.580	2/16	0.0012	0.444	133
15	15,900,251.1	2/10	<0.001	0.999	173
16	538.717	2/11	<0.001	0.834	169
17	1557.022	2/10	<0.001	0.984	169
18	466736.053	2/4	<0.001	0.999	103

Table 2. Relationship between sex singing time vs. partner waiting time in *C. semibadius* pairs.

Pair	Singing time of male vs. Waiting time of female (R ² - value)	Slope	p	Singing time of female vs. Waiting time of male (R ² - value)	Slope	p
1	0.19	0.125	0.13	0.0078	0.088	0.637
2	0.17	-0.108	0.048	0.27	-0.0629	0.015
3	0.21	-0.061	0.076	0.72	-0.448	0.00013
4	0.49	0.115	<0.001	0.019	-0.121	0.56
5	0.045	-0.179	0.32	0.78	-0.788	<0.0001
6	0.35	0.132	<0.0001	0.063	-0.0935	0.050
7	0.33	0.273	0.085	0.36	0.35	0.067
8	0.81	-0.308	<0.0001	0.56	0.275	0.0033
9	0.45	-0.522	0.032	0.065	0.685	0.45
10	0.23	-0.565	0.34	0.039	-0.264	0.64
11	0.40	-0.397	0.37	0.52	-0.858	0.10
12	0.25	0.134	0.0026	0.0078	0.088	0.64
13	0.41	-0.164	0.0029	0.51	-0.688	0.00044
14	0.36	-0.756	0.0089	0.053	0.411	0.34
15	0.49	-0.225	0.017	0.047	-0.211	0.50
16	0.70	-0.625	0.00038	0.11	-0.262	0.25
17	0.61	1.344	0.0015	0.54	-0.632	0.0063

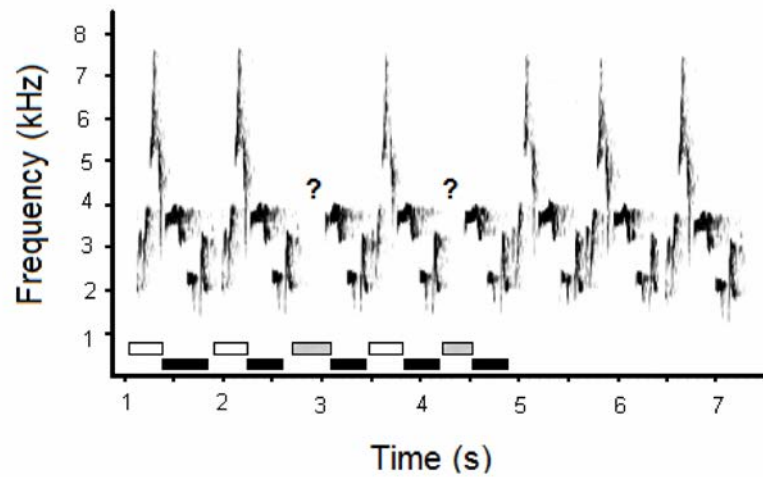


Figure 1. Sound spectrogram of one duet of *C. semibadius*. Bars underscore the elements contribution by each sex (female white, male black). In a few cases, during duetting, an individual stop singing, leaving a gap where its elements were suppose to be (gray bars) if the individual's elements classification I did was correct based on an antiphonal duet with intercalated elements between female and male. This helped me to confirm that I classified individual's elements correctly.

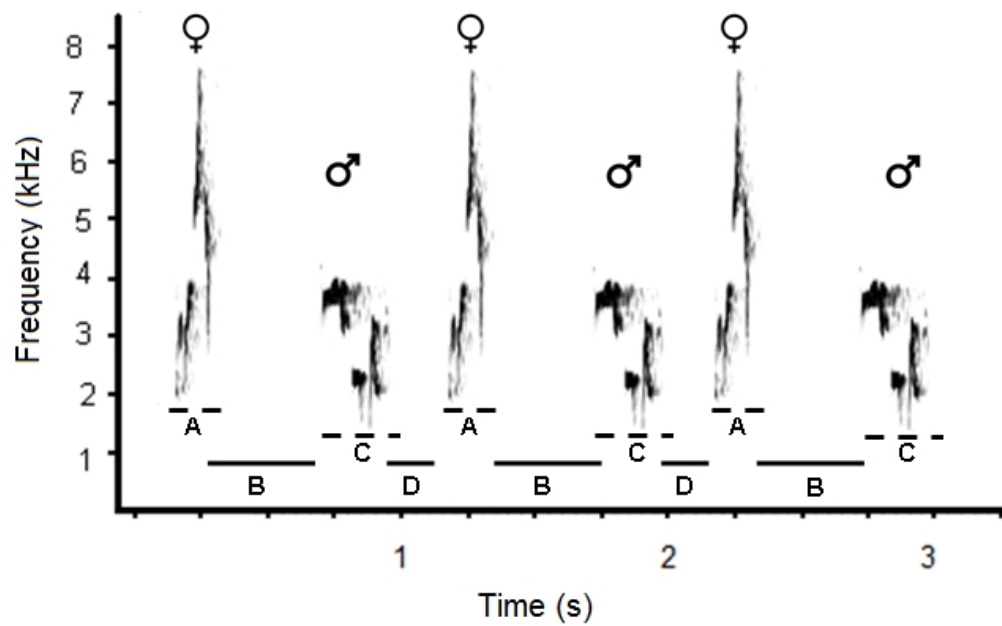


Figure 2. Temporal variables considered to analyzed duets of *C. semibadius*. Stripped lines show singing times (A: female; C: male), continuous line represents the time an individual waits until start to sing its part in a duet (waiting time), B: waiting time of male, and D: waiting time of female.

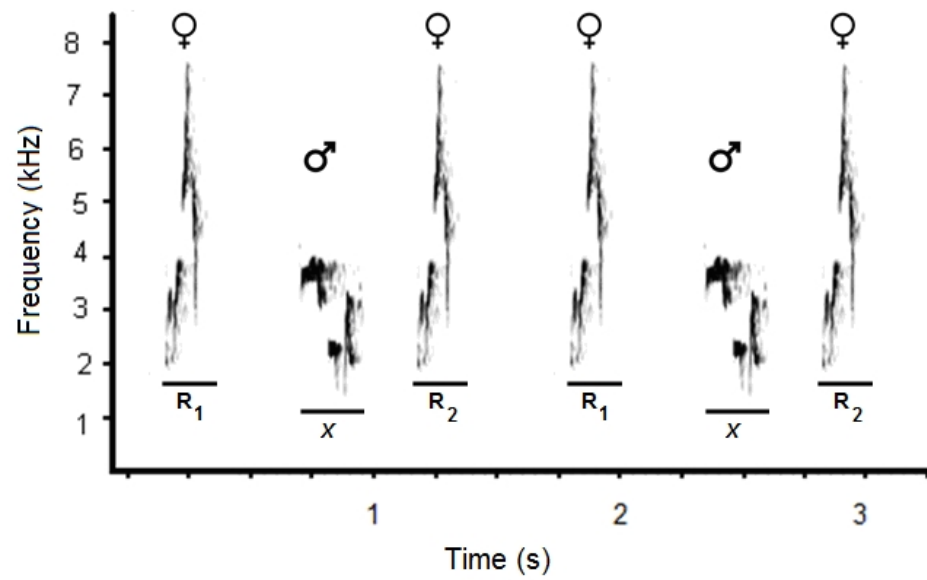


Figure 3. Triads of elements sang by both individuals in a duet of *C. semibadius* used to calculate the periodicity of the elements for one individual relative to its partner in the duet.

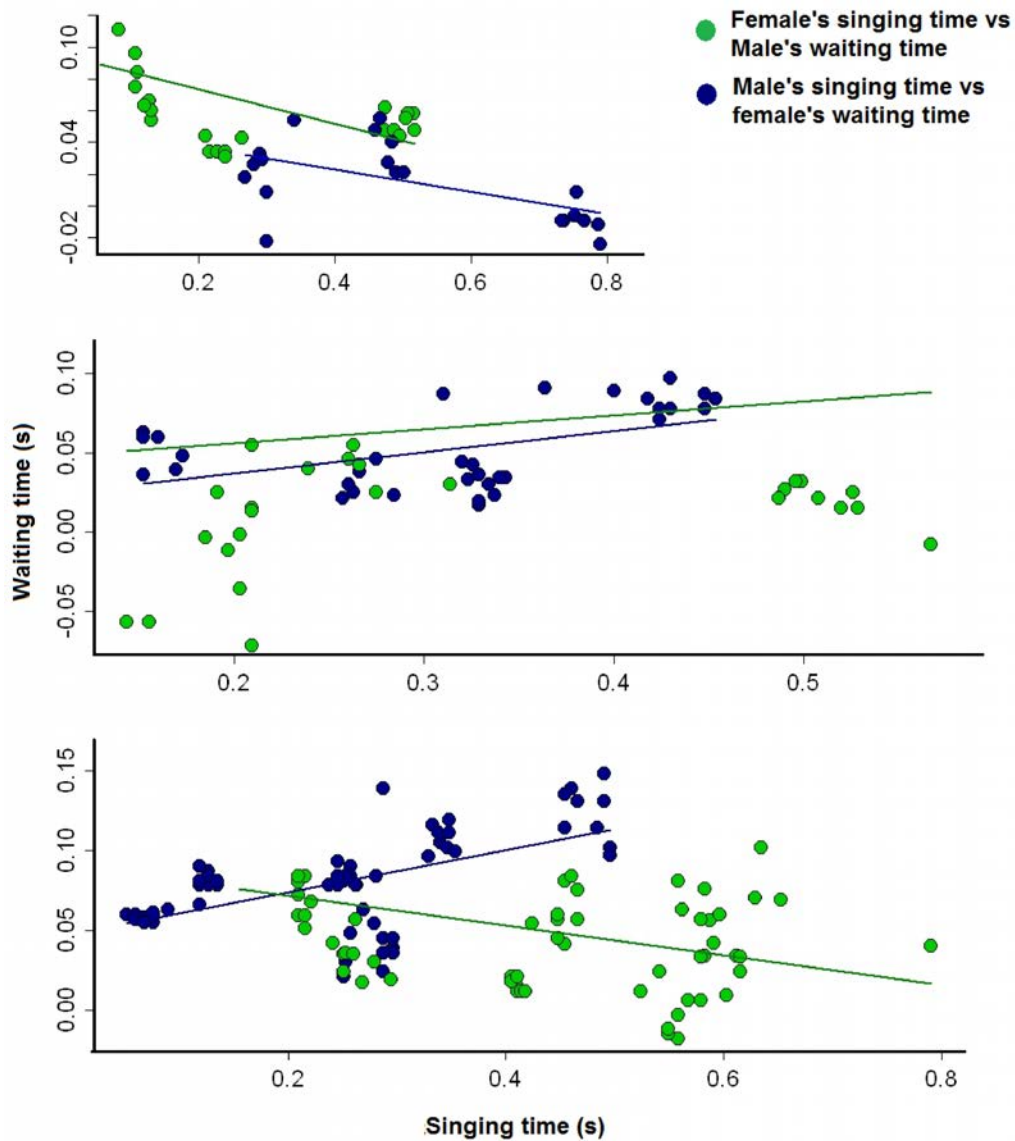


Figure 4. Flexibility patterns found in *C. semibadius* pair's timing periods during duetting. In a pair, an individual can respond with short or long waiting times when its partner sang reducing its singing times periods; in other pairs, as one individual sang with a short singing time, its pair responded with a short waiting time as well.

Capítulo 2. Natural history and acoustic repertoire of *Pezopetes capitalis*, a highland endemic bird of Costa Rica and Western Panama

(con formato para *ORNITOLOGÍA NEOTROPICAL*)

Abstract. - *Pezopetes capitalis* is an endemic species common in montane forest understory in the highlands of Costa Rica and western Panama. It is monogamous and territorial, and reproduces more than once a year during a non-synchronic reproductive season. Both sexes participate in nest construction and care for the offspring (usually one chick per breeding period). The acoustic repertoire of *P. capitalis* consists of two songs which differ in acoustical characteristics such as frequency range). The first song is a solo used by males, in two contexts: morning songs and territorial displays. The second song is a highly synchronize duet, sung by both sexes, though sometimes the male sings its part of the duet alone. The duet is sung when a pair reunited after a spatial separation, or more frequently as a territorial display.

Key words: endemic bird, habitat use, biparental care, acoustic repertoire, duet, territory defense.

INTRODUCTION

Costa Rican avifauna is characterized by a high diversity of highland endemic species (Slud 1964, Stiles & Skutch 1989, Hernandez-Baños *et al.* 1995). The assemblage of this endemic avifauna has been due to both historical and ecological factors (Drake 1991, Barrantes 2009). A complex geological history, including the formation of the cordilleras, and cold climatic conditions during the upper Pleistocene, promoted dispersal of bird species from the Nearctic and the Neotropical regions, especially from the Andes. Periods of inter-glacial conditions reduced the connectivity between these regions, isolating populations of the species established in the highlands from their ancestral populations, and promoting subsequent speciation (Barrantes 2009).

The highland avifauna of Costa Rica and western Panama includes 85 regular or temporary resident species (Barrantes 2009), 34 of which are endemic to these highlands. The composition of this avifauna was first described by Slud (1964) and a series of subsequent papers described general aspects of their natural history (Wolf 1969, Colwell *et al.* 1974, Naoki 1996, Wilms & Kappelle 2006, Barrantes 2009, Barrantes *et al.* 2011), morphological and genetic divergence (Stiles 1998, 1985,

Barrantes & Sánchez 2000, Chavarría *et al.* 2011), and feeding and behavioral aspects of some species, particularly hummingbirds (Wolf *et al.* 1976, Stiles & Freeman 1993, Fuchs *et al.* 2010, Ávalos *et al.* 2012). However, despite the uniqueness of this diverse, endemic avifauna and the interest in preserving this entire ecosystem (Kappelle 1996, Sánchez & Barrantes 2011), detailed information on the natural history and reproductive biology is available for only few species (Hunt 1971, Barrantes & Loiselle 2009).

Pezopetes capitalis (Large-footed finch) is a common endemic species of Costa Rica and western Panama. In Costa Rica, it inhabits the understory of forest in the Central and Talamanca Cordilleras (Slud 1964, Stiles & Skutch 1989). This species is the most common ground-foraging finch in these highlands, being found in thickets covered with a thick layer of leaf litter (Wolf 1976, Stiles & Skutch 1989). It breeds only in dense forest undergrowth, forest clearings and borders; its nest is a massive cup made of seed-stalks and bamboo leaves, and is constructed on thick bushes or bamboo stems around 1.5 to 2 m above the ground (Klein *et al.* 1991). The clutch consists of one long and elliptical or subelliptical shaped egg (Stiles & Skutch 1989, Klein *et al.* 1991). Other information on the reproductive biology and natural history of this species is poorly known. Here, I describe habitat use, reproductive behavior, parental care, and the acoustic repertoire of *P. capitalis*.

METHODS

Study Population. I observed *P. capitalis* at the Estación Biológica Cerro de la Muerte (09°34'N; 83°41'W; 3150 m elevation) at 2200 to 3350 m el. from April 2009 to May 2009, and March 2011 to December 2012. The study site is characterized by an oak second growth forest (*Quercus costaricensis*), with its understory dominated by dense thickets of bamboo (*Chusquea* spp.) (Stiles & Skutch 1989), and some ericaceous and melastomataceous bushes and treelets.

Natural history. I observed 17 pairs. To determine the territory of each mated pair I followed them from one to 15 non-consecutive days, marking foraging area and routes with flagging tape. To recognize individuals, I mist-netted and banded, with a unique

combination of colors, at least one individual from 13 of the mated pairs; I recognized the other four pairs based on their presence in limited areas and previous observations of territory fidelity in this species. Descriptions of territories, foraging behavior, reproductive behavior, and parental care are based on direct observations and video recordings of some pairs made with a digital video camera (Sony HDR-SR11) in the field.

For each pair I classified observation periods in two categories: a) Non reproductive period: when birds were only foraging, without any behavior related to courtship or nesting construction. b) Reproductive period: when one or both pair members carried material for nest construction, members of the pair foraged alone (possibly because the other was on the nest?), and caring for offspring. Based on my field observations, I divided youngsters in three qualitative, age categories: 1) Chick: a baby outside its nest, with a yellow bill, a strongly barred chest, and a tail no longer than 3 cm. 2) Pre-juvenile: an individual with yellow bill, a barred chest, a tail as long as that of an adult, and green head with black stripes. 3) Juvenile: an individual with black bill, barely barred chest, a tail as long as that of an adult, a head with the same color pattern as an adult. Juveniles foraged actively with their parents.

Song repertoire. I recorded solo songs from 5 pairs in 2009 and duet songs from 13 pairs from 2011 to 2012. In cases where an individual or a mated pair did not sing, I used playbacks from other individuals to provoke a response. I used two playbacks (LCH 12-001 and LCH 12-003) from birds recorded in Barva National Park (74 km away from the study site), obtained from the Bioacoustic Lab, University of Costa Rica); the third playback was from a bird recorded in 2009 at the study site.

For all recordings I used a directional microphone Sennheiser ME66 and a solid state digital recorder Marantz PMD 620 (from April to May 2009), and a Marantz PMD 661 (March 2011-December 2012). I saved digital recordings as uncompressed monoaural WAV files (24-bit and 48-bit, 44 kHz) and analyzed them using Raven pro 1.4. (Bioacoustics Research Program 2011). To identify which elements corresponded to each individual in a pair within a duet, I used two methods: 1) I recorded videos in HD

definition using a Sony HDR-SR11, for three mated pairs (two banded pairs and one unbanded) in which I knew before hand the sex of each individual (based on behavior during duetting and foraging, and morphometric measures), allowing me to determine their duetting order; 2) In playbacks experiments, I directed the microphone to one individual during the time they were responding, so this would be reflected on the spectrograms as a contrast in color, having a more intense color those elements belonging to the bird I was focusing on. I defined an element as a discrete sound that can have modulation in frequency (Hz) and time, and that can be separated temporally or in frequency of other elements.

RESULTS AND DISCUSSION

Habitat use and abundance. I observed pairs foraging together all year around, mostly in the understory of subalpine, and montane oak forest (*Quercus costaricensis*), second growth forests, *Chusquea* sp. tickets, and open areas dominated by Ericaceae and Rosaceae bushes. The density of *P. capitalis* was 30% higher in oak forest than on adjacent non-forested areas (Oostra *et al.* 2008).

Foraging activity goes from 04:50 h to approximately 18:00 h. Activity initiated with solo songs sung by males from dense thickets. Singing continued intermittently for periods of 10 to 20 minutes, until foraging activity began. The birds foraged in pairs, scratching the leaf litter, and occasionally going up in a bush, looking for small (unidentified) insects and occasionally some berries (i.e., *Rubus* sp). These diet observations are similar to those of Wolf (1976), who reported insects, seeds, and fruits, especially of *Pernettya*, as the main food items for this species.

I observed pairs actively foraging in the same are for more than one year. They fed, bred, and slept in their territories. In two of the territories I also saw the territory owners collecting material to construct their nests (also noted by Klein *et al.* 1991). These pairs attacked con-specifics when they intruded into these areas, and also responded intensely, both physically (e.g., constant movements between brushes) and acoustically, when I used playbacks stimuli to simulate territory intrusion. Thus concluded that *P. capitalis* is a territorial species. I counted 19 pairs in a 50 ha area, but

I was unable to monitor the entire site, so there may have been more pairs than those I observed, especially since the estimated territory size for a pair is about one hectare (F. G. Stiles com. pers). When a pair perceived an intrusion of conspecifics (a playback recording) in their territory, the male first approached the source of the song, followed shortly by the female. When the male arrived alone, he usually sang a sequence of solo songs that may last as long as 5 min, as he moved between branches. When the female approached the male within about 1 m, the pair sang a sequence of duets (from 1 to 4).

Within their territories *P. capitalis* pairs seemed to follow particular foraging routes each day. I recorded this pattern in six pairs, in which I saw them foraging on the same area almost at the same time for several days (3 to 10 days). The foraging areas often overlapped between adjacent territories ($N = 8$), but birds did not enter far into neighboring territories, and did not enter at all when the other pair was present. The same behavior was described by Wolf (1976), who stated that pairs seemed to restrict their activities to one area, but more than one pair was often seen foraging in the same territory.

Reproductive behavior and parental care .— Most pairs ($N = 11$ of the 13 pairs banded) remained together for more than 18 months. From these pairs I registered two divorces. In one case, I saw the male with a new mate and a chick five months later, foraging close to the male's former territory. For the second pair, I saw the female with a new mate six months later, and the male with a new mate and a chick eight months after the divorce. In this particular case, the female maintained the same territory she had prior to divorce, while the male was seen foraging in an adjacent territory. Divorce is a common strategy in birds and likely affects the individual's relative fitness (McNamara & Forslund 1996). Despite the amount of studies of avian mating systems, the reasons for divorce in monogamous birds are still poorly understood. It is thought that at least for one of the pair mates its fitness increases by divorcing a current partner to re-pair with a higher quality mate (Choudhury 1995, Otter & Ratcliffe 1996), but only long-term studies combined with studies of paternity will provide information on fitness of divorce individuals.

The reproduction was asynchronous in different pairs, and occurred nearly throughout the entire year. I registered pairs with youngsters from April to August (Fig 1.). Some pairs had multiple reproductive events in a year. One pair had three breeding events in one year, raising one chick each time. Nearly always a pair raised a single chick (16 out of 17 pairs), but one pair raised two chicks in one occasion.

Reproduction began with construction of a new nest, which was described by Klein *et al.* (1991) as a massive cup built with bamboo (*Chusquea* sp.) leaves, grasses, mosses, stems, and sticks. They mentioned that in eight of nine nests the clutch consisted of only one egg; I did not check nest contents so cannot add to this. The period of time that a chick remains with its parents was approximately three months (Fig 1: see pairs 2, 3 and 5). I estimated this time by accounting the time from the first observation I had of a pair with a chick until the chick left with its parents. For 3 pairs the period between the initiation of nesting events was at least five months (Fig 1: see pair 3).

Both parents fed the chicks. Both chicks and juveniles produced a low intensity begging call (*peep peep*) as their parents were foraging nearby. Every time I heard this begging call (N = 6), both parents proceeded to feed their offspring immediately. All three young stages (chicks, pre-juveniles, and juveniles) scratched the litter as adult do, but only pre-juveniles and juveniles were occasionally captured prey. While foraging, all family members remained less than 5 m apart. When I got close to a family (around 5 m), the male approached me and then perched on branch or stem, while the female continued foraging with their offspring, about 10m away from the male. I saw this behavior in 6 pairs while they were foraging with their offspring. Another response when parents detected my intrusion was walking away with their offspring until they hid their chicks or juveniles in dense vegetation. After this, the chick or juvenile remained very quiet and silent, and both parents immediately returned to foraging.

The observations above suggest that *P. capitalis* shows strongly biparental investment in parental care, at least in time. The low environmental temperature prevailing on the highlands inhabited by *P. capitalis* is likely may have promoted the evolution of both the high biparental inversion and the extremely small clutch size in this

species. Such small clutch size may be compensated by the capability of this bird species of reproducing up to three times a year.

Acoustic repertoire.— This species produced three different vocalizations, which were sung all year around: 1) a solo song (“species song” hereafter) sung only by males (Fig. 2); 2) duets which consisted by a sequence of temporally highly coordinated elements produced by both male and female with stereotyped acoustic pattern (Farabaugh 1982, Langmore 1998) (Fig. 3); and 3) a solo song produced by males that has the same structure (e.g., frequency and order in which every element was sung) and elements used by a pair member in a duet (Fig. 4). I defined a song as a group of stereotyped, long, and complex (modulation in frequency and time) vocalizations produced by males or females.

The species song consist of 10 to 18 different elements, which can be repeated, especially at the end of the song (Fig. 2). The beginning of the song was variable within males ($N=5$), but the final part was always the same in all male songs, this part was more conservative in the type of elements (Fig 2: groups of elements A to C) and in the order each of them was sung. This song presented differences in its length and the acoustic frequency among males (Table 1; I only measured the conservative elements because they were always present in all males songs).

The entire duet was divided in four sections (Fig. 3a-d), which varied in length, and frequency (Table 1), but only the middle and final sections were present in all duets ($N= 68$). During the duet the elements produced by both sexes overlapped in time and/or frequency along most of this vocalization. The introductory twitter of the duet consisted of a twitter-like sound that can be sung by either sex, and the bird that sang this section was not the same that initiated the middle section, because both sections overlapped temporally. This introductory twitter section was absent in most duets, so for my analyses I considered the middle section as the initial part of *P. capitalis* duets.

The middle section consisted of a group of alternate overlapping elements sung by both members of a pair. The number of elements per individual in this section was 5 ± 1.4 (range from 2 to 9 elements). The final section consisted of 10 ± 4.6 elements

(range from 1 to 21 elements) sung by each sex in alternate fashion, and most duets ended with this section, but some duets ($N = 10$ of 45 duets) had an additional section of 6 ± 2.8 (range from 2 to 10 elements) elements (Fig. 3d), I did not measure frequency (Hz) or element's length on this sections because I was unable to determine which sex sang this section or if both individuals singing it alternating their elements.

The duet was produced in two different contexts. The first was when a pair perceived an intrusion of conspecifics (i.e., a playback) in their territory, and the second when the members of a pair got together (seen only twice) after having being some distance apart (i.e., more than 10 m apart). The only function of the duet proposed for *P. capitalis* was mate recognition (Wolf 1976, Stiles & Skutch 1989). The duet in *P. capitalis* likely serves multiple functions (i.e., territory defense, mate recognition and contact maintenance) as suggested by Hall (2009). On five occasions, I recorded a male singing alone its section of the duet in response to a playback.

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Table 1. Acoustic parameters of *Pezopetes capitalis*' vocalizations: Species song ($N= 5$ males) and duet song ($N=12$ pairs).

Type of song	Time (s)	High frequency (Hz)	Low frequency (Hz)
<i>Species song</i>			
A	0.34± 0.11	9920± 125	1439± 489
B	0.192±0.048	10357±1136	1710±899
C	0.206± 0.025	9376± 594	1801± 222
<i>Duet</i>			
Introductory twitter	0.61±0.22	2766±469	552±136
Middle section	1.98±0.31	10100±210	7238±219
Final section	2.46±0.54	5732±299	1050±320

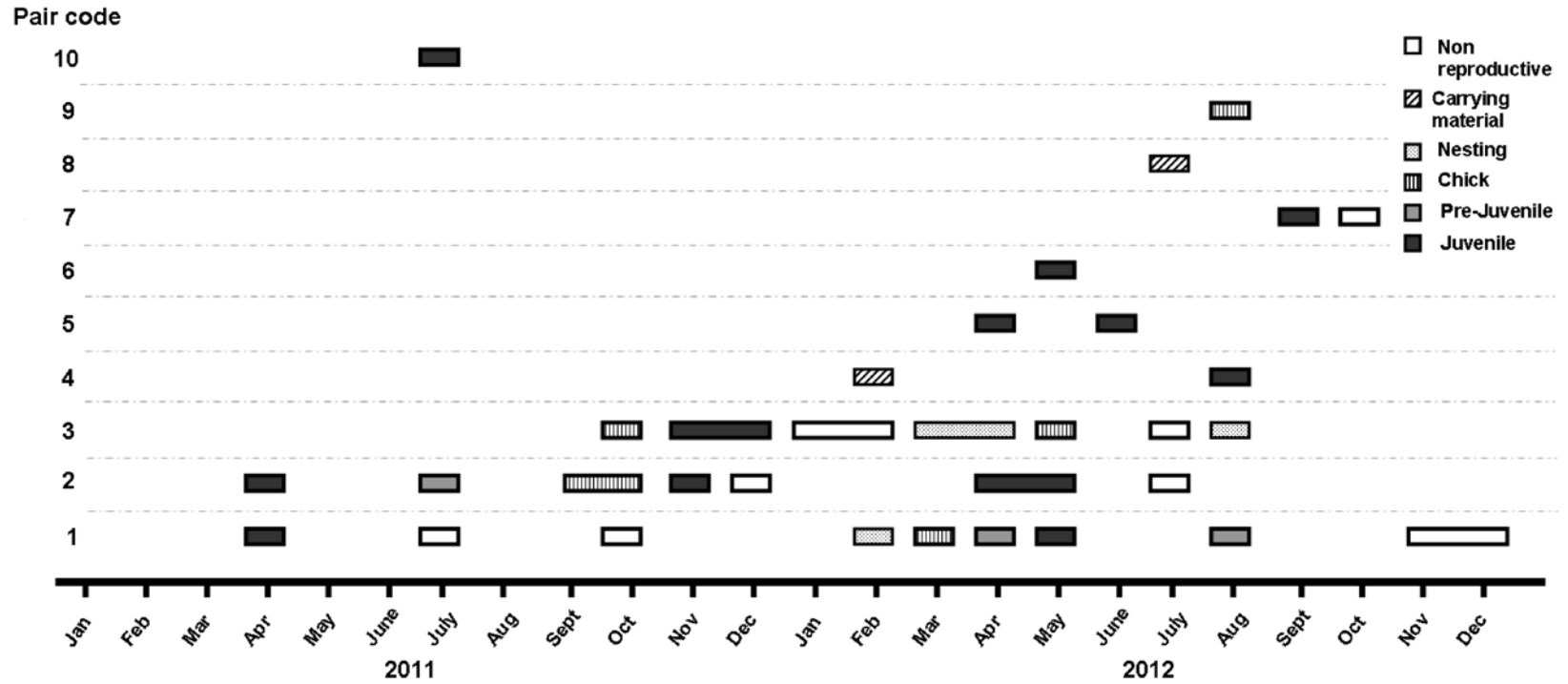


Figure 1. Period of time of reproductive and non-reproductive stages invested by pairs of *Pezopetes capitalis*.

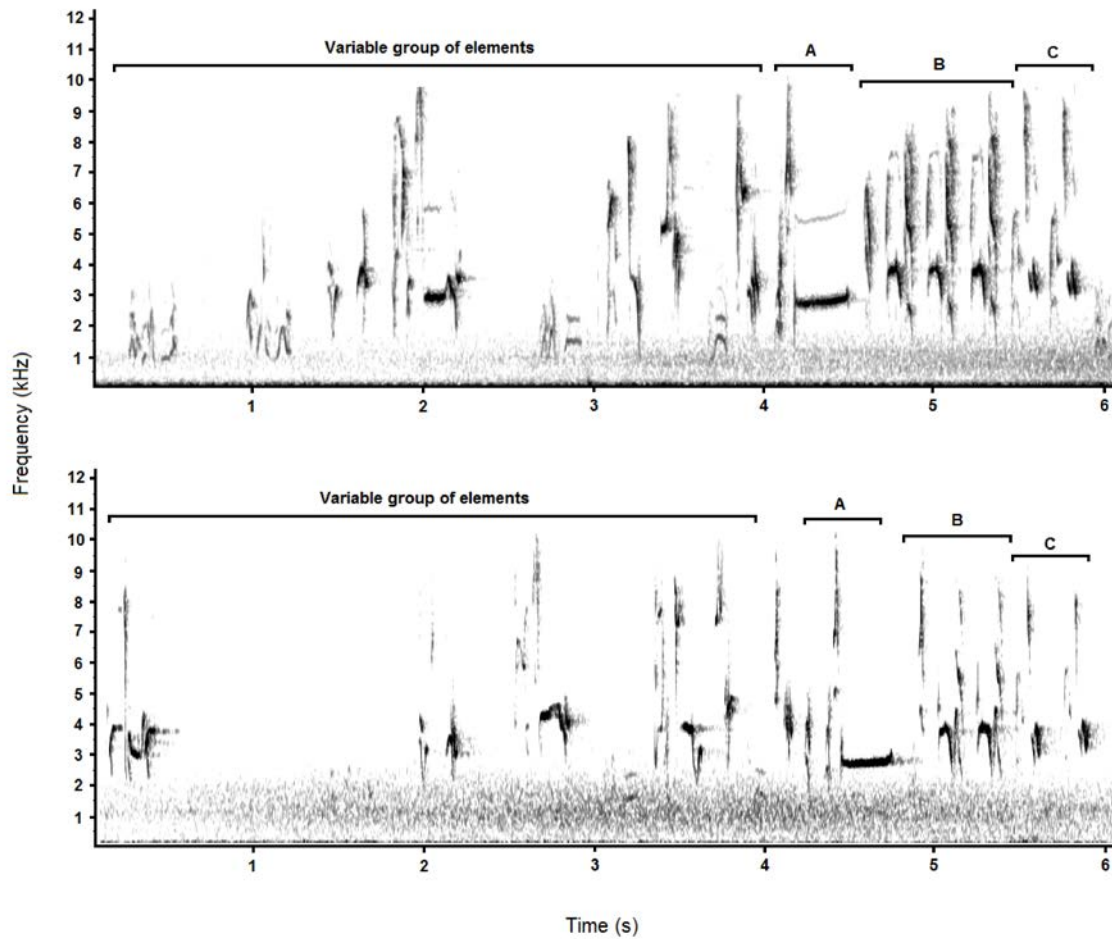


Figure 2. Sound spectrograms depicting two solo songs (species song) sung only by males of *Pezopetes capitalis*. The first part of a solo song, its variable between males, and it is compound of different elements. A, B,C: represent groups of elements always present in this solo songs, and that are always sing in the same order.

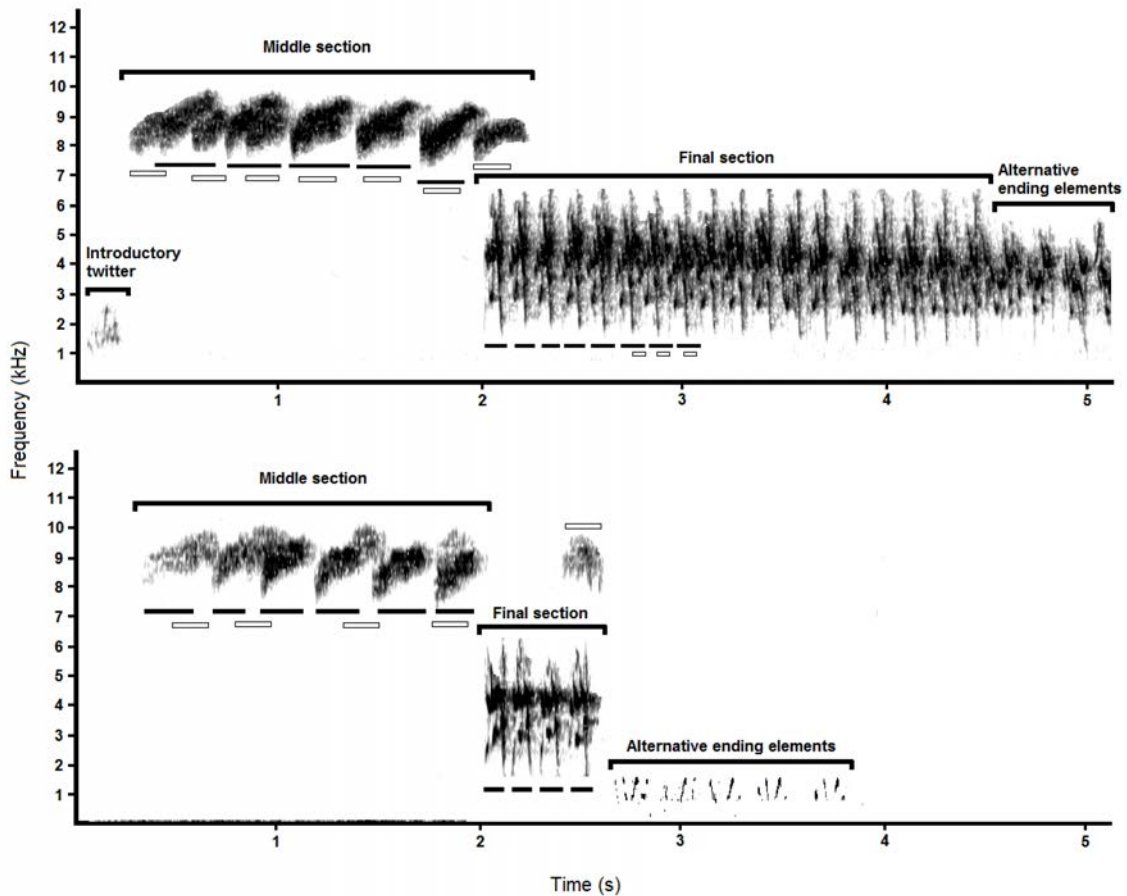


Figure 3. Sound spectrograms of typical duets of *Pezopetes capitalis*, which consist of 1) introductory twitter elements: can be sung by both sexes but are not present in all duets. 2) Middle section: group of overlapping elements that can be initiated by either the male or the female. 3) Final section: formed by a group of repeated and intercalated elements between both members of a mated pair. (d) Variable group of elements that are not present in every duet. When present, males and females sing the same overlapping elements. Spectrograms show elements sung by "individual 1" (black bars) and elements by "individual 2" (white bars).

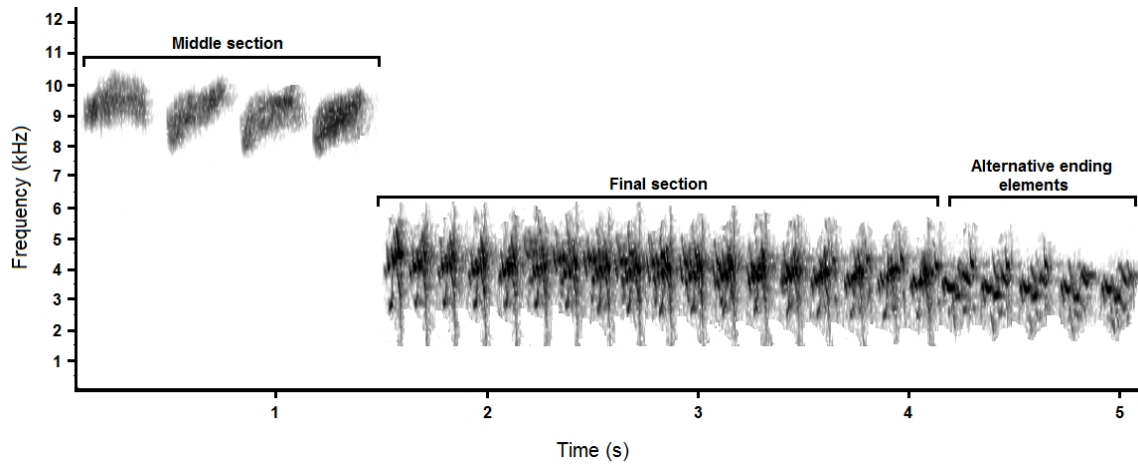


Figure 4. Solo song of *Pezopetes capitalis*. This song shares the same structure and elements as the duets, but is only sung by a male.

Capítulo 3. Acoustic description and synchronization of the duetting species
Pezopetes capitalis, Costa Rica

Abstract

Duetting has been widely studied, and its function vary between species, though in all cases temporal synchrony of the elements sang by each sex in the duet seems to play an important role. This is the first study in *Pezopetes capitalis* that analyze the temporal synchronization (low variation in its temporal variables), of both members in a mated pair during the duetting. My goals in this study where to describe the structure of the duet, and the degree of temporal synchronization of each individual of the pair during duetting. Duets of *P. capitalis* consist of overlapping elements between both members of a mated pair and can be initiated by either sex, but more often by males. Individuals sung their elements randomly as well as periodically during duetting. Synchronization was similar between both individuals. The second individual overlapped more frequently than the first (First individual $N=18$, second individual $N=33$ of 39 duets), both in frequency and duration of overlap. For 11 pairs I analyzed, I found that both, females ($N=10$ pairs) and males ($N=9$ pairs), reduced their silence intervals before sung a new element as a response to an increase in the duration of its partner's elements. I found that both mates decreases their elements high frequency, as the duet continued, with a similar decrease pattern, despite females joined males later on the second section, which can be a possible evidence of frequency coordination on the second section of the duet. I also found that pairs sang with a higher high frequency and increased the number of elements sang per duration of duets, when they were provoked; duet's elements duration and maximum frequency did not change significantly between treatments. Duets in *P. capitalis* serves as a joint defense of territory and as a way to recognized mates when a pair reunited. Further studies are needed to determine the functions within a duet of the possible frequency coordination found on this species.

Key words. Large footed finch, acoustic frequency coordination, overlapping, temporal coordination, endemic bird.

In nearly 450 bird species, representing 40% of the world families, both males and females vocalize with temporal coordination to produce a stereotyped acoustic

pattern known as a duet (Farabaugh 1982; Logue 2007; Hall 2009). Duets have evolved independently in phylogenetically distinct groups (Rogers *et al.* 2007), which according to Hall (2009) suggest that there it is a strong selection for duetting.

So far, there have been published extensive papers about bird duetting related to aspects as their structure (i.e., Brumm and Slater 2007, Hall 2009, Douglas and Mennill 2010) and functions (i.e., Farabaugh 1982, Langmore 1998, Hall 2004). However, a significantly part of all duets researches have been accomplished studying the wren family troglodytidae (i.e., Levin 1996, Logue *et al.* 2008, Barker and Mennill 2009, Fortune *et al.* 2011).

One of the most cited characteristic associated with duets is temporal coordination (synchronization), as most duetters involve together in a highly coordinated acoustic display. It has been proposed that the biological meaning of this coordination can be associated with individual quality (Hall and Magrath 2007), a way to avoid misdirected aggression when pairs are involved in territorial encounters (Farabaugh 1982), and to avoid signal masking (Brumm and Slater 2007). This is one of the first studies to describe the duet vocal structure and temporal synchronization of both individuals during duetting in a species of the family emberizidae.

The family Emberizidae has around 310 species around the world. Nevertheless, Farabaugh (1982) reported only two emberizid duetter species in the Panamanian region, which can be found both in Costa Rica. Nowadays, it is known that there are at least eight duetting species in the region, including *Pezopetes capitalis* (Large-footed finch).

P. capitalis is a highland endemic species to Costa Rica and western Panama. In Costa Rica, it is a fairly common residence in the upper parts of Central Cordillera and Talamanca Cordillera, (Stiles and Skutch 1989). There have not been detailed researches about this monogeneric species and its natural history.

Considering the little information on the structure of duets and the possible role of each mate of *P. capitalis* during duetting, I propose three main goals in this study. First, to describe the duet's structure according to each sex elements and its temporal patterns. Second, to determine the degree of temporal synchronization, of each individual of the pair during duetting. Finally, to test whether females and males adhere

strictly to duet codes, like timing in singing and waiting time to answer a mate. This is the first study in the species *P. capitalis* that analyze the temporal synchronization of both individuals during the duetting period. In addition, I discuss on the possible role of duetting synchronization.

Material and methods

Study Population.— I conducted the recordings and playbacks trails in Estación Biológica Cerro de la Muerte (09°34'N; 83°41'W, at 3150 m elevation) from March 2011 to October 2012. The study site is, and is characterized by the presence of an oak forest (*Quercus costaricensis*), its understory it is generally compound by a dense thicket of bamboo (*Chusquea* spp) (Stiles & Skutch 1989).

I mist netted and banded with a unique combination of ring colors, at least one individual from 12 mated pairs. To determine each mated pair potential territory to record them, I followed each of them during the day and put flagging marks at the edges of the areas where each pair were foraging (Chapter 2, unpublished data). I recorded duets of six of these mated pairs during one hour starting at 4:40 h, the time when mated pairs started to sing (personal observations) around the roosting and nesting sites (L. Sandoval com. pers).

This species maintain the same territories for at least two years (Chapter 2, unpublished data). Thus, to increase the sample size I included other seven (unbanded) mated pairs that maintained the same territories during the study period.

Playbacks experiments.— I used a directional microphone Sennheiser ME66 and a solid state digital recorder Marantz PMD 661. I saved digital recordings as uncompressed monoaural WAV files (48-bit, 44 kHz).

To a duet response, from each pair, I used three playbacks containing only duets, two of them (LCH 12-001 and LCH 12-003) recorded in Barva National Park (73 km away from my study site), and the third playback was a recorder in 2009 at Cerro de la Muerte. The recordings used as playbacks are deposited at the Laboratorio de Bioacústica, Escuela de Biología, Universidad de Costa Rica,

For playback trials, I used each one of the playbacks randomly, and did not play each playback more than three times to avoid that birds learn the playback songs and limit their response. All trials were conducted between 5:30 a.m. and 7:00 a.m., the period of highest acoustic activity of *P. capitalis* (personal observations). I only used one of the playbacks per day, to ensure responses were a consequence of that playback.

Analysis of vocalizations.— I analyzed all playbacks and recordings using Raven pro 1.4 (Bioacoustics Research Program 2011). To identify which elements corresponded to each individual in a pair, I used two methods: 1) I recorded videos in HD using a Sony HDR-SR11, for three banded mated pairs that allowed me to determine their duetting order; 2) In playback trials, I directed the microphone to one individual as they were responding to the playback. In this situation, the spectrogram of the bird singing directly toward the microphone is darker, than that of the other bird. This allowed identification of the sex singing each part of the duet.

For all analyses I divided all duets in two sections (Fig. 1). I measured for each section of the duet two temporal acoustical variables: element's duration and silence interval between elements. The silence interval corresponded to the time between the end of the element of one individual and the beginning of the next element corresponding to its partner (e.g., the time it takes for one individual to respond to its partner). When temporal overlap occurred, I measured the overlapping time and assigned it as a negative value to differentiate it from non-overlapping elements.

Here I defined an element as a discrete sound that can have modulation in frequency (Hz) and time, and that can be separated temporally or in frequency of other elements. Also, I defined *synchronization* as the temporal coordination of the elements in a duet sang by both birds. Temporal coordination could occur whether or not elements overlap in the duet.

Statistical analysis.— Duets in *P. capitalis* are composed of repetitions of similar notes, which are emitted with apparently regular time intervals (periodicity). Given this periodical nature, it is possible to represent the elements of the duet with a sine function.

To calculate the periodicity of the elements for one individual relative to the other individual in the duet of *P. capitalis* (reference individual), I used circular statistical calculations following the methods outlined in Zar (2010) and the modified equation (equation 1) used by Maynard *et al.* (2012). This equation includes triads of elements as the sampling unit (Fig. 3). The triads are composed by a sequence of elements in which the first (R_1) and third (R_2) element of the triad belongs to one bird (e.g., male) and the second element (X) belongs to the second bird (e.g., female). Then the time between the beginning of R_1 and the beginning of X , and between the beginning of R_2 and the beginning of R_1 are measured and included in the equation A , which transform these time intervals to degrees.

$$\text{(Equation 1)} \quad A = \frac{360(X - R_1)}{R_2 - R_1}$$

For instance, if the element of the female is exactly halfway between the two elements of the male the value of A is 90° . I calculated a mean value of A for the female and male within each pair.

For each value of A , I calculated the sine and cosine to obtain the r-vector, which represents the periodicity between the time the elements of both individuals are emitted; r-vector varies from 0 to 1, where a value of 0 indicates absence of periodicity, meanwhile a value of 1 indicates that the elements in a duet were sung periodically. I then calculated the mean angle for each duet sang by every pair and used it in a second order sample parametric analysis (Zar 2010, page 645) to statistically test whether or not the time between elements of the duet are periodically for one or both duetting birds.

To compare the synchronization of each pair during duetting, I first obtained, the mean of silent interval time or overlapping time for each individual. For this analysis, I considered as the first individual, the one who started the duet, and as the second individual, the one responding to the first individual's elements (in most cases it was the male who initiated the duet). I calculated the CV of each individual and estimated which sex was more coordinated by dividing the CV of the second individual by the CV of the first individual; this indicates difference in synchronization between both birds. I considered pairs with lower CV values as more coordinated in comparison with ones

with higher CV values, because birds with low CV values implies less variation in their timing.

To determine whether both members of a mated pair adjusted their timings (duration of element and silent intervals), according to changes in its partner's timing, I applied linear regression analyses (e.g., duration of elements of one individual vs. silent intervals of its partner). Visually, in the second section of the duet (Fig.1) the acoustic frequency of the elements seemed to decrease with time (e.g., high frequency decreases with time). This acoustic behavior was also seen when a male sang alone his corresponding section of the duet. To determine if frequency of elements changed with time, I measured the high frequency of each individual element, and then compared the frequency (e.g., high frequency) of each element against the order in which each element was sang: 1 being the first element of the section of the duet analyzed. I did not include low frequency because the lower limit of each element was difficult to define in the spectrogram. To compare the reduction in high frequency between sexes I regressed the order of the elements against the high frequency for each bird and then compared the slopes and intercepts between sexes. Regressions were calculated for those sections of the duet in which both birds participate in the duet.

To evaluate the effect of playbacks I compared the acoustic structure of natural duets with that of duets provoked with playbacks using generalized linear mixed models (GLMM) for four response variables: 1) Duration of duet, 2) High frequency, 3) Maximum frequency, and 4) the ratio between number of elements and the duration of duet. The first variable was measured on the whole duet, and the last three variables were measured for each section of the duet. I included in the analysis two explanatory categorical variables: 1) Pair, and 2) Treatment, which involved natural duets, and duets sang in response to a playback stimulus, and included the number of duets recorded as a random factor. I performed circular statistics analyses using Microsoft Excel 2003. The rest of the analyses were performed using R software (R Core Team 2012).

Results

During duetting, some pairs of *Pezopetes capitalis* appeared to sing their elements randomly, but others sang their elements periodically (synchronic). Considering the first section of the duet, six pairs ($N = 6$) sang the elements of the duet randomly and the other pairs synchronized temporally their elements. For the second section, four out of ten pairs synchronized their elements temporally, the remaining six pairs did not synchronize the elements between both individuals (Table 1). The synchrony measured by the CV was similar for both individuals on both sections of the duet ($t = -0.31$, $df = 11$, $p = 0.759$ for the first section and $t = 0.19$, $df = 10$, $p = 0.853$, for the second section). CV for both individuals were low, on the first section the CV for the first individual was 0.14, and for the second individual was 0.12. For the second section of the duet the CV of the first individual was 0.16, and 0.18 for the second individual.

For the first section ($N = 39$ duets) the first individual overlapped with 11% to 100% of the elements of the second individual, which represented a mean time overlapping of 0.762 ± 0.623 s of the singing time of the first individual; this time corresponded to 34% of the mean duration of the elements sung by this individual in this section. For the second individual overlapping with the elements of the first individual was between 17% to 100% of the elements, the mean time of these overlapping was 0.568 ± 0.540 s of the singing time for the second individual, which represented 27% of mean duration of elements sung in the first section.

For the second section of the duets ($N = 28$), only the second individual overlapped with the elements of the first 79% to 100% of the cases. These individuals presented a great variation in the time they overlapped (0.545 ± 0.856 s). The second individual overlapped 33% of the mean duration of its elements. In addition the duration of elements and silence intervals decreased for both individuals (first individual $N = 10$, second individual $N = 9$) along the second section of the duet (Table 2).

In 7 out of 9 pairs, the high frequency of the elements of the second section of the duet decreased from the first to the last element (Fig. 2). In 6 of these 9 pairs, the high frequency decreased similarly (similar slopes) for both mates as duet progressed

(Table 3). This suggests that even those individuals (second individual) that began to sing later the second section of the duet coordinate the high frequency with the first individual. The number of elements included in the analysis of the second individual was lower than for the first, because often the second individual began to sing after the first individual had initiated the second part of the duet.

In response to playbacks *P. capitalis* increased high frequency of the second section of duets in comparison with the natural duets (unprovoked duets). Maximum frequency was higher in both sections of the duet, in response to playbacks; pairs increased the number of elements in the first section while responding to playback 2, and in response to playback 1 on the second section. The duration of duets did not change in response to playbacks (Figs. 3-6; Table 4).

Discussion

Coordination (synchronization) is a characteristic common to nearly duets, as most duetters engage together in a highly coordinated acoustic display. In duets, coordination within a pair birds varies from coordination in timing to coordination of song types (Hall 2009), depending on how their duet is structured. In duets of *P. capitalis*, some pairs within a mated pair sing their elements randomly, and others synchronically. In both cases with high overlapped in time and between elements. Same temporal synchronization in both members of a mated pair, was reported also by Marshall-Ball and collaborators (2006), in pairs of plain wrens (*Thryothorus modestus*) that had been together for years.

Pezopetes capitalis duets when a pair reunited, when other pair approach their territory or when they are provoked by playbacks, showing in this case an apparent aggressive behavior against the source of sound and singing closer to each other (Chapter 2, unpublished data). It has been suggested that duetting functions to maintain pair bond and the joint defense of resources (Farabaugh 1982, Langmore 1998, Hall 2004, Logue 2005), which may also be functions for the duet of *P. capitalis*. Evidence for these hypothesis is scarce and in all cases correlative. The Australian magpie-lark

increases the song rate in response to highly synchronized duets (Hall 2000, Hall and Magrath 2007). This change is interpreted as a more effective territorial, though direct evidence is lacking.

In this species, Hall and Magrath (2007) also proposed that precise temporal coordination (synchronization) serves as honest signal of coalition strength during territorial displays. However they reached this conclusion based on a human communication system (Hagen and Bryant 2003), and those results not necessarily apply or can be extrapolated to an avian system. In humans coalition quality depends on motivation and ability to act collectively. Hall and Magrath (2007) considered coordination in duetting as the ongoing motivational signal and coordination precision as an index of the capacity to act collectively. Thus, the evidence for the functions of duets is only correlative and until a more experimental approach be taken, these functions will remain unclear.

In natural contexts birds tend to avoid overlapping in acoustical signals to avoid being masked by acoustical signals of another bird (Todt and Naguib 2000, Searcy and Beecher 2009). However, under certain conditions overlapping can be inevitable depending on factors as the random timing of elements and the limitations of acoustic space (time), were the only chance for example for one individual to respond to another individual is to produce a song with overlapping elements (Todt and Naguib 2000, Naguib and Mennill 2010). Considering the short time between two consecutive elements of a single individual that the other bird in a duet of *P. capitalis* has to sing its own elements, and the random emission of elements in some of these birds, is highly improbable that elements do not overlap within a duet. However, the overlapping time is relatively low in this species, allowing signals of both individuals to be heard by neighbors or potential competitors. The changes in silent intervals detected along the duet of *P. c.* could be a mechanism to adjust to variation in duration of the elements of its partner and thus to reduce acoustical overlap. Todt and Naguib (2000) suggest (with little evidence) that the degree of overlap indicates the state or status of an individual.

The biological importance of producing duets with overlapping elements could also be related to producing more threatening signals than those signals produced with a

solo song by one individual or non-overlapping duets, because acoustical signals could be reinforced with the combination of elements of both mated birds (Todt and Naguib 2000, Fitzimmons *et al.* 2008). This would support the function of joint resources defense of duets (Hall 2004).

Comparing the slope of both sexes, high frequency versus their elements sequence, the results suggests that there is coordination in the frequency. This would be the first report of this vocal behavior in duetting birds, since only coordination in timing and coordination of song types have been previously reported (see Farabaugh 1982, Brumm and Slater 2007, Hall 2009, Maynard *et al.* 2012). If this type of coordination occurs in *P. capitalis*, it would imply a high level of attentiveness and an extraordinary neural capacity that allow fine/scale adjustments, on a scale of milliseconds to perceive and produce highly coordinated duets in both timing and frequency (Hall 2009). The reduction in high frequency presented by both individuals in a mated pair as the second section of the duet progresses, could also be produced by fatigue of muscles associated to song production (Suthers *et al.* 1999). The frequency could decrease as fatigue increases. However, it is unlikely that the second bird that began to sing after the first had initiated this part of the duet, begins singing with similar frequency than the first bird.

Pairs of *P. capitalis* changed the characteristics of some acoustical variables in response to playbacks: high frequency in the second section of the duet, and the number of elements/duration in both sections of the duet. These changes in the acoustical characteristics of the duet suggest an aggressive response to potential competitors (playbacks). In Australian magpie larks, Hall and Magrath (2007) found that pairs had the ability to modify the temporal characteristics of their duets depending on the characteristics of the playbacks they were using to elicit a response, such as percentage of overlapping and temporal coordination.

The results obtained in this study suggest that duets in *P. capitalis* are important in territory defense, and may also be important in recognition when a pair reunited. In their duets, *P. capitalis* synchronizes the timing and the frequencies and both timing and frequency vary across pairs. The role of both types of synchronization in the duet of *P.*

capitalis is still unclear and an experimental approach is necessary to determine, first the function of the duet in this species and second, to examine how the synchronization in time and frequency affect these functions.

Temporal coordination (synchronization) has been considered as one of the common characteristics associated with duets, as most duetters involve together in a highly coordinated acoustic display. In duets, the way a pair communicate can vary from coordination of timing to coordination of song types (Hall 2009), and the way their duet is structured. In *P. capitalis* duets, mated individuals sang their elements randomly as well as synchronically, where time overlapping elements represent a high percentage of the duet vocal structure.

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Table 1. Results of the circular statistical analysis by each section of duets of *Pezopetes capitalis*. Some pairs timed their elements randomly, and other sung their elements in a periodically way.

Pair code	First Section of the duet					Second section of the duet				
	F-value	DF	p	r-vector	Mean angle	F-value	DF	p	r-vector	Mean angle
1	2.97	2, 29	0.0668	0.29	104	5.86	2, 49	0.00521	0.26	149
2	1.18	2, 12	0.34	0.26	167	3.07	2, 19	0.0701	0.36	146
3	0.88	2, 22	0.428	0.19	104	6.59	2, 32	0.00402	0.40	173
4	6.08	2, 28	0.0064	0.38	161	1.15	2, 62	0.324	0.13	176
5	9.67	2, 30	<0.001	0.48	152	6.25	2, 37	0.00458	0.41	127
6	7.12	2, 24	0.00373	0.47	165	--	--	--	--	--
7	27.87	2, 25	<0.001	0.59	150	28.02	2, 60	<0.001	0.50	153
8	40.06	2, 20	<0.001	0.72	142	0.97	2, 40	0.387	0.13	170
9	0.68	2, 4	0.55	0.30	172	--	--	--	--	--
10	0.53	2, 16	0.60	0.19	134	227.867	2, 20	<0.001	0.85	115
11	20.59	2, 25	<0.001	0.58	168	0.59	2, 35	0.558	0.13	136
12	4.17	2, 17	0.0336	0.33	12	0.68	2, 15	0.519	0.22	83

Table 2. Relationship between each sex element's duration vs. its partner silence interval or overlapping time in duetting pairs of *Pezopetes capitalis*. Individuals response to an increase in their partners element's duration was a decrease in the duration of their silence interval until start singing their next element.

Pair code	Silence interval of the second individual vs. duration of elements of the first individual (R²-value)	Regression slope	DF	p	Silence interval of the first individual vs. duration of elements of the second individual (R²-value)	DF	Regression slope	p
1	0.0068	0.0865	105	0.400	0.18	102	-0.495	<0.0001
2	0.059	-0.189	38	0.132	0.025	36	-0.157	0.339
3	0.22	-0.540	60	0.000138	0.12	57	-0.373	0.00673
4	0.18	-0.361	99	<0.0001	0.25	102	-0.496	<0.0001
5	0.26	-0.531	90	<0.0001	0.10	77	-0.211	0.00444
6	0.15	-0.541	31	0.0261	0.30	30	-0.573	0.00115
7	0.12	-0.242	95	0.00041	0.23	89	-0.332	<0.0001
8	0.25	-0.339	66	<0.0001	0.27	64	-0.299	<0.0001
10	0.30	-0.738	49	<0.0001	0.34	39	-0.526	<0.0001
11	0.49	-0.640	69	<0.0001	0.27	65	-0.412	<0.0001
12	0.11	-0.360	38	0.0382	0.24	39	-0.619	0.00126

Table 3. Relationship between the sequence of the elements of each individual vs. the high frequency of their elements in duets of *Pezopetes capitalis*.

Pair code	Sequence of elements of first individual vs. its high frequency				Sequence of elements of second individual vs. its high frequency				Slope Analysis		Intercept Analysis	
	R ²	b	a	p	R ²	b	a	p	T-test	p	T-test	p
1	0.16	-21.182	5066.93	<0.0001	0.00013	1.054	5247.82	0.908	-2.16	0.0320	-1.36	0.174
2	0.41	-37.33	5717.27	0.00174	0.0018	-2.696	5326.60	0.854	-1.95	0.0583	2.97	0.00514
3	0.12	-20.330	5195.28	0.0337	0.040	-9.794	5151.87	0.236	-0.86	0.393	0.28	0.777
4	0.43	-62.285	5034.88	<0.0001	0.26	-48.75	4953.28	<0.0001	-0.90	0.3700	0.73	0.465
5	0.022	-24.81	5466.36	0.357	0.00074	-5.195	5346.09	0.866	--	--	--	--
7	0.43	-63.73	5766.73	<0.0001	0.19	-40.15	5511.66	0.00230	-1.42	0.159	1.80	0.0748
8	0.62	-45.18	5187.48	<0.0001	0.68	-74.43	5439.82	<0.0001	3.36	0.00111	-2.46	0.0154
10	0.62	-92.62	5589.97	<0.0001	0.60	-96.62	5581.57	<0.0001	0.17	0.862	0.049	0.961
11	0.054	-103.3	6082.71	0.140	0.11	-180.80	6624.66	0.0281	0.738	0.462	-0.749	0.456
12	0.25	-66.48	5473.29	0.0389	0.47	-69.52	5029.79	0.00234	0.086	0.931	2.28	0.0298

Table 4. Comparison of acoustical variables of unprovoked duets and duets elicited by playbacks, *Pezopetes capitalis*.

Acoustical variables	F-value	DF	Probability
Duration of the duet	0.153	3, 53	0.927
First section of the duet			
High frequency	1.22	3, 50	0.314
Maximum frequency	0.028	3, 50	0.994
# elements/duration	4.63	3, 52	0.006
Second section of the duet			
High frequency	3.19	3, 28	0.0389
Maximum frequency	2.88	3, 28	0.0537
Number of elements/duration	3.37	3, 30	0.0314

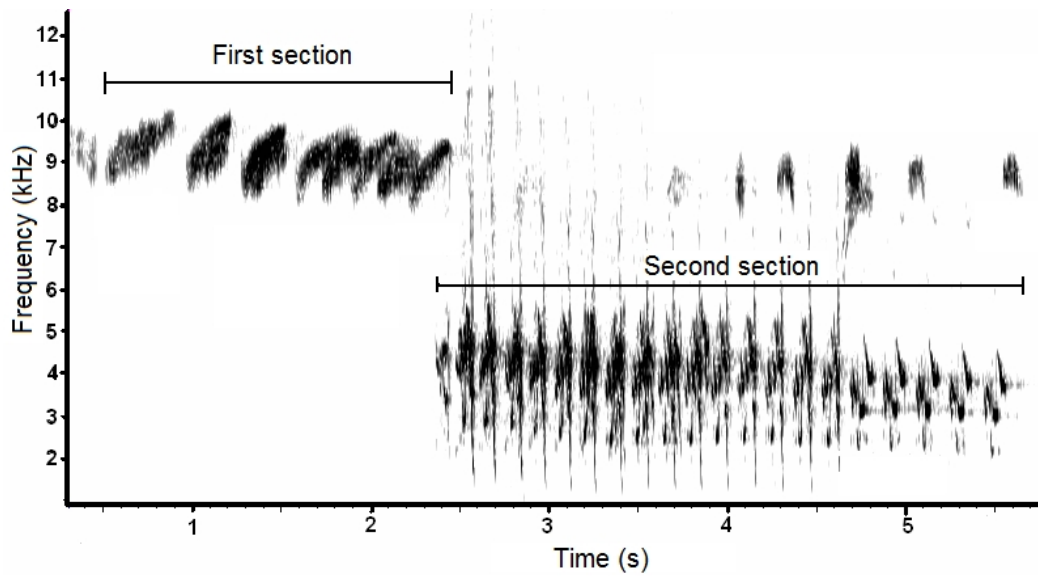


Figure 1. Sound spectrogram of a typical duet of *Pezopetes capitalis* signaling the sections used to analyzed temporal overlapping.

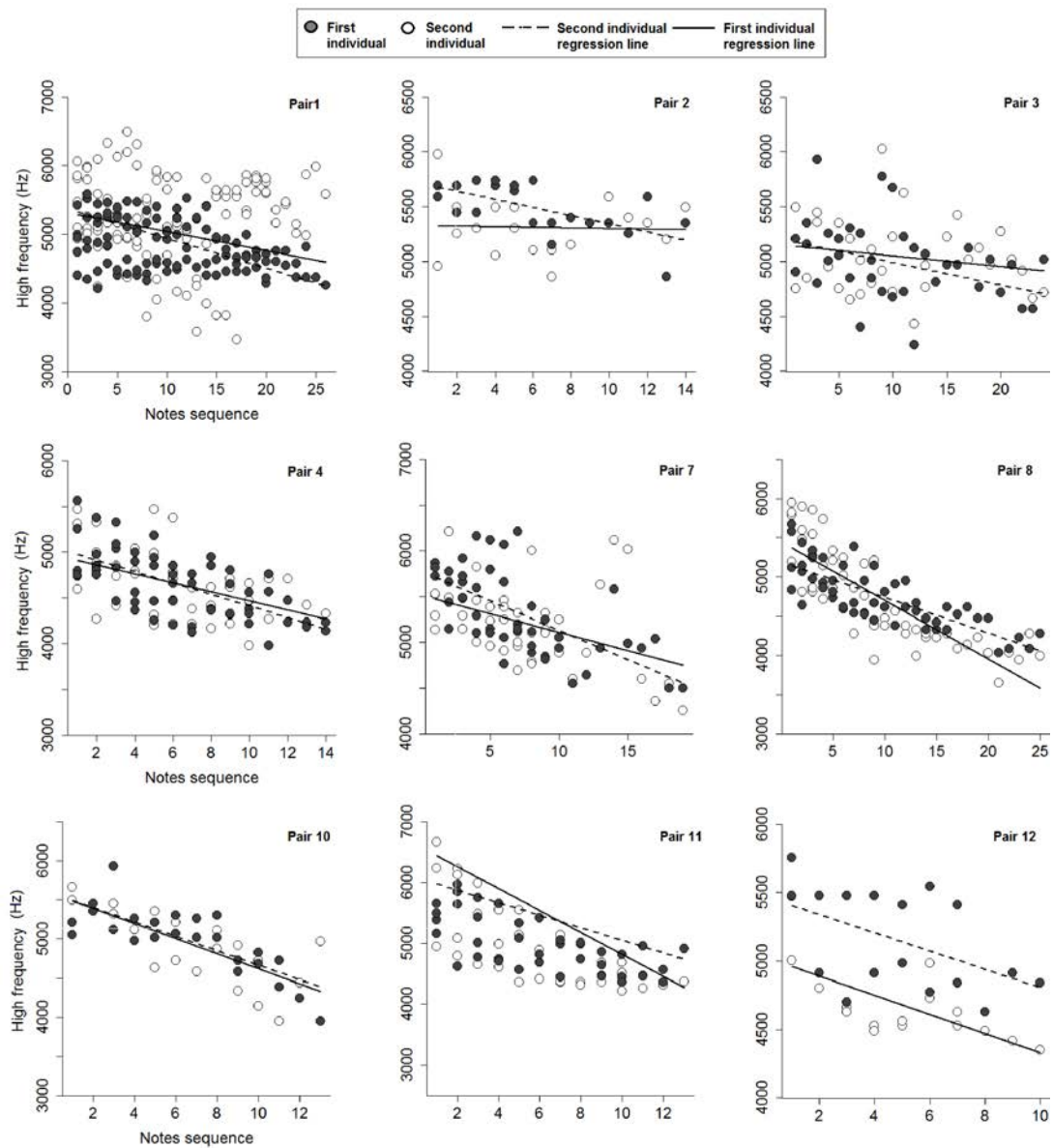


Figure 2. Relationship between each individual's elements sequence vs. note's high frequency of *Pezopetes capitalis* duets. Slope analysis suggest a possible evidence of frequency coordination, considering that second individuals joined their partners later in the duet and start with the same frequency as well.

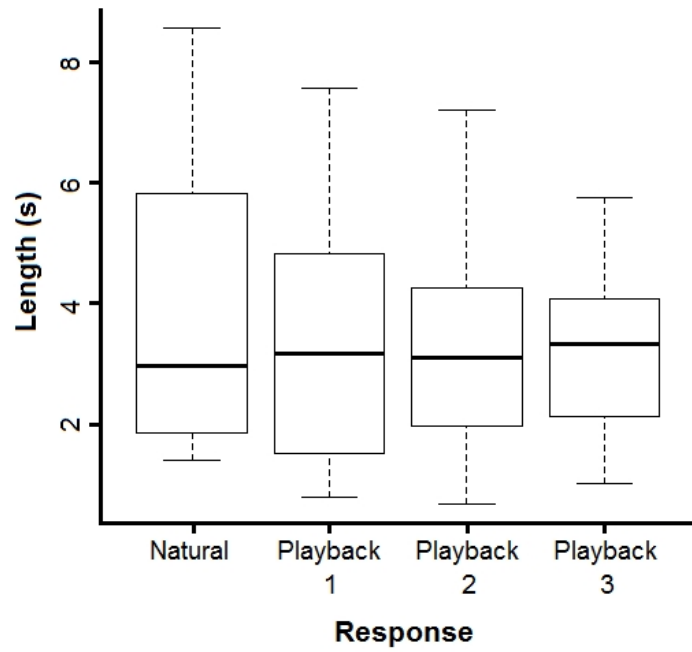


Figure 3. Mean duration of duets were similar during natural recordings and playback treatments of *Pezopetes capitalis*.

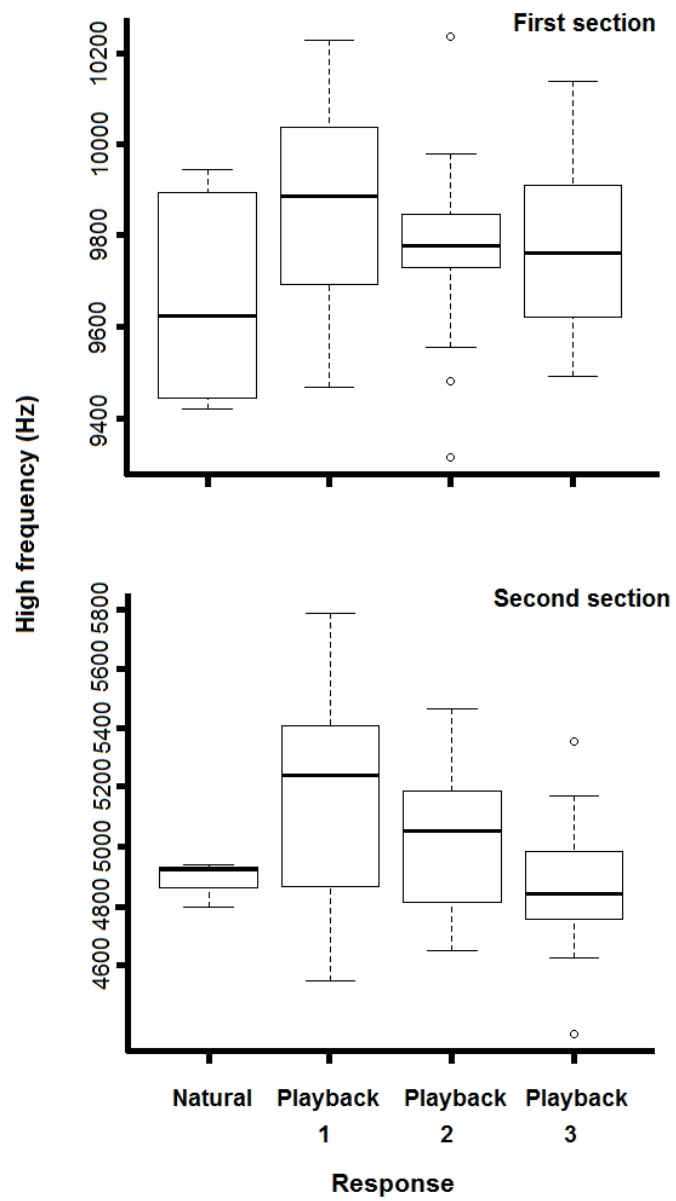


Figure 4. Pairs of the Large-footed finch (*Pezopetes capitalis*) varied the high frequency of their elements during natural recording duets and playback responses.

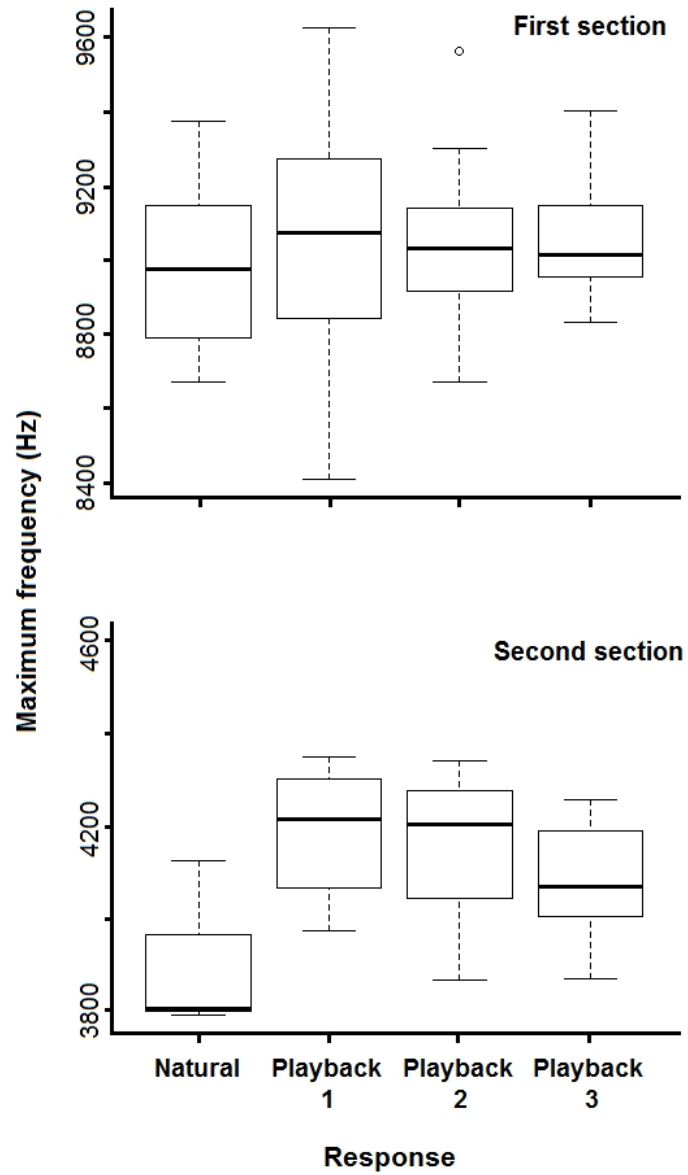


Figure 5. Pairs of *Pezopetes capitalis* sang elements with a higher maximum frequency while responding to playbacks than during natural recording duets.

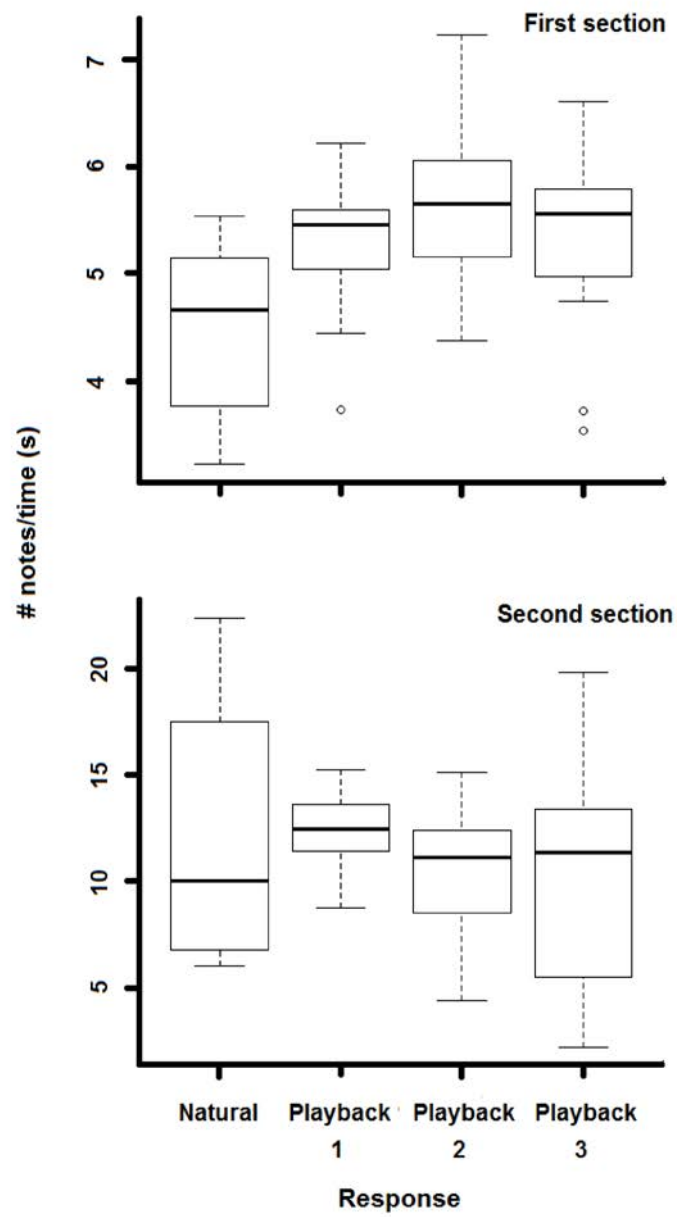


Figure 6. Pairs of *Pezopetes capitalis* responded with a higher number of elements per time while responding to playbacks than during natural recordings.