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VOCALIZAÇÃO DO SAGUI COMUM: INFLUÊNCIAS SOCIAIS E ONTOGÊNICAS EM AMBIENTE NATURAL

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Dissertação apresentada ao Curso de Mestrado em Biologia Animal da Universidade Federal de Pernambuco, como parte dos requisitos para obtenção do grau de Mestre em Ciências Biológicas na área de Biologia Animal.

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… Some things are meant to be the way they gonna be, you can’t stop time or change history. Sometimes all you saw were things you wanted to see…

by Sandi Thom

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ÍNDICE

Resumo

Os sagüis comuns, *Callithrix jacchus* (Callithrichidae, Primates), vivem em grupos de três a quinze indivíduos, havendo um sistema de dominância e a possibilidade de viver em monogamia, poliginia, poliandria ou poliginandria. Eles são primatas neotropicais arbóreos, endêmicos da região Nordeste do Brasil, mas que nos últimos anos foram amplamente introduzidos em outras regiões do país. O presente estudo foi conduzido em um fragmento de Floresta Atlântica no Nordeste do Brasil e investigou um total de 30 sagüis comuns. Os objetivos do presente estudo foram: (i) apresentar uma descrição quantitativa do repertório vocal de sagüis comuns em ambiente natural, baseando-se na categorização das vocalizações e nas características físicas destas; (ii) investigar se existem diferenças no repertório vocal entre animais de diferentes idades; (iii) comparar o repertório vocal de sagüis comuns selvagens com o repertório previamente descrito para essa espécie em cativeiro; (iv) investigar o contexto comportamental associado com certas vocalizações; (v) investigar se a freqüência de uso das vocalizações é afetada pela idade, sexo e posição hierárquica dos animais no grupo; (vi) e, por fim, investigar se as características físicas dos sinais acústicos estão relacionadas com a idade dos animais, através do estudo do efeito da idade sobre as características físicas da vocalização de contato "trill". O repertório vocal dos sagüis comuns em liberdade foi separado em 13 sinais acústicos e alguns destes se mostraram exclusivos para certas idades (e.g. "loud squeal" para infantes e vocalizações de alarme para os adultos). Algumas vocalizações estão mais aptas a serem emitidas associadas com certos contextos comportamentais ou como resposta a outras vocalizações. Algumas vocalizações que antes foram descritas para animais em condições de cativeiro não foram observadas em ambiente natural e vice-versa.

Durante maior parte do dia, os adultos vocalizaram mais que juvenis e infantes. Entretanto, não houve diferença quanto à freqüência de uso das vocalizações de acordo com a posição hierárquica ou gênero dos animais. A vocalização "trill" emitida por animais mais jovens se mostrou com características físicas (freqüências dos sons) mais altas que aquelas emitidas por animais adultos. De uma maneira geral, nossos resultados sugerem que a comunicação auditiva dos sagüis comuns está mais relacionada com a idade dos animais, pelo menos em termos de repertório, freqüência de uso das vocalizações e características físicas da vocalização "trill". Considerando o complexo sistema social e o hábito arborícola da espécie, já previamos a existência um intricado sistema de comunicação através das vocalizações. Nossos resultados, juntamente com os dados obtidos em animais de cativeiro, confirmaram tal predição.

Abstract

Common marmosets, *Callithrix jacchus* (Callithrichidae, Primates), live in groups comprising three to 15 individuals. There is a hierarchical structure and the possibility of living in monogamy, polygyny, polyandry or polygynandry. They are arboreal Neotropical primates, endemic from the Northeast Brazil, but they already were introduced in several other regions of the country. The present study was carried out in a fragment of Atlantic rain Forest in the Northeast, Brazil and investigated a total of 30 wild common marmosets. The aims of the study were (i) to provide a detailed, quantitative description of the vocal repertoire of common marmosets in the wild based on categorising their vocalisations and then reporting the physical characteristics of those vocalisations; (ii) to investigate if there are differences in vocal repertoire between animals of different age; (iii) to compare the vocal repertoire of wild common marmosets with the repertoire described for this species living in captive conditions; (iv) to ascertain the behavioral contexts associated with certain vocalisations; (v) to investigate whether the rate of vocalisations of common marmosets is affected by age, gender and hierarchic position; (vi) and to investigated whether call characteristics were related to the age of the caller by studying the affect of age on the physical characteristics of a contact vocalisation, the trill call. The vocal repertoire of wild common marmosets was separated into 13 different calls, with some of these calls being exclusive to certain age groups (e.g. loud squeal to infants and alarm calls to adults). Some call types are most likely to be associated with certain behavioral contexts or as a response to other particular calls. Some call types that were previously described in captive conditions were not observed in wild conditions and vice-versa. During most of the day, adults vocalised more than both juveniles and infants. However, no differences were found

between either gender or hierarchic position with respect to rate of vocalisations. The trill calls emitted by young common marmosets were of a higher pitch than those emitted by adults. Our results suggest that the auditory communications of wild common marmosets are related to the age of the animals, at least in terms of call types present in the vocal repertoire, the rate of vocalisations and the physical characteristics of the trill call. ConsideringThe complex social organization of this species and the arboreal status already predicted an intricate communication system through vocalisations. Our study together with the data previously coming from captive studies confirmed such prediction.

CAPÍTULO I

Revisão Bibliográfica

Aspectos pertinentes sobre a espécie em estudo

O *Callithrix jacchus* é um primata neotropical popularmente chamado de sagüi comum, sagüi-do-Nordeste ou sagüi-de-tufo branco. É pertencente à família Callithrichidae, onde dentre as suas principais características encontramos o tamanho corporal reduzido. Este aspecto, juntamente com a presença de unhas em forma de garras bem resistentes e desenvolvidas, lhes permite se apoiar em posição vertical nos galhos e troncos, facilitando a locomoção e o consumo de goma. Tais características representam um importante ponto para o sucesso ecológico em termos de distribuição e adaptação destes animais (Garber, 1992; Ferrari, 1993). Eles ainda apresentam tufos de pêlos brancos circum-auriculares por trás e acima; coloração do corpo acinzentado claro com reflexos castanhos e pretos; uma cauda apresentando faixas transversais; e dimorfismo sexual não acentuado (Hershkovitz, 1977; Sussman & Kinzey, 1984; Auricchio, 1995). Os sagüis comuns apresentam uma dentição especializada, com os incisivos grandes e afiados, o que de certa forma os auxilia na habilidade de roer troncos de árvores em busca de goma (Hershkovitz, 1977).

Os sagüis comuns são animais sociais que formam grupos de três a 15 indivíduos, apresentando, geralmente, uma área de uso específica (Stevenson & Rylands, 1988; Mendes Pontes & Monteiro da Cruz, 1995; Monteiro da Cruz, 1998). O período de gestação desses animais varia em torno de 140 a 148 dias, sendo os filhotes, em geral, gêmeos e tendo a capacidade de se agarrarem ao pêlo da mãe segundos após o parto (Hershkovitz, 1977; Hearn, 1983; Yamamoto, 1991; Fleagle, 1999). Apesar da presença de uma fêmea e de um macho dominante no grupo, eles possuem uma organização social em que todos os membros cooperam nos cuidados com a prole (Ingram, 1977; Rothe & Darms, 1993). Contudo, é importante salientar que estudos em campo e em cativeiro já revelaram a existência de monogamia, poliginia, poliandria e ainda poliginandria em grupos de *C. jacchus* (Dixson, 1993; Roda & Mendes Pontes, 1998; Arruda et al., 2005; Bezerra et al., *in press*).

O sagüi comum é endêmico do nordeste brasileiro, ocorrendo ao norte do rio São Francisco, ao leste do Rio Parnaíba (Auricchio, 1995) e tendo o Rio São Francisco como limite sul (Rylands et al., 1993). Entretanto, essa espécie já foi amplamente introduzida em várias matas do Brasil, principalmente no Sudeste, como Serra da Carioca e Tijuca no Rio de Janeiro, Serra da Cantareira e em vários parques da cidade de São Paulo (Auricchio, 1995). No Rio de Janeiro inclusive, o sagüi comum e o vem se tornando um problema nos esforços de conservação do mico leão dourado, *Leontopithecus rosalia*, por conta da competição de uma maneira geral entre esses primatas (e.g. Ruiz-Miranda et al., 2006). O sagüi comum tem um habitat bastante diversificado, podendo ser encontrado em áreas de Caatinga, Cerrado, Mata Atlântica, mangue e plantações (Hershkovitz, 1977; Stevenson & Rylands, 1988; Mendes Pontes, 1989; Rylands & de Faria, 1993, Auricchio, 1995).

É valido salientar que os sagüis comuns foram selecionados como uma espécie de grande interesse científico, sendo inclusive a espécie número um na Europa em pesquisas envolvendo neurotoxinologia neurofamacologia e fisiologia reprodutiva (Newman, 1995). Dentre as razões para essa preferência pela espécie encontramos a fácil adaptação a ambiente de cativeiro, o baixo custo de manutenção de colônias da espécie e o fato de gerar gêmeos idênticos numa freqüência relativamente alta, o que permite a manutenção de colônias auto-suficientes por um determinado período (e.g. Hearn, 1983).

Comunicação dos animais

A comunicação dos animais se dá por diversos motivos, tais como reprodução, agressão, predação ou alimentação (Marler, 1961; Shettleworth,1998). Ela pode ser definida como um processo em que um animal influencia o comportamento do outro através da transmissão de sinais (Krebs & Davies, 1996; Pearce, 1997; Shettleworth, 1998). Estes sinais podem ser transmitidos de forma olfativa, visual, tátil ou auditiva (Krebs & Davies, 1996; Dyer & Brockman 1996), e irão depender principalmente das restrições impostas pelos hábitos e habitat das espécies (Krebs & Davies, 1996; Brumm et al., 2003). Em particular os sinais acústicos tem a propriedade de ampla transmissão, ou seja, é geralmente possível saber de onde vem um som, sem necessariamente estar olhando para e/ou próximo da fonte, ao contrário do que acontece com os sinais visuais/gestuais e os olfatórios (Altman, 1974). Entretanto, não podemos desconsiderar que a percepção do sinal acústico também vai depender do receptor. Para um melhor entendimento da comunicação auditiva, a consideração das vocalizações, tanto do aspecto comportamental como estrutural é fundamental (McLanahan & Green, 1977).

A comunicação vocal envolve um comunicador, um sinal e um receptor (McLanahan & Green, 1977). Os sons presentes nessa comunicação fazem parte de uma classe especial de som que é caracterizada pela complexidade acústica, pela importância biológica e pelo fato de que também é produzida e percebida pela mesma espécie (Wang, 2000). O estudo da comunicação vocal nos animais pode revelar diversos aspectos ecológicos e comportamentais de uma espécie. Por exemplo, a produção de um determinado som poderá indicar sucesso em atrair um parceiro ou em repelir um adversário (Gerhardt, 1998). Este caso acontece freqüentemente entre vários primatas como resposta à vocalização longa, *long call* (Gautier & Gautier, 1977 *apud* Snowdon 1993).

É crescente o número de trabalhos envolvendo vocalização de diversos animais (e.g. Griffin & Galambs, 1941; von Frisch & Lindauer, 1956; Griffin et al., 1960; Roeder. & Treat 1961; Wilson & Bossert, 1963; Rosemary, 1977; Snowdon, 1993; Roush & Snowdon, 1994; Crocroft & Ryan, 1995; Catchpole & Slater, 1995, Herzing, 1996; Dudzinnski, 1998; Miller & Tyack, 1998; Riede, 1998; Dudzinnski, 1999; McCowan & Hooper, 2001; Nagarajan et al., 2002; Corewyn, 2003; Mendes & Ades 2004). Tendo o processo de comunicação vocal dos primatas, em particular, recebido bastante atenção por parte dos pesquisadores (Tomasello & Call, 1997).

Os primatas de um modo geral podem se comunicar através de uma ampla variedade de sinais olfativos, táteis, auditivos e visuais/gestuais (Altman, 1967; Napier & Napier, 1996; Corewyn, 2003). O conhecimento sobre a vocalização desses animais contribui inclusive para os estudos da taxonomia dos mesmos (Marler & Mitani, 1988; Snowdon, 1993; Mendes et al., 2006; Konrad & Geissmann, 2006). De acordo com Ghanzafar & Hauser (2001) as diferenças na estrutura dos sinais auditivos em primatas não somente codificam diferentes categorias de vocalização, mas também codificam características individuais, sexuais, de identificação grupal e do estado de motivação do animal. O reconhecimento grupal e individual tem importantes implicações para a evolução do comportamento social (e.g. Rendal et al., 1996).

Os sinais auditivos são de extrema importância para a comunicação dos primatas arborícolas visto que a folhagem interfere bastante, bloqueando o campo visual (Altmann 1967; Epple, 1968; Yamamoto, 1991; Geiss & Schrader, 1996; Napier & Napier, 1996). Informações quanto à idade e sexo do animal, assim como uma íntima consideração do contexto da vocalização e do ambiente em que a vocalização ocorre são pré-requisitos importantes para o entendimento da função do sinal vocal (McLanahan & Green, 1977). O repertório vocal dos primatas em geral é bem variado e comumente apresenta-se associado a um determinado comportamento. Um exemplo é o das vocalizações de alarme apresentadas pelo *Cercopithecus aethiops*, que causam uma resposta diferente nos indivíduos do grupo para cada tipo de predador (Struhsaker, 1967; Seyfarth et al., 1980 a e b). Ainda para o *Cercopithecus aethiops*, existem diferenças nas respostas a vocalizações de acordo com o gênero e a posição hierárquica do indivíduo emissor do sinal acústico no grupo (Cheney & Seyfarth, 1990). Um outro exemplo seria o comportamento agonístico de apresentação da genitália pelos calitriquídeos que é geralmente acompanhado por vocalizações peculiares (Auricchio, 1995). Eles ainda apresentam uma vocalização longa (*long call)*, que parece ser usada em vários contextos tais como defesa do grupo contra invasores da mesma espécie, defesa do território, fazer contato com indivíduos dispersos do grupo e, possivelmente, atração sexual (Snowdon, 1993; Roush & Snowdon, 1999; Mendes et al., 2006). O *Saguinus oedipus* apresenta uma vocalização do tipo curta e alta C e D (*C and D chirps*) durante forrageio e alimentação, que está positivamente correlacionada a preferência alimentar individual (Roush & Snowdon, 1999). Os infantes de *Cebuella pygmaea* apresentam vocalizações rápidas (*babbling calls*) que consistem de uma reprodução imatura dos sinais acústicos produzidos pelos adultos e estão relacionadas a interações sociais. Os infantes que mais utilizam essas vocalizações tendem a ser mais carregados pelos outros indivíduos do grupo (Snowdon, 2001).

Contudo, é válido salientar que nem sempre se pensava assim quanto às funções e importância das vocalizações dos primatas não humanos. Na década de setenta e início dos anos oitenta, acreditava-se que as vocalizações de primatas não humanos eram relativamente involuntárias, ocorrendo somente em situações de elevada emoção, e estavam sobre um controle limitado do córtex cerebral. Assim, ao contrário dos seres humanos, os sinais vocais nos outros primatas não representavam nada além do estado emocional do indivíduo ou do comportamento sendo executado naquele momento (Cheney and Seyfarth, 1990). Hoje se sabe que o córtex cerebral tem significativa importância no processamento das vocalizações espécie-específica, pois, por exemplo, lesões nessa área (i.e. área de Wernicke) do cérebro causam déficit na discriminação das vocalizações em primatas não-humanos e na compreensão da fala em humanos (e.g. Wang, 2000).

Vocalização do sagüi comum

O sagüi comum tem sido extensivamente estudado com relação a sua ecologia e forrageio (e.g. Rylands & de Faria, 1993; Mendes Pontes & Monteiro da Cruz, 1995; Monteiro da Cruz, 1998; Souto et al., 2007), tendo recentemente recebido uma especial atenção quanto a sua capacidade cognitiva (e.g. Bugnyar & Huber, 1997; Voelkl & Huber, 2000; Halsey et al., 2006; Schiel & Huber, 2006) e também quanto a sua comunicação vocal (e.g. Schrader & Todt, 1993; Jones et al., 1993; Norcross & Newman, 1993; Norcross et al., 1994; Geiss & Schrader, 1996; Hook-Costingan & Rogers, 1998; Norcross et al., 1999; Snowdon, 2001; Nagarajan et al., 2002; Brumm et al., 2003; Cross & Rogers, 2006).

Os sinais acústicos produzidos pelo sagüi comum são de grande importância para coordenar as atividades sociais do grupo (Hook-Costingan & Rogers, 1998). Epple (1968), Pook (1977), Winter (1977) e Winter & Rothe (1979) fizeram uma descrição detalhada das vocalizações produzidas pelo *C. jacchus* em grupos vivendo em ambiente de cativeiro. Os infantes apresentam vocalizações específicas como “phee”, “tsik-tsik” e o “nga”, que são em geral usadas no intuito de retomar contato com outros animais do grupo. Os adultos e juvenis apresentam um repertório de vocalização mais diversificado constituído basicamente de 11 grupos de vocalização: *phee*, *twitter, chatter, tsee, tsik,* vocalizações ultrasonicas, *egg, ock, whistle, squea* e *scream*.

Algumas espécies de calitriquídeos não vocalizam muito sob condições de cativeiro (Epple, 1968). Contudo, eles apresentam um amplo e variado repertório vocal, o qual difere de várias maneiras de acordo com a espécie, podendo isto ser um reflexo das variações na organização social e ecológica em ambiente natural (Pook, 1977). Tendo em vista que os estudos voltados especificamente para a vocalização do sagüi comum foram realizados, em sua quase totalidade, em ambiente de cativeiro, ainda tem-se muito a investigar sobre os aspectos da comunicação vocal da espécie. Os estudos em ambiente natural são essenciais e de significativa importância para um entendimento mais profundo acerca do comportamento comunicativo das espécies. Por exemplo, no esquilo terrestre, *Spermophilus beldingi*, foram encontradas diferenças nas respostas a certas vocalizações quando comparados animais de cativeiro e de vida livre (Mateo & Holmes, 1999). Dessa forma, uma comparação dos dados de estudo de campo com os de cativeiro permitirão uma compreensão mais ampla e precisa acerca do comportamento do sagüi comum (Yamamoto, 1991).

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CAPÍTULO II

The vocal repertoire of wild common marmosets

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Abstract

The vocal repertoire and the behavior of animals from three groups of wild common marmosets, *Callithrix jacchus*, were recorded through *ad libitum* and focal sampling techniques in a fragment of Atlantic Rain Forest in Pernambuco, Northeast Brazil. The aims of the present study were to: (i) provide a detailed, quantitative description of the vocal repertoire of common marmosets in the wild based on a categorisation of their vocalisations and an analysis of the physical characteristics of those vocalisations; (ii) investigate if there are differences in vocal repertoire between animals of different age; (iii) compare the vocal repertoire of wild common marmosets with that described for this species in captive conditions; (iv) ascertain the behavioral contexts associated with specific vocalisations of wild common marmosets. The vocal repertoire of wild common marmosets was separated into 13 different calls. Some of which were exclusive to certain age groups (e.g. loud squeal to infants and alarm calls to adults). Others are most likely to be associated with certain behavioral contexts or as a response to other particular calls. Some of the call types previously described for animals in captive conditions were not observed in wild conditions and vice-versa. The behavior of the caller as well as the behavior of conspecifics and/or unknown individuals was associated with the vocalisations.

Key Words: Wild common marmosets, Callithrichidae, *Callithrix jacchus*, calls, vocal repertoire.

Introduction

Primates are known to communicate through olfactory, visual and/or auditory signals (Napier & Napier, 1996; Corewyn, 2003). Vocal signals are a particularly important tool for communication in arboreal, social primates, due to the poor visibility within their habitats (Altmann, 1967; Yamamoto, 1991; Geiss & Schrader, 1996; Napier & Napier, 1996; Prescott, 2006). Understanding the vocalisations of primates is an important step to better understanding their behavior, sociality and ecology. According to Ghanzafar & Hauser (2001), differences in the structure of vocalisations may occur not only inter-specifically but also intra-specifically, between genders, groups and same sex individuals within a group. Information about the age and gender of a vocalising animal, as well as a close consideration of the behavioral and environmental context of the vocalisation, are prerequisites for ascertaining the function of the vocalisation (McLanahan & Green, 1977).

The vocal repertoires of primates are usually associated with the behavioral context. For example, *Cercopithecus aethiops* produces different predator alarm calls depending upon the type of predator that has been seen, which result in predator specific responses by the group (Cheney & Seyfarth, 1990). Cotton-top tamarin, *Saguinus Oedipus* present short, high pitched calls during foraging, which seem to be related to individual food preferences (Roush & Snowdon, 1999). Infants of *Cebuella pygmaea* present babbling calls that consist of an immature version of the vocal signals presented by the adults, and seem to be related to social interactions. The infants that use this vocalisation more frequently are also those that are more often carried by older group members (Snowdon, 2001).

Marmoset species, in general, have a large and varied vocal repertoire (Cleveland & Snowdon, 1982), and the use of vocalisations differs from species to species, in part reflecting the variations in their social organization and ecology (Pook, 1977). It is not surprising that common marmosets, *Callithrix jacchus*, have a wide repertoire of vocalisations since they possess a complex social system (e.g. Schiel & Huber, 2006) and live in an arboreal habitat (Stevenson & Rylands, 1988). Epple (1968), Winter (1977), Pook (1977) and Winter & Rothe (1979) have produced general descriptions of the vocal repertoire of common marmosets living in captive conditions. Captivity is particularly different from the natural environment for primates (Boere, 2001) with the opportunities for wide ranging behaviors clearly more prevalent in the wild. A comparison between field and captive data allows a much better understanding of the behavior of *Callithrix* species (Yamamoto, 1991). However, as far as we are aware, there are no studies showing the vocal repertoire of common marmosets in the wild.

Thus, the aims of the present study are to: (i) provide a detailed quantitative description of the vocalisations and vocal repertoire of common marmosets in the wild based on categorising their vocalisations and then reporting the physical characteristics of those vocalisations; (ii) investigate if there are differences in vocal repertoire between animals of different age; (iii) compare the vocal repertoire of wild common marmosets with the repertoire described for this species living in captive conditions; (iv) ascertain the behavioral contexts associated with certain vocalisations in wild living common marmosets.

Methods

Study site

The study was carried out in a fragment of Atlantic Rain Forest. The 32 ha study site is located in Camaragibe, State of Pernambuco, Northeast Brazil (7°56’97’’S, 35°1’23’’W) and also in its surroundings where a small condominium mostly occupied during the summer months is present. The condominium consists of 70 houses with gardens connecting each house to the surrounding forest. The gardens usually include trees. Trees are also commonly found alongside the unpaved, narrow roadways of the condominium. For a detailed descripton of the study site see Souto et al. (2007). Observations were taken both in the forest and in the gardens since the gardens also provided sources of food for the marmosets due to the presence of fruit and gommivory trees.

Subjects

We studied 30 animals across three social groups. Before observations were taken, the animals were classified into three broad age categories following Stevenson and Rylands (1988): adults (>15 months; 17 individuals); juveniles (6-10 months; 6 individuals) and infants (0-5 months; 7 individuals). All study animals were wild.

The subjects were identified without capture, by their natural features (size and color of the ear-tufts, scars, natural mutilations, and fur coloration). In two twin infants, a small portion of the tail fur was cut with a pair of scissors once every 40 days to further facilitate identification (for a detailed descripton of this marking procedure see Souto et al., 2007). Data for the present study was collected from December 2004 to April 2005 and from July to September 2005, during daily observations.

Recording vocal repertoires

We used focal animal and *ad libitum* sampling techniques (Altman, 1974) to obtain recordings of the vocal repertoire of wild common marmosets. All recordings were made between 05:00 and 17:30, which were daylight hours. We recorded vocalisations using an

AKG C1000S II hypercardioid microphone (linear frequency response within the range 50 Hz to 20 kHz), which is well suited for camcorders (Shopmann, 1999). We connected the microphone to a digital camcorder, Panasonic PV-GS400, linear frequency response within the range 50 Hz to 20 kHz (at a 16-bit quantization and 48 KHz sampling rate) (Biebel, 2004). A sampling frequency of 48 kHz can result in a reliable frequency response of up to 22 kHz. Camcorders have been used in a number of studies for recording audio in studies on marine mammals (e.g. Herzing, 1996; Dudzinnski, 1998; Dudzinnski, 1999) but less so in studies on terrestrial mammals (see, however, the study by Taglialatela et al., 2003 on *Pan paniscus*). The advantage of using an appropriate video camera is having both audio and video records for subsequent behavioral analysis (Taglialatela et al., 2003). We used a Hosa® cable to connect the microphone with the camcorder and earphones (Intersound, linear frequency response within the range 20 Hz to 20 kHz) in order to monitor the sound while recording. This system is sufficient both to capture the behaviors of the study animals and the full bandwidth (of the fundamental frequencies) of their vocalisations.

The recordings were conducted at a distance of 2 – 5 m from the subjects. Once acquired, the vocalisations were digitally transferred, via firewire cable, from the video camera to a PC, through MediaStudio Pro 6.5 (Ulead System, Inc.) software, settled to capture DV 1 at 16-bits and at 48 kHz sampling rate. Each vocalisation was saved in WAV format (without compression) and then analysed through SYRINX-PC sound-analysis software (J. Burt, Seattle, Washington – available upon request), with which sonograms were produced. A sonogram is a graphical representation of a vocal signal as frequency against time (e.g. Regas, 1983; Owren & Linker, 1995). We recorded more than 1000 vocalisations in total. However, after the removal of certain vocalisations due to the presence of interfering background noise, 754 remained for analysis. The physical characteristics used to describe these vocalisations were: the number of syllables, syllable duration, duration of inter-syllable interval, the highest frequency of the vocalisation, the lowest frequency, the range of frequencies, the start and end frequencies, the duration from the start of the vocalisation to the highest frequency, the duration from the time of the highest frequency to the end of the vocalisation, the number of harmonics in the vocalisation (up to 22 kHz) and the interval between harmonics. These measures were extracted from the sonograms (based on the methodology of Jones et al., 1993, Newton-Fisher et al., 1993 and Norcross et al., 1999).

Recording the frequency of behaviors

Bezerra used the focal sampling technique (Altmann, 1974) to register the frequency of behaviors of the study animals. All observations were made between 05:00 and 17:30. The maximum distance that the animals were observed was 5 m, since from greater distances it was not possible to hear clearly some vocalisations. Information about the observations were recorded by dictation onto a tape recorder (Sony-M-529V) during 5 min sessions (date, time, location, description of the behaviors and/or vocalisations (initial and responses) of the focal animal, and register of the individuals within the vicinity of the focal animal (within 5 m)). The dictations did not appear to disturb the animals. A vocalisation was considered as initial when it followed at least 10 s of vocal silence and as a response when it was performed within 4 s of an initial vocalisation. A behavior was considered as a response when it was performed within 4 s of an initial vocalisation (adapted from Soltis et al., 2002). In the present study we selected common behaviors in order to ascertain the behavioral contexts associated with certain vocalisations. Concerning the initial vocalisations, we selected three long distance contact calls that were most frequently heard in the wild: (1) the twitter call (Epple, 1968; Winter 1977; Winter and Rothe 1979), (2) the phee call (Epple, 1968; Winter 1977) (we used a combination of long phee call plus brief phee call 1) and (3) the loud cry. See the Results section for descriptions of these different calls.

According to Maurus et al. (1988), the recognition of call types by listening depends on the physical ability of the observer to distinguish the acoustical structures of a call and on their propensities for categorizing sounds. In the present study, before the start of data collection (November 2004), Bezerra was submitted to a battery of medical tests in two different hospitals to ascertain her auditory capacity. The results from both hospitals attested that Bezerra is able to hear the full bandwidth of fundamental frequencies of the vocalisations emitted by common marmosets (i.e. from 250Hz to 20 kHz (Winter, 1977)). Also, since Bezerra has been conducting behavioral observations of common marmosets in the area since 2001, she is well practised in distinguishing by ear the vocalisations of common marmosets.

Due to background noise present in the recordings (e.g. wind, bird and insect sounds), we were not able to generate sonograms for all of the types of calls of juveniles and infants. However, these calls were included in the description of the vocal repertoires of juveniles and infants.

Statistical analyses

We used the software packages SPSS for Windows v. 8.0 (SPSS Inc. Chicago, IL, USA) and Excel (Microsoft Corporation, Redmond, WA, USA) for the statistical analyses. The physical characteristics of the vocalisations (Table I) are presented as means ± SEM.

We used Friedman two-way of analyses of variance by ranks to look for differences in the frequency of more than two paired samples (i.e. intra-age comparisons of the use of different call types during selected behavioral contexts; and intra-age comparisons of the vocal and behavioral responses to the selected long distance calls/initial vocalisations). The percentages of each call type and/or behaviors are shown for each specific behavioral context and/or initial vocalisation. All tests were two-tailed and significance was set at $p \leq 0.05$.

Results

Description of vocal repertoire

Both by ear and based on the physical characteristics of the vocalisations, 13 different call types could be distinguished in wild common marmosets: (1) trill call; (2) twitter call; (3) tsik call; (4) tsê call; (5) egg call; (6) chatter call; (7) squeal calls (consisting of the loud squeal and of the submissive squeal); (8) moaning call; (9) food call; (10) bird alarm; (11) dog alarm; (12) scream call; (13) phee calls (consisting of long phee call, brief phee call 1; brief phee call 2; brief phee call 3).

The sonograms of the different call types (Figure 1), together with the physical characteristics (Table I) and the brief description of each call type provide a detailed description of the vocal repertoire of wild common marmosets.

1) Trill call (Whirrs – Pook, 1968; Phee call – Epple, 1988, Winter, 1977 and Winter & Rothe, 1979; trill call - Norcross & Newman, 1994): A relatively quiet call uttered with the mouth almost closed. Uttered in isolation or in combination with squeal and/or tsik calls.

2) Twitter call (Epple, 1968 and Winter, 1977; Zwitscher-Laute - Winter & Rothe, 1979; Gorgeio decrescivo - Camarotti & Monteiro da Cruz, 1997): Relatively loud sound, characterized by a series of short syllables at intervals of less than 0.1 s. It sounds like a warble.

3) Tsik call (Epple, 1968; Winter, 1977 and Winter & Rothe, 1979): Uttered singly or in series. In the wild, the tsik call, when uttered in series, is used as a mobbing call against unknown conspecifics, unknown humans and potential predators moving along the ground or in the trees (e.g. Coati, *Nasua nasua* and Tayra, *Eira barbara* – Bezerra et al. *in prep)*. In the case of predators, all the individuals of the group apart from infants continue to emit the tsik call and follow the potential predator until it retreats. Finally, the tsik call, uttered in series, can be associated with a distressed animal due to unusual noises (e.g. the falling of large branches in the forest).

4) Tsê call: Sound similar to, but distinguishable from, the tsik call. This call is uttered singly of in combination with the egg call and/or tsik call.

5) Egg call (Egg call – Epple, 1968, Winter, 1977 and Winter & Rothe, 1979): This is a very short call with a few harmonics. In the wild it can be uttered singly, in series (up to 3 syllables) or in combination with tsê or tsik calls (usually one tsê or one tsik call is followed by up to three egg calls). Normally, the egg call is associated with vigilance behavior, for example when a strange human approaches the group or when the calling marmoset must go to the ground in an area of sparse vegetation (See Souto et al., 2007, for a definition of dense and sparse vegetation in the study site).

6) Chatter call (Chatter call: Epple, 1968 and Winter, 1977; kecker-Laute - Winter & Rothe, 1979; erh-erh – Stevenson & Pool, 1976; que que que - Alonso & Langguth,

1989): Given in series with very short intervals between the syllables. Associated with intra and inter group aggression (Table III).

7) Squeal call (Squeal call – Epple, 1968 and Winter, 1977; Quärr-Laute - Winter & Rothe, 1979; nhe-nhe - Alonso & Langguth, 1989): There are two easily distinguishable squeal calls, the submissive squeal and the loud squeal. Both variations of squeal call are uttered in combination with tsik and trill calls. The combination of submissive squeal plus tsik and trill is here termed a submissive cry. The combination of loud squeal plus tsik call plus trill call was termed a loud cry.
8) Moaning call: A faint call with some similarity to the squeal call, that can be uttered singly or in series (usually up to 3 syllables). Mainly young animals utter this call during play behavior between individuals, when play appears to become too intense.
9) Food call: A short, high-pitched call uttered in series and with the mouth wide opened. This call is relatively rare and tends to be emitted when the marmosets have found a relatively large amount of food (e.g. an open jackfruit or a mango on the ground). Animals that hear this call tend to approach the animal that was vocalising.
10) Bird alarm (Warning call – Epple, 1968; Alarm call - Pook, 1977): A short, sharp whistle. Usually after hearing this alarm call, group members move to denser vegetation.
11) Dog alarm (Warning call – Epple, 1968; Alarm call - Pook, 1977; Lautgruppen 02 - Winter & Rothe, 1979): A short, sharp whistle emitted while the animal make is making a soft 'haa' like exhalation of breath. After hearing the dog alarm, group members tend to remain motionless for several seconds until the potential predator (domestic dogs) disappears.

12) Scream call: (Scream call – Epple, 1968 and Winter, 1977; Schrei-Laute - Winter & Rothe, 1979): Uttered singly or in series. This call is relatively rarely observed and is usually uttered by animals either trying to steal food or being seriously injured by a conspecifc.

13) Phee calls (Phee calls – Epple, 1968 and Winter, 1977; Shirilling call – Pook, 1977; Phii-Laute - Winter & Rothe, 1979; Long call – Snowdon, 1989; Silvo longo - Camarotti & Monteiro da Cruz, 1997): Easily distinguished into four main types: long phee call (more than 1 s duration, loud and uttered with the mouth wide open), brief phee call 1 (less than 1 s duration, loud and uttered with the mouth wide open); brief phee call 2 (often more than one s in duration, less loud than the long phee call and uttered with the mouth less open); brief phee call 3 (usually less than 0.7 s duration, faint and uttered with the mouth less open). This call type was used generally to (i) make contact with conspecifics when in the presence of another group of common marmosets or an unknown individual; (ii) begin to bring group members together prior to nightfall, (iii) when the vocalising animal has been alone, relatively far from the rest of the group for a relatively long period of time, (in this case, marmosets usually utter a long phee call and a brief phee call 1); (iv) when the vocalising marmoset is in close visual contact with a conspecifc (under such circumstances, the brief phee call 2 and 3 are usually uttered).

Vocal repertoire of adults, juveniles and infants

The vocal repertoire of adults consisted of 12 calls: twitter call; phee call (divided in: long phee call, brief phee call 1, brief phee call 2; brief phee call 3); trill call; tsik call;

egg call; scream call; chatter call; bird alarm call; dog alarm call; tsê call; food call, submissive squeal call.

The vocal repertoire of juveniles consisted of 11 calls: twitter call; phee call (consisting of long phee call, brief phee call 1, brief phee call 2; brief phee call 3); trill call; tsik call; egg call; scream call; chatter call; tsê call; food call; submissive squeal; moaning call. Due to background noise, unfortunately we didn't get any proper sonograms of the following vocal signs to juveniles: phee calls, food call, and submissive squeal call.

The vocal repertoire of infants consisted of 9 calls: phee call (infants were observed only emitting brief phee call 1, 2 and 3); trill call; tsik call (emitted singly and in series); tsê call; egg call; scream call; chatter call; loud squeal and submissive squeal; and moaning call. Due to background noise, we were unfortunately unable to obtain proper sonograms of the following infant vocal signs: phee call, tsê call, egg call, chatter call and moaning call.

Table I details information on the physical characteristics of the vocalisations emitted by adult, juvenile and infant common marmosets in the wild.

Context of vocalisations

We found significant differences in the frequency of use of different call types according to behavioral context (see Table II for a description of recorded behaviors) and as a response to the selected initial vocalisations.

In terms of foraging behavior, adults, juveniles and infants showed variations in the use of call types. The call type most often uttered during foraging behavior was the trill call. During vigilance behavior, a combination of two call types was more likely to be uttered, the tsê call plus the egg call. During periods of solitary rest, only adults and juveniles vocalised. Vocalisations that were more likely to be uttered during solitary rest were the twitter, trill and phee calls. During social rest, only the adults vocalised and again, twitter, trill and phee calls were more likely to be uttered. While capturing prey or eating, the common marmosets did not vocalise. When watching conspecifics and unknown individuals in the wild, a couple of different call types tend to be uttered (Table III).

Concerning the responses of marmosets to certain vocal types: twitter calls are more likely to be responded with another twitter call and/or with the animal stopping its behavior for a little while. Loud cries tend to be responded with the animal approaching and interacting with the infant caller. The combination of long phee calls plus brief phee call 1 tended to be responded with twitter call and/or with phee calls, and with the animal locomoting in the direction of the initial caller (Table IV).

Discussion

Adults, juveniles and infants show different quantities of call types in their vocal repertoire (12, 11 and 9 call types, respectively). Moreover, some calls were exclusive to marmosets of certain age (e.g. loud squeals by infants and alarm calls by adults). There are reports of age-related variations in the call types present in the vocal repertoire of captive common marmosets (e.g. Epple, 1968), in the vocal repertoire of other primates species such as Japanese monkeys, *Macaca fuscata* (Itani, 1963); vervet monkeys, *Cecopithecus aethiops* (Struhsaker, 1967); squirrel monkeys, *Saimiri sciureus* (Ploog, 1967); pygmy marmoset, *Cebuella pygmaea* (Snowdon, 1988); and also in the vocal repertoire of non-primate species such as the red fox, *Vulpes vulpes* (Newton-Fisher et al., 1993). This age-related variation can be due both to physical development (Snowdon 1988; Corewyn, 2003) and behavioral changes with age, which may at least partially explain the age-related variation in the vocal repertoires of wild common marmosets.

The vocal repertoire of common marmosets in the wild is somewhat different from the vocal repertoire previously described by Epple (1968), Winter (1977), Pook (1977) and Winter and Rothe (1979) for captive individuals. For instance, the tsee call, as described in the sonogram of Epple (1968), was not recorded from our subjects. Furthermore, Winter (1977), Pook (1977) and Winter and Rothe (1979) did not record the tsee call in their captive animals. Epple (1968) described this tsee call as sounding similar to the tsik call. Indeed we also observed a vocalisation that sounded similar to the tsik call. However, the sonograms obtained from this vocalisation are clearly different from the one showed by Epple (1968) for the call that sounded similar to the tsik call. Hence we named this new call ‘tsê’.

Concerning the warning call described by Epple (1968) (alarm calls by Pook, 1977; Lautgruppen by Winter & Rothe, 1979) for animals in captive conditions, we recorded two different kinds of warning calls in the wild: the bird alarm and the dog alarm. These calls are easily distinguished when viewed as sound sonograms and also by ear. The sonogram of the dog alarm is very similar to the sonograms presented by Epple (1968) and Pook (1977) for alarm calls in captive animals. The sonogram of the bird alarm looked very similar to one of the sonograms presented by Winter & Rothe (1979) in a group of calls termed in German as “Lautgruppen 02” (or ‘call group 02’). We considered bird and dog alarms as warning calls since both were connected to the sudden appearance of potential predators, as seen in captive conditions.

According to Cheney & Wrangham (1987) the anti-predator behavior of small primates (< 1 kg body mass) consists mainly of concealment, vigilance and flight rather than attack, even though many species are reported to present mobbing behavior. The same researchers suggest that diurnal callithrichid species seem to be adapted to avoid rather than to challenge predators. Common marmosets are small, diurnal primates and the anti-predator behaviors of wild individuals support some of these predictions for anti-predator behavior. The common marmosets investigated in the present study uttered the bird alarm when aerial raptors (potential predators) and smaller aggressive birds (e.g. *Turdus rufiventris* and *Pitangus sulphuratus*) suddenly appeared in the surrounding area. It is common to see *Turdus rufiventris* and *Pitangus sulphuratus* mobbing and attacking common marmoset in the study site (Bezerra et al., *in press*). After hearing a bird alarm, common marmosets flee to more dense vegetation, presumably making it more difficult for the birds to attack them. The dog alarm was uttered only when domestic dogs appeared suddenly very close to the edge of the forest. The stillness of the marmosets in response to hearing the dog alarm is quite probably an attempt to limit the chances of being spotted by a dog. In another fragment of Atlantic Rain Forest, the Dois Irmãos forest (08º04’00”S, 34º52’00”W) 20 km far from the study site, there have been reports of predation on common marmoset by domestic dogs (Mendes Pontes & Soares, 2005). Similar to wild animals, Pook (1977) reported that captive common marmosets respond to alarm calls by instantaneous alertness and by fleeing to a more secure position, like the nest box or under branches and platforms.

Another call type connected to the appearance of a potential predator in the wild is the tsik call given in series as a mobbing call. This mobbing call was also observed for captive animals (e.g. Epple, 1968). In our study area, marmosets were repeatedly observed emitting the mobbing vocalisation in the presence of coati and tayra. In one occasion one juvenile marmoset was captured by a tayra (Bezerra et al., *in prep*).

Alarm calls have been reported for almost all primate species and they appear to have different alarm calls for different types of predators (Cheney & Wrangham, 1987).

For common marmosets living in wild conditions, we managed to distinguish by ear and by sonograms, two different alarm calls and one mobbing call, each associated with the appearance of a different kind of predator.

Some of the ‘phee calls’ presented by Epple (1968), Winter (1977) and Winter and Rothe (1979) as a phee call for infant common marmosets had a sine like ascending and descending frequency. We also observed the same kind of vocalisation in wild animals, however, not only for infants. Adults and juveniles also presented this vocalisation. Pook (1977) also recorded this vocalisation being uttered by adult captive animals and he named the vocalisation as “whirrs call”. However, as Norcross et al. (1994), we term this vocalisation a ‘trill call’. This vocalisation for common marmosets looks like the trill call described in the sonograms for other primate species such as *Callithrix argentata* (Epple, 1968; Regas, 1983), *Cebuella pygmaea* (e.g. Snowdon, 1988), *Leontopithecus rosalia* (Epple, 1968; McLanahan & Green, 1977), *Cebus capucinus* (Boinsk & Campbell, 1995; Gros-Louis, 2000) and *Microcebus ssp*. (Zimmermann & Hafen, 2001).

Most call types present in the vocal repertoire of wild common marmosets tended to occur in a variety of behavioral contexts. However, some of the call types were more likely to be uttered within some specific behavioral contexts (e.g. alarm calls previously discussed). During foraging behavior, the call type more likely to be uttered is trill call singly. This call is relatively quiet and is known to be uttered for close visual contact with conspecifics in captive conditions (Pook, 1977). The trill call seems to be suitable to foraging behavior since it makes more difficult to the prey detect the predator common marmoset, at least because of the noise. Capturing a prey or eating is not accompanied with vocalisations, which is reasonable since such situations apparently may not require vocalisations. During vigilant behavior, the combination of tsê call plus egg call was more likely to be uttered. These call types are relatively high pitched and very short and, thus, may be useful to warn the conspecifics about the fact that vigilance might be required in the moment the call had been uttered. In solitary and social rest, the vocalisations that were more likely to be uttered were twitter, trill and phee calls. And when watching conspecifics and strange individuals in the wild, a couple of different call types tended to be uttered. The pattern of use of contact calls in wild common marmosets seemed to be affected by the behavior of the caller and to some extent by the behaviors and/or the vocalisations in which a strange individual and/or a conspecific were engaged as also reported by Pook (1977) for captive animals.

The vocal repertoire of wild common marmosets showed to be fairly large and varied, having vocal signals with complex physical characteristics never showed before in fully details for this species, neither in captivity nor in wild conditions. The age of the animals showed to influence in the call types present in the vocal repertoire. In addition, the behavior of the caller as well as the behavior of conspecifics and/or strange individuals seemed to affect the vocalisations of wild common marmosets. The complex social organization of this species and the arboreal status already predicted an intricate communication system through vocalisations. Our study together with the data previously coming from captive studies also confirmed such prediction.

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Legends

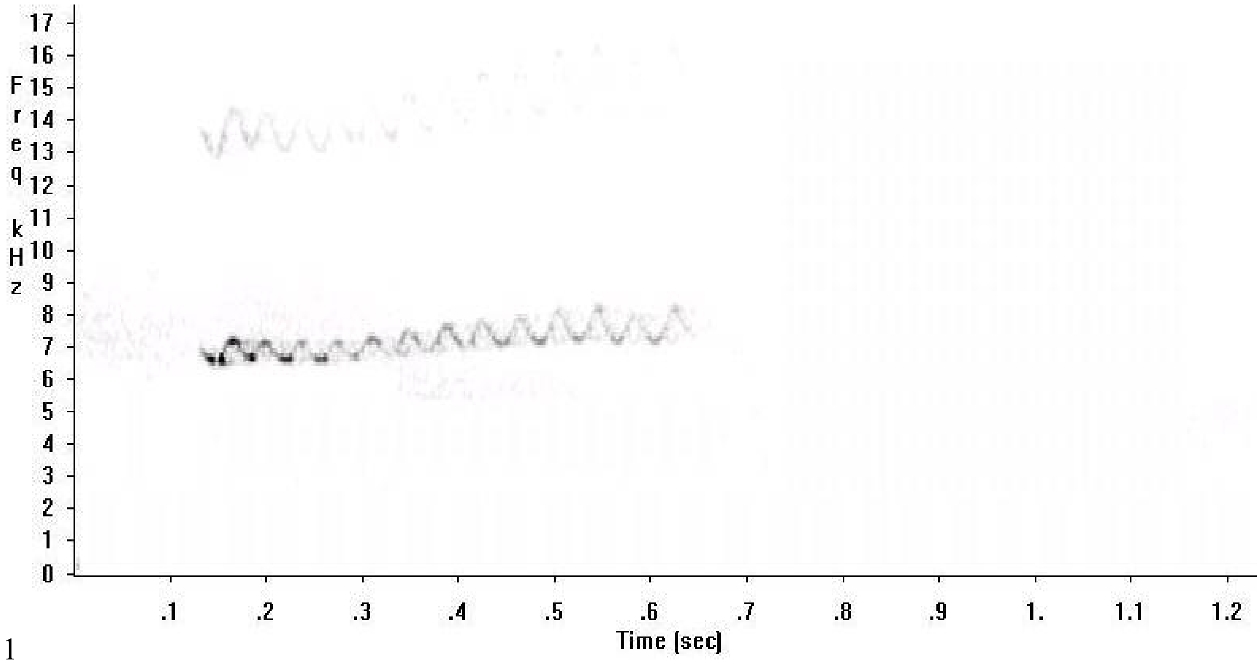
Figure 1. Sonograms of the different vocalisations collected from wild common marmosets. (a) Trill call; (b) Twitter call; (c) Tisik call; (d) Tsê call; (e) Egg call; (f) Chatter call; (g) Submissive squeal; (h) Loud squeal; (i) Moaning; (j) Food call; (k) Bird alarm; (l) Dog alarm; (m) Scream call; (n) Long phee call + Brief free call 1; (o) Brief phee call 2; (p) Brief phee call 3.

Table I. Features of the vocal signals emitted by wild common marmosets. Age: A= adults; J= juveniles; I= infants. N: Number of vocal signals analysed through sonograms. Call dur: Call duration; Num Syl: Number of syllable; Syl dur: Duration of syllable; ISI; Intersyllable interval; ↑ Freq: higher frequency; ↓ Freq: Lower frequency; ∆ Freq: Range frequency; ←Freq: start frequency; → Freq: end frequency; Dur start-peak: duration from the start to the higher or peak frequency of the vocal signal; Dur peak-end: Duration from the higher or peak frequency to the end of the vocal signal; Num H: number of harmonics; IBH: Interval between harmonics; n/a = non applicable.

Table II. Description of behaviours.

Table III. Behavioural contexts and the vocalisations that were more likely to be uttered (n_1: number of animals; n_2: number of times the behaviour was performed; n_3: number of vocalisations performed; *$p \leq 0.05$; ** $p \leq 0.01$; *** $p \leq 0.0001$; Age: A - adult, J - juvenile, I - Infant).

Table IV. Initial vocalisations and their vocal and/or behavioural responses (n_1: number of animals; n_2: number of times the initial vocalisation was performed; n_3: number of times that vocal responses were performed; n_4: number of times the behavioural responses were performed. * $p \leq 0.01$; ** $p \leq 0.001$; ***$p \leq 0.0001$; Age: A - adult, J - juvenile, I - Infant)



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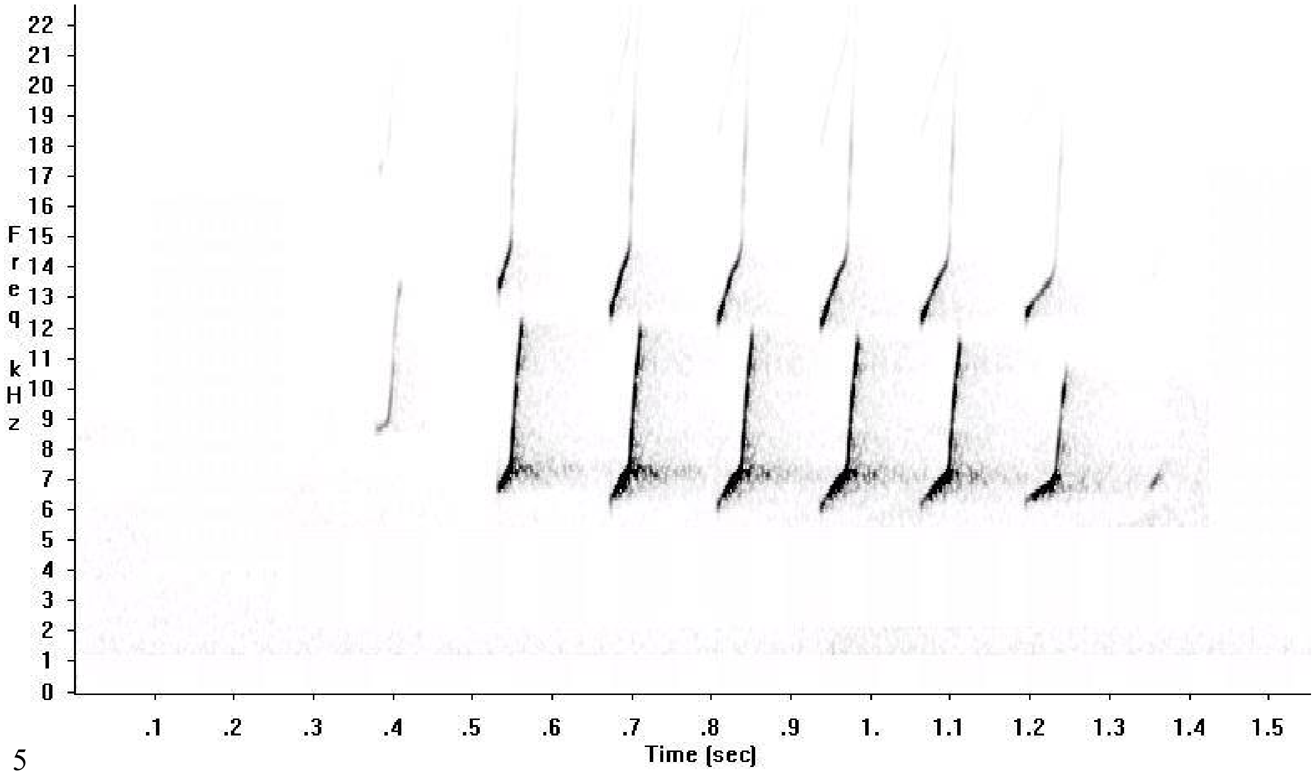

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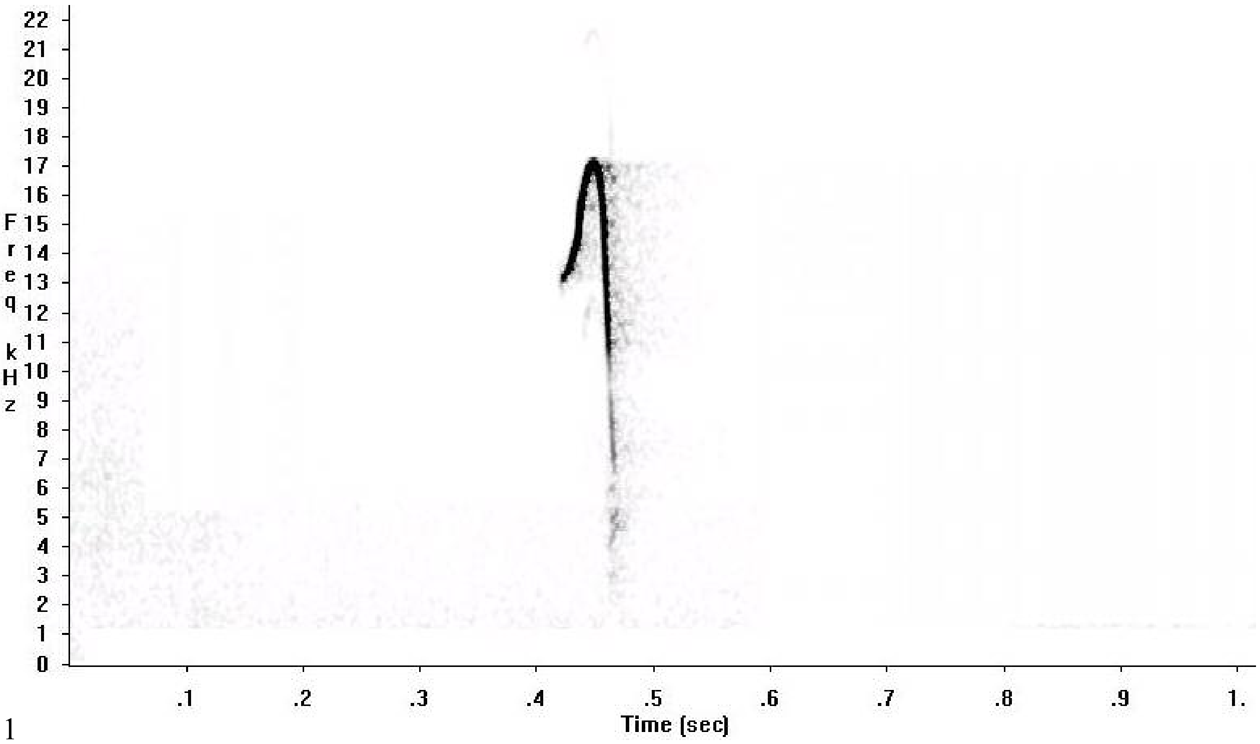

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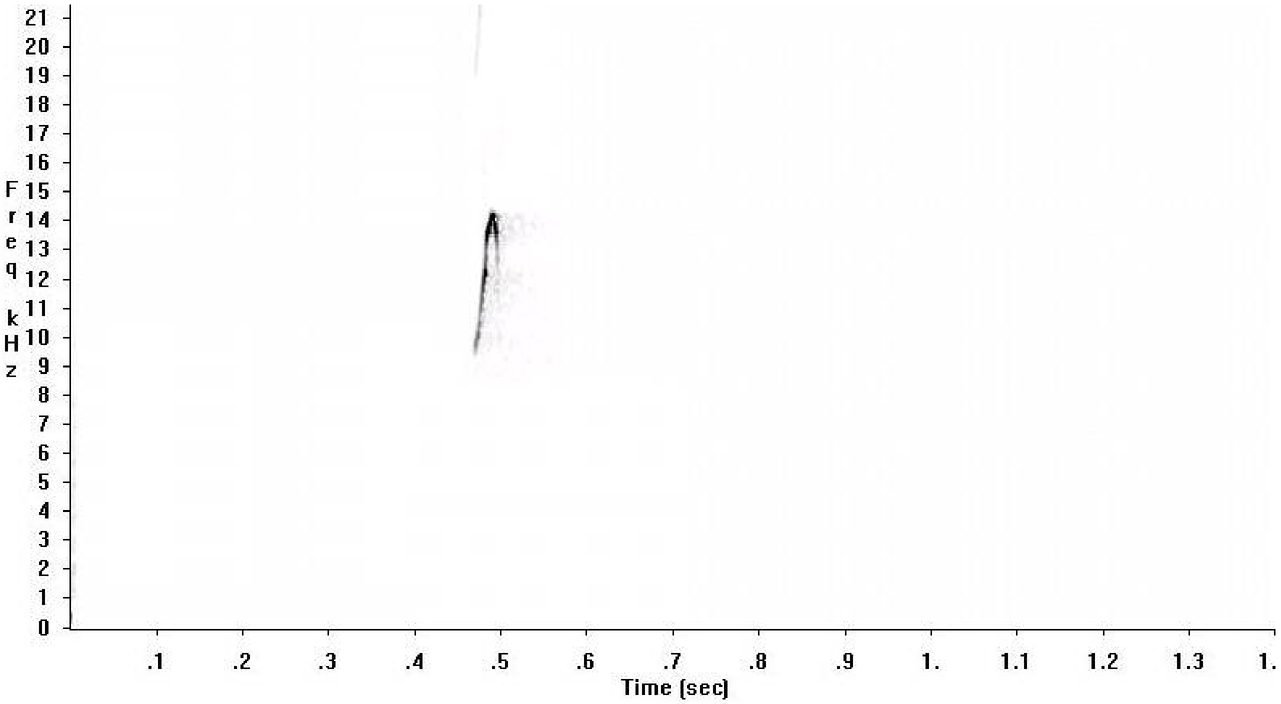

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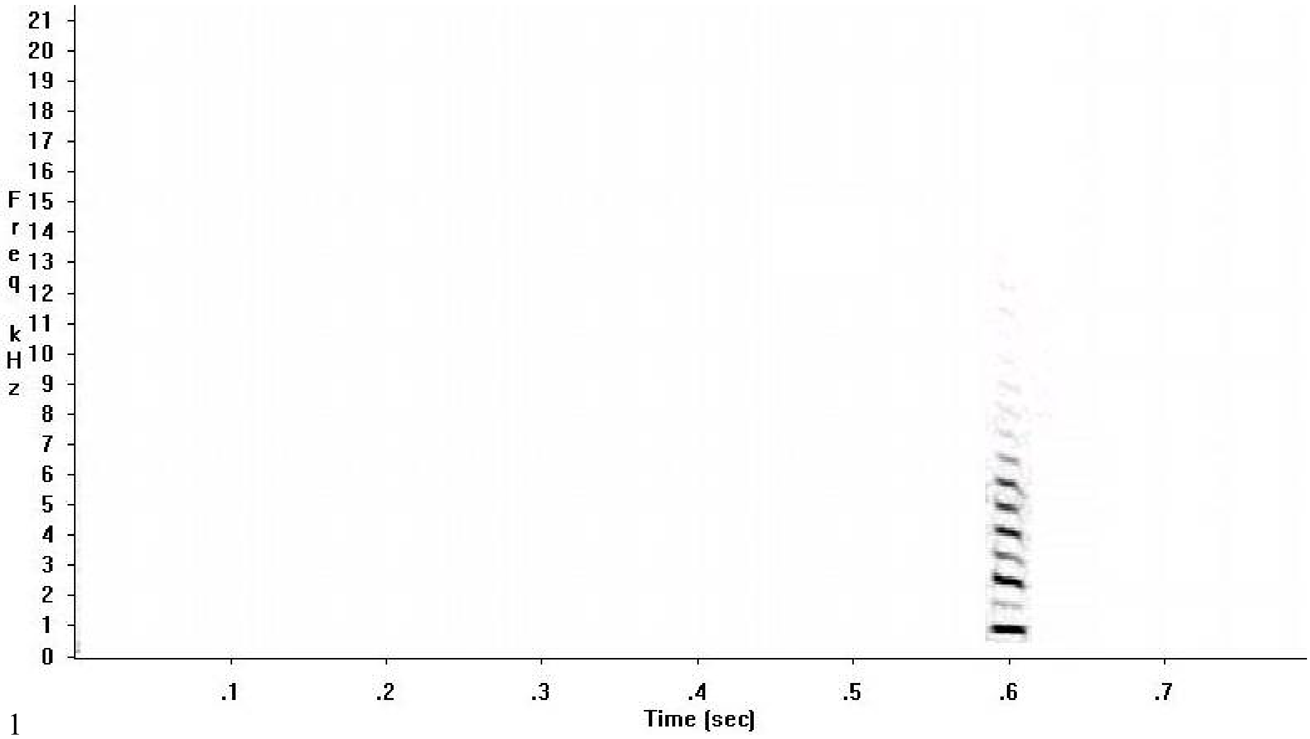

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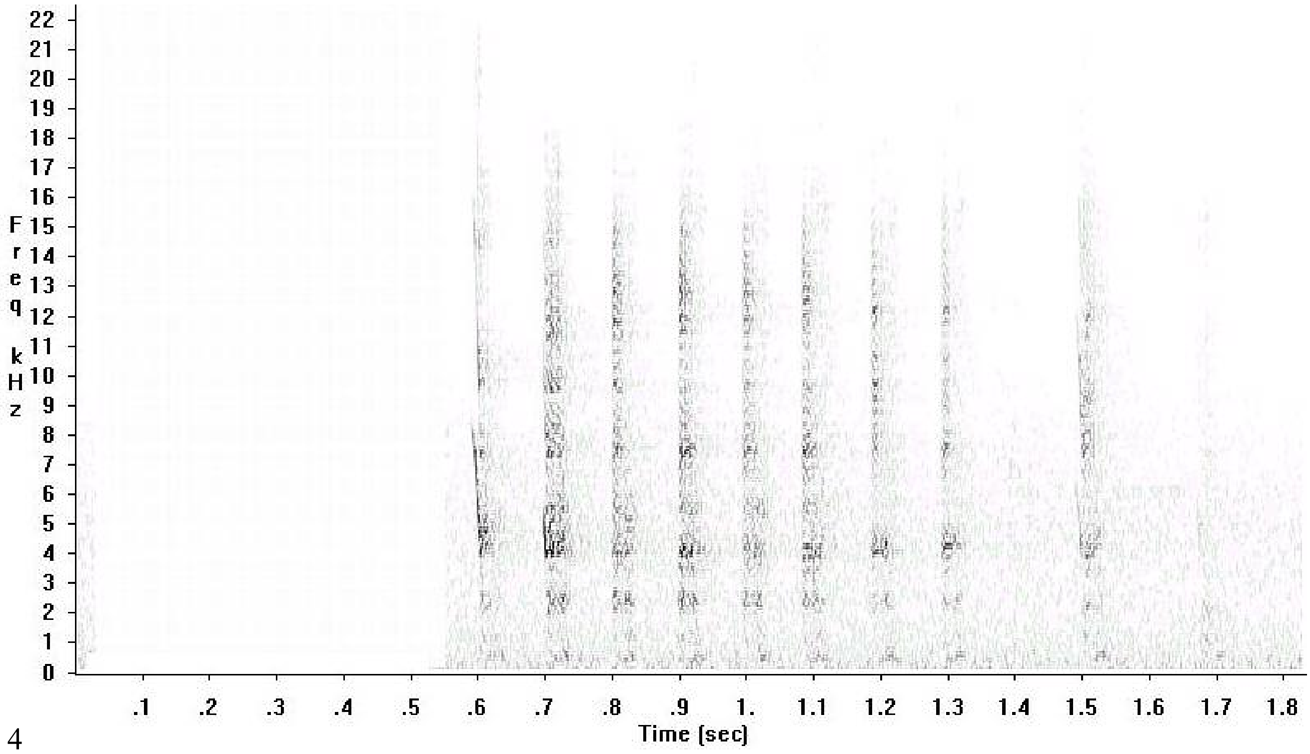

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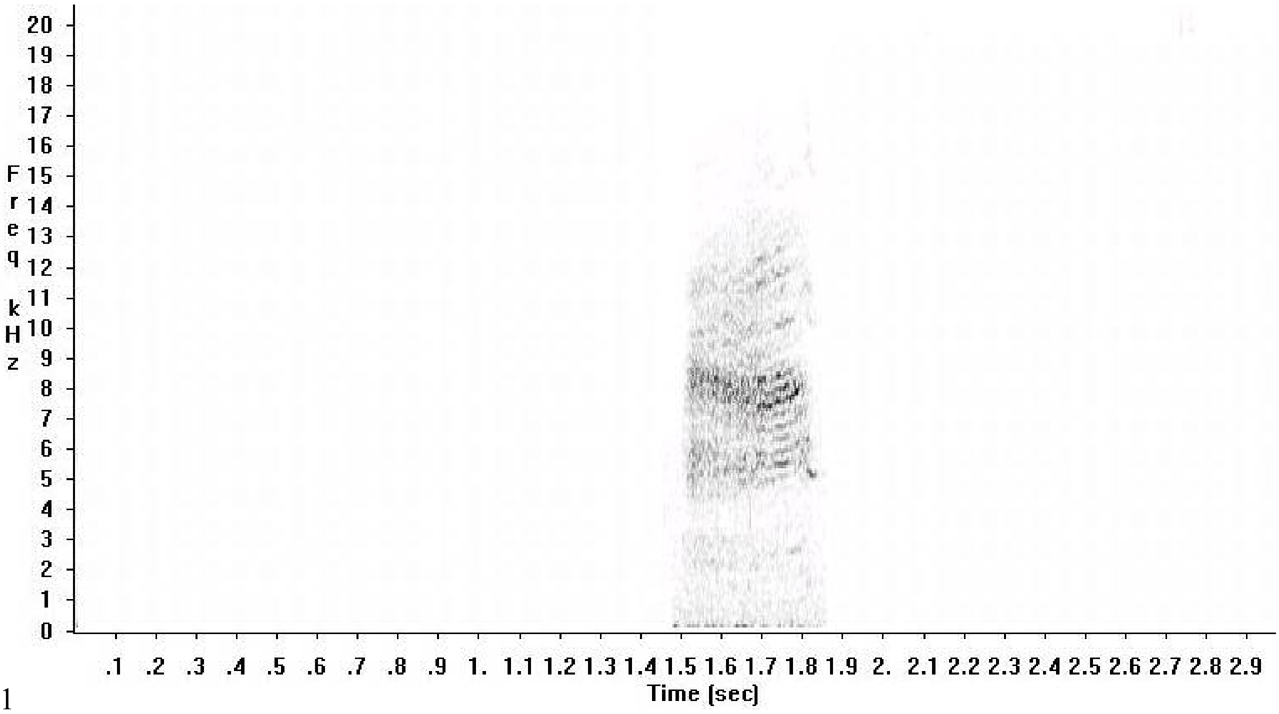

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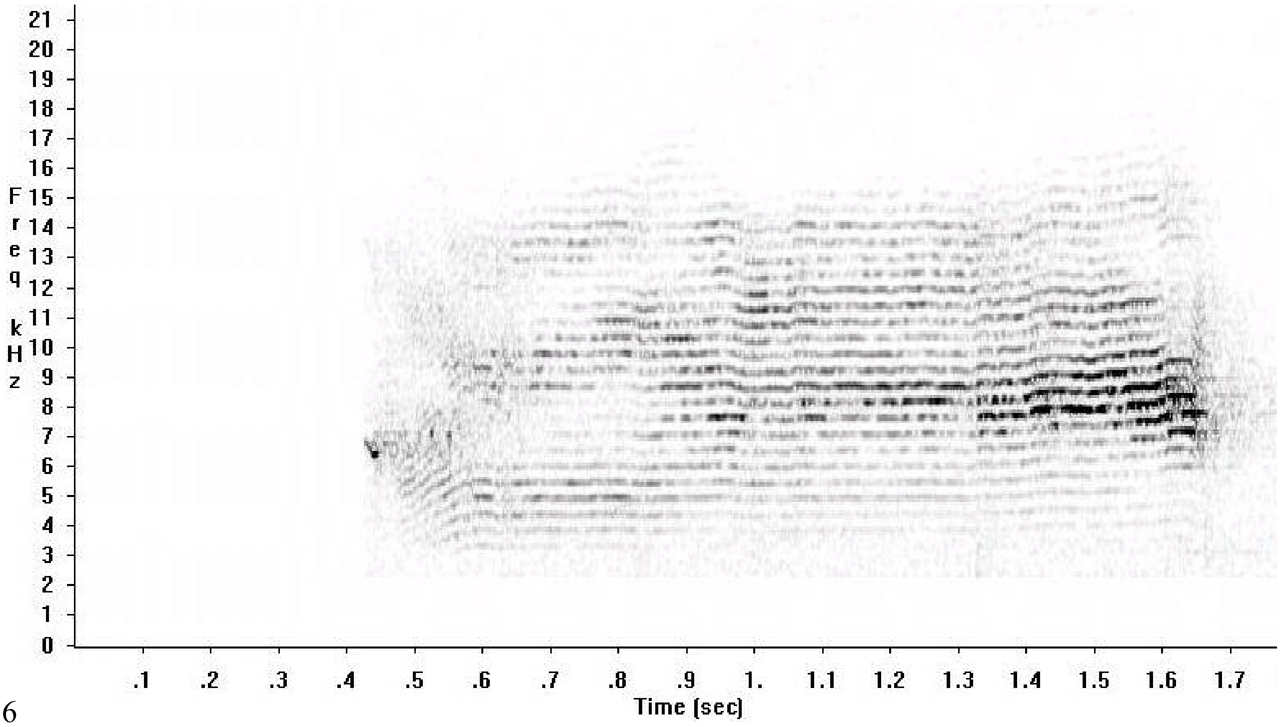

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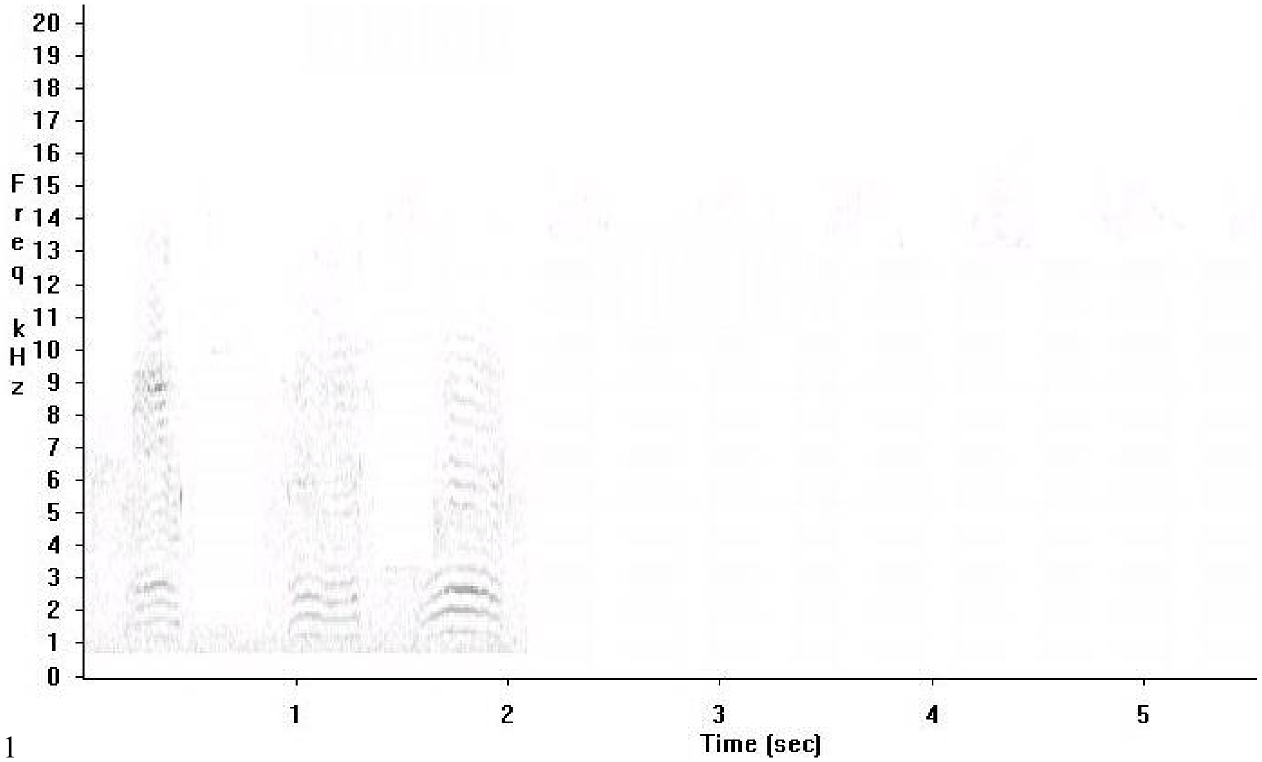

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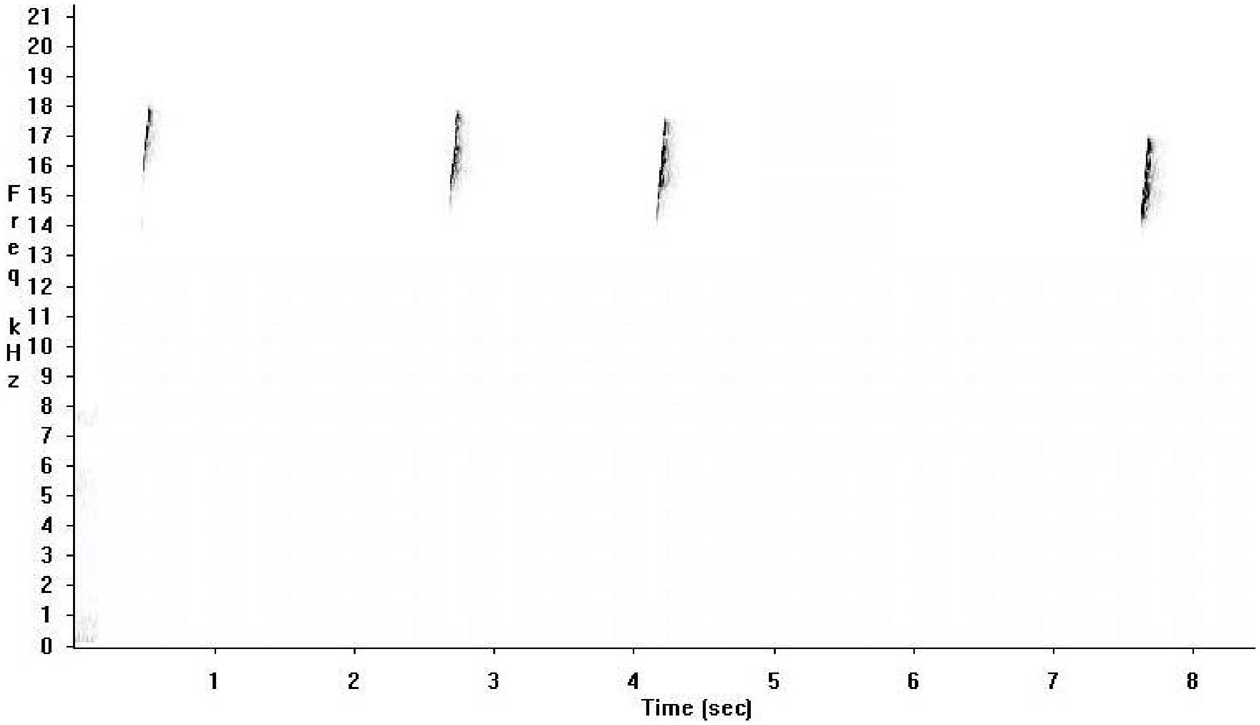
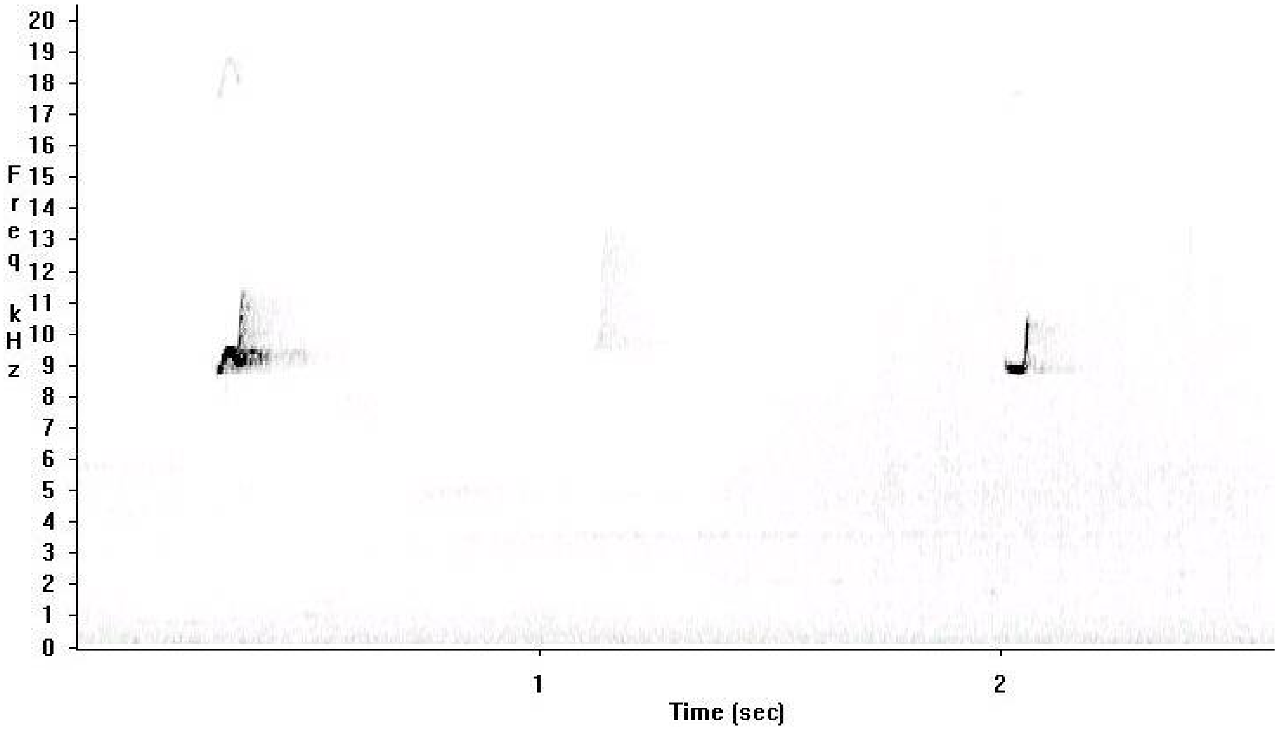


Figure 1j



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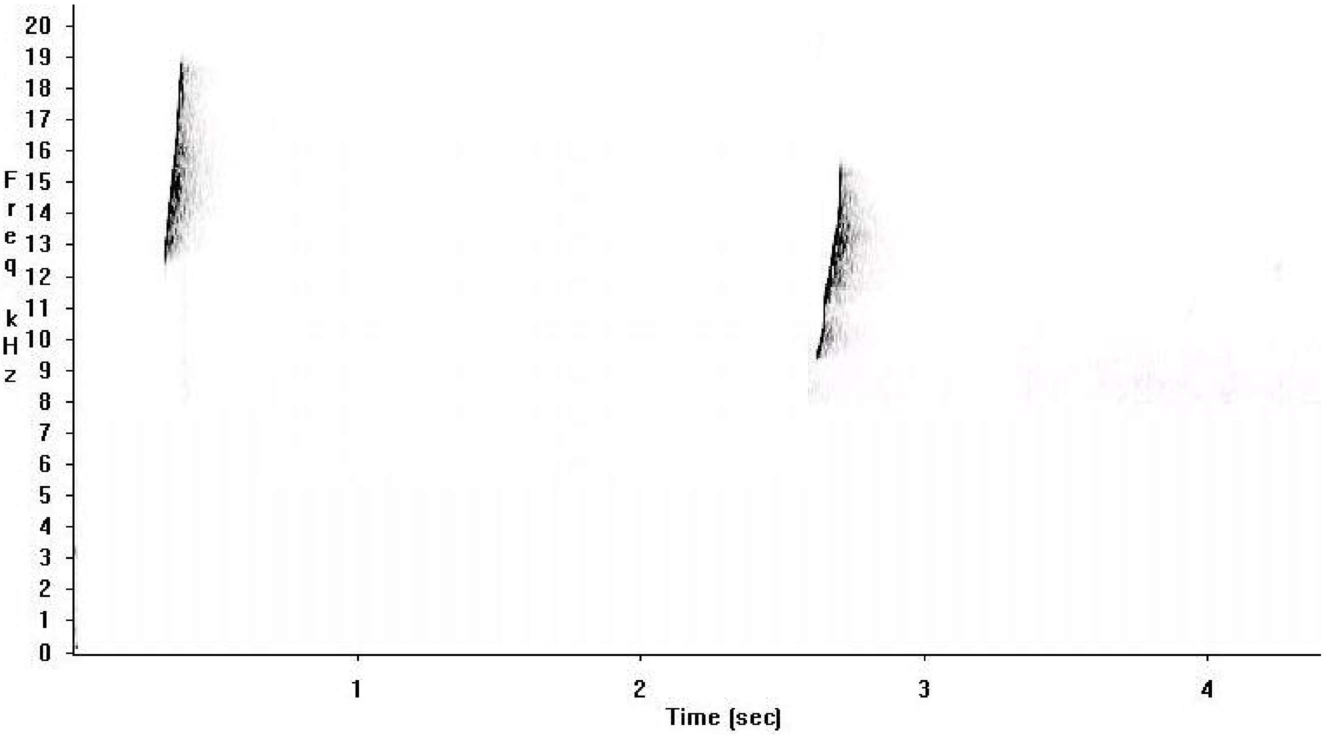

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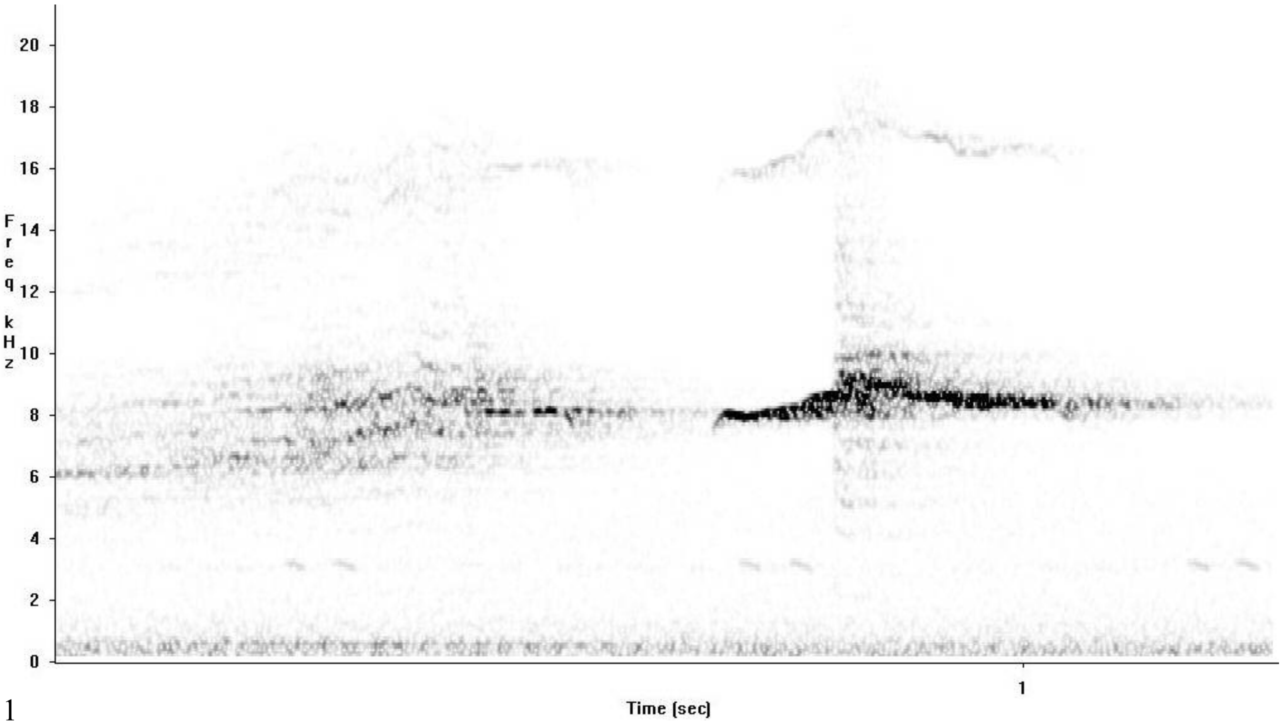

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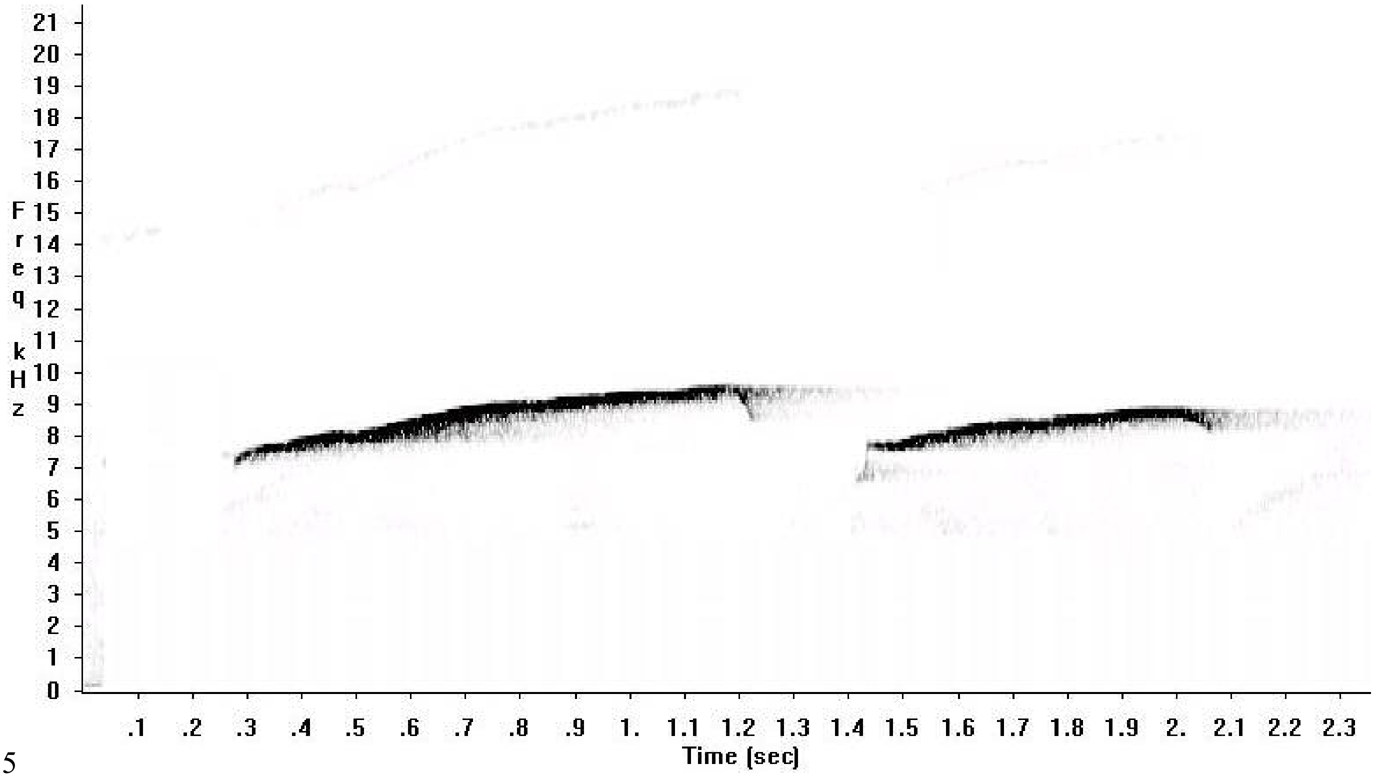

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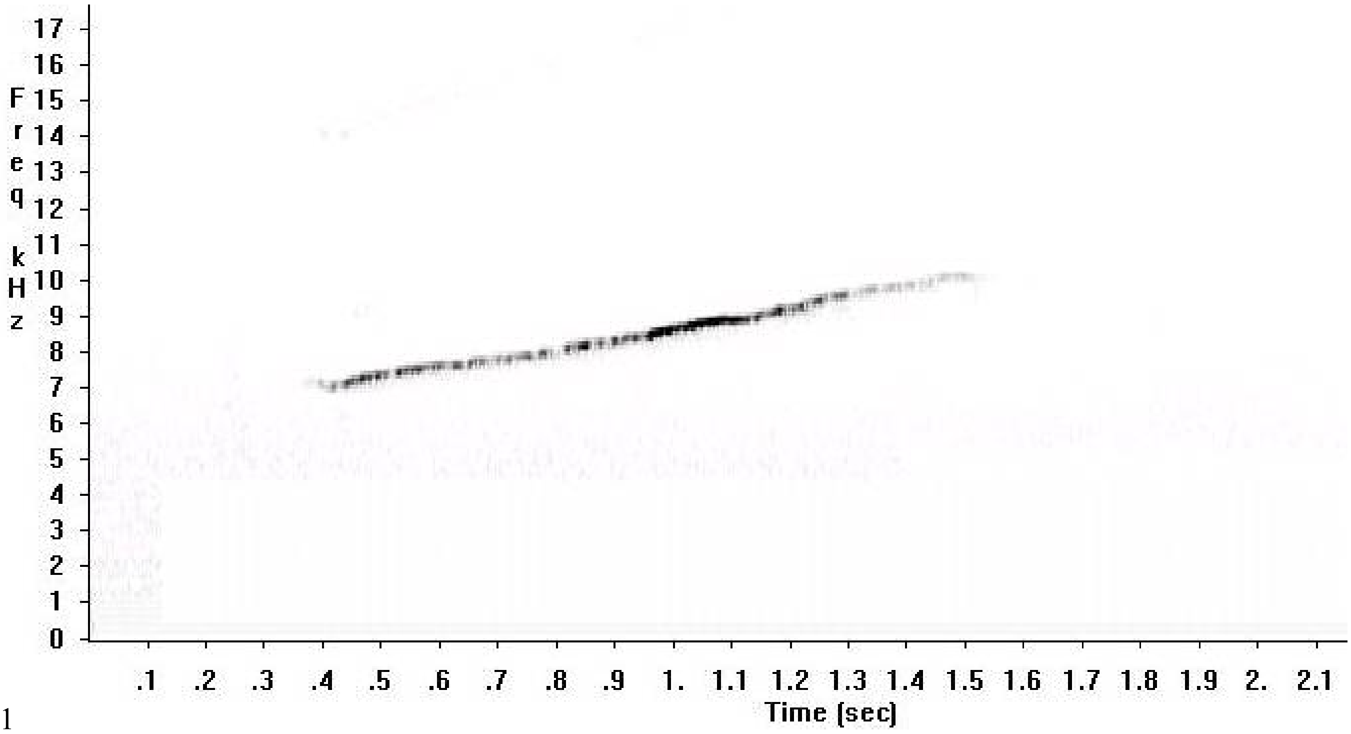

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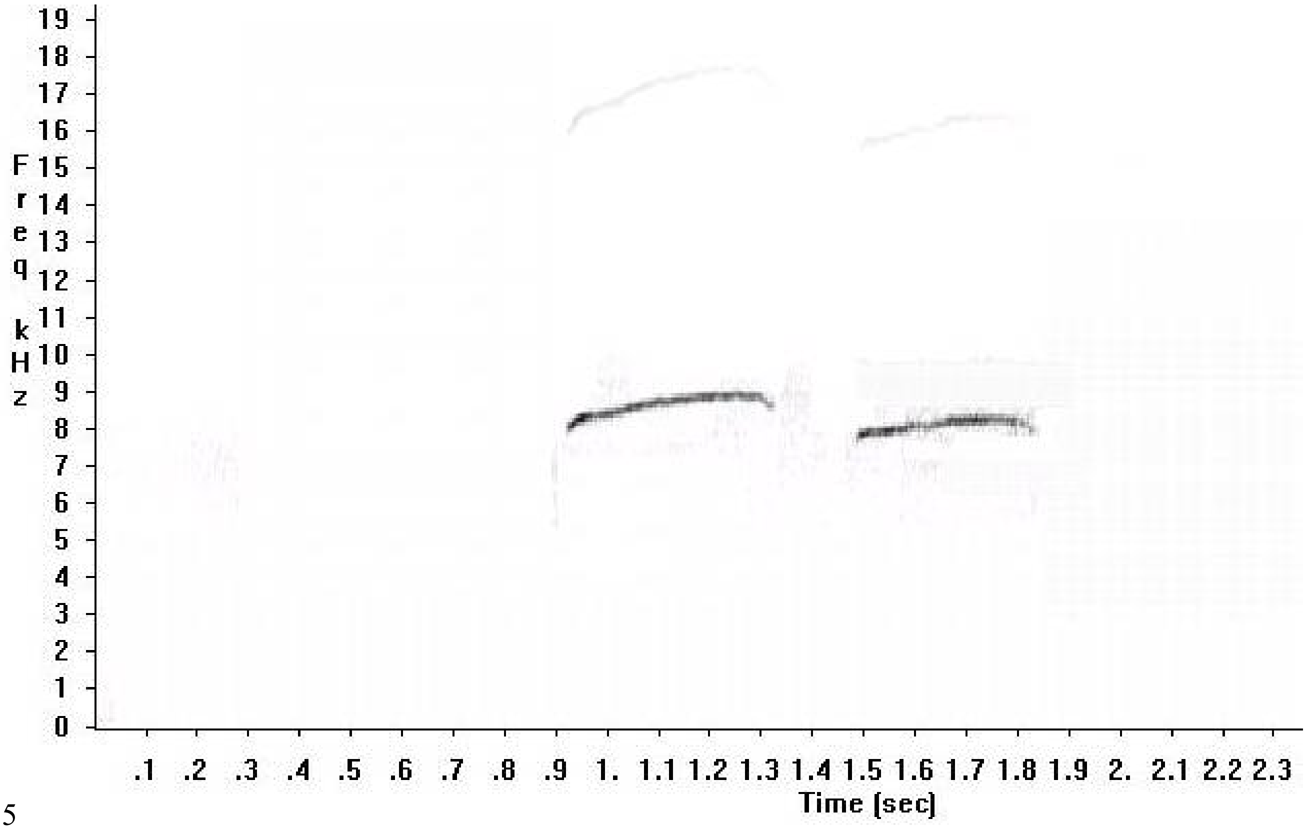

Figure 1p

Table I.

Vocal sign	Age	N	Call Dur	SE	Num Syl	SE	Syl Dur	SE	ISI	SE	↑ Freq	SE	↓ Freq	SE	Δ Freq	SE
Trill	A	106	0,37	± 0,02	1,00		0,37	± 0,02	n/a		8,13	± 0,10	6,37	± 0,10	1,77	± 0,05
	J	66	0,37	± 0,05	1,00		0,37	± 0,05	n/a		9,03	± 0,20	6,95	± 0,14	2,08	± 0,10
	I	13	0,37	± 0,07	1,00		0,37	± 0,07	n/a		9,78	± 0,65	7,29	± 0,18	2,49	± 0,48
Twitter	A	39	1,12	± 0,10	9,63	± 0,76	0,06	± 0,00	0,09	± 0,02	13,08	± 0,22	5,49	± 0,12	7,60	± 0,18
	J	10	0,96	± 0,17	8,29	± 0,14	0,05	± 0,01	0,08	± 0,00	12,75	± 0,31	5,82	± 0,09	6,94	± 0,30
Tsik	A	84	n/a		n/a		0,05	± 0,00	n/a		14,63	± 0,63	2,72	± 0,39	11,91	± 0,57
	J	30	n/a		n/a		0,04	± 0,00	n/a		14,96	± 0,78	3,58	± 0,73	11,38	± 0,83
	I	68	n/a		n/a		0,04	± 0,01	n/a		14,09	± 0,91	3,64	± 0,40	10,45	± 0,51
Tse	A	22	n/a		n/a		0,04	± 0,01	n/a		16,91	± 0,76	11,82	± 0,65	5,10	± 0,31
	J	9	n/a		n/a		0,04	± 0,00	n/a		16,47	± 0,56	13,65	± 0,68	2,83	± 0,24
Egg	A	14	n/a		n/a		0,04	± 0,00	n/a		16,69	± 1,67	12,73	± 0,06	3,96	± 1,62
	J	19	n/a		n/a		0,04	± 0,01	n/a		16,69	± 1,45	12,73	± 0,06	3,96	± 1,41
Chatter	A	47	n/a		n/a		0,06	± 0,01	0,06	± 0,02	21,96	± 0,57	0,25	± 0,00	21,71	± 0,57
Submissive squeal	A	25	n/a		n/a		0,49	± 0,04	n/a		20,55	± 0,32	1,49	± 0,10	19,06	± 0,33
Loud squeal	I	39	n/a		n/a		0,93	± 0,26	n/a		21,69	± 0,64	1,12	± 0,60	20,58	± 0,04
Moaning	J	10	n/a		n/a		0,27	± 0,00	n/a		15,57	± 0,60	0,81	± 0,02	14,76	± 0,58
Food call	A	6	n/a		n/a		0,11	± 0,01	n/a		17,39	± 0,24	14,68	± 0,29	2,72	± 0,17
Bird alarm	A	8	n/a		n/a		0,12	± 0,01	n/a		10,85	± 0,10	8,66	± 0,14	2,19	± 0,07
Dog alarm	A	4	n/a		n/a		0,10	± 0,02	n/a		16,86	± 0,49	10,25	± 0,25	6,61	± 0,74
Scream	I	2	n/a		n/a		0,63	± 0,05	n/a		20,00	± 0,75	1,90	± 0,10	18,10	± 0,65
Long phee call	A	68	n/a		n/a		1,38	± 0,04	n/a		8,80	± 0,08	7,07	± 0,08	1,73	± 0,10
Brief phee call 1	A	38	n/a		n/a		0,80	± 0,03	n/a		8,91	± 0,08	7,24	± 0,10	1,67	± 0,09
Brief phee call 2	A	4	n/a		n/a		1,04	± 0,05	n/a		10,06	± 0,36	7,65	± 0,31	2,41	± 0,55
Brief phee call 3	A	16	n/a		n/a		0,54	± 0,10	n/a		8,61	± 0,24	7,47	± 0,15	1,14	± 0,15

Table I. (*Cont.*).

Vocal sign	Age	N	← Freq	SE	→ Freq	SE	Dur start-peak	SE	Dur peak-end	SE	NH	SE
Trill	A	106	7,03	± 0,13	7,23	± 0,10	0,21	± 0,02	0,16	± 0,02	up to 1	
	J	66	8,18	± 0,33	7,80	± 0,21	0,20	± 0,05	0,17	± 0,03	up to 1	
	I	13	8,85	± 0,32	7,71	± 0,13	0,16	± 0,08	0,21	± 0,01	up to 1	
Twitter	A	39	8,43	± 0,18	8,04	± 0,39	0,10	± 0,09	1,03	± 0,12	up to 1	
	J	10	8,61	± 0,31	8,74	± 0,67	0,13	± 0,00	0,83	± 0,00	up to 1	
Tsik	A	84	12,05	± 0,95	2,80	± 0,45	0,02	± 0,00	0,03	± 0,00	0 to 2	
	J	30	13,27	± 0,91	3,59	± 0,73	0,02	± 0,00	0,02	± 0,00	0 to 2	
	I	68	11,76	± 0,95	4,36	± 0,12	0,03	± 0,01	0,04	± 0,00	0 to 2	
Tse	A	22	12,04	± 0,59	15,44	± 0,90	0,03	± 0,01	0,01	± 0,00	0,00	
	J	9	13,65	± 0,68	14,90	± 0,39	0,03	± 0,00	0,01	± 0,00	0,00	
Egg	A	14	n/a		n/a		n/a		n/a		12,29	± 0,86
	J	19	n/a		n/a		n/a		n/a		11,33	± 1,57
Chatter	A	47	n/a		n/a		n/a		n/a		n/a	
Submissive squeal	A	25	n/a		n/a		n/a		n/a		31,68	± 1,28
Loud squeal	I	39	n/a		n/a		n/a		n/a		39,02	± 0,87
Moaning	J	10	n/a		n/a		n/a		n/a		39,02	± 1,71
Food call	A	6	14,68	± 0,29	17,51	± 0,35	0,09	± 0,02	0,02	± 0,01	up to 1	
Bird alarm	A	8	8,76	± 0,12	8,31	± 0,18	0,07	± 0,01	0,05	± 0,01	0,00	
Dog alarm	A	4	10,25	± 0,25	16,38	± 0,03	0,09	± 0,02	0,00	± 0,00	n/a	
Scream	I	2	n/a	±	n/a	±	n/a	±	n/a	±	n/a	
Long phee call	A	68	7,21	± 0,12	7,87	± 0,14	1,15	± 0,06	0,23	± 0,05	up to 2	
Brief phee call 1	A	38	7,24	± 0,10	8,35	± 0,15	0,69	± 0,04	0,10	± 0,03	up to 2	
Brief phee call 2	A	4	7,99	± 0,41	9,79	± 0,49	0,98	± 0,05	0,06	± 0,01	up to 1	
Brief phee call 3	A	16	7,48	± 0,16	8,41	± 0,21	0,48	± 0,09	0,06	± 0,02	up to 1	

Table I. (*Cont.*).

Vocal sign	Age	N	IBH	SE	Obs.
Trill	A	106	n/a		
	J	66	n/a		
	I	13	n/a		
Twitter	A	39	n/a		
	J	10	n/a		
Tsik	A	84	n/a		
	J	30	n/a		
	I	68	n/a		
Tse	A	22	n/a		
	J	9	n/a		
Egg	A	14	0,61	± 0,07	The higher frequence is the frequence of the last harmonic
	J	19	0,68	± 0,04	The higher frequence is the frequence of the last harmonic
Chatter	A	47	n/a		
Submissive squeal	A	25	0,43	± 0,09	The higher frequence is the frequence of the last harmonic
Loud squeal	I	39	0,26	± 0,00	The higher frequence is the frequence of the last harmonic
Moaning	J	10	0,26	± 0,07	The higher frequence is the frequence of the last harmonic
Food call	A	6	n/a		
Bird alarm	A	8	n/a		
Dog alarm	A	4	0,00		
Scream	I	2	n/a		Maximum intensity between 6 and 10,75kHz
Long phee call	A	68	n/a		
Brief phee call 1	A	38	n/a		
Brief phee call 2	A	4			
Brief phee call 3	A	16			

Table II.

Behaviour category	**Behaviors**
Foraging behaviour	Saltatory search: Searching for animal prey in a 'stop and go' pattern (Souto et al., 2007). Careful search: Carefully watching and, simultaneously, manipulating a leaf, branch or tree hole.
Vigilance	Looking around quickly into the surrounding vegetation while stationary (Halsey et al., 2006).
Rest	Solitary rest: Resting or self-grooming while stationary with no other marmoset within at least 2 m. Social rest: Stationary with another marmoset in bodily contact, the former either resting, grooming the conspecific or being groomed.
Play	Solitary play: Playing alone by undertaking 'frisk-hops' and/or locomoting over short distances (< 1 m). Social play: Playing while interaction with conspecifics. Play consists of pretend fighting, either on the ground or in the trees; chasing each other around tree trunks or over branches.
Eat	Consumption of either animal prey (e.g. cicada, grasshopper, ant, small frogs, small lizards) or vegetable matter (e.g. fruit, flowers, seeds).
Capture	The act of capturing a prey item (Maier et al., 1982; Schiel, 2000).
Aggression	Intra-group aggression (Stevenson & Poole, 1976).

	Inter-group aggression: (Stevenson & Poole, 1976).
Social watch	Watching a known conspecific: Stationary, watching a group member that is undertaking behaviors (Schiel & Huber, 2006).
	Watching an unknown conspecific: Stationary, watching an individual of another social group undertaking behaviors.
Locomote to caller	Locomoting in the direction of a caller.
Locomote away from caller	Locomote away from a caller.
Approach	Approach only: Locomoting to get closer to another individual (≅1 m distance) without physical contact.
	Approach with interaction: Approaching another marmoset and then interacting with it by grooming it, carrying it (when it is an infant) or through aggressive behaviors.
Look at call direction	Looking in the direction from which a call has eminated (either being able to see the caller or otherwise)
Pause	Stopping the current behavior and remaining stationary for several seconds.
Flee	Moving away rapidly from a negative stimulus.
Frozen	Staying in a stationary position and not moving any body parts, including the head.

Table II (*Cont.*)

Table III.

Behavioral context	**n_1**	**Age**	**Friedman's test**	**n_2**	**n_3**	**% of vocalisations related to the behavioral context**
Foraging behavior	14	A	50.969***	738	525	94,3% trill; 3.6% brief phee call 3; 2.5% twitter; 2.3% brief phee call 2; 0.38% tsik and brief phee call 1; 0.19% tsê + egg
	6	J	24.842**	284	114	83.3% trill; 7.9% brief phee call 3; 2.6% twitter; 1.75% tsik; 0.88% egg, tsik, tsik + egg, tsê + egg, submissive squeal and brief phee call 2
	5	I	8.727*	176	29	86,2 % trill; 6.9% brief phee call 3; 3.45% tsê and submissive squeal.
Vigilance	10	A	18.088**	71	158	89.2% tsê + egg; 3.8% twiter and very brief whistle; 1.9% brief phee call 2; 0.6 brief phee call 1 and tsik.
	5	J	3.868	26	46	80,4% tsê + egg; 10.9% very brief whistle; 6.52% tsik; 2.17% tsik + egg.
Solitary rest	13	A	10.892	105	51	60.8% twitter; 11.8% trill; 7.8% Long phee call e brief phee call 3; 5.9% brief phee call 1; 3.9% long phee call + brief phee call 1; 1.96% brief phee call 2.
	5	J	3.000	49	21	85.7% twitter; 9.5% brief phee call 3; 4.76% trill.
	4	I	_	21	_	The infants did not vocalise during the times they were observed.

Table III. (*Cont.*)

Behavioral context	**N_1**	**Age**	**Friedman's test**	**n_2**	**n_3**	**% of vocalisations related to the behavioral context**
Social rest	11	A	10.069*	106	64	32.8% trill; 31.2% twitter; 28,1% brief phee call 3; 4.7% brief phee call 2; 3.1% brief phee call 1
	5	J	_	8	_	The juveniles did not vocalise during the times they were observed.
	5	I	_	115	1	The infants did not vocalise during the times they were observed. Except for one single time in which one infant uttered a singly trill.
Solitary play	2	A	_	2	0	_
	6	J	_	26	3	From the 26 times that the juveniles were observed on solitary play, they were silent 23 times. On three occasions one juvenile uttered a trill single.
	5	I	_	108	0	_
Social play	8	A	_	24	0	
	6	J	8.643	72	19	47% moaning; 26.3% tsik; 15.8% trill; 5.3% twitter.
	5	I	_	111	36	100% moaning.

Table III. (*Cont.*)

Behavioral context	**n_1**	**Age**	**Friedman's test**	**n_2**	**n_3**	**% of vocalisations related to the behavioral context**
Eat	14	A	_	137	0	
	6	J	_	158	1	All juveniles kept silent while eating, except for one animal that once uttered a tsê + egg call.
	5	I	_	77	0	
Capture	14	A	_	79	0	
	6	J	_	82	0	
	5	I	_	10	0	
Intra-group aggression	6	A	6.000**	19	16	93.75% chatter; 6.25% tsê.
	2	J		12	7	85.7% chatter; 14.3% egg
	3	I		8	8	75% chatter; 25% submissive cry (submissive squeal + trill + tsik)

Table III. (*Cont.*)

Behavioral context	**n_1**	**Age**	**Friedman's test**	**n_2**	**n_3**	**% of vocalisations related to the behavioral context**
Inter-group aggression	6	A	11.000***	32	14	64.3% chatter; 14.3% twitter and tsê + egg; 7.14% scream
Watch a known conspecific	11	A	19.95**	39	49	32.6% twitter; 18.37% very brief whistle; 12,24% brief phee call 3; 6.12% tsê and submissive cry; 4.08% brief phee call 1; 2.04% tsik + egg and brief phee call 2.
	5	J	11.478	59	54	35.18% submissive squeal; 20.4% twitter; 18,5% tsik; 14.8% trill; 3.7% tsik + egg and brief phee call 1; 1.85% tsê and tsê + egg.
	5	I	24.986**	178	172	61.05% loud cry (Loud squeal + trill + tsik); 18.02% submissive cry; 1.74% tsik + egg; 1.16% tsê, tsê + egg and brief phee call 2 and 0.58% moaning.
Watch an unknown conspecific	4	A	9.659	36	61	68.8% long phee call; 11.5% twiter; 6.56% brief phee call 1; 4.92% tsik; 1.64% long phee call + brief phee call 1, brief phee call 3, chatter; tsik + egg and tsik series.
	4	J	7.402	64	66	31.8% twitter; 25.8% brief phee call 3; 22.7% trill; 7.58% brief phee call 1; 6.06% submissive cry; 3.03% brief phee call 2; 1.5% long phee call.

Table IV.

Initial vocalisation	**n_1**	**Age**	**Vocal responses Friedman's test**	**n_2**	**n_3**	**% Vocal responses**	**Behavioral responses Friedman't test**	**n_4**	**% Behavioral responses**
Twitter call	10	A	10.000*	71	60	93% twitter; 6.7% brief phee call 1	23.131***	88	42% Pause; 9.17% Locomote to caller
	5	J	_	29	23	100% twitter	3000	31	82.3% Pause; 17.6% Locomote to caller;
Loud Cry (Combination of Loud squeal + tsik + trill)	10	A	_	27	5	80% very brief whistle; 20% twitter.	4.361	30	60% Approach with interaction; 10% Approach only; Look at call direction; 3.3% others.
	4	J	_	15	0		_	16	56% Approach with interaction; 18.75% Approach only; 6.25% Locomote to caller, 6.25%

									Look at call direction; 6.25% others.
Long Phee call (ALA) + Brief phee call 1 (ABA)	11	A	18.198**	49	32	59.4% twitter; 18.75% long phee call + brief phee call 1; 6.25% brief phee call 1; 6.25% brief phee call 2.	12.200*	41	51% Locomote to caller; 46.3% Pause; 2.4% Look at call direction.

Table IV (*Cont.*).

CAPÍTULO III

Social and ontogenetic influences on the vocalisations of wild common marmosets

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Vocalisations of wild common marmosets

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Abstract

The vocalisations of 30 wild common marmosets, *Callithrix jacchus*, living in a fragment of Atlantic Rain Forest were recorded to investigate whether the rate their vocalisations is affected by (i) age, (ii) gender and (iii) hierarchic position. We also investigated whether call characteristics were related to the age of the caller by studying the affect of age on the physical characteristics of a common, contact vocalisation, the trill call. During most of the day, adults vocalised more than both juveniles and infants. However, no differences were found between either gender or hierarchic position with respect to rate of vocalisations. The trill calls emitted by young common marmosets were of a higher pitch than those emitted by adults. Thus we conclude that at least part of the auditory communication of wild common marmosets is directly related to the age of the animals, both in terms of the rate of vocalisations and the physical characteristics of vocalisations.

Key words: age-related variations, *Callithrix jacchus*, common marmoset, vocal communication, vocalisation.

Introduction

Common marmosets are small, diurnal, social primates living in groups of up to 15 individuals and usually have a specific home range (Hershkovitz, 1977; Stevenson & Rylands, 1988; Mendes Pontes & Monteiro da Cruz, 1995; Monteiro da Cruz, 1998). The social organisation of this species is complex (e.g. Schiel & Huber 2006) and a group may be monogamous, polygynous, polyandrous or polygyandrous (Ferrari & Lopes Ferrari, 1989; Dixson, 1993; Koenig, 1995; Roda & Mendes Pontes, 1998; Nievergelt et al., 2000;

Bezerra et al., *submitted*) but always includes a dominant reproductive couple (Stevenson & Rylands, 1988).

Common marmosets, *Callithrix jacchus*, can communicate through olfactory signals (e.g. scent marks), visual signals (e.g. piloerection, genital presentation) and vocal signals (calls) (Stevenson & Rylands, 1988; Yamamoto, 1991; Smith, 2006). The poor visibility provided by the arboreal environment in which common marmosets live (Altmann, 1967; Epple, 1968; Yamamoto, 1991; Geiss & Schrader, 1996; Napier & Napier, 1996) makes vocal signalling extremely important for coordinating the social activities and behaviors of the group (Geiss & Schrader, 1996; Hook-Costingan & Rogers, 1998). Indeed, previous studies have shown that common marmosets vocalise frequently in keeping with their extended social structure and territoriality (Norcross and Newman, 1993; Hook-Costingan & Rogers, 1998; Lazaro-Perea, 2001). The vocal repertoire of common marmosets has been described for captive groups (Epple, 1968; Winter, 1977; Pook, 1977 and Winter & Rothe, 1979), and more recently for groups living in the wild (Bezerra & Souto, *submitted*).

There is some evidence that the ontogeny of vocalisation in non-human primates may result from the social organisation, ecology and physical changes of the species (Corewyn, 2003). The physical structure of the vocalisations encodes information about the caller, including the gender of the caller, the behavioral context and the social context of the call (Norcross & Newman, 1993; Schrader & Todt, 1993; Geiss & Schrader, 1996; Norcross et al., 1999; Rukstalis et al., 2003). While the ecology, behavior and sociality of common marmosets has been studied in some detail (e.g. Stevenson & Poole, 1976; Stevenson & Rylands, 1988; Alonso & Langguth, 1989; Ferrari & Lopes Ferrari, 1989; Rothe & Darms, 1993; Monteiro da Cruz, 1998; Nievergelt et al., 2000; Souto et al., 2007;

Bezerra et al., *in press)*, the influences of age, gender and hierarchic position on the rate of vocalisations of common marmosets is unknown.

Thus, the present study investigates whether the rate of vocalisations of common marmosets in the wild is affected by (i) age, (ii) sex and (iii) hierarchic position. We also investigate whether information about the age of the caller is included in their vocalisations by studying the affect of age on the physical characteristics of a call typically used by common marmosets to contact conspecifics (the trill call; Norcross et al., 1994; previously termed the whirr call; Pook, 1977). An understanding of how gender, social position and age influence the vocalisations of individuals is important if we are to further develop our knowledge about the behavior and sociality of this species in the wild.

Methods

Study site

The study was carried out in a fragment of Atlantic Rain Forest. The 32 ha study site is located in Camaragibe, State of Pernambuco, Northeast Brazil (7°56’97’’S, 35°1’23’’W) (for a detailed descripton of the study site see Souto et al., 2007).

Subjects

We studied 30 common marmosets distributed into three social groups. The subjects were classified into three broad age categories following Stevenson and Rylands (1988): adults (> 15 months; 17 individuals); juveniles (6-10 months; 6 individuals) and infants (0-5 months; 7 individuals). Subjects were wild and were not provisioned for.

The subjects were identified without capturing, through their natural features (size and colour of the ear-tufts, scars, natural mutilations, and small variations in fur coloration).

In two of the infants, a small portion of the tail fur was cut with a pair of scissors, to facilitate distinguishing the twins (see Souto et al., 2007 for a detailed description of this marking procedure). The hierarchic structure of the group was ascertained (as Bezerra et al., *in press*) on the basis of aggressive and submissive interactions (Saltzman et al., 1996) and on affiliative behavior e.g. allo-grooming (Kirkpatrick-Tanner, 1998; Albuquerque et al., 2000; Lazaro-Perea, 2001).

Data collection

The focal sampling technique (Altmann, 1974) was used to record the rate of vocalisations performed by the study animals. All observations were carried out between 05:00 and 17:30, i.e. daylight hours. The maximum distance that the animals were observed was 5 m, since from greater distances it was not possible to hear all vocalisations clearly. The observations were dictated onto a tape recorder (Sony M-529V) during 5 min sessions and included date, time, location and description of the vocalisations. A total of 1105 observational sessions were conducted from December 2004 to April 2005.

According to Maurus et al. (1988), the recognition of call types from listening depends on the physical ability of the observer to distinguish the acoustic structures of a call and on their propensities for categorizing sounds. In the present study, before the start of data collection (November 2004), Bezerra was submitted to a battery of medical tests in two hospitals to ascertain her auditory capacity. The results from both hospitals attested that Bezerra is able to hear the full bandwidth of the fundamental frequencies of the vocalisations emitted by common marmosets. Also, since Bezerra has been conducting behavioral observations of common marmosets in the area since 2001, she is well practised in distinguishing the vocalisations of common marmosets by ear.

Callithrix species present a general pattern of activities for 10 to 12 hours per day i.e. the daylight hours (e.g. Yamamoto, 1991; Kantha & Suzuki, 2006). After nightfall and before daybreak, marmosets rest and sleep. It is known that the behavioral time budgeting of common marmosets is influenced by time of day (e.g. rate of foraging behavior, Alonso & Langguth, 1989; visiting different areas of the home range, Mendes Pontes & Monteiro da Cruz, 1995; rates of scent-marking behavior, Nogueira et al., 2003). The data were arbitrarily divided into three periods: (i) beginning of the day: 05:00 to 10:00; (ii) middle of the day: 10:00 to 15:00 and (iii) end of the day: 15:00 to 17:30, such that variations in vocal behavior through the day could be investigated.

Recording the trill calls

We used the focal animal and *ad libitum* sampling techniques (Altmann, 1974) to obtain recordings of the vocal repertoire of wild common marmosets. All recordings were made between 05:00 and 17:30. We recorded vocalisations using an AKG C1000S II hypercardioid microphone (linear frequency response within the range 50 Hz to 20 kHz), which is well suited for camcorders (Shopmann, 1999). We connected the microphone to a digital camcorder, Panasonic PV-GS400, linear frequency response within the range 50 Hz to 20 kHz (at a 16-bit and 48 kHz sampling rate) (Biebel, 2004). A sampling frequency of 48 kHz can result in a reliable frequency response of up to 22 kHz. Camcorders have been used in a number of studies for recording audio in studies on marine mammals (e.g. Herzing, 1996; Dudzinnski, 1998; Dudzinnski, 1999) but less so in studies on terrestrial mammals (see, however, Taglialatela et al., 2003, on *Pan paniscus*). The advantage of using an appropriate video camera is having both audio and video records for subsequent behavioral analysis (Taglialatela et al., 2003). We used a Hosa® cable to connect the microphone with the camcorder and earphones (Intersound, linear frequency response within the range 20 Hz to 20 kHz) in order to monitor the sound while recording. This system is sufficient both to capture the behaviors of the study animals and the full bandwidth (of the fundamental frequencies) of their vocalisations.

The recordings were conducted at a distance of 2 – 5 m from the subjects. Once acquired, the vocalisations were digitally transferred, via firewire cable, from the video camera to a PC, through MediaStudio Pro 6.5 (Ulead System, Inc.) software, settled to capture DV 1, at a 16-bit quantization and 48 kHz sampling rate. Each vocalisation was saved in WAV format (without compression) and then analysed through SYRINX-PC sound-analysis software (J. Burt, Seattle, Washington – available upon request). This allowed us to build sonograms of trill calls and to obtain a number of variables representing the physical characteristics of those calls (Jones et al., 1993, Newton-Fisher et al., 1993 and Norcross et al., 1999).

Statistical analyses

The software packages SPSS v. 8.0 (SPSS Inc. Chicago, IL, USA) and Excel (Microsoft Corporation, Redmond, WA, USA) were used for data analysis. Mann-Whitney U tests were used for comparisons of two independent samples [i.e. (i) inter and intra-age comparisons of the rate of vocalisations; when considering hierarch position and gender, comparisons were made only between adults since the other age classes did not include sufficient animals for robust statistical analyses. (ii) inter-age comparisons of the physical characteristics of the ‘trill call’; we compared six physical characteristics of the trill calls of adults and juveniles (the highest, lowest, start and end frequencies, the frequency range and the call duration)]. The physical characteristics of the trill calls of the infants were not included in inter-age analysis because such vocalisations had only been recorded for two individuals. However, the mean values for the physical characteristics of the trill calls of these infants are included in Figure 3.

We used Friedman two-way analyses of variance by ranks to calculate possible differences in the frequency of more than two paired samples (i.e. intra-age comparisons between the three periods of the day).

P values ≤ 0.05 (two-tailed) were considered to indicate significant effects.

Results

Rate of vocalisations: Inter-age group comparisons

Across the day (between 05:00 to 17:30), adults and juveniles performed significantly more 'vocalisations' than did infants (n_1=11; n_2 = 5, $U = 0$, $p = 0.002$ and n_1 = 6, n_2 = 5, $U = 3$, $p = 0.018$, respectively), while there was no significant difference between adults and juveniles (n_1 = 11, n_2 = 6, $U = 20$, ns) (Figure 1).

Between 05:00 and 10:00, adults vocalised significantly more than did juveniles or infants (n_1=11; n_2 = 6, $U = 11$, $p = 0.027$ and n_1 = 11, n_2 = 5, $U = 3$, $p = 0.003$, respectively), whereas no significant difference between juveniles and infants was found in this period of the day (n_1 = 6, n_2 = 5, $U = 13$, ns). Adults vocalised significantly more than juveniles and infants between 10:00 and 15:00 (n_1=10; n_2 = 4, $U = 2$, $p = 0.01$ and n_1 = 10, n_2 = 5, $U = 3$, $p = 0.007$, respectively). There was no significant difference between juveniles and infants (n_1 = 6, n_2 = 5, $U = 9$, ns). Adults and juveniles vocalised more than infants between 15:00 and 17:30 (n_1 = 10; n_2 = 5, $U = 5$, $p = 0.01$ and n_1 = 6, n_2 = 5, $U = 2$,

p = 0.018, respectively), and vocalised a similar amount to each other in this period (n_1 = 11, n_2 = 6, U = 30, ns) (Figure 2).

Rate of vocalisations: Intra-age group comparison

The rate of vocalisations in adults and in infants did not differ significantly through the day (adults: N = 10, F_r = 2.600, df = 2, ns; infants: N = 5, F_r = 3.600, df = 2, ns; Friedman two-way analyses of variance by ranks). However, the rate of vocalisations of juveniles did vary significantly through the day (N = 10, F_r = 8.000, df = 2, p=0.018; Friedman two-way analyses of variance by ranks). Juveniles vocalised at the highest rate between 15:00 and 17:30.

Vocalisations: gender and hierarchy

There was no statistical difference in the rate of vocalisations between male and female adults (n_1 = 6, n_2 = 5, U = 10, ns). There was no statistical difference in the rate of vocalisations across the day between dominant and subordinate adults (n_1 = 5, n_2 = 6, U = 8, ns).

Influence of age on the physical features of trill calls

A total of 172 trill calls were included in these analyses. Significant differences between adults and juveniles were found for all of the measured frequency characteristics of the trill call (highest frequency: n_1=12; n_2 = 9, U = 11, p = 0.002; lowest frequency: n_1= 12; n_2 = 9, U = 16, p = 0.007; start frequency: n_1= 12; n_2 = 9, U = 14, p = 0.004; end frequency: n_1= 12; n_2 = 9, U = 25, p = 0.039; frequency range: n_1= 12; n_2 = 9, U = 23, p = 0.028; Figure 3). The trill calls of juveniles were significantly higher in frequency than those of adults. No difference in call duration was found between adults and juveniles (n_1= 12; n_2 = 9, U = 54, ns).

Discussion

Across the entire period of daylight, which is when marmosets are active, infants vocalised less than juveniles and adults. While adults and juveniles vocalised the same amount across a day, there were differences during specific parts of the day. Adults vocalised significantly more than juveniles, and infants, between both 05:00 and 10:00 and between 10:00 and 15:00. It is known that for primates, some activities such as territorial defence and organization of social structure are coordinated by the adults of a group (e.g. Walters, 1987; Lazaro Perea, 2001). Vocalisations seem to be an important component of the behaviors displayed by common marmosets during intra-group interactions as well as during intergroup interactions, particularly those related to territory defence (Norcross and Newman, 1993; Hook-Costingan & Rogers, 1998; Lazaro-Perea, 2001). The latter is also true for other primate species such as moustached tamarin monkeys, *Saguinus mystax* (Garber et al., 2006). Adult common marmosets use several calls to establish or maintain contact between individuals (Jones et al., 1993) and it is also known that intergroup encounters are frequent in wild groups of this species (Lazaro-Perea, 2001). During the present study, 75% of the intergroup encounters occurred before 15:00 (Bezerra et al., *unpublished data*). Hence this may help to explain, in part, why adults vocalised more than did younger individuals before 15:00. Further studies focusing directly on time budgeting of intra-group behaviors and inter-group behaviors in common marmosets over the day are required to fully uncover the reasons for the differences in vocalisation rate between age groups during the early and mid parts of the day.

Between 15:00 and 17:30, juveniles vocalised more than they did earlier in the day and, indeed, as frequently as adults. Both adults and juveniles were again more vocal than infants during this period. 15:00 to 17:30 corresponds to the hours of daylight closest to the long period of inactivity by common marmosets during the night. This increase in vocalising during the latter part of the day is specific to juveniles, since the frequency of calls by adults and infants were relatively consistent throughout the day. Camaroti & Monteiro da Cruz (1997) also found that during the two hours prior to nightfall, adult common marmosets tended to be quieter than earlier in the day. However, chemical communication through scent-marking behavior in adult common marmosets tends to increase from 15:00 to 17:00 (Nogueira et al., 2003). It is possible, therefore, that juveniles do not use scent marking to the same extent as do adults, and instead continue to rely on vocal communication as nighttime approaches. Communication at this time of the day may tend to focus on finding and organizing conspecifics ready for sleeping.

The hierarchical system present in the social organization of common marmosets can lead to differences in the intensity of social interactions between individuals in the group (e.g. Yamamoto, 1991) and also lead to sexual and hormonal suppression of subordinate individuals (e.g. Hershkovitz, 1977; Abbott, 1986). Furthermore, the gender and hierarchic position of an individual influences its reactions to unknown conspecifics (e.g. Epple, 1970). Nevertheless, despite the fact that gender and hierarchical position play an important role in the life of common marmosets, these characteristics did not influence the rate of vocalisations of the animals in the present study. In captive groups, for the specific vocalisation ‘phee call’, there was also found to be no gender difference in the rate of production of this call (Norcross & Newman, 1993). These data from field and captive groups support the proposition that gender does not influence vocalisation rates.

In captive conditions, the vocalisations of infant common marmosets were, on average, of a higher pitch (Newman, 1995) than those of adults. This is supported by the data in the present study, which show that juvenile animals living in the wild tend to make the trill call at a higher frequency than do adult individuals. It can be seen that the physical characteristics of the trill calls of the two infants are considerably higher in frequency than those of the juveniles. Therefore it may be reasonable to suppose that the trill calls of infants in general are of a higher pitch than those of juveniles and, indeed, adults. This is supported by the finding that the trill calls of infant pygmy marmosets, *Cebuella pygmaea*, are also of a higher pitch than those of adults (Snowdon 1988). Age related variations in the physical characteristics of this call may be related to physiological and morphological changes during maturation in the animal (Snowdon 1988; Corewyn, 2003; Rukstalis et al., 2003), and it seems to be the case in certain vocalisations of other primate species such as pygmy marmosets, vervet monkeys (*Cercopithecus aethiops*) and rhesus macaques (*Macaca mulatta*) (Rukstalis et al., 2003). The morphological and physiological developments, along with the changes in general behaviors of infant common marmosets over time (Ingran, 1977; Hearn, 1983; Yamamoto et al., 1996), presumably help to explain these age-related differences in the physical characteristics of the trill call.

As is the case for other behavioral activities (e.g. foraging behavior, see Souto et al., 2007), the auditory communication of wild common marmosets seems to be associated with age. This is shown both by the physical characteristics of the trill call and the rate of vocalisations in general. Despite playing an important role in the social life of common marmosets, the gender and hierarchical position of individuals does not appear to have an influence on the rate of vocalisations. Further studies uncovering the reasons for differences in rates of vocalisations, including about specific calls, are required to further lay bare the complexities of marmoset behavior and sociality.

Acknowledgments

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Legends

Figure 1. Average rate of vocalisations throughout daylight hours of adults, juveniles and infants. Data are presented as means ± SEM. Mann-Whitney *U* test (two-tailed); * $p \leq 0.05$, ** $p \leq 0.01$, ns: not significant.

Figure 2. Rate of vocalisations in each of the three periods of the day. Data are presented as means ± SEM. Inter-age comparisons - Mann-Whitney *U* test (two-tailed). * $p \leq 0.05$, ** $p \leq 0.01$, ns: not significant.

Figure 3. Physical features of the trill call of adults, juveniles and infants. Highest = highest frequency; Lowest = lowest frequency; Start = start frequency; End = end frequency; Range = frequency range. Data are presented as means ± SEM. Mann-Whitney *U* test (two-tailed); * $p \leq 0.05$, ** $p \leq 0.01$.

Figure 1.

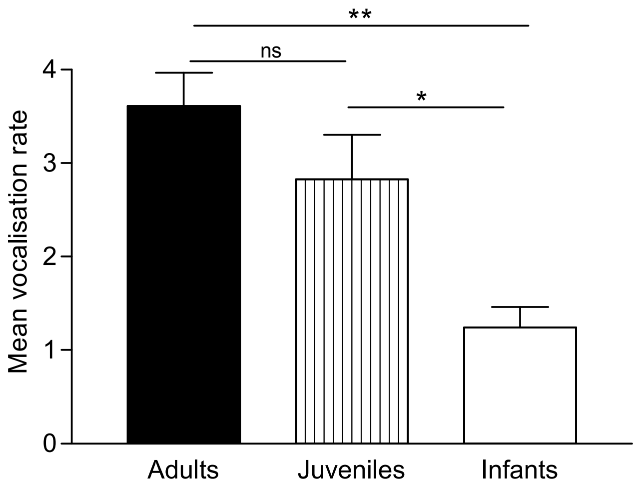


Figure 2.

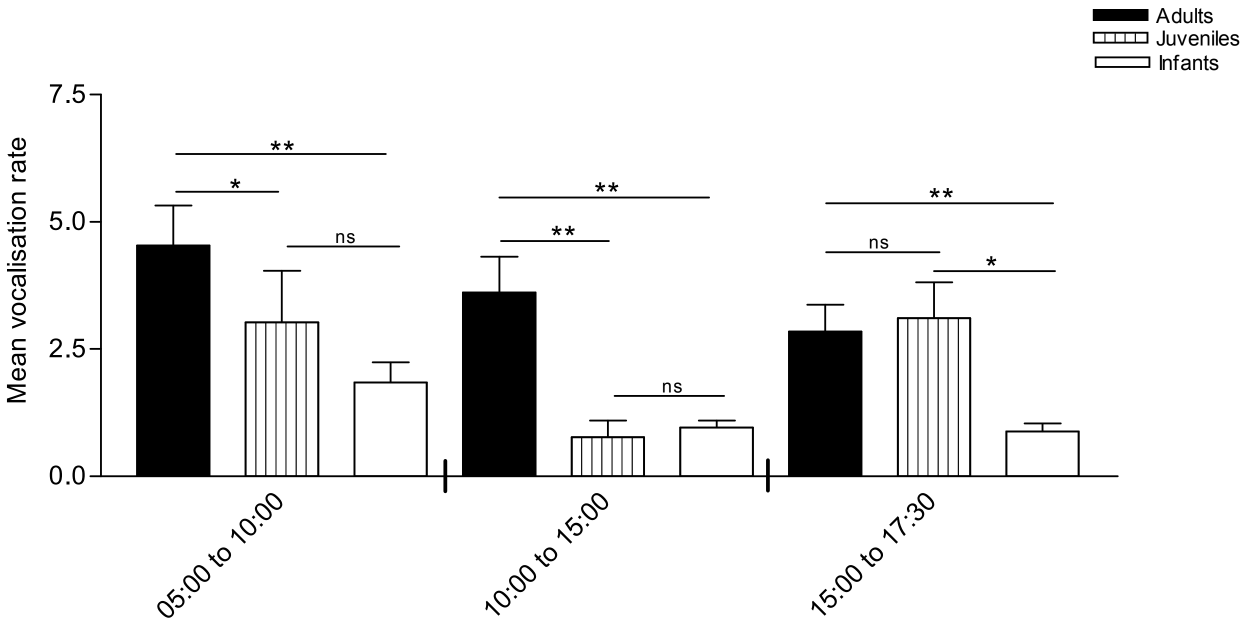
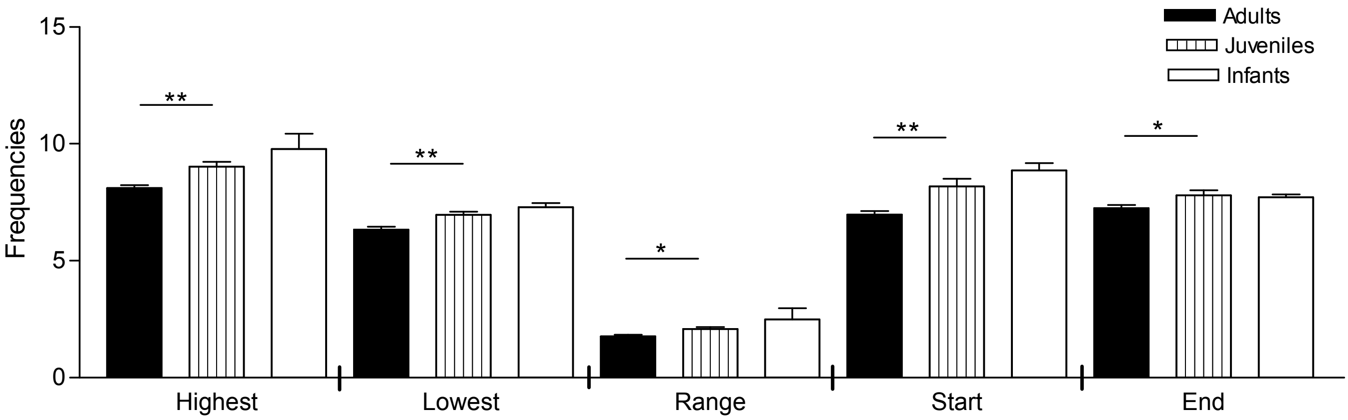


Figure 3.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CAPÍTULO IV

Conclusão Geral

Tendo em vista a complexa organização social e o hábito arbóreo de sagüis comuns em liberdade, já prevíamos um intricado sistema de comunicação através de vocalizações para espécie em questão. Dessa forma, o presente estudo, juntamente com aqueles previamente publicados para animais de cativeiro, veio a confirmar tal predição. O repertório vocal de sagüis comuns se mostrou amplo e variado, com complexos sinais acústicos. A idade dos animais não somente influenciou nos tipos de vocalizações presentes no repertório, como também na freqüência de uso das vocalizações e nas características físicas das mesmas. De uma maneira geral, os adultos apresentaram um repertório vocal mais amplo, tenderam a vocalizar mais e apresentaram vocalizações com freqüências mais baixas que a dos animais mais jovens. O comportamento de indivíduos estranhos e indivíduos do grupo pareceram de certa forma influenciar nas vocalizações dos sagüis selvagens. O repertório vocal previamente descrito para animais de cativeiro e o repertório de animais em liberdade investigado mostraram algumas dissimilaridades. Certas vocalizações encontradas em campo, não foram encontradas em cativeiro e vice e versa. Um outro ponto interessante é que os sagüis comuns em liberdade apresentaram três diferentes tipos de vocalizações de alarme ligados à presença de diferentes predadores ou potenciais predadores. Futuros trabalhos envolvendo especificamente as respostas comportamentais dos sagüis comuns em liberdade, através, por exemplo, do uso de experimentos de playback, ainda se fazem necessários para um consolidar os conhecimentos acerca da comunicação vocal dos sagüis comuns.

ANEXO

Regras de submissão das revistas referidas nos capítulos 2 e 3 da presente dissertação.

International Journal of Primatology

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Abstract, Key Words, Text, Acknowledgements, References, and Table and Figure legends must be typed, double-spaced in 12-point font. Original and 3 clear copies of all figures and tables are required.

The Title Page should list the affiliations of all authors and the full traditional mail address, telephone and FAX numbers and e-mail address of the author with whom the editor and publisher will correspond.

A ≤250-word Abstract and 4-5 Key Words, which express the precise content of the manuscript for indexing, should directly follow the Title Page.

The Abstract and main text should be written in active voice throughout, i.e. employ I/we in relating what you did, observed, etc. Every sentence should have an explicit subject; if you were the actor, use I or we as appropriate for the number of actors. Use last names of authors or field assistants if you wish to signal individual observers who conducted specific components of your study versus the collective we throughout the text. FAILURE TO USE ACTIVE VOICE REQUIRES RETURN OF THE MS TO THE CORRESPONDING AUTHOR FOR AMENDMENT AND MIGHT OTHERWISE DELAY ITS PUBLICATION.

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For Linnaean nomina and common names of species use the lexicons in Grubb et al. (IJP 24(6): 1301-1357, 2003) & Brandon-Jones (IJP 25(1); 97-164, 2004) for Old World monkeys and apes and Colin Grove's Primate Taxonomy (2001, Smithsonian Institution Press) for New World monkeys, tarsiers and lemurs, unless your subject is a new species. Do not use Linnaean nomina adjectivally, e.g. write "habitats of Pan paniscus," not "Pan paniscus habitats."

Do not abbreviate taxa except within a sentence wherein you have already written out the same taxon. For example, "Pan troglodytes and P. paniscus live in Africa." is acceptable, but "P. troglodytes and P. paniscus live in Africa." is not acceptable, even if you have written the genus (Pan) in a previous sentence of the text.

Avoid nicknames such as chimps for chimpanzees, orangs for orangutans, ringtails for ring-tailed lemurs, etc.

Do not use Italics or bold fonts for emphasis in the text. Also do not use quotation marks for terms with which you may not fully agree. Quotation marks should embrace substantial quotes only.

Do not write parenthetic instructions to readers in the text, i.e. avoid embedded fragments such as (see Darwin, 1859 for fuller discussion on the origin of species). The reference (Darwin, 1959) is sufficient to direct the reader to a fuller source of information on a topic.

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