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ECOLOGIA ESPACIAL E COMUNICAÇÃO VOCAL DE ARIRANHAS (*PTERONURA BRASILIENSIS*) NO PANTANAL

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Manaus, Amazonas
Dezembro de 2012

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Sinopse:

Estudei o padrão de atividade, ecologia espacial e comunicação vocal de ariranhas, *Pteronura brasiliensis* no Pantanal Sul, Brasil. Monitorei os grupos através de observações diretas, rádio-telemetria e armadilhas fotográficas. Gravei vocalizações de diferentes grupos e o comportamento dos emissores. Aspectos como área de vida, seleção de caracterísitcas da paisagem, territorialidade, repertório vocal e variações acústicas individuais foram avaliados.

Palavras- chave: Ariranhas – Comportamento, Bioacústica, Ecologia de populações, Vocalização

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RESUMO

Ariranhas vivem em grupos coesos, que defendem ativamente territórios, durante a estação seca. Durante o período de inundação, a ecologia espacial da espécie é pouco é conhecida, quando acredita-se que os grupos abandonam seus territórios. Grupos de ariranhas são coesão e territoriais, indicando que a espécie utilize um elaborado sistema de comunicação vocal, para garantir a estabilidade e comunicação dentro e entre os grupos. O presente estudo teve como objetivos gerais: 1) descrever o padrão de atividade de grupos de ariranhas no Pantanal; 2) estimar o tamanho de área de vida e o padrão de seleção de habitat de grupos de ariranhas em um ambiente sazonal; 3) compreender os efeitos da sazonalidade no tamanho de território e de territórios exclusivos, e do comportamento territorial de grupos de ariranhas; 4) descrever o repertório vocal da espécie, relacionando os tipos sonoros com o contexto comportamental em que foram emitidos; 5) testar se sons de alarme apresentam características acústicas potenciais para codificação individual. Dez grupos de ariranhas foram monitorados através de observações diretas entre junho de 2009 e junho de 2011 nos rios Vermelho e Miranda, e outros sete grupos foram monitorados no rio Negro entre setembro de 2009 e junho de 2011. Três machos adultos de diferentes grupos foram monitorados com rádio-telemetria entre novembro de 2009 e junho de 2011 na primeira área de estudo. Armadilhas fotográficas foram armadas em locas e latrinas ativas de oito grupos de ariranhas nas duas áreas de estudo, a fim de registrar atividades em ciclos de 24-h. Vocalizações e o comportamento dos emissores foram gravados ao longo das campanhas. Os grupos apresentaram um padrão de atividade crepuscular e diurno, mas 31% dos registros de armadilhas fotográficas ocorreram no período noturno. A área de vida dos grupos foi de 4 a 59 vezes maior no período chuvoso e alguns grupos abandonaram seus territórios durante a inundação. Alguns grupos sobrepuseram os limites de seus territórios com grupos vizinhos. O tamanho dos territórios foi correlacionado com o tamanho do grupo em ambas as estações. O tamanho dos territórios exclusivos foi negativamente relacionado com a pressão de intrusos. O repertório vocal da espécie foi classificado em 15 tipos sonoros emitidos em diferentes contextos. Sons de alarme variaram significativamente entre grupos e indivíduos, com uma discriminação maior entre fêmeas e machos, o que pode estar relacionado ao tamanho corporal dos emissores e, consequente dimorfismo sexual.

ABSTRACT

Spatial ecology and vocal communication of giant otters (*Pteronura brasiliensis*) in Pantanal

Giant otters live in cohesive groups, which defend territories during the dry season. Little is known about the spatial ecology of the species during the flooding period, when it is believed that groups abandon their territories. The strong cohesion between group members and the territorial behavior of the species indicate that giant otters use a complex vocalization system, to provide the stability and communication within and among groups. The present study aimed to: 1) to describe the activity pattern of giant otter groups in the Pantanal; 2) to estimate home range size of groups and landscape selection patterns between dry and wet seasons in Pantanal; 3) to look for the effect of season on territory size, territory exclusivity and territorial behaviour of giant otter groups; 4) to describe the vocal repertoire of the species, according to the behavioral context in which sound were emitted; and 5) to test if alarm sounds may present potential identity coding. Ten giant otter groups were monitored through visual observations between June 2009 and June 2011 in the Vermelho and Miranda Rivers, and another seven groups were monitored in the Negro River from September 2009 to June 2011. Three adult males of different groups were monitored with radio-telemetry between November 2009 and June 2011 in the first study area. Camera traps were located on active dens and latrines to record activity patterns in 24-h cycles. Vocalizations and the behavior of senders were recorded during the field campaigns. Groups presented a crepuscular and diurnal activity pattern, but 31% of photographic records occurred at night. The home range size of groups increased from 4 to 59 times during the wet seasons and some groups left their territories during flooding. Some groups overlapped the territories boundaries of neighboring groups. Territory size was correlated with group size in both seasons. The size of exclusive territories of giant otter groups was negatively related with intruder pressure. The vocal repertoire of the species was classified from 15 sounds emitted in different behavioral contexts. Alarm sounds varied significantly among groups and individuals, with a higher discrimination between females and males, which may be related to the body size of the senders and, consequently, sexual dimorphism.

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INTRODUÇÃO GERAL

Ariranhas (*Pteronura brasiliensis*; Zimmermann, 1780), são sociais e são consideradas as maiores lontras do mundo (Kruuk, 2006). A espécie é endêmica da América do Sul e, devido principalmente à caça ilegal que ocorreu até meados da década de 80, muitas populações de ariranhas foram dizimadas ou reduzidas a valores críticos (Schweizer, 1992; Carter & Rosas, 1997) Atualmente no Brasil,populações estáveis e em recuperação da espécie parecem ser limitadas ao Pantanal e à Bacia Amazônia (Leuchtenberger & Mourão, 2008; Rosas *et al.*, 2008). No entanto, devido ao crescimento populacional humano, destruição de habitat, entre outros fatores como a superexploração da pesca, contaminação dos corpos d'água, caça ilegal, turismo desordenado e comercialização de filhotes como animais de estimação (Gómez *et al.*, 1999; Lima, 2009as ariranhas são classificadas como em perigo de extinção na lista vermelha da IUCN (2011) e como vulneráveis no Brasil (Rosas *et al.* 2008).

Ariranhas vivem em grupos monogâmicos, formados por um casal dominante não relacionado geneticamente e parentes próximos (Duplaix, 1980; Ribas 2012). No entanto, o grau de parentesco entre os indivíduos do grupo é variável e alguns grupos podem ser formados por indivíduos sem relação genética (Ribas, 2012). Os grupos estão organizados sob cooperação reprodutiva e compreendem de dois a 20 indivíduos (Duplaix, 1980; Schweizer, 1992). Machos dominantes apresentam um papel importante na defesa do grupo e do território (Duplaix 1980), uma vez que se envolvem com maior frequência na demarcação territorial e sobremarcam o cheiro dos demais indivíduos do grupo (Leuchtenberger & Mourão 2009). Fêmeas dominantes são responsável pelo coordenação das atividades do grupo e são reconhecidas durante o período reprodutivo por apresentarem estado de lactação (Duplaix, 1980).

Ariranhas se alimentam principalmente de peixes, podendo eventualmente consumir invertebrados e outros vertebrados (Duplaix, 1980; Rosas et al. 1999). A espécie pode se alimentar de presas maiores, como jacarés do Pantanal (*Caiman yacare*), como observado em grupos que habitavam lagos artificiais ao longo da Estrada Parque do Pantanal, o que pode ser um efeito da escassez de recursos e do aumento da densidade populacional da área (Ribas et al. 2012). Os indivíduos se orientam visualmente para capturar seu alimento (Duplaix, 1980, Rosas *et al.*, 1999), o que parece limitar a atividade da espécie ao período diurno (Schweizer, 1992; Kruuk, 2006).

Os grupos são fortemente coesos e realizam grande parte de suas atividades diárias em conjunto (Duplaix, 1980; Leuchtenberger & Mourão, 2008). As atividades iniciam quando o grupo deixa a sua loca ao amanhecer e encerram no final do dia com o retorno do grupo ao refúgio (Duplaix, 1980; Schweizer, 1992; Staib, 2005). Estudos sobre a atividade da espécie são limitados a observações oportunísticas e de animais em cativeiro (Duplaix, 1980; Staib, 2005; Carter & Rosas, 1997), o que dificulta a detecção de padrões temporais em condições naturais.

Em ambientes sazonais, grupos de ariranhas mantêm territórios ao longo dos corpos d'água durante o período seco (Duplaix, 1980; Laidler, 1984; Schweizer, 1992; Tomas *et al.*, 2000; Ribas, 2004; Utreras *et al*., 2005; Leuchtenberger & Mourão, 2008; Evangelista & Rosas, 2011a). Neste período, os peixes estão confinados ao leito dos rios, baías e corpos d'água marginais (Wantzen *et al.*, 2002) e os barrancos elevados proporcionam disponibilidade de refúgios. O estabelecimento de territórios quando recursos importantes ainda estão disponíveis em um ambiente sazonal pode garantir a manutenção dessas áreas ao longo das estações (Stamps, 1990). A familiaridade com o ambiente favorece o sucesso reprodutivo do dono da área, uma vez que aumenta sua habilidade de forragear e de se mover em áreas mais seguras (Stamps, 1995).

Alterações sazonais na disponibilidade de recursos e de habitat podem afetar a organização espacial e seleção de habitat de muitas espécies (Erlinge & Sandell, 1986; Arthur *et al*., 1996), levando algumas delas a aumentar a sua área de vida e outras a abandonarem seus territórios durante a estação desfavorável (Stamps, 1990; Maher & Lott, 2000). Durante a estação chuvosa, a inundação das planícies e das áreas marginais aos rios causa a dispersão dos peixes e o alagamento dos barrancos (Wantzen et al. 2002). Segundo Duplaix (1980), durante a estação chuvosa os grupos de ariranhas abandonam seus territórios, seguindo a migração de peixes para as áreas inundadas e apenas os barrancos mais elevados são visitados, para a construção de locas e latrinas comunais. Além disso, a dispersão dos grupos durante a estação chuvosa pode ocasionar um aumento de 4 a 13 vezes nas suas áreas de vidas, como estimado por Utreras *et al.* (2005) na Amazônia do Equador. O monitoramento da espécie durante o período de inundação, no entanto, é ineficiente sem o uso de tecnologias adequadas e a possível alteração na organização espacial dos grupos durante este período ainda é desconhecida.

Os grupos de ariranhas defendem ativamente seus territórios através de um sistema avançado de comunicação, que envolve sinais olfativos e acústicos (Duplaix, 1980; Ribas & Mourão, 2004; Leuchtenberger & Mourão, 2009). Encontros agonísticos entre grupos de ariranhas e solitários, como também canibalismo, registrados no Pantanal (Schweizer, 1992; Mourão & Carvalho, 2001; Ribas & Mourão, 2004; Leuchtenberger & Mourão, 2009) ressaltam o comportamento territorial da espécie. Marcações de cheiro e latrinas comunais são depositados ao longo dos barrancos em acampamentos e locas (Carter & Rosas, 1997). Sinais químicos são eficientes para demarcação territorial uma vez que transmitem informações sobre o dono do território, mesmo na sua ausência (Gosling, 1982) e geralmente são depositados em locais onde há uma maior pressão de intrusos (Sillero-Zubiri & Macdonald, 1998). Sinais químicos parecem exercer um importante papel na comunicação entre indivíduos e grupos de ariranhas e podem representar um mecanismo de supressão reprodutiva dos indivíduos subordinados (Leuchtenberger & Mourão, 2009).

A forte coesão social entre os indivíduos do mesmo grupo e o comportamento territorial da espécie podem ser sustentados por um elaborado sistema de comunicação vocal, que garanta a estabilidade e comunicação entre os grupos (Schassburger, 1993). Entre os mustelídeos, ariranhas (*Pteronura brasiliensis*), lontras marinhas (*Enhydra lutrisi*) e texugos (*Meles meles*), apresentam os sistemas de organização social mais complexos da família e seus repertórios vocais são os mais variados (Duplaix, 1980; McShane *et al.*, 1995; Wong *et al.*,1999). O conhecimento sobre o repertório vocal de ariranhas é limitado ao estudo de Duplaix (1980), que descreveu qualitativamente nove tipos sonoros emitidos em diferentes contextos sociais. Bezerra et al. (2010) apresentou a descrição sonográfica de cinco dos tipos sonoros classificados por Duplaix (1980) e sugeriram a possibilidade de variações individuais em sons de alarme (*snort*).Variações acústicas podem carregar codificações individuais que facilitam a coordenação das atividades dos indivíduos e podem proporcionar a coesão dos grupos (Janik & Slater 1998; Fitchel & Manser 2010). Tais variações são geralmente determinadas por características ambientais e genéticas (Bradbury & Vehrencamp 1998), enquanto que algumas variações podem ser aprendidas e fixadas através do comportamento, criando padrões de variação acústicas geográfica (Mitani et al. 1999; Collins & Terhune 2007; Delgado 2007), entre grupos e indivíduos (Weilgart & Whitehead 1997; Boughman 1998; Janik & Slater 1998; Sousa-Lima et al. 2002, 2008; McComb et al. 2003; Crockford et al. 2004).

Informações sobre a área de vida de uma espécie, as características ambientais e os demais fatores que determinam a sua manutenção no espaço e no tempo, são ferramentas importantes para ações de conservação. Além disso, o estudo do sistema de comunicação vocal e de variações acústicas de uma espécie podem gerar informações sobre sua história de vida, comportamento, bem como padrões de dispersão e isolamento genético de populações, o que pode afetar decisões de manejo e conservação de espécies ameaçadas (Terry et al. 2005).

Considerando a complexidade de fatores que afetam a organização espacial e o sistema de comunicação de ariranhas. Essa tese teve como objetivos gerais: 1) descrever o padrão de atividade de grupos de ariranhas no Pantanal; 2) estimar o tamanho de área de vida de grupos de ariranhas durante estações secas e chuvosas no Pantanal e comparar o padrão de seleção de características da paisagem durante ambas as estações; 3) compreender os efeitos da sazonalidade no tamanho de território e de territórios exclusivos, e do comportamento territorial de grupos de ariranhas no Pantanal;; 4) descrever o repertório vocal da espécie no Pantanal, relacionando os tipos sonoros com o contexto comportamental em que foram emitidos; 5) testar se sons de alarme apresentam características acústicas potenciais para codificação idividual.

Sendo assim, a tese está organizada em cinco capítulos: Capítulo 1 – "Activity patterns of giant otters recorded by telemetry and camera traps", onde descrevemos o padrão de atividade de grupos de ariranhas monitorados através de rádio telemetria e armadilhas fotográficas nos rios Miranda, Vermelho e Negro, no Patnanal, apresentando registros de atividade noturna; Capítulo 2 – "Space use by giant otter groups in the Brazilian Pantanal", no qual o tamanho da área de vida e o padrão de seleção de habitat de diferentes grupos de ariranhas foram analisados em estações secas e chuvosas nos rios Miranda e Vermelho, no Pantanal; Capítulo 3 – "Territoriality of giant otter groups in an area with seasonal flooding", neste capítulo analisamos o efeito da sazonalidade na fidelidade dos grupos aos seus territórios, bem como no tamanho dos territórios e territórios exclusivos, além de relações entre o tamanho de território com o número de sinais químicos depositados por diferentes grupos, com o tamanho de grupo e com a pressão de intrusos; Capítulo 4 – "A sentence is more than the sum of its words: vocal repertoire of giant otter", no qual descrevemos 15 tipos sonoros compondo o repertório vocal da espécie e o contexto comportamental em que eles foram emitidos; Capítulo 5 – "Acoustic variation in giant otter alarm calls", neste capítulo analisamos variações acústicas presentes em sons de alarme de diferentes grupos e indivíduos, apresentando discriminações acústicas significativas entre grupos, indivíduos e entre machos e fêmeas.

OBJETIVOS

O presente estudo teve como objetivos gerais:

1) descrever o padrão de atividade de grupos de ariranhas no Pantanal;

2) estimar o tamanho de área de vida e o padrão de seleção de características da paisagem de grupos de ariranhas em um ambiente sazonal;

3) compreender os efeitos da sazonalidade no tamanho de território e de territórios exclusivos, e do comportamento territorial de grupos de ariranhas no Pantanal;

4) descrever o repertório vocal da espécie no Pantanal, relacionando os tipos sonoros com o contexto comportamental em que foram emitidos;

5) testar se sons de alarme apresentam características acústicas potenciais para codificação individual.

CAPÍTULO 1

Leuchtenberger, C; Zucco, C.A.; Ribas, C.; Magnusson, W. & Mourão, G. Activity patterns of giant otters recorded by telemetry and camera traps. Manuscrito submetido à *Ethology Ecology & Evolution*.

Activity patterns of giant otters recorded by telemetry and camera traps

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ABSTRACT

The giant otter is a social species that defends territories along water bodies. Although some researchers have visually monitored otters during long periods at night no nocturnal activity of the species has been recorded and giant otters are currently believed to be strictly diurnal. In this study, we present information about the activity patterns of groups of giant otters in the Pantanal of Brazil, using radio telemetry and camera trap data. We captured, implanted transmitters and monitored three male giant otters from different groups in the Miranda and the Vermelho Rivers between November 2009 and July 2010. The locations and behavior of the group were recorded at 30-min intervals from 05:00 to 19:00 h. Camera traps were positioned at the active dens and latrines, located in the territories of eight groups of giant otters in the rivers Miranda, Vermelho and Negro between June 2010 and October 2011. The groups of giant otters were more crepuscular and diurnal, but 31% of the camera trap recordings were nocturnal. Fishing was the most frequent (64%) behavior recorded by telemetry. Giant otters were recorded exiting the den mostly in the early morning (06:00 h) and entering the den at the end of the day (16:00 to 19:00 h). Nocturnal activity appeared to be associated with the need to defecate, prey availability nearby the den and predation risk.

KEY WORDS: *Pteronura brasiliensis*, den, latrine, prey availability, predation risk, scent-mark, night activity

RESUMO

Ariranha é uma espécie socia que defende territórios ao longo dos corpos d'água. Apesar de alguns pesquisadores terem monitorado a espécie visualmente durante long visually monitored otters during long periods at nigs períodos durante a noite, nenhuma atividade noturna foi registrada e ariranhas são consideradas estritamente diurnas. Neste estudo, nós apresentamos informações sobre padrões de atividade de grupos de ariranhas no Patnanal do Brasil, usando dados de rádio telemetria e armadilhas fotográficas. Nós capturamos, implantamos transmissores e monitoramos três machos adultos de ariranhas de diferentes grupos nos rios Vermelho e Miranda entre Novembro de 2009 e Julho de 2010. As localizações e o comportamento do grupo foram registrados em intervalos de 30 minutos entre 05:00 e 19:00 h. Armadilhas fotográficas foram posicionadas em locas e latrinas ativas, localizadas nos territórios de oito grupos de ariranhas nos rios Miranda, Vermelho e Negro entre Junho de 2010 e Outubro de 2011. Os grupos de ariranhas foram mais crepusculares e diurnos, mas 31% dos registros de armadilhas fotográficas foram noturnos. Pesca foi o comportamento mais frequente (64%) registrado por telemetria. Ariranhas foram registradas saindo da loca com maior frequência no início da manhã (06:00 h) e entrando na loca no final do dia (16:00 to 19:00 h). Atividade noturna parece estar associada com a necessidade de defecar, disponibilidade de presas próximo à loca e risco de predação.

PALAVRAS-CHAVE: *Pteronura brasiliensis*, loca, latrina, disponibilidade de presas, risco de predação, marcação, atividade noturna

The activity pattern of most animals is related to circadian rhythms and periodical changes in environmental stimuli (ASCHOFF 1966). Carnivores usually exhibit daily cycles of activity, which seem to be a function of prey activity and feeding tactics (GERELL 1969; ZIELINSKI 1988; LODE 1995). Some otters change activity patterns seasonally according to prey availability (MELQUIST & HORNOCKER 1983; KRUUK 2006; GARCIA DE LEANIZ et al. 2006), and individual variation in activity patterns may be a strategy to avoid intraspecific competition (RALLS & SINIFF 1990).

The giant otter (*Pteronura brasiliensis*) is a social species that eats mainly fish (DUPLAIX 1980; ROSAS et al. 1999). Foraging is visually oriented, which seems to limit the species' activity to daylight hours (KRUUK 2006). Information about giant otter activity patterns comes from direct field observations and captive individuals (CARTER & ROSAS 1997; STAIB 2005).

Some authors have described that giant-otter groups leave their dens in the early morning, scent-marking latrines near the den before they go fishing during the whole day and returning at the end of the day to the main den, where they stay during the night (DUPLAIX 1980; SCHWEIZER 1992; CARTER & ROSAS 1997; STAIB 2005). Although some researchers have monitored visually otters during long periods at night (DUPLAIX 1980; SCHWEIZER 1992), no nocturnal activity of the species has been recorded and giant otters are currently believed to be strictly diurnal (DUPLAIX 1980; SCHWEIZER 1992; CARTER & ROSAS 1997; STAIB 2005).

Diurnal activity of giant otters involves territory patrolling and demarcation. Groups mark their territories using communal latrines, which can be located at dens or at sites along the banks (DUPLAIX 1980; LEUCHTENBERGER & MOURÃO 2009). Dens are tunnels systems built along river banks, under roots or fallen trees, with one to seven entrances (DUPLAIX 1980; CARTER & ROSAS

1997). Giant otters may use different dens for resting at night and for temporary refuge during the day. Therefore, the monitoring of dens and latrines can provide information on activity patterns (SERVHEEN & KLAVER 1983; LIM AND NG 2008; STEVEN & SERFASS 2008).

Although radio telemetry and camera traps are wide used methods, these technologies have just recently become more powerful tools for studying giant otters, improving the monitoring of groups in the field and providing new information about the biology and ecology of the species (UTRERAS & PINOS 2003; PICKLES et al. 2011; SILVEIRA et al. 2011). In this study we used telemetry and camera trap data to describe the activity pattern of giant otters groups in the Brazilian Pantanal wetlands.

2. MATERIALS AND METHODS

We studied giant otter activity in the southern Pantanal of Brazil. The region receives an annual precipitation of about 1200 mm, with most of the rain falling between November and March, providing a flooding season from December to June. Discharge of the rivers that flow from surrounding uplands result in seasonal inundation of the Pantanal (HAMILTON et al. 1996). This study was carried out at a site that includes a stretch of the Miranda River and its smaller tributary, the Vermelho River (19°34'S; 57 °01'W), and a stretch of the Negro River (19°34'S; 56 °09'W) about 60 km east of the Miranda River site.

2.1. Data collection

Activity patterns were described based both on radio telemetry and on camera trapping. Between November 2009 and July 2010, we captured two dominant males and one adult subordinate male (average of body weight 31 ±1.7 kg) from three different groups of giant otters (coding of groups: G2, G10 and G12) in the Miranda and Vermelho Rivers. A funnel-shaped net was used at the den entrance to capture animals, following techniques described by SILVEIRA et al. (2011). The animals were immobilized chemically using a dosage of 2.0 mg/kg of a 1:1 combination of tiletamine and zolazepam (Zoletil®, Virbac, Carros-Cedex, France) and received a complementary dosage of 1.5 mg/kg ketamine hydrochloride 10% (Vetaset®, Fort dodge, Campinas, Brasil) combined with 0.25 mg/kg midazolam (Midapine®). Individuals were tagged with intraperitoneally implanted transmitters (Advanced Telemetry System, Isanti, Minnesota), weighting approximately 42 g (~0. 1% body weight). All the handling and surgical procedures followed the guidelines of the American Society of Mammalogists for the use of wild mammals in research (SIKES et al. 2011), and were authorized under permit no. 12794/4 of the Brazilian Federal Environment Agency (IBAMA).

Tracking of radio-tagged animals was carried out from 05:00 to 19:00 h during 8 to 10 days every month, from November 2009 to June 2010 for the group G2 and from July 2010 to June 2011 for the groups G10 and G12 (making a total of 153 monitored days). The animals were radio-tracked by boat and their location recorded every 30-min. Since they were in the same area, the groups of G10 and G12 were monitored in alternate periods (05:00 to 12:00 h or 12:30 to 19:00 h) in each day. Whenever visual observation was possible, the predominant behavior of the majority of the group was observed and classified by focal group sampling (ALTMAN 1973) as: a) fishing (FS), when the individuals were foraging or eating; b) swimming (SW), when the individuals were seen moving through the area; c) scent-marking at the den (SMD), when the individuals were scent-marking and/or using the latrines near den entrances; d) scent-marking at latrines (SML), when the individuals were scent-marking and/or using a latrine far from the den (i.e., usually >1000 m); e) social interaction (SI), considering all affiliative interactions between members of the same group, such as grooming, cub caring and play; f) in the den (ID), when individuals were in a den; and g) resting outside the den (RC), when individuals rested at sites along the bank. Periods when animals could not be located were not included in the analysis. We also conducted 20 nighttime radio tracking sessions (19:00 to 24:00 h), recording the same behaviors in same monitoring intervals as described above.

Camera traps (Bushnell® Trophy Cam 8MP, Overland Park, KS) were positioned monthly (during a period of 2 to 30 days) at the entrances of active dens and on latrines. We monitored 10 dens and 13 latrines of six groups of giant otters (G2, G3, G9, G10, G12, G13; n = 35 individuals) in the Miranda and Vermelho Rivers in June 2010, from December 2010 to June 2011, and at four dens and one latrine near the den of two giant-otter groups (G18, G19; n = 7 individuals) in the Negro River between June and October 2011 (Fig. 1). The camera traps were programmed to operate 24 h/day with 15 seconds-intervals between photographs and to record the date and time of each shot. The behavior recorded by camera traps was classified as: a) entering the den (EN), when the photographed individual was facing the den, b) exiting the den (EX) when the individual was facing the water, c) scent-marking at the den (SMD) when the individual was scent-marking and/or using the latrines at the den site, and d) scent-marking other latrines (SML) when the individual was scent-marking and/or using latrines more than 1000 m distant from dens (Fig. 2).

2.2. *Data analysis*

As photoperiod in our study area ranged from 10h57min length in winter to 13h19min in summer, we fitted all data in a common standardized diurnal time scale, in which sunrise and sunset were fixed at 06:00 and 18:00 h respectively. Taking into account the actual sunrise and sunset time of the date each photo was taken, we calculated through interpolation a new time for that photograph in the standardized scale. This assured that, a photo taken near the light threshold will always refer to the same standardized time, no matter if it was taken in mid-summer or mid-winter. We used this standardized time in results and discussion. To determine the activity pattern by camera trap method, we considered just the independent records.

Photographs of giant otters showing the same behavior at the same trap station were considered independent only if taken at >30-min intervals. Activity patterns were, then, determined for each method (radio-telemetry and camera trap) as the proportion of each behavior recorded in 1-h intervals throughout the day, based on the standardized record times.

Additionally, considering only the camera trap records, we split the daily cycle in three periods: day (07:00 – 17:00), night (18:30 – 05:30) and crepuscular (05:30 – 07:00 and 17:00 – 18:30), to test for differences in the use of the time. Electivity of each period was tested by adapting the Ivlev Electivity index (IVLEV 1961), which is usually used to quantify an individual or population preference for food types, taking into account the relative availability of food types in the environment and their relative occurrence in the diet of organisms. We calculated “relative use” as the proportion of photo taken in a given period and “relative availability” as the number of hours of that period/24. We accessed the significance of the index by bootstrap resampling of the photographs 1000 times. Resampling was performed with replacement and the same sample size as the original sample.

We have been studying giant otters for eight years at the Miranda River site and for three years at the Negro River. Therefore, most of individuals were recognizable based on their throat and chest markings. Whenever possible, we identified group events from the complete series of photographs as a set of consecutive records of different individuals performing the same movement (in or out of the den) in a short interval of time (<10-min) at a given camera station. Classification of these events required only the conclusion that more than half the group was involved in the activity, and it was not necessary to identify each individual. The chronology of group events was then used to estimate the time the group spent outside the den. In the case of nighttime photographs, we identified individuals that moved in or out of the den to estimate the time that they spent outside, and to determine which individuals scent-marked. This could not be done in the daytime because the intense activity of the animals hindered our attempts to associate specific activities to individuals. All the analyses were performed using R 2.13 software (R Development Core Team).

3. RESULTS

We obtained 2323 behavioral records from telemetry data for the three marked groups (G2, n = 956; G10, n = 801; G12, n = 566) between 05:00 and 19:00 h (Fig. 3). The overall time budget recorded by telemetry was 64% fishing (FS, n =1477), 18% resting in a den (ID, n = 411), 5% swimming (SW, n = 118), 5% scent marking at a den (SMD, n = 110), 4% scent marking at a latrine (SML, n = 96), 3% resting outside the den (RC, n = 81), and 1% social interactions (SI, n = 30). FS was recorded more frequently between 07:00 and 11:00 h and from 14:00 to 16:00 h. Scent-marking events (SMD and SML) were observed throughout the day, with higher peaks at 06:00 h for SMD and 18:00 h for SML. Activity at the den was recorded in higher proportion (more than 40% of the behavior ID) at 05:00 h, before the animals left the den at the beginning of the day and at 18:00 h, generally indicating the moment that animals entered the den at the end of the day, with a lower peak of resting between 11:00 and 14:00 h. Resting outside the den occurred more frequently at noon.

We obtained 1163 photographs (456 independent records) during a total camera trapping effort of 362 camera days. However, our sample refers to 90 daily cycles, for which we had at least one record. Photographs were taken at all the 28 trapping stations, with 17 stations having more than 5 independent records and a single station with up to 84 independent records.

Most of the records were taken during the day (n = 215), however otter activity was concentrated mostly in the crepuscular period (98 records, Ivlev index = 0.26, $P<0.001$), followed by daylight (Ivlev index = 0.06, $P<0.001$), while night period was avoided (143 records, Ivlev index = -0.19, *P*<0.001). Entering the den (EN) was the most common behavior, corresponding to 34% (n= 153) of the records, followed by exiting the den (EX) with 30% (n = 135), scent-marking at the den (SMD) with 26% (n = 119) and scent-marking at latrines (SML) with 11% (n = 49) (Fig 4).

Giant otters were recorded exiting the den mostly in the early morning (06:00 h) and entering the den at the end of the day (16:00 to 19:00 h). There were also peaks of entering and leaving the den between 11:00 and 13:00 h and about two hours after dusk (20:00 – 22:00 h). Peak scent-marking near the den coincided with the beginning of outdoor activity in the morning and preceded den entering at the end of the day. A third peak was synchronous with movements around the den in the early evening. Scent-marking at latrines far from dens occurred almost exclusively during the day, peaking between 11:00 and 12:00 h. Pooling all the behaviors, 80% (n = 114) of nocturnal activity outside the den occurred in the first half of the night (18:30 to 24:00 h).

All but one of the 51 group events identified in the photographs (n = 1163) occurred from 05:00 to 19:00 h. The average time groups spent outside the den during the daytime was 356 min (SD=228). Coincidentally, the only nocturnal group event outside that period occurred at a den of the group G10 during a nocturnal radio tracking session, enabling us to directly observe the cause. The group members were surprised by a jaguar a few meters above the den entrance while trying to enter the den at 18:16 h. The group immediately left the area, moving downstream to a latrine, where they spent approximately 3-h before returning to the den only after 21:00 h.

In 19 nocturnal individual forays that we could confidently monitor with the camera traps, individuals spent a median of 5 min outside the den (varying from 1 to 50 min). In 12 nocturnal scent-marking events (from 28 photographic records) of which we were able to identify the individual, four cases involved dominant females, three cases involved dominant males, three cases of subordinate females, 2 cases of subordinate males and no records of immature otters.

During 20 nights of telemetry monitoring (between December 2010 and June 2011), nocturnal fishing by the group G10 was observed on two occasions. Both events occurred during the high-water season, which extended from February to June. On one of these events, a large fish shoal migrating upriver passed in front of the den. One individual that had remained outside the den at dusk vocalized “coo” and “hum-purr” sequences at the den entrance. The other group members then left the den and fished successfully for about 20 minutes before returning to the den. The second event was at the peak of the high-water season, when fish are usually scattered and difficult to catch, and the group may have taken advantage of the light of the full moon for fishing until about 21:00 h.

4. DISCUSSION

Giant otter activity was more intense during daylight (from 05:00 to 18:00 h), with more animals exiting the den in the early morning and entering at dusk, as observed previously by many authors (DUPLAIX 1980; LAIDLER 1984; SCHWEIZER 1992; CARTER & ROSAS 1997; STAIB 2005). Lower peaks in the den or resting at latrines were recorded during the day. DUPLAIX (1980) observed that resting periods during the day followed fishing sequences and usually lasted about 50 min, but could take up to 1.5-h. Direct observations indicated that fishing was the most frequent activity recorded from 06:00 to 18:00 h, with peaks in the morning and mid-afternoon, as observed in Peru (LAIDLER 1984). The resting peak at noon has been recorded previously in the Pantanal (SCHWEIZER 1992) and among captive animals (CARTER & ROSAS 1997).

Scent-marking was more intense during the daytime, with the highest peak in den scent-marking recorded by both methods in the early morning and a lower peak at dusk. SCHWEIZER

(1992) stated that groups of giant otters in the Negro River spent more time on territory demarcation in the early morning. Like other otter species (MELQUIST & HORNOCKER 1983; KRUUK 2006), giant otters scent-mark frequently throughout the day during foraging sessions. Latrine scent-marking was recorded almost exclusively during the day, with higher peaks at noon and on the end of the day. In Bolivia, camera traps positioned at giant otter latrines recorded scent-marking events from 06:00 to 18:00 h, with higher peaks from 08:00 to 12:00 h and from 14:00 to 18:00 h (PICKLES et al. 2011).

Although several authors have spent many nights monitoring giant otters, no nocturnal activity had previously been recorded (DUPLAIX 1980; SCHWEIZER 1992). In our study, 31% of the activities recorded by camera traps corresponded to nocturnal activity at dens and latrines, suggesting that the species is not exclusively diurnal, although groups seemed to avoid the nocturnal period. Scent-marking activity at night may be associated with the passage of food through the digestive tract, which takes about 3-h (CARTER et al. 1999), since the peak of nighttime exiting the den was about 3-h after the peak of entering the den at dusk. Defecation by one individual may trigger a similar response in other members of the group, as has been observed in *Lontra canadensis* (MELQUIST & HORNOCKER 1983), but usually only one or two giant otters left the den at any one time during the night.

Scent-marking is an important mechanism of communication among otters (ROSTAIN et al. 2004; KRUUK 2006; KEAN et al. 2011). The scent-marking rate of giant otters plays an important role in intraspecific defense and is related to the sexual and social status of group members (LEUCHTENBERGER & MOURÃO 2009), which can lead to the reproductive suppression of subordinate individuals. Therefore, scent-marking at night may be related with territorial defense and may also be a strategy used by individuals to provide information about their reproductive status and improve their fitness. However, we were unable to identify sufficient individuals in nighttime photographs to fully support this explanation. In any case, it is notable that immature otters were not recorded at night activities.

Activity patterns may be affected by predation risk (DALY et al. 1992). The presence of a jaguar apparently prevented one group from entering a den and provoked a shift of about three hours in their denning time. Otters can also change their activity because of individual strategies (RALLS & SINIFF 1990), mainly due to prey availability (MELQUIST & HORNOCKER 1983; GARCIA DE LEANIZ et al. 2006; KRUUK 2006). Giant otters are visually oriented (CARTER & ROSAS 1997) and usually need daylight to find fishes that are motionless and/or hidden under banks. Although our night observations were limited to the high-water season, the nocturnal fishing events reported in this study may be due the high availability of prey provided by a fish shoal, and food scarcity during the high water season. The “coo” and “hum-purr” sounds vocalized before a fishing event seem to have been used to advise other members of a fishing opportunity. DUPLAIX (1980) classified these sounds as close-contact vocalizations, which are used before departure from the resting site or when the individuals are reunited after a brief absence during fishing sequences.

The results reported here demonstrate that giant otters are not strictly diurnal, and further studies should be undertaken to determine whether the same behaviors occur in other populations.

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6. REFERENCES

ASCHOFF J. 1966. Circadian activity pattern with two peaks. *Ecology* 47:657-662.

CARTER S.K. & ROSAS F.C.W. 1997. Biology and conservation of the giant otter *Pteronura brasiliensis*. *Mammal Review* 27:1-26.

CARTER S.K., ROSAS F.C.W., COOPER A.B. & CORDEIRO-DUARTE A.C. 1999. Consumption rate, food preferences and transit time of captive giant otter *Pteronura brasiliensis*: Implications for the study of wild populations. *Aquatic Mammals* 25 (2):79-90.

DUPLAIX N. 1980. Observations on the ecology and behavior of the giant river otter *Pteronura brasiliensis* in Suriname. *Revue Ecologique (Terre Vie)* 34:496-620.

DALY M., BEHRENDS P.R., WILSON M.I. & JACOBS L.F. 1992. Behavioral modulation of predation risk: moonlight avoidance and crepuscular compensation in a nocturnal desert rodent, *Dipodomys merriami*. *Animal Behaviour* 44:1-9.

GARCIA DE LEANIZ C., FORMAN D.W., DAVIES S. & THOMSON A. 2006. Non-intrusive monitoring of otters (*Lutra lutra*) using infrared technology. *Journal of Zoology* 270:577-584.

GERELL R. 1969. Activity patterns of the mink *Mustela vison* Schreber in southern Sweden. *Oikos* 20:451-460.

HAMILTON S.K., SIPPEL S.J. & MELACK J.M. 1996. Inundation patterns in the Pantanal wetland of South America determined from passive microwave remote sensing. *Archiv für Hydrobiologie* 137:1-23.

IVLEV V.S. 1961. Experimental ecology of the feeding of fishes. *Yale University Press, New Haven, Connecticut, USA.*

KEAN E.F., MÜLLER C.T. & CHADWICK E.A. 2011. Otter scent signals age, sex, and reproductive status. *Chemical Senses* 36:555-564.

KRUUK H. 2006. Otters: Ecology, behavior and conservation. *Oxford University Press Inc., New York.*

LAIDLER L. 1984. The behavioral ecology of the giant otter in Guyana. *Master dissertation, University of Cambridge.*

LEUCHTENBERGER C. & MOURÃO G. 2009. Scent-marking of giant otter in the Southern Pantanal, Brazil. *Ethology* 115:210-216.

LIM N.T.L. & NG P.K.L. 2008. Home range, activity cycle and natal den usage of a female Sunda pangolin *Manis javanica* (Mammalia: Pholidota) in Singapore. *Endangered Species Research* 4:233-240.

LODE T. 1995. Activity pattern of polectas *Mustela putorius* L. in relation to food habits and prey activity. *Ethology* 100:295-308.

MELQUIST W. E. & HORNOCKER M.G. 1983. Ecology of river otters in west Central Idaho. *Wildlife Monographs* 83:1-60.

PICKLES R., ZAMBRANA V., JORDAN B., HOFFMANN-HEAP I., SALINAS A., GROOMBRIDGE J. & DAMME P.V. 2011. An evalutaion of the utility of camera traps in monitoring giant otter populations. *IUCN Otter Specialist Group Bulletin* 28:39-45.

RALLS K. & SINIFF D.B. 1990. Time budget and activity patterns in California sea otters. *The Journal of Wildlife Management* 54:251-259.

ROSAS F.C.W., ZUANON J.A.S. & CARTER S.K. 1999. Feeding ecology of the giant otter, *Pteronura brasiliensis*. *Biotropica* 31:502-506.

ROSTAIN R.R., BEN-DAVID M., GROVES P. & RANDALL J.A. 2004. Why do river otters scent-mark? An experimental test of several hypotheses. *Animal Behaviour* 68:703-711.

SCHWEIZER J. 1992. Ariranhas no Pantanal: Ecologia e comportamento de *Pteronura brasiliensis*. *Edibran-Editora Brasil Natureza Ltda, Curitiba, Paraná*.

SERVHEEN C. & KLAVER R. 1983. Grizzly bear dens and denning activity in the Mission and Rattlesnake Mountains, Montana. *Bears: Their Biology and Management* 5:201-207.

SILVEIRA L., FURTADO M.M., ROSAS F.C.W., SILVA L.C., CABRAL M.M.M., TORRES N.M., SOLLMANN R., KOUBA A. & JÁCOMO A.T.A**.** 2011. Tagging giant otters (*Pteronura brasiliensis*) (Carnivora, Mustelidae) for radio-telemetry studies. *Aquatic Mammals* 37:208-212.

SIKES R.S., GANNON W.L. & THE ANIMAL CARE AND USE COMMITTEE OF THE AMERICAN SOCIETY OF MAMMALOGISTS. 2011. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *Journal of Mammalogy* 92:235-253.

STAIB E. 2005. Eco-Etología del Lobo de Río (*Pteronura brasiliensis*) en el Sureste del Perú. *PhD Tesis*. *Sociedad Zoológica de Francfort Perú.*

STEVENS S.S. & SERFASS T.L. 2008. Visitation patterns and behavior of nearctic river otters (*Lontra canadensis*) at latrines. *Northeastern Naturalist* 15:1-12.

UTRERAS V. & PINOS L. 2003. Camera trap use for studying giant otters (*Pteronura brasiliensis*) in the Yasuní Biosphere Reserve, Ecuadorian Amazon. *IUCN Otter Specialist Group Bulletin* 20:12-13.

ZIELINSKI W.J. 1988. The influence of daily variation in foraging cost on the activity of small carnivores. *Animal Behaviour* 36:239-249.

FIGURE CAPTIONS

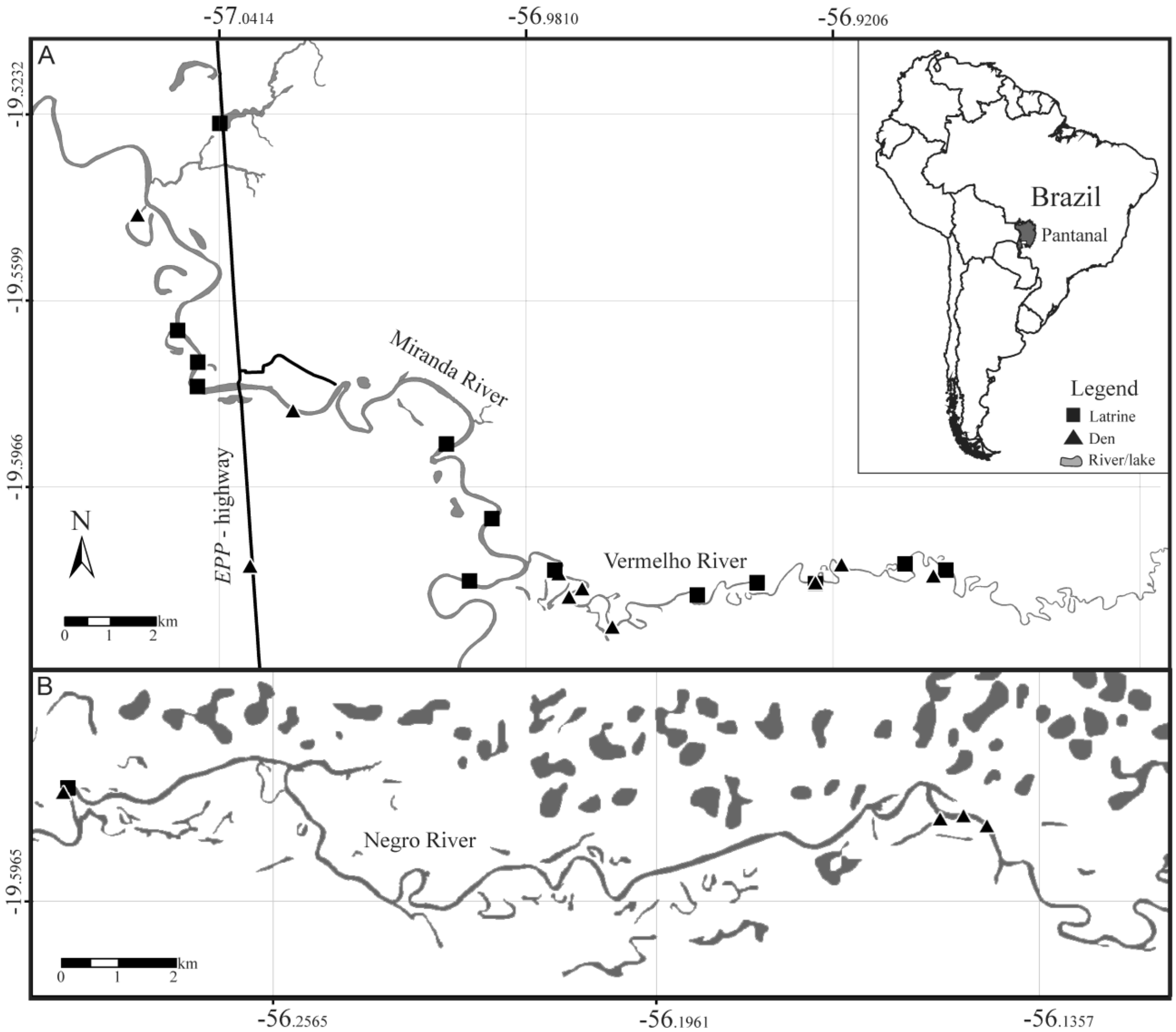

Fig. 1. — Map of the study area showing the location of camera traps at dens (triangles) and latrines (squares) of groups of giant otters on the Miranda and Vermelho Rivers (a) and on the Negro River (b) in the southern Brazilian Pantanal.

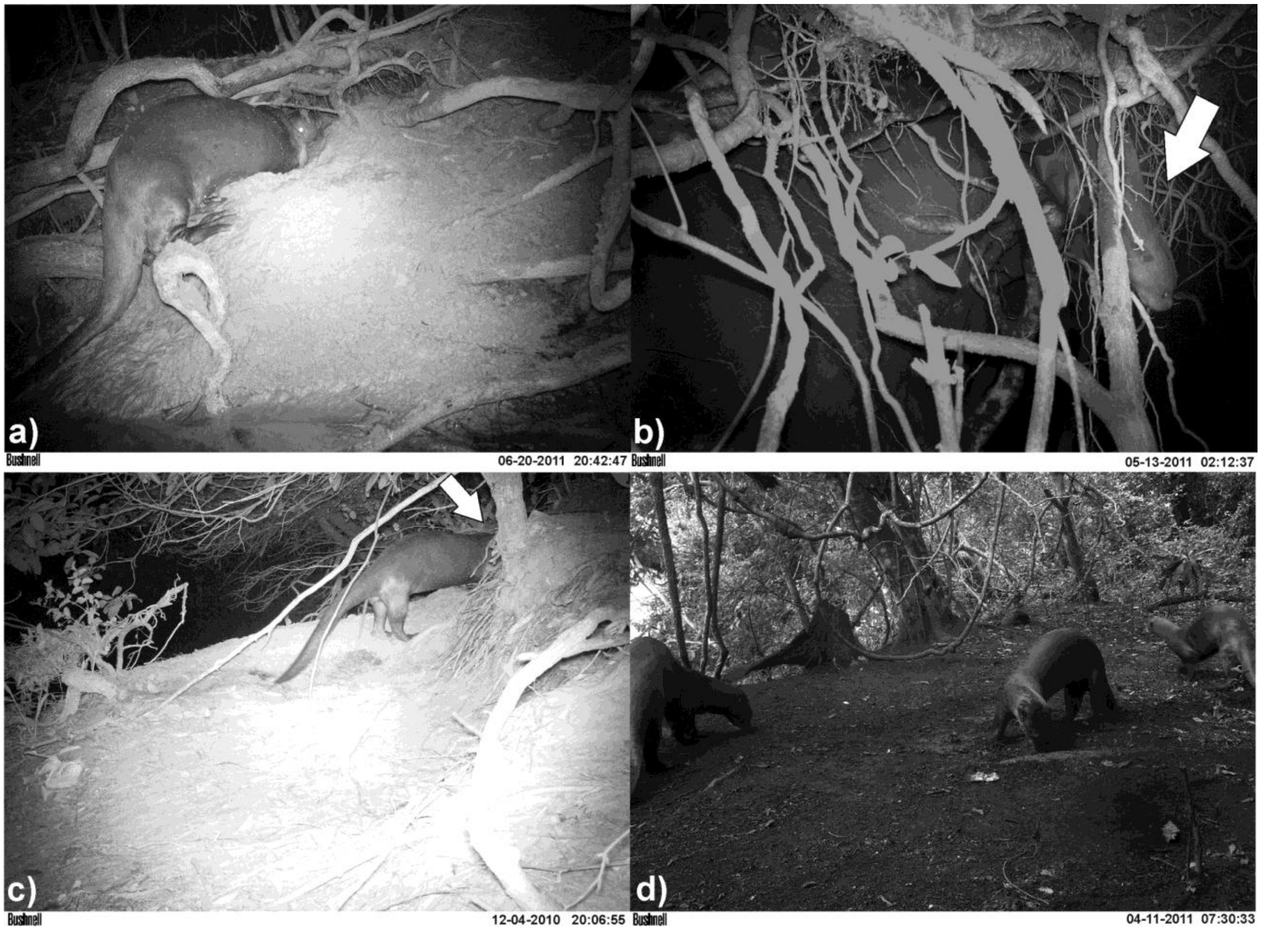

Fig. 2. — Giant otter activities recorded by camera traps positioned at dens and latrines in the Miranda, Vermelho and Negro Rivers, in the southern Brazilian Pantanal. a) (EN) entering the den, b) (EX) exiting the den (see arrow), c) (SMD) scent-marking and/or using the latrines at the den (arrow), d) (SML) scent-marking and/or latrine use at latrines distant from the den.

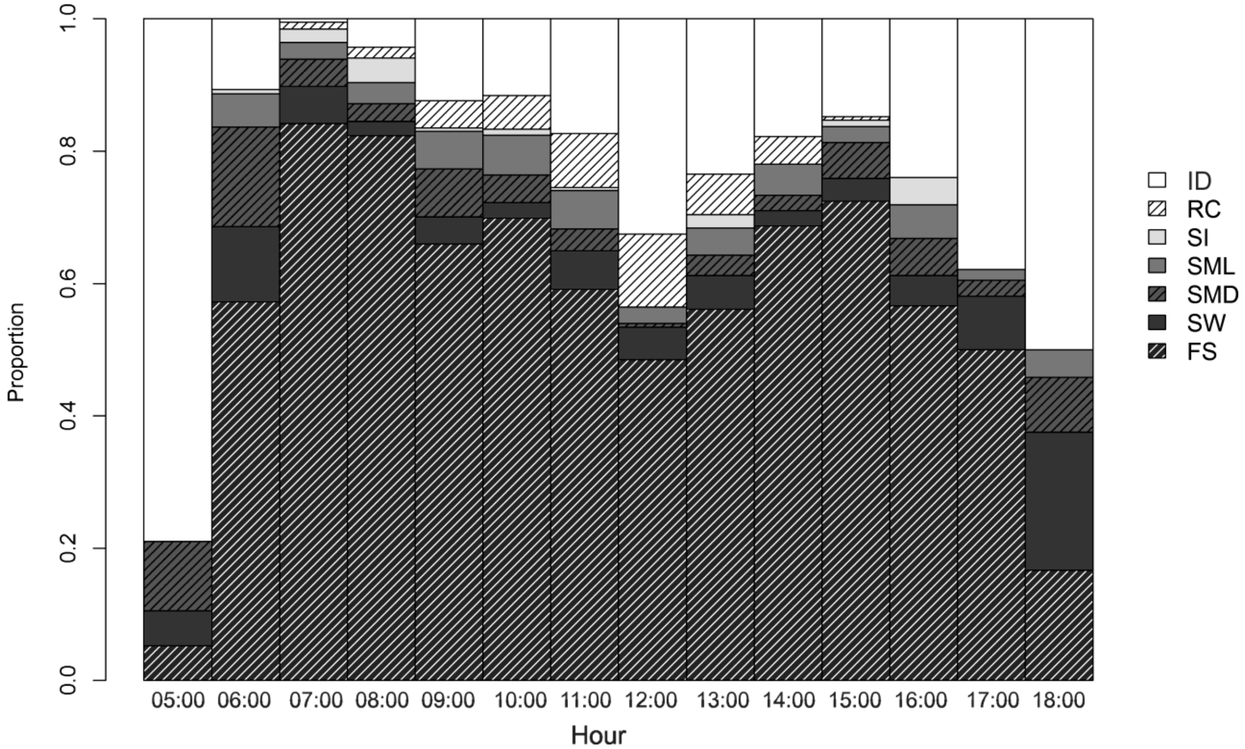

Fig. 3. — Diurnal (05:00 – 19:00 h) activity patterns of three groups of giant otters monitored by radio telemetry in the Miranda and Vermelho Rivers, southern Brazilian Pantanal, between November 2009 and June 2011. The numbers above each bar indicate the sample size for that hourly period. ID – in the den; RC – resting outside the den; SI – social interactions; SML – scent-marking and/or latrine use at latrines distant from the den; SMD – scent-marking and/or latrine use at the den; SW – swimming; FS – fishing.

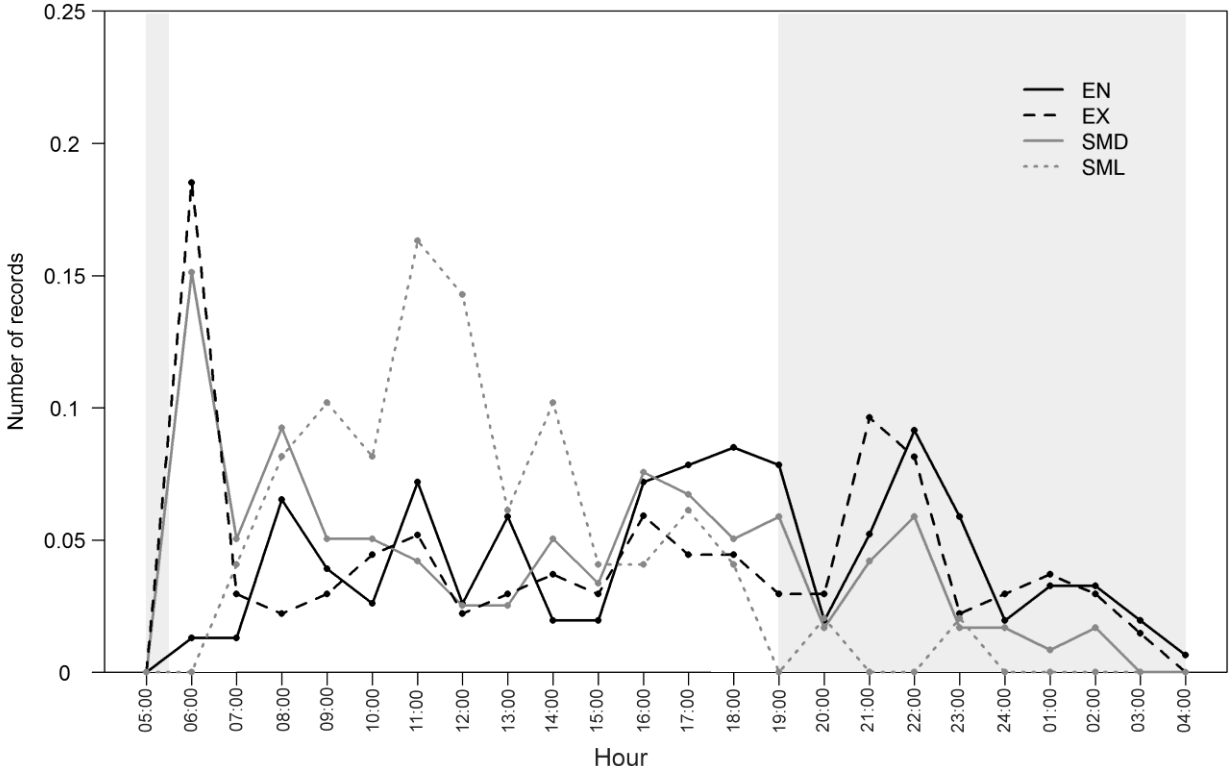

Fig. 4. — Patterns of den use and scent-marking of giant otters recorded by camera traps positioned at dens and latrines (June 2010; December 2010 to October 2011) in the Miranda, Vermelho and Negro rivers, southern Brazilian Pantanal. The proportions are relative to the total number of records for each behaviour (n = 456). EN – entering at den, EX – exiting from den, SMD – scent-marking and/or latrine use at the den, SML – scent-marking and/or latrine use at latrines distant from the den. The light gray area in the graph indicates the crepuscular period period and the dark gray area represents the nighttime darkness.

CAPÍTULO 2

Leuchtenberger, C; Oliveira-Santos, L.G.; Magnusson, W. & Mourão, G. Space use by giant otter groups in the Brazilian Pantanal**.** *Journal of Mammalogy* (no prelo).

Space use by giant otter groups in the Brazilian Pantanal

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Giant otters (*Pteronura brasiliensis)* are social and feed mainly on fish. Information on the spatial organization of giant otters is limited to dry-season observations. However, groups may abandon their territories to follow spawning fish into flooded areas during the wet season. Therefore, we studied the spatial ecology of giant otter groups during dry and wet seasons in the Vermelho and Miranda Rivers in the Brazilian Pantanal. We monitored 10 giant otter groups monthly from June 2009 to June 2011. Locations of dens, campsites and visual observations of the groups were recorded. Three of the groups were monitored monthly by radio-telemetry between November 2009 and June 2011 during daylight hours and their locations were recorded at 30 minute intervals. We estimated home-range size for all groups with the following methods: (1) linear river length, considering the extreme locations of each group, and (2) fixed kernel. For the radio-tracked groups, we also used (3) the *k*-LoCoh method. Spatial fidelity was calculated as the percentage of home range and core area overlapped between seasons. Habitat selection of giant otter groups was analyzed considering the landscape composition during the dry and wet seasons. During the dry season, the home range of giant otter groups estimated by linear and 95% fixed-kernel methods varied, respectively, from 1.8 to 22.9 km and from 1.1 to 3.2 km^2. During the wet season, these estimates varied, respectively, from 14.8 to 31.7 km and from 1 to 3.9 km^2. Based on *k*-LoCoh (98%) method, home range sizes during the wet season (3.6 - 7.9 km^2) were 4 to 59 times larger than during the dry season (0.1 - 2.3 km^2). Home-range fidelity between seasons varied among giant otter groups from 0% to 87%, and 2 radio-tagged groups shifted to flooded areas during the wet seasons. Giant otter groups were selective in relation to the composition of the landscape available during the dry seasons, when the river was used more intensively than other landscape features. However, they seemed to be less selective in positioning activity ranges during the wet season. During this season, giant otters were frequently observed fishing in the areas adjacent to the river, such as flooded forest, grassland and swamps.

Key-words: home range, *Pteronura brasiliensis*, selection of landscape features, site fidelity

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Animals adopt different strategies to deal with spatial and temporal heterogeneity of environmental features. Most species constrain their activities to an area on the landscape defined as a home range, which comprises areas used in diverse ways for survival, reproduction and other activities that maximize fitness (Krebs & Davies 1997; Powell 2000). Some core areas are used more intensely within the boundaries of the home range and commonly contain refuges and more defendable food sources (Kernohan et al. 2001; Samuel et al. 1985). The maintenance of the home range in space and time is favored by a cognitive map (Spencer 2012) that provides site familiarity, which enhances the owners' fitness, increasing their ability to forage and to move rapidly and safely in the area (Stamps 1995).

Some landscape features are used more by a species than their proportional availability in the environment (Aebischer et al. 1993; Johnson 1980). However, under highly seasonal fluctuations, changes in habitat and resource availability may induce a shift in the animal's spatial organization and habitat use through different seasons (Arthur et al. 1996). Availability and abundance of food resources, together with the metabolic needs of each species, seem to be the most important variables determining the home range size and habitat selection of carnivores (e.g., Dillon & Kelly 2008; Macdonald 1983; Valenzuela & Ceballos 2000). Space use by semi-aquatic mammals is strongly affected by the availability of water bodies and prey, and such relationships have been reported for several species of otters (Blundell et al. 2000; Garcia de Leaniz et al. 2006; Kruuk 2006; Melquist and Hornocker 1983). In places with well-defined hydrological cycles, flooding increases the amount of water in the landscape and may result in the dispersal of fish assemblages across vast flooded areas (Wantzen et al. 2002; Winemiller & Jepsen 1998), which may attract fish predators and induce predictable movement patterns of the piscivores.

Giant otters (*Pteronura brasiliensis*) feed mainly on fish, and information on their spatial ecology is limited to direct observations during the dry season, when groups maintain linear territories along water bodies (Duplaix 1980; Evangelista & Rosas 2011a; Laidler 1984; Leuchtenberger & Mourão 2008; Ribas 2004; Schweizer 1992; Tomas et al. 2000; Utreras et al. 2005). Groups build dens and campsites with communal latrines throughout their home ranges that are used for resting, scent-marking and rearing cubs (Duplaix 1980; Leuchtenberger & Mourão 2009; Lima et al. 2012). During the rainy season, giant otters seem to relinquish their territories to follow spawning fish into the flooded forest and swamps, and to search for emergent sites for building dens and campsites (Duplaix 1980). Seasonal shifts in movement patterns can increase home-range sizes of giant otter groups, which have been estimated to be 4 to 13 times larger during the rainy season (Utreras et al. 2005). However, in the absence of fluctuating water levels, giant otter groups seem to maintain their territories throughout the year (Laidler 1984).

The Pantanal is an extensive wetland located near the centre of South America and it is subject to a strong annual flood pulse, which is considered to be the most important ecological phenomenon for the maintenance of local biodiversity (Alho 2008). Giant otters are locally abundant and distributed throughout this region (Leuchtenberger & Mourão 2008; Tomas et al. 2000). In this paper, we examine home-range size, home-range fidelity and habitat selection of giant otters in the Brazilian Pantanal based on direct observations and radio-telemetry, with the aim of answering the following questions: Is home-range size during the wet season larger than in the dry season? Do giant otter groups show home-range fidelity within and between seasons? Do habitat-selection patterns differ between seasons?

MATERIAL AND METHODS

From June 2009 to June 2011, we monitored 10 giant otter groups in the Vermelho River (19°34'S; 57°01'W) and a stretch of the Miranda River (19°36'S, 57°00'W), totaling 119 linear km of river, in the southern Pantanal of Brazil. The annual precipitation in the region is about 1,200 mm, with most of the rain falling between November and March (Hamilton et al. 1996). Due to the low declivity and seasonal inundation, almost 80% of the plain undergoes transition from terrestrial to aquatic habitat during the rainy season (Alho 2008). We measured the level of the Miranda River every day at a fixed station (19°34'S, 57°01'W), and it varied from 126 to 481 cm during the study period. Flooding tended to be abrupt, and the transition from wet to dry occurred within a few weeks. Based on the river-level measurements, we recognized 2 dry seasons (June-December 2009 and July 2010-January 2011) and 2 wet seasons (January-June 2010 and February-June 2011) during the study.

We monitored giant otter groups by boat, using a video camera (Canon HF-200) to record individual natural marks on the throat of otters and their behaviors. This allowed us to identify the sex, position in the group hierarchy, group composition and other details about the individuals. The location of individuals, groups, dens, latrines and other vestiges were registered by a global positioning system receptor (Garmin Etrex®, Inc., Olathe, KS).

Between November 2009 and July 2010, we undertook three 10-day field trips to capture and implant radio-transmitters in individuals from different groups of giant otters. In each campaign, we first searched for active dens suitable for setting traps (i.e. dens with one or few entrances relatively free of entanglements of roots and vegetation). We blocked the den entrance with a funnel-shaped net late at night, as described by Silveira et al. (2011), and waited in the vicinity of the den to capture the individuals in the early morning. We captured 2 dominant males (from groups G2 and G12) and 1 adult subordinate male (group G10). The mean weight of captured individuals was 30.97 kg (SD=1.75) and the mean total body length of 178 cm (SD=6.25).

We chemically immobilized the animals after capture using a dosage of 2.0 mg/kg of a combination of tiletamine and zolazepam (Zoletil$^{®}$, Virbac, Carros-Cedex, France) and applied a complementary dosage of 1.5 mg/kg ketamine hydrochloride 10% (Vetaset$^{®}$, Fort Dodge, Campinas, Brasil) combined with 0.25 mg/kg midazolam (Midapine$^{®}$). Radios were implanted intraperitoneally by a registered veterinarian. During surgery, we applied 0.5 ml of intramuscular penicillin (Pentabiótico Veterinário®, Fort Dodge Animal Health, Campinas, Brazil) and a subcutaneous dosage of 2mg/kg of anti-inflammatory/analgesic (Ketoprofen 1%, Merial Animal Health, Paulínea, Brazil). We examined each captured individual for general body condition, photographed their throat markings and took body measurements. The radio transmitter (M1245B, Advanced Telemetry System®, Isanti, Minnesota), which weighed 42 g (~0.1% of body weight). All handling and surgery procedures followed the guidelines of the American Society of Mammalogists for the use of wild mammals in research (Sikes et al. 2011), and were authorized under license No. 12794/4 of the Brazilian Federal Environment Agency (IBAMA). We released the radio-tagged giant otters after they recovered from the anesthesia, at the place of capture or near their group.

We radio-tracked animals by boat or walking on the bank with a Yagi antenna (RA-17, Telonics®, Mesa, Arizona) attached to a 2.5m pole and connected to a TR4-receiver (Telonics®, Mesa, Arizona). One group (G2) was monitored from November 2009 to June 2010, and 2 groups (G10 and G12) from July 2010 to June 2011, totaling 153 days of monitoring. Radio-tagged animals were monitored from 05:00 h, when almost all members of the group had left the den, to 19:00 h or when the whole group had entered the den, during 8-10 consecutive days every month. On two occasions, when the tagged animals were not found for two consecutive months, we undertook aerial surveys with a fixed-wing aircraft (CESSNA-182) to locate them. Once located from the ground, we followed the animals as silently as possible, keeping a distance that apparently did not disturb their behavior. We recorded locations with the GPS every 30 min when the group could be seen until we lost the radio signal. Since groups G10 and G12 had territories near each other, we monitored these groups in alternate periods (05:00-12:00 or 12:30-19:00). We undertook nocturnal monitoring irregularly, but these data were not considered for home range and habitat-use analyses, as movements were very limited at night. We used only locations recorded more than 10 days after capture in the analyses to avoid abnormal behavior due to the effects of capture and handling.

Home range. – Removal of sequential data to increase independence of locations can reduce the biological meaning of the information (Blundell et al. 2001; De Solla et al. 1999; Reynolds & Laundre 1990; Rooney et al. 1998). Also, giant otters cover much of their home range every day, so observations taken over 6-13 hs per day tend not to be clustered in a limited part of the home range. Therefore, we considered all sequential locations (*n* = 2,321) acquired by radio telemetry for home range analysis, as well as some visual locations of the group G2 (*n* = 38) made before the capture event.

To allow comparison with other studies, we estimated home range for all groups as linear river length (RL) within the extreme locations of each group, which is commonly used to estimate giant otter linear home range (Evangelista & Rosas 2011a), and the fixed-kernel estimator with *ad hoc* estimation of the *h* value. For the radio-tracked groups, for which we obtained more locations, we also used the *k*-LoCoh method (Getz & Wilmers, 2004). Because groups sometimes shifted their areas from one season to another (Leuchtenberger & Mourão 2008), we stratified the home-range estimates by seasons in cases where we had more than 20 locations for a given group in a given season. All home-range analyses were undertaken in the R software (version 2.13, The R Foundation for Statistical Computing), using the packages ade4 (Thioulouse et al. 1997), adehabitat and adehabitatHR (Callenge 2006), gpclib, maptools (Lewin-Koh et al. 2009), rgdal (Keitt et al. 2010), rgeos (Renard & Bez 2005) and shapefiles (Stabler 2003). We calculated 98% and 95% isopleths for *k*-LoCoh analyses and 95% isopleths for the kernel estimator of total home-range size and the 50% isopleths to delimit core areas.

We measured the linear extension of river (RL) and/or other water bodies, such as ponds, streams or flooded areas along roads, within the extreme locations of each monitored group using the GPS Track Maker software (Geo Studio Technology Ltda., Brasil). For the kernel analysis, we tried to use the Least-Square Cross-Validation (LSCV) method, but this analysis did not converge. Therefore, we chose the h-value of $h = 80$ and $h = 100$, respectively, for the dry and wet seasons analyses of all groups, as they resulted in kernel-contour shapes that visually better accommodated the group locations.

To evaluate if we had enough locations to determine the home-range areas of radio-tracked giant otter groups, we plotted the cumulative estimated LoCoh 100% areas chronologically. For this analysis, we fixed the number of nearest-neighbor locations (*k)* to five. However, to estimate the appropriate *k* for calculation of the group's home range area, we followed the procedure described in Ryan et al. (2006). That is, we plotted the home-range areas based on 100% of locations, calculated with *k* values varying from 2 to 30 (100% isopleths) for each group. The asymptote of the 3 radio-tagged groups was estimated to be approximated at $k = 16$, which was the value used for the *k*-LoCoh analyses.

We overlapped the home ranges and core areas (estimated with the kernel and LoCoh methods) of groups that were monitored in consecutive seasons to estimate the percentage of area fidelity. These were estimated with ArcMap 10.0 software (Environmental Systems Research

Institute, Inc., Redlands, California), using the clip function. We also calculated the daily speed of each radio-tracked group by season, dividing the daily mean of the Euclidean distance traveled among consecutive locations by the respective mean of time interval.

Selection of landscape features. — Here we use habitat to mean a category of physical environment that occurs in a circumscribed area that is available to an organism or group of organisms. In this sense, habitats include areas that may never be used by the organism under study. Used in this way, habitats are not necessarily related to particular organisms, and do not exist as inherent natural objects in the landscape, but are merely convenient categories that humans use to get a preliminary understanding of the spatial relationships of organisms to their environment. We created 3 landscape-category maps, representing 3 seasons (dry, wet 2010 and wet 2011), due to the differences in the flood levels of the wet seasons during the study period. We classified Landsat (TM5) satellite images within seasons using the Kmedia method in the Spring v.4.3.3 (DPI/Inpe) software. We digitalized an image taken during the dry season of 2009 in Google Earth and classified it in ArcMap 10.0 software. The wet-season images were overlapped on this dry-season image, recovering some landscape-unit types that could not be classified automatically. We used six landscape-unit categories: (1) river; (2) pond (comprising permanent and temporary freshwater ponds, and artificial ponds created during the construction of roads or water reservoirs used for cattle); (3) swamp (water bodies that act as a transition between the aquatic and terrestrial, normally found at the edge of ponds, streams and rivers, and that are dominated by grasses sometimes including isolated trees and shrubs); (4) seasonally flooded grassland (seasonally flooded plains, including the grasslands); (5) forest (riparian forest, semi-deciduous forest and/or woodland savanna); (6) grassland (non-flooded matrix of grasses and herbs, we also included in this class roads and a few riparian human communities that were established in areas that originally had this vegetation cover).

We analyzed landscape-category selection of giant otter groups using a log-ratio compositional analysis (Aebisher et al. 1993) with 2,000 permutations in the R 2.13 software, using the packages adehabitat (Callenge 2006), maptools (Lewin-Koh et al. 2009), raster (Hijmans & van Etten 2010), rgdal (Keitt et al. 2010), rgeos (Renard & Bez 2005) and shapefiles (Stabler 2003). We undertook landscape-category selection analysis for eight groups (G1-G4, G8-G12) within the second and third levels proposed by Johnson (1980), which are the home-range area selected by each group in the study area, and space use (locations) of the groups within their home ranges. A buffer of 2 km was incorporated around each location of giant otters during the monitoring period in the study area (Blundell et al. 2001) using ArcMap 10.0 software. This buffer range was considered the study area for compositional analysis within home ranges. For home range availability, we used the fixed-kernel contours with *ad hoc* estimation of the *h* values. We undertook eigen analysis of selection ratio as described by Callenge & Duffor (2006), which assigns scores to each giant otter group and habitat, resulting in a measure of habitat selection for each group. We counted the number of dens and campsites built by giant otter groups in each landscape feature to analyze the proportion of refuge and site locations in each habitat.

RESULTS

From June 2009 to June 2011 (*n* = 188 days), we visually monitored 10 giant otter groups (*n* = 361 locations), totaling 77 individuals in groups (20 females, 26 males and 31 indeterminate) with an average of six individuals per group (varying from 2 to 15, Tab. 1). Three giant otter males (2 dominant and 1 subordinate) of different groups (G2, G12 and G10) were radio-tracked from November 2009 to June 2011, resulting in 2,321 locations (591-937 locations per group) in 151 days of monitoring (69-81 days per group). The relationship between the number of locations and the cumulative home range presented a punctuated equilibrium, approaching multiple asymptotes with different sample size for each group (Fig. 1). This pattern may be explained by the shift of home range areas during the wet season, associated with territorial expansion of the groups within the season.

Home range. – The linear river extent of home range of the 8 groups monitored during both dry seasons ranged from 1.8 to 22.9 km (Tab. 2). During the wet seasons, the linear home ranges for five groups varied from 14.8 to 31.7 km. Based on the 95% fixed-kernel method, during the dry season, the home-range size of 8 groups varied from 0.5 to 3.2 km^2 (Tab. 1), while the home-range sizes of the five groups monitored during the wet season varied from 1.0 to 12.0 km^2. However, these values may be underestimated due to differences in sampling effort and should be treated with caution. The 98% *k*-LoCoh home-range sizes (Fig. 2) for the radio-tagged groups G2, G10 and G12 during the dry season were, respectively, 1.0, 2.3 and 0.1 km^2, while during the wet season they were 3.9, 7.9 and 3.6 km^2, respectively (Tab. 1), which represents an increase of 4 to 59 times in home-range size during the wet season.

The 3 radio-tagged groups reared cubs during the monitoring period. Group G2 had 3 cubs during the wet season of 2010 (born in March), while the groups G10 and G12 had, respectively, 6 and 2 cubs during the dry season of 2010 (born in September and August). Groups G10 and G12 had larger core areas during the wet season (*k*-LoCoh 50% = 0.5 and 0.01 km^2) than during the dry season, but group G2 reduced its core area by about 10 times from 0.03 to 0.003 km^2 between the dry season and the following wet season (Tab. 1). The daily speed of movement followed the same pattern, since during the wet season the mean daily speeds of groups G2, G10 and G12 were respectively, 0.5 (0.03-1.9) km/h, 1.3 (0-4.7) km/h and 0.8 (0.3-1.7) km/h, while during the dry season these values were 0.9 (0-3) km/h, 0.9 (0.04-4.6) km/h and 0.4 (0.1-0.5) km/h.

It was not feasible to monitor all groups during the wet season. Therefore, we estimated home-range fidelity only for the radio-tagged groups and 2 other groups (G1 and G3). Home-range overlap varied from 0% to 87% between seasons (Tab. 1). The radio-tagged groups G2 and G10 used 78% and 87%, respectively, of their dry-season home ranges (*k*-LoCoh 98%) during the consecutive wet season. The area occupied during the wet season of 2011 by group G12 did not overlap its home range in the previous dry season of 2010. Groups G2 and G12 both dispersed to flooded plains at the beginning of the wet season, abandoning the home ranges used during the previous dry season until the middle of the wet season. These groups used temporary streams and constructed dens and campsites on the banks of artificial ponds and on the roadside of the *Estrada Parque Pantanal* (EPP). The EPP is a dirt road with 1-2 m elevation that crosses a section of the Southern Pantanal. From March to April 2011, the water level was at its highest and almost all river banks in the study area were submerged. During this time, groups G10 and G12 broke branches of emerged shrubs to construct clumsy nests, which the animals used to rest and defecate. The radio-tagged groups were not neighbors during the study. Therefore, none of them overlapped the home range areas of other radio-tagged groups in the same season. Groups G2 and G10 partially overlapped their own core areas (*k*-LoCoh 50%) in consecutive wet and dry seasons by 17% and 13%, respectively.

Selection of landscape features. – During the wet seasons, groups did not select any of the landscape categories to establish home ranges ($\Lambda = 0.05$, $P = 0.121$) or select landscape elements within the home ranges ($\Lambda = 0.059$, $P = 0.13$). During the dry season, selection for landscape features to establish home ranges differed significantly from random (Λ = 0.007, *P* = 0.017). The ranking matrix ordered the habitat types as river = forest = swamp = ponds > grassland (Tab. 3A). Changes in use of landscape features between seasons seemed to differ among groups. During the wet seasons, group G1 continued using the river more intensively than other landscape elements, while group G12 selected seasonally flooded grassland and grassland habitats. During dry season, group G12 selected ponds, whereas the other groups selected the river and forest habitats (Fig. 3). Seasonally flooded grassland occurred within only one of the home ranges of the eight groups studied during the dry seasons. Therefore, we excluded this landscape feature from the analyses related to this season.

During the dry season, giant otters groups did not select landscape elements within the home ranges (Λ = 0.186, *P* = 0.07), but the low probability for the null hypothesis indicates a likely type-II error. The ranking matrix of landscape-element selection suggests that the river was proportionally more used than expected from availability relative to the other landscape elements (Tab. 3B). Forest was used mainly to build dens and campsites, and 83% of dens (*n* = 156) and 77 % of campsites (*n* = 92) were located in riparian forest (Tab. 4).

DISCUSSION

Home range. – Despite the increasing knowledge of the ecology of giant otters since the reference study by Duplaix (1980), data on the spatial ecology of the species has been restricted to observations made during the dry season, and most of these observations were reported as linear home ranges. Here we provide two-dimensional as well as linear estimates of home ranges for giant otter groups in an area of the southern Pantanal, in both dry and wet seasons. During the dry seasons, the linear home ranges varied from 1.8 to 22.9 km, with a median of 13.7 km and were of same magnitude as the linear home ranges for giant otters inhabiting areas in Guyana and the Amazon (Duplaix 1980; Evangelista & Rosas 2011a). Laidler (1984) suggested a home range of 32 km of creek or 20 km^2 of a lake in Guyana, based on the assumption that the groups cyclically move among different hunting places. However, such cyclic movements were not observed in our study site (Leuchtenberger & Mourão 2008) or elsewhere (Duplaix 1980; Evangelista & Rosas 2011a; Staib 2005). Using the two-dimensional locations of our radio-tagged groups, the home-range estimates for the dry season ranged from 0.1 to 2.3 km^2 (LoCoh 98%), which is similar to the two-dimensional home ranges reported for giant otters in areas of the Amazon (0.6–1.1 km^2, Staib 2005; and 0.5–2.8 km^2, Utreras et al. 2005).

Site fidelity of radio-tagged groups between seasons varied from 0% to 87% of overlapping. During the wet season, 2 of the 3 radio-tagged groups left the area they used during the dry season partially or entirely to move into the flooded plains. Seasonal shifts in home-range size have been observed for many carnivores (Curtis & Zaramody 1998; Dillon & Kelly 2008; Valenzuela & Ceballos 2000), including otters (Blundell et al. 2000), and seems to be strongly related to resource availability. Duplaix (1980) stated that giant otter groups abandon their ranges during the rainy season to follow dispersing fish into the flooded forest and swamps, and to search for higher banks for building dens and campsites. The availability of banks may not be restrictive, as the otters can use emerged shrubs to rest during flooding (this study). One group we radio-tracked remained in its original stretch of river, but frequently used the flooded marginal areas. Giant otters can increase their home ranges at least fourfold during the wet season in the Pantanal (this study) and in an area in the Amazon (Utreras et al. 2005), by taking advantage of the flooded areas along the river courses.

Core areas comprised less than 7% of the home ranges of the groups and usually contained dens, latrines and intensive foraging sites, as suggested by Duplaix (1980). During the first months of cub rearing, giant otter groups reduced their movements and limited their core areas to extremely small sizes (e.g., group G12 used a pond of 1.3 ha), as previously reported for the species (Duplaix 2004; Evangelista & Rosas 2011a; Laidler 1984) and other otters (Erlinge 1967; Hussain & Choudhury 1995; Melquist & Hornoker 1983; Ruiz-Olmo et al. 2005). The restriction of movement and reduction of ranges during the first four months of cub rearing may be a strategy to improve the raising success, as this is the critical period for lactation and cub learning (Evangelista & Rosas 2011b), and cub mortality may be higher in this period (Schweizer 1992).

Selection of landscape features. – Changes in availability of landscape features may induce changes in habitat-selection patterns (Arthur et al. 1996, Humphrey & Zinn 1982). Giant otter groups were selective in relation to their use of landscape elements available during the dry season. However they seemed to be less selective in positioning activity ranges during the wet season. According to Duplaix (1980), food availability is one of the key factors that affect habitat choice by giant otters. Therefore, when their prey becomes more dispersed through the floodplains, groups may move more unpredictably with regard to landscape elements when searching for food as a foraging strategy to maximize food gain, as is expected for an animal using an optimal foraging strategy (Schoener 1971).

During the wet season, giant otters were frequently observed fishing in the areas adjacent to the river, such as flooded forest, grassland and swamps. These areas have shallow water, which is preferred for foraging by many otter species (Anoop & Hussain 2004; Hussain & Choudhury 1995; Kruuk 2006; Laidler 1984), presumably due to the higher concentration of prey during the flood season (Wantzen et al. 2002; Winemiller & Jepsen 1998). During the dry season, the river was most intensively used in relation to other landscape features that were available within the home range. However, there was variation in use of landscape elements between groups. Some groups selected marginal habitats, such as freshwater ponds and artificial ponds beside roads, during the dry season, and seasonally flooded grassland during the wet season. However, this apparent preference may be an artifact of territoriality, since the groups that inhabited those marginal habitats were smaller than their neighboring groups. The use of such habitats by giant otter groups may be a result of lack of space in areas where the species has reached carrying capacity (Ribas et al. 2012). However, these marginal habitats may not support larger groups for long, as the fish stocks in these habitats are rapidly and drastically reduced due to the high rate of predation by piscivorous animals (Ribas et al. 2012) and deterioration of water conditions (Winemiller & Jepsen 1998).

The selection of forest by most of the groups during the dry season is probably related to the use of banks with vegetative cover near water bodies to build dens and campsites (Carter & Rosas 1997; Duplaix, 1980; Lima et al. 2012; Schenck 1999; Schweizer 1992; Souza 2004). Banks covered by vegetation are less impacted by erosion and may offer more protection of dens from predators (Lima et al. 2012; Souza 2004). During the wet season, groups continued to use the highest forested banks available in their territories to build dens and campsites, and some groups used emerged shrubs to build temporary platforms in marginal flooded areas and swamps. The importance of vegetation cover has been noted for other otter species (*Lutrogale perspiscillata,* Anoop & Hussain 2004; Nawab & Hussain 2012; *Lutra lutra,* Macdonald & Mason 1983; *Lontra provocax,* Medina-Vogel et al. 2003; *Lutra maculicollis, Aonyx capensis*, Perrin & Carugati 2000). The removal of riparian vegetation by canalization of rivers and streams has affected the habitat and prey of *L. provocax* in Chile and led to declines in density (Medina-Vogel et al. 2003). Vegetation cover on the bank seems to be important for all otter species (Anoop & Hussain 2004; Nawab & Hussain 2012) and should be considered as a key factor for the maintenance of giant otter groups.

Many studies have investigated the relationship between home-range size and individual- or group-mass and diet (e.g., Gittleman & Harvey 1982; Lindstedt et al. 1986; Ottaviani et al. 2006). Based on the relationship presented by Gittleman and Harvey (1982), social mustelids as giant otters, sea otters (*Enhydra lutris*) and European badgers (*Meles meles*) have an unusually smaller home range than expected for a strict carnivore (Johnson et al. 2000). The home range size of giant otter groups was similar to the home ranges estimates for other social otters, as *L. perspicillata* (2.1 to 6.6 km^2, Hussain & Chudoury 1995), *L. maculicollis* (1.1 to 9.5 km^2, Perrin et al. 2000) and male groups of *E. lutris* outside the breeding season (0.6 to 1 km^2, Jameson 1989), despite differences in data analysis and on their social system. This suggests that the home ranges of giant otter groups in our study have a large and dense prey base that supports that large otters in such small areas, which also demands healthy habitat. As the flood pulse is often linked to high fish productivity (Welcomme 1985; 1990), the maintenance of the annual hydrological fluctuations should be considered a priority for the conservation of vulnerable species which have fish as their principal prey. This is particularly worrying for giant otters in the Pantanal, because 70 small dams for hydroelectric purposes are planned and another 44 have already been constructed on streams that flow into the Paraguay River Basin (Mourão et al. 2010), and these may promote drastic changes in the flood pulse of this large wetland.

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RESUMO

Ariranhas (*Pteronura brasiliensis)* são sociais e se alimentam principalmente de peixes. Informação sobre a organização espacial de ariranhas é limitada a observações durante estações secas. No entanto, grupos podem abandonam seus territórios para seguir a dispersão de peixes para áreas inundadas durante a estação chuvosa. Por isso, nós estudamos a ecologia especial de grupos de ariranhas durante as estações seca e chuvosa nos rios Vermelho e Miranda no Pantanal brasileiro. Nós monitoramos dez grupos de ariranhas mensalmente entre junho de 2009 e junho de 2011. Localizações de locas, latrinas e observações visuais de grupos ou indivíduos foram registradas. Três grupos foram monitorados mensalmente com rádio-telemetria entre novembro de 2009 e junho de 2011 durante o dia e suas localizações foram registradas em intervalos de 30 minutos. Nós estimamos o tamanho da área de vida de todos os grupos através dos seguintes métodos: (1) comprimento linear do rio, considerando as localizações extremas de cada grupo, e (2) kernel fixo. Para os grupos monitorados com telemetria nós também usamos o método (3) *k*-LoCoh. Fidelidade de espaço foi calculada como a porcentagem de área de vida e área núcleo sobrepostas entre estações. Seleção de habitat de grupos de ariranhas foi analisada considerando a composição da paisagem durante as estações seca e chuvosa. Durante a estação seca as áreas de vida de grupos de ariranhas estimada através dos métodos lineares e kernel 95% variaram, respectivamente, de 1.8 a 22.9 km e de 1.1 a 3.9 km^2. Durante a estação chuvosa, estas estimativas variaram, respectivamente, de 14.8 a 31.7 km e de 1 a 3.9 km^2. Baseado no método de k-LoCoh (98%), os tamanhos das áreas de vidas durante a estação chuvosa (3.6 - 7.9 km^2) foram 4 a 59 vezes maiores do que durante as estações secas (0.1 - 2.3 km^2). Fidelidade de área de vida entre estações variou de 0% to 87% entre os grupos de ariranhas e dois grupos monitorados com rádio-telemetria dispersaram para áreas inundadas durante as estações chuvosas. Grupos de ariranhas foram seletivos em relação à composição da paisagem durante as estações secas, quando o rio foi mais intensamente utilizado em relação a outras características da paisagem.. No entanto, eles pareceram ser menos seletivos no posicionamento de suas atividades durante as estações chuvosas. Durante a estação chuvosa ariranhas foram freqüentemente observadas pescando em áreas adjacentes ao rio, como florestas inundadas, campos e brejos.

LITERATURE CITED

AEBISCHER, N. J., P. A. ROBERTSON, AND R. E. KENWARD. 1993. Compositional analysis of habitat use from animal radio-tracking data. Ecology 74(5):1313−1325.

ALHO, C. J. R. 2008. Biodiversity of the Pantanal: response to seasonal flooding regime and to environmental degradation. Brazilian Journal of Biology 68(4, Suppl.):957−966.

ANOOP, K. R., AND S. A. HUSSAIN. 2004. Factors affecting habitat selection by smooth-coated otters (*Lutrogale perspicillata*) in Kerala, India. Journal of Zoology 263:417–423.

ARTHUR, S. M., B. F. J. MANLY, L. L. MCDONALD, AND G. W. GARNER. 1996. Assessing habitat selection when availability changes. Ecology 77(1):215-227.

BLUNDELL, G. M., R. T. BOWYER, M. BEN-DAVID, T. A. DEAN, AND S. C. JEWETT. 2000. Effects of food resources on spacing behavior of river otters: does forage abundance control home-range size?. Pp. 325-333 in Biotelemetry 15: Proceedings of the Fifteenth

International Symposium on Biotelemetry (J. H. Eiler, D. J. Alcorn and M. R. Neuman, eds.). International Society of Biotelemetry, Wageningen, Netherlands.

BLUNDELL, G. M., J. A. K. MAIER AND E. M. DEBEVEC. 2001. Linear home ranges: effects of smoothing, sample size, and autocorrelation on kernel estimates. Ecological Monographs 71(3):469−489.

CALLENGE, C. 2006. The package "adehabitat" for the R software: A tool for the analysis of space and habitat use by animals. Ecological Modelling 197:516–519.

CALLENGE, C., AND A. B. DUFOUR. 2006. Eigenanalysis of selection ratios from animal radio-tracking data. Ecology 87(9):2349–2355.

CARTER, S., AND F. C. W. ROSAS. 1997. Biology and conservation of the giant otter *Pteronura brasiliensis*. Mammal Review 27(1):1−26.

CURTIS, D. J. AND A. ZARAMODY. 1998. Group size, home range use, and seasonal variation in the ecology of *Eulemur mongoz*. International Journal of Primatology 19 (5):811-835.

DE SOLLA, S. R., R. BONDURIANSKY, AND R. J. BROOKS. 1999. Eliminating autocorrelation reduces biological relevance of home range estimates. The Journal of Animal Ecology 68(2):221−234.

DILLON, A., AND M. J. KELLY. 2008. Ocelot home range, overlap and density: comparing radio telemetry with camera trapping. Journal of Zoology 275:391–398.

DUPLAIX, N. 1980. Observations on the ecology and behavior of the giant otter *Pteronura brasiliensis* in Suriname. Revue Ecologique (Terre Vie) 34:495−620.

DUPLAIX, N. 2004. Guyana giant otter project: 2002-2004 research results. Oceanic Society. San Francisco, California, USA: 44 p. http://www.giantotterresearch.com/articles/OCEANIC_SOCIETY_Guyana_Project_Report_2002-2004.pdf

ERLINGE, S. 1967. Home range of the otter *Lutra lutra* L. in southern Sweden. Oikos 18(2):186−209.

EVANGELISTA, E., AND F. C. W., ROSAS. 2011a. The home range and movements of giant otters (*Pteronura brasiliensis*) in the Xixuaú Reserve, Roraima, Brazil, IUCN Otter Specialist Group Bulletin 28(A):31−37.

EVANGELISTA, E., AND F. C. W. ROSAS. 2011b. Breeding behavior of giant otter (*Pteronura brasiliensis*) in the Xixuaú Reserve, Roraima, Brazil. IUCN Otter Specialist Group Bulletin 28(A):5−10.

GARCIA DE LEANIZ, C., D. W. FORMAN, S. DAVIES, AND A. THOMSON. 2006. Non-intrusive monitoring of otters (*Lutra lutra*) using infrared technology. Journal of Zoology 270:577–584.

GETZ, W. M., AND C. C. WILMERS. 2004. A local nearest-neighbor convex-hull construction of home ranges and utilization distributions. Ecography 27:489−505.

GITTLEMAN, J. L., AND P. H. HARVEY. 1982. Carnivore home-range size, metabolic needs and ecology. Behavioral Ecology and Sociobiology 10(1):57−63.

HAMILTON, S. K., S. J. SIPPEL, AND J. M. MELACK. 1996. Inundation patterns in the Pantanal wetland of South America determined from passive microwave remote sensing. Archiv für Hydrobiologie 137:1−23.

HIJMANS, R. J., AND J. VAN ETTEN. 2010. Raster: package for reading, writing, and manipulating raster (grid) type geographic (spatial) data. http://cran.r-project.org/web/packages/raster/index.html.

HUMPHREY, S. R., AND T. L. ZINN. 1982.Seasonal habitat use by river otters and everglades mink in Florida. The Journal of Wildlife Management 46:375–381.

HUSSAIN S. A., AND B. C. CHOUDHURY 1995. Seasonal movement, home range and habitat utilization by smooth-coated otter in National Chambal Sanctuary. Habitat 11:45–55.

JAMESON, R. J. 1989. Movements, home range and territories of male sea ottersof Central California. Marine Mammal Science 5(2):159-172.

JOHNSON, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61(1):65−71.

JOHNSON, D. D. P., D. W. MACDONALD, AND A. J. DICKMAN. 2000. An analysis and review of models of the sociobiology of the Mustelidae. Mammal Review 30(3 & 4): 171-196.

KEITT, T. H., R. BIVAND, E. PEBESMA, AND B. ROWLINGSON. 2010. Rgdal: bindings for the geospatial data abstraction library. R package version 0.6-24. http://CRAN.R-project.org/package=rgdal

KERNOHAN, B. J., R. A. GITZEN, AND J. J. MILLSPAUGH. 2001. Analysis of animal space use and movements. Pp. 125-166 in: Radio tracking and animal populations. (J. J. Millspaugh and J. M. Marzluff, eds.). San Diego: Academic press.

KREBS, J. R., AND N. B. DAVIES. 1997. Behavioural ecology: an evolutionary approach, 4th ed. Oxford, UK: Blackwell.

KRUUK, H. 2006. Otters: Ecology, behavior and conservation. Oxford University Press Inc., New York.

LAIDLER, L. 1984. The behavioral ecology of the giant otter in Guyana. Master dissertation, University of Cambridge.

LEUCHTENBERGER, C., AND G. MOURÃO. 2008. Social organization and territoriality of giant otters (Carnivora : Mustelidae) in a Seasonally Flooded Savanna in Brazil. Sociobiology 52(2):257−270.

LEUCHTENBERGER, C., AND G. MOURÃO. 2009. Scent-marking of giant otter in the Southern Pantanal, Brazil. Ethology 115:210−216.

LEWIN-KOH, N. J., ET AL. 2009. Maptools: Tools for reading and handling spatial objects. R package version 0.7-29. http://CRAN.R-project.org/package=maptools

LIMA, D. DOS S., M. MARMONTEL, AND E. BERNARD. 2012. Site and refuge use by giant river otters (*Pteronura brasiliensis*) in the Western Brazilian Amazonia. Journal of Natural History 46(11-12):729−739.

LINDSTEDT, S. L., B. J. MILLER, AND S. W. BUSKIRK. 1986 Home Range, time, and body size in mammals. Ecology 67(2):413-418.

MACDONALD, D. W. 1983. The ecology of carnivore social behaviour. Nature 301:379−384.

MACDONALD, S. M., AND C. F. MASON. 1983. Some factors influencing the distribution of otters (*Lutra lutra*). Mammal Review 13:1–10.

MEDINA-VOGEL, G., V. S. KAUFMAN, R. MONSALVE, AND V. GOMEZ. 2003. The influence of riparian vegetation, woody debris, stream morphology and human activity on the use of rivers by southern river otters in *Lontra provocax* in Chile. Oryx 37(4):422−430.

MELQUIST, W. E., AND M. G. HORNOKER. 1983 Ecology of river otters in West Central Idahos. Wildlife Monographs 83:3−60.

MOURÃO, G., W. TOMAS, AND Z. CAMPOS. 2010. How much can the number of jabiru stork (Ciconiidae) nests vary due to change of flood extension in a large Neotropical floodplain? Zoologia 27(5):751−756.

NAWAB, A., AND S. A. HUSSAIN. 2012. Factors affecting the occurrence of smooth-coated otter in aquatic systems of the Upper Gangetic Plains, India. Aquatic Conservation.

OTTAVIANI, D., S. C. CAIRNS, M. OLIVERIO, AND L. BOITANI. 2006. Body mass as a predictive variable of home-range size among Italian mammals and birds. Journal of Zoology 269:317–330.

PERRIN, M. R., I. D. CARRANZA, AND I. J. LINN. 2000. Use of space by the spotted-necked otter in the KwaZulu-Natal Drakensberg, South Africa. South African Journal of Wildlife Research 30(1):15-21.

PERRIN, M. R., AND C. CARUGATI. 2000. Habitat use by the cape clawless otter and the spotted-necked otter in the KwaZulu-Natal Drakensberg, South Africa. South African Journal of Wildlife Research 30(3):103−113.

POWELL, R. A. 2000. Animal home ranges and territories and home range estimators. Pp. 65-110 in Research techniques in animal ecology: controversies and consequences (L. Boitani and T. K. Fuller, eds). Columbia University Press, New York.

RENARD, D., AND N. BEZ. 2005. RGeoS: geostatistical package. R package. Version 2.1. Centre de Géostatistique, Ecole des Mines de Paris, Fontainebleau, France.

REYNOLDS, T. D., AND J. W. LAUNDRE. 1990. Time intervals for estimating pronghorn and coyote home ranges and daily movements. The Journal of Wildlife Management 54(2):316−322.

RIBAS, C. 2004. Desenvolvimento de um programa de monitoramento em longo prazo das ariranhas (*Pteronura brasiliensis*) no pantanal brasileiro. Master dissertation, Federal University of Mato Grosso do Sul, Brazil.

RIBAS, C., G. DAMASCENO, W. MAGNUSSON, C. LEUCHTENBERGER, AND G. MOURÃO. 2012. Giant otters feeding on caiman: evidence for an expanded trophic niche of recovering populations. Studies on Neotropical Fauna and Environment 47(1):19−23.

ROOONEY, S. M., A. WOLFE, AND T. J. HAYDEN. 1998. Autocorrelated data in telemetry studies: time to independence and the problem of behavioural effects. Mammal Review 28(2):89–98.

RUIZ-OLMO, J., A. MARGALIDA, AND A. BATET. 2005. Use of small rich patches by Eurasian otter (*Lutra lutra* L.) females and cubs during the pre-dispersal period. Journal of Zoology 265:339–346.

RYAN, S. J., C. U. KNECHTEL, AND W. M. GETZ. 2006. Range and Habitat Selection of African Buffalo in South Africa. Journal of Wildlife Management 70(3):764−776.

SAMUEL, M. D., D. J. PIERCE, AND E. O. GARTON. 1985. Identifying areas of concentrated use within the home range. Journal of Animal Ecology 54(3):711−719.

SCHENCK, C. 1999. Lobo de Rio (*Pteronura brasiliensis*). Presencia, uso del hábitat y protección en el Perú. GTZ/INRENA, Lima, Peru.

SCHOENER, T. W. 1971. Theory of Feeding Strategies. Annual Review of Ecology and Systematics 2:369−404

SCHWEIZER, J. 1992. Ariranhas no pantanal: ecologia e comportamento de *Pteronura brasiliensis*. Edibran-Editora Brasil Natureza Ltda, Curitiba, Paraná.

SIKES, R. S., W. L. GANNON, AND THE ANIMAL CARE AND USE COMMITTEE OF THE AMERICAN SOCIETY OF MAMMALOGISTS. 2011. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. Journal of Mammalogy 92:235−253.

SILVEIRA, L., M. M. FURTADO, F. C. W. ROSAS, L. C. SILVA, M. M. M. CABRAL, N. M. TORRES, R. SOLLMANN, A. KOUBA, AND A. T. A. JÁCOMO. 2011. Tagging giant otters (*Pteronura brasiliensis*) (Carnivora, Mustelidae) for radio-telemetry studies. Aquatic Mammals 37:208−212.

SOUZA, J. D. de. 2004. Estudos ecológicos da ariranha, *Pteronura brasiliensis* (Zimmermann, 1780) (Carnivora: Mustelidae) no Pantanal Mato-Grossense. Master dissertation, Federal University of Mato Grosso, Brazil.

SPENCER, W. D. 2012. Home ranges and the value of spatial information. Journal of Mammalogy 93(4):929–947.

STAIB, E. 2005. Eco-Etología del Lobo de Río (*Pteronura brasiliensis*) en el Sureste del Perú. PhD dissertation, Sociedad Zoológica de Francfort Perú.

STABLER, B. 2003. Shapefiles, version 0.3. R package. http://cran.r-project.org.

STAMPS, J. A. 1995. Motor learning and the value of familiar space. The American Naturalist 146(1):41−58.

THIOULOUSE, J., D. CHESSEL, S. DOLEDEC, AND J. M. OLIVIER. 1997. Ade-4: a multivariate analysis and graphical display software. Statistics and computing 7:75–83.

TOMAS, W., P. A. L. BORGES, H. J. F. ROCHA, R. SÁ FILHO, F. KUTCHENSKI JR, AND T. V. UDRY. 2000. Potencial dos Rios Aquidauana e Miranda, no Pantanal de Mato Grosso do Sul, para a conservação da ariranha (*Pteronura brasiliensis*). Pp 1-12. in III Simpósio sobre Recursos Naturais e Sócio-econômicos do Pantanal: Os Desafios do Novo Milênio (Embrapa Pantanal, eds.), Corumbá, Brazil.

UTRERAS, V. B., E. R. SUÁREZ, G. ZAPATA-RÍOS, G. LASSO, AND L. PINOS. 2005. Dry and rainy season estimations of giant otter, *Pteronura brasiliensis*, home range in the Yasuní National Park, Ecuador. The Latin American Journal of Aquatic Mammals 4 (2):1–4.

VALENZUELA, D., AND G. CEBALLOS. 2000. Habitat Selection, Home Range, and Activity of the White-Nosed Coati (*Nasua narica*) in a Mexican Tropical Dry Forest. Journal of Mammalogy 81 (3):810−819.

WANTZEN, K. M., F. DE A. MACHADO, M. VOSS, H. BORISS, AND W. J. JUNK. 2002. Seasonal isotopic shifts in fish of the Pantanal wetland, Brazil. Aquatic Sciences 64:239–251.

WELCOMME, R. L. 1985. River fisheries. FAO Fish. Technical Paper, 262.

WELCOMME, R.L. 1990. Status of fisheries in South American rivers. Interciência 15(6):337−345.

WINEMILLER, K. O., AND D. B. JEPSEN. 1998. Effects of seasonality and fish movement on tropical river food webs. Journal of Fish Biology 53A:267–296.

FIGURE LEGENDS

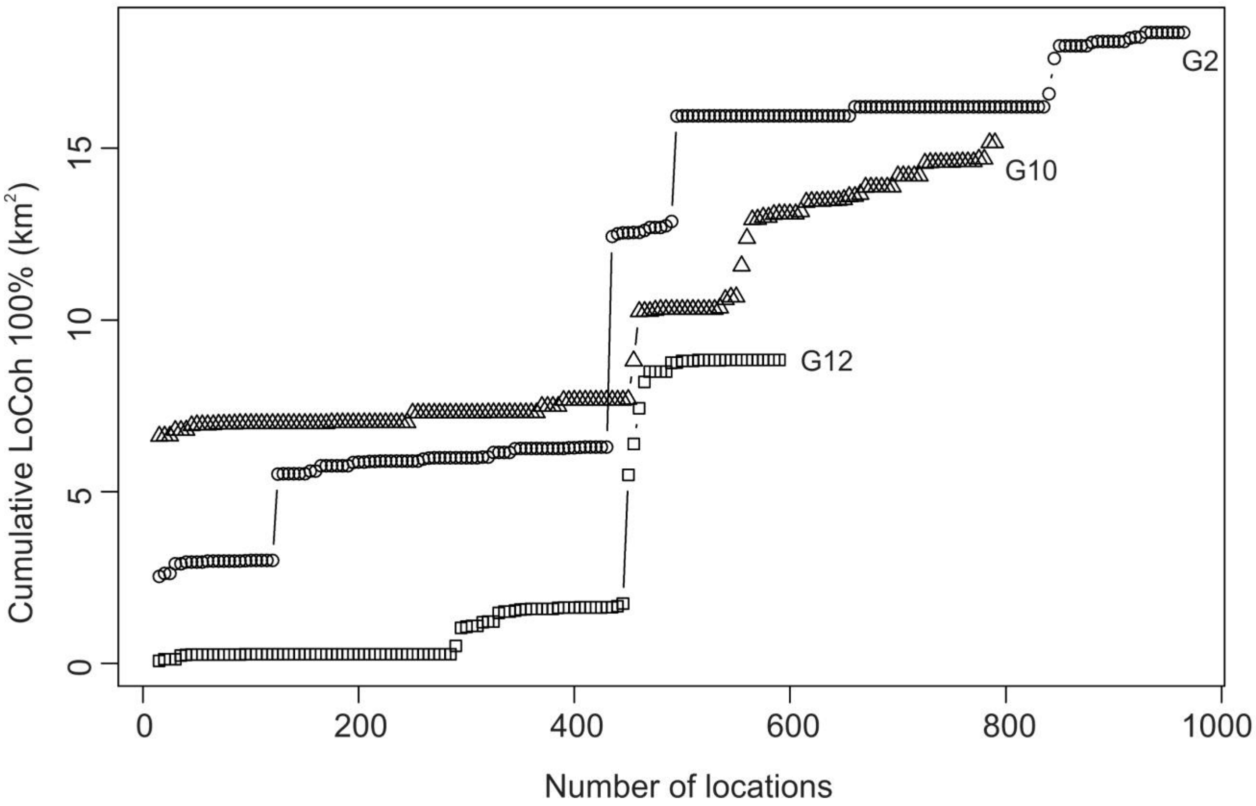

Figure 1 – Cumulative estimated area used (LoCoh 100%) in relation to the number of chronological locations of 3 groups of giant otters radio-tracked from November 2009 to June 2011, in the southern Pantanal of Brazil.

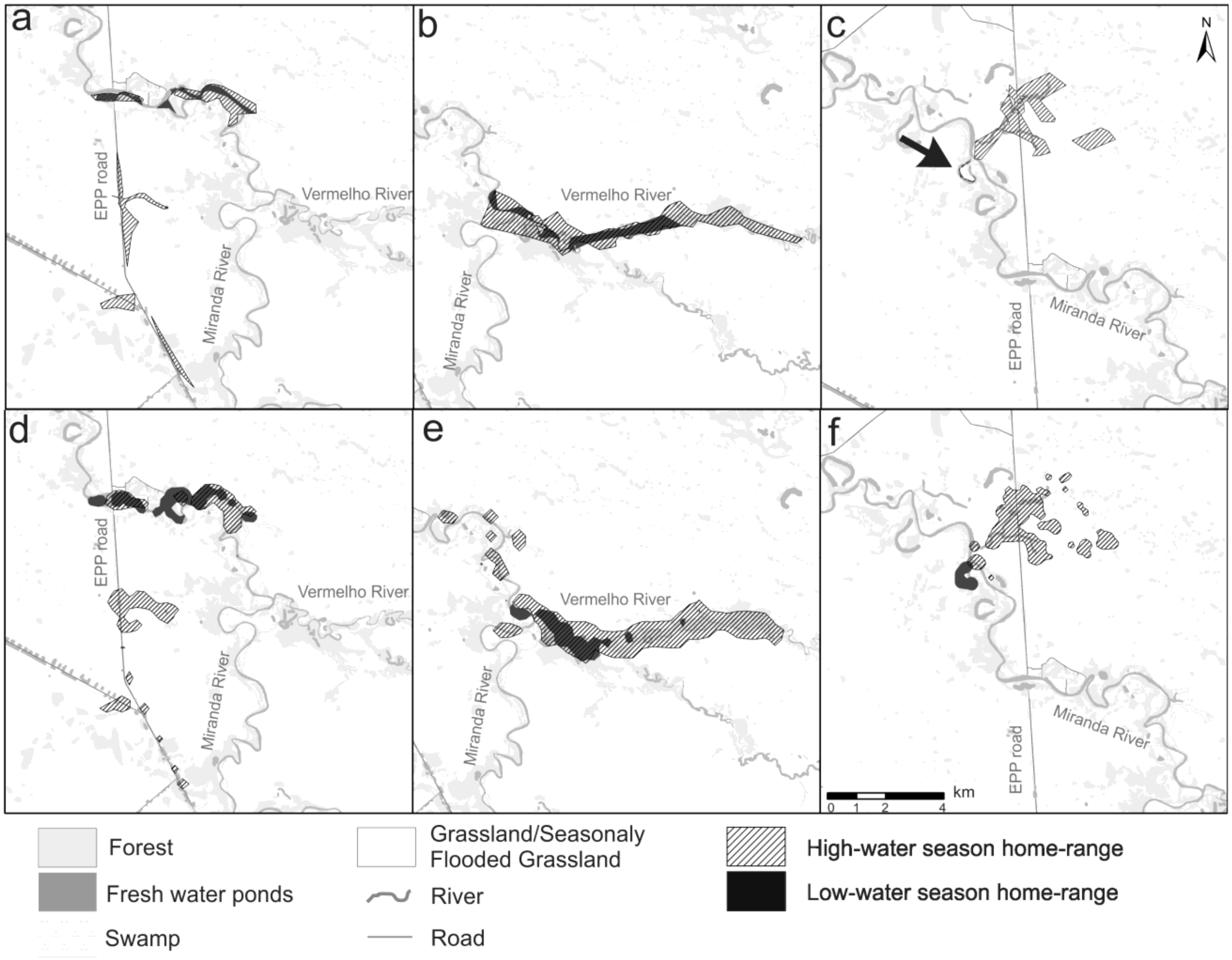

Figure 2 – Seasonal home ranges of three giant otter groups monitored by radio telemetry between November 2009 and June 2011, in the southern Brazilian Pantanal. Upper figures: *k*-LoCoh 98% of (a) group G2, (b) group G10, and (c) group G12. The black arrow indicates the location of the reduced home-range of group G12 during the dry season. Lower figures: Kernel 95% of (d) group G2; (e) group G10; (f) group G12.

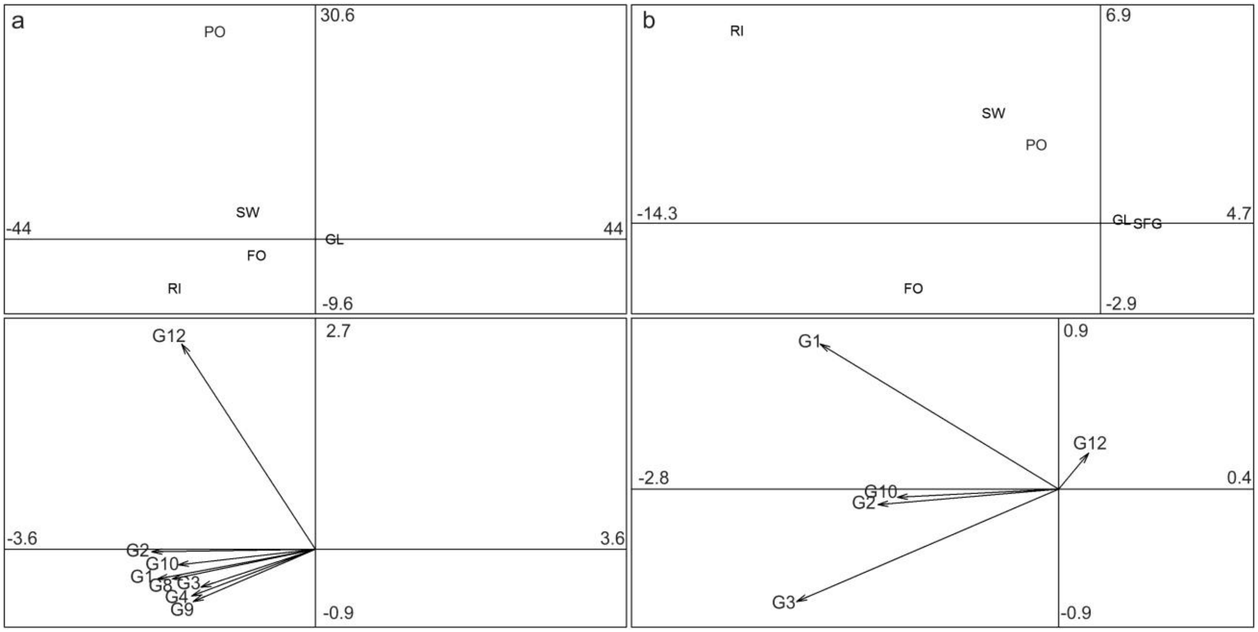

Figure 3 – Results of eigenanalysis of landscape-element selection ratio by giant otter groups for six landscape elements (FO – Forest, PO –ponds, GL – grassland, SFG – seasonal flooded grassland, SW – swamp, RI – river), from June 2009 to June 2011 in the southern Brazilian Pantanal. (a) During the dry season (groups G1–G4, G8–G10, G12) and (b) during the wet season (groups G1–G3, G10, G12). Upper graphs show the landscape-element loadings on the first two factorial axes and lower graphs show the groups' scores on the first factorial plane.

TABLES

Table 1 - Home-range size (km^2) and overlap area (km^2 and %) between dry (DS) and wet (WS) seasons of 10 giant otter groups (ID=G1-G4, G8-G13, G size=range of number of individuals that composed the group during the monitoring period) monitored by radio telemetry (RT) and direct observations (DO) from June 2009 to June 2011, in southern Pantanal, Brazil. Home ranges were estimated with *k*-LoCoh (isopleths 98%, 95% and 50%) and Kernel *ad hoc* (*h*=80 for dry season and *h*=100 for wet season) methods.

						k-LoCoh									Kernel					
						DS			WS			Overlap			DS		WS		Overlap	
	ID	G size	Period	Days	Locations	98%	95%	50%	98%	95%	50%	98%	95%	50%	95%	50%	95%	50%	95%	50%
RT	G2	3	14/08/09-10/6/10	79	965	0.99	0.8	0.03	3.9	3.12	0.003	0.77 (78%)	0.58 (73%)	0.005 (17%)	2.66	0.28	5.28	0.06	1.36 (51%)	0
	G10	9-15	4/8/09-21/6/11	81	793	2.31	1.67	0.03	7.86	7.86	0.53	2 (87%)	1.42 (85%)	0.004 (13%)	2.38	0.3	11.97	0.06	1.98 (83%)	0.007 (2%)
	G12	2-3	4/8/09-20/6/11	69	591	0.1	0.04	0.004	3.6	2.32	0.01				0.52	0.1	4.34	0.3	0.03 (6%)	0
	G1	5-8	5/6/09-21/6/11	57	177										3.15	0.28	3.88	0.23	2.75 (87%)	0
	G3	3-9	3/6/09-17/3/11	26	71										3.17	0.12	0.98	0.16	0.53 (17%)	0.01 (8%)
	G4	7	3/6/09-17/6/11	11	43										1.11	0.1	-	-	-	-

DO	G8	8	2/6/09-15/12/09	22	80	2.28	0.3	-	-	-	-
	G9	2-6	15/8/09-18/6/11	31	72	2.1	0.19	-	-	-	-
	G11	4-6	22/7/10-18/5/11	9	18	-	-	-	-	-	-
	G13	3	15/2/11-11/5/11	6	7	-	-	-	-	-	-

Table 2 - Linear home-range estimate (km) of ten giant otter groups monitored by radio-telemetry (RT) and direct observation (DO), during four seasons (DS 2009 - dry season of 2009, WS 2010 - wet season of 2010, DS 2010 - dry season of 2010, WS 2011- wet season of 2011), from June 2009 to June 2011, in the southern Pantanal of Brazil.

Method	Groups	DS 2009	WS 2010	DS 2010	WS 2011
RT	G2	10.5	22.7		
	G10		9.1*	22.9	31.7
	G12			1.8	15.6
DO	G1	18.0	23.1	20.1*	6.4*
	G3	14.2	14.8	13.7	4.9*
	G4	17.2	6.7*	0.3*	4.1*
	G8	12.1			
	G9	13.0	8.5*		11.5*
	G11			9.4*	1.8*
	G13				1.6*
	Median	13.6	22.7	13.7	23.6

(*Estimates should be accepted with caution, as they are based on few locations (<20), and therefore were not used to calculate the medians).

Table 3 - Ranking matrix of habitat types (RI – river, PO –pond, FO – forest, SW – swamp, GL – grassland) selected by eight giant otter groups during the dry seasons, from June 2009 to January 2011 in the southern Pantanal of Brazil. A) proportional habitat use within group's kernel home ranges with proportion of total available habitat types within study area; B) proportions of independent locations for each group in each habitat type within group's kernel home range. Each mean element in the matrix was replaced by its sign, a triple sign represents significant deviation from random at $P<0.05$. Plus sign indicates that the habitat was positively selected.

A) Home range vs. landscape

Habitat type	RI	FO	SW	PO	GL
RI	0	+	+	+	+++
FO	---	0	+	+	+++
SW	---	-	0	+	+++
FP	---	---	---	0	+++
GL	---	---	---	---	0

B) Radio locations vs. home range

Habitat type	RI	PO	FO	SW	GL
RI	0	+	+++	+++	+++
PO	-	0	+	+	+++
FO	-	-	0	+	+++
SW	-	-	-	0	+
GL	---	---	---	---	0

Table 4 – Number of dens and campsites built by ten giant otter groups in different landscape features (SW – swamp, GL – grassland, SFL – seasonal flooded grassland, FO – forest) during four seasons (DS 2009 – dry season of 2009, WS 2010 – wet season of 2010, DS 2010 – dry season of 2010, WS 2011- wet season of 2011) from June 2009 to June 2011, in the southern Pantanal of Brazil.

	DS 2009		WS 2010		DS 2010		WS 2011		TOTAL	
Habitat	den	campsite	den	campsite	den	campsite	den	Campsite	den	campsite
SW	8	5	1	2	2	7	1	0	12	14
GL	5	2	1	2	2	0	2	2	10	6
SGL	0	0	2	1	0	0	2	0	4	1
FO	70	17	16	14	31	18	13	22	130	71
TOTAL	83	24	20	19	35	25	18	24	156	92

CAPÍTULO 3

Leuchtenberger, C.; Magnusson. W. & Mourão, G. Territoriality of giant otter groups in an area with seasonal flooding. Manuscrito formatado para *Journal of Zoology*.

Territoriality of giant otter groups in an area with seasonal flooding

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Abstract

Territoriality carries costs and benefits, which are commonly affected by the spatial and temporal abundance and predictability of food, and by intruder pressure. Giant otters live in groups that defend territories along water bodies during the dry season, using chemical signals, loud vocalizations and agonistic encounters. However, little is known about the territoriality of giant otters during the rainy season, when groups leave their territories and follow fish dispersing into flooded areas. The objective of this study was to analyze long-term territoriality of giant otter groups in a seasonal environment. The linear extensions of the territories of 10 giant otter groups were determined based on locations of active dens, latrines and scent-marks in each season. Some groups overlapped the limits of neighboring territories. The total territory extent of giant otters was correlated with group size in both seasons. The extent of exclusive territories of giant otter groups was negatively related to the number of adults present in adjacent groups. Territory fidelity ranged from 0 to 100% between seasons. Some groups maintained their territory for long periods, which demanded constant effort in marking and re-establishing their territories during the wet season. These results indicate that the defense capacity of groups had an important role in the maintenance of their territories across seasons, which may also affect the reproductive success of giant otter alpha pairs.

Key-words: *Pteronura brasiliensis*, territory size, exclusive territory, overlap, chemical signal, agonistic encounters.

Resumo

Territorialidade implica em custos e benefícios, que são geralmente afetados pela abundância e previsibilidade de alimento no tempo e espaço, e por pressão de intrusos. Ariranhas vivem em grupos que defendem territórios ao longo de corpos d’água durante a estação seca utilizando sinais químicos, vocalizações estridentes e encontros agonísticos. No entanto, pouco é conhecido sobre a territorialidade de ariranhas durante a estação chuvosa, quando se acredita que grupos abandonam seus territórios e seguem a dispersão de peixes para áreas inundadas. O objetivo deste estudo foi entender a territorialidade de grupos de ariranhas em um ambiente sazonal por longo tempo. Alguns grupos fizeram incursões em territórios vizinhos. O tamanho de território de ariranhas foi correlacionado com o tamanho de grupo em ambas as estações. A extensão dos territórios exclusivos de grupos de ariranhas foi negativamente relacionada com o número de adultos presentes em grupos adjacentes. A fidelidade de território variou de 0 a 100% entre estações. Alguns grupos mantiveram seus territórios por longos períodos, os quais demandaram constantes esforços em marcação e restabelecimento de território durante a estação chuvosa. Estes resultados indicam que a capacidade de defesa do grupo tem um importante papel na manutenção de seus territórios ao longo das estações, que pode também afetar o sucesso reprodutivo dos casais dominantes.

Palavras-chaves: *Pteronura brasiliensis*, tamanho de território, território exclusivo, sobreposição, sinais químicos, encontros agonísticos.

Introduction

Most of social species defend territories within their home range in an attempt to have exclusive access to important resources (Brown & Orians, 1970; Grant *et al.*, 1992; Kruuk, 1992). However, territories may be more or less exclusive and some overlap with neighboring intruders may occur (Stamps, 1990; Stamps & Kirschnan, 1990; Wolf, 1993, Adams 2001). An important strategy to avoid conspecific rivals is to inform ownership to intruders, such as through chemical signals, which are an efficient communication tool, even in the absence of the signaler (e.g., Gosling, 1982; Sillero-Zubiri & Macdonald, 1998; Zub *et al.*, 2003). Scent-marking may inform intruders about the composition and strength of the group, and the aversion to marks left by strangers may constrain owners to their territories (Sillero-Zubiri & Macdonald, 1998). Species adopt different patterns of territory marking, and in heterogeneous habitat signals are commonly concentrated in areas where the threat of intrusion is highest (Kruuk *et al.*, 1984; Sillero-Zubiri & Macdonald, 1998; Gosling & Roberts, 2001; Zub *et al.*, 2003; Herr & Rosell, 2004).

Territoriality carries costs and benefits, which are commonly affected by the abundance and predictability of food in time and space (Maher & Lott, 2000). The Resource Dispersion Hypothesis (RDH) suggests that the territory size of carnivores is determined by resource dispersion, while group size is related to the richness of patches (Macdonald, 1983). Assuming that territory size and shape represent an economic optimum (Maher & Lott, 2000), the minimum defensible territory would contain enough resources to maintain a minimum breeding unit, and areas with more abundant resources will support additional individuals, increasing group size (Macdonald, 1983; Doncaster & Macdonald, 1992; Revilla & Palomares, 2002). Therefore, when resources are widely distributed, the size of territories may be related to the metabolic needs of individuals (Gittleman & Harvey, 1982) and consequently to group size (Macdonald, 1983; Kruuk & Macdonald, 1985; Adams, 2001), although the relation between group and territory size is potentially complicated by other factors that benefit group-living, such as hunting and breeding cooperation (Brown, 1982).

In seasonal environments, some species maintain territories only in the period during which important resources are available (Stamps & Kirschnan, 1990). As groups select and establish territories in a given area, the order of territory establishment may affect the final size of the territory and the fitness of the owners for the entire territorial season, since the first groups that establish territories during this period will have territories of optimal size, and later groups will have to establish their territories in the remaining space (Stamps & Kirschnan, 1990; Adams, 1994). Therefore, neighbor pressure may prevent expansion of territories and result in conflicts and territory overlap (Erlinge, 1968; Stamps, 1990; Stamps & Kirschnan, 1990; Wolf, 1993; Powel, 2000; Herr & Rossell, 2004; Tallents *et al.*, 2012). In such situations, the size of exclusive territories may have a negative correlation with intruder pressure (Stamps, 1990), with greater overlap in areas with more conflicts.

The pressure of neighboring groups may have negative consequences because of agonistic encounters (White & Harris, 1994; Sillero-Zubiri & Macdonald, 1998; Zub *et al.*, 2003), which may affect the maintenance of territories (Stamps & Kirschnan, 1999). Groups that remain in the same territory for longer periods will become more familiar with the area, which may also improve fitness and defense capacity, since owners learn to explore their territory more efficiently and to defend those areas that are more frequently invaded by intruders (Stamps, 1995). Giant otters live in cohesive groups ranging from two to 20 individuals, which cooperate with the care of the offspring of the dominant pair (Duplaix, 1980). Giant otter groups mark their territories with scent-marks and communal latrines, which are located at dens and campsites along the banks of water bodies (Duplaix, 1980; Leuchtenberger & Mourão, 2009). Agonistic encounters result in fighting and loud vocalizations when a group or a solitary individual is detected within the territory of a resident group (Schweizer, 1992; Ribas & Mourão, 2004; Leuchtenberger & Mourão, 2009; Ribas *et al.*, 2012). Estimates of territory sizes of giant otter groups have been made during dry seasons in Guyana and Suriname, and in the Amazon and Paraguay River basins (Duplaix, 1980; Laidler, 1984; Tomas *et al.*, 2000; Staib, 2005; Ribas, 2004; Leuchtenberger & Mourão, 2008; Evangelista & Rosas, 2011). However, little is known about the territoriality of giant otters during the rainy season, when groups are believed to leave their territories and follow fish dispersing into flooded areas (Duplaix, 1980; Carter & Rosas, 1997). We analyzed long-term territoriality of giant otter groups in a seasonal environment with the aim to look at the effects of season on territory size and fidelity, territory exclusivity, and territorial defense behavior. Since territoriality implies costs with defense and intruders pressures, we expected that: giant otter groups deposit more chemical signals at the borders of their territories and larger territories may present more chemical signals; since defense capacity may increase with group size, we hypothesized that larger groups maintain larger territories; and the size of territories may be limited by the number of intruders present in adjacent groups. Considering that territoriality is benefited by resource concentration and abundance, during the flooding season groups are expected to increase their territory size, following the resources dispersion, which may lead some groups to leave their territories and decrease the investment in chemical signalling.

Material and Methods

The Pantanal is a large wetland covering approximately 160 000 km^2, located in areas of western Brazil, Bolivia and Paraguay. The hydrological regime is regulated by seasonal rains, which fall mostly between November and March and result in the inundation of almost 80% of the area (Hamilton *et al.*, 1996).

From June 2009 to June 2011, we studied home-range size and habitat selection of ten giant otter groups inhabiting stretches of the Miranda and Vermelho Rivers in the southern Pantanal. We use these data, together with data on home-range sizes of these groups that has been published previously (Leuchtenberger & Mourão, 2008; Chapter 2), to examine aspects of the long-term stability of territories of giant otter groups in a seasonal environment.

Ten giant otter groups were monitored (G1-G4, G8-G13) for 8-10 consecutive days every month, interspaced by two to three weeks, along 119 km of the Vermelho (19^{o}34'S; 57^{o}01'W) and Miranda Rivers (19°36'S, 57°00'W) in the southern Pantanal (Chapter 2). Monitoring was undertaken during the daytime (05:00-19:00), when we searched for individuals or groups, active dens, campsites, scent-marks and other signs (see Groenendijk *et al.*, 2005), and registered the locations with a global positioning system receptor (Garmin Etrex, Inc., Olathe, KS). Giant otters were video recorded (Canon HF-200), which allowed identification of their natural individualistic marks on the throat, and their sex and behavior whenever possible. The hierarchical status of individual within the group was identified according to their behavior and other cues (Leuchtenberger & Mourão 2009). Two dominant males and one subordinate male from different giant otter groups (G2, G10 and G12) were radio-tracked from November 2009 to June 2011. For more details see Chapter 2.

Based on the Miranda River level, we recognized two dry seasons (June-December 2009 and July 2010-January 2011) and two wet seasons (January-June 2010 and February-June 2011) during the study period (Chapter 2).

We measured the linear extent of territories of all groups observed, based on the extreme locations of active dens, latrines and scent-marks in each season. We also measured the exclusive stretches within the territories, which were defined as the core area defended only by the resident group that did not overlap with areas defended by adjacent groups (Brown & Orians, 1970). We calculated territory overlap between groups as the proportion of the territory of one group that overlapped the territory of another group. These overlaps are asymmetrical between groups (Kernohan *et al.*, 2001).

We combined latrines and isolated scent-marks as chemical-signal sites. The density of chemical signals was estimated for each group along the linear extent of river within the exclusive and overlapping areas and these estimates were averaged for dry and wet seasons. We used a two-way-ANOVA to test the difference between the densities of chemical-signals sites between exclusive and overlap areas and seasons.

Group size was considered the number of individuals in the group during each season, including juveniles 6-months-old or more, since they were usually already integrated in the daily activities of the group. Potential intruder pressure was estimated by summing the number of adults and sub-adults (>1 year old) present in adjacent groups during each season. We estimated means of total-territory extent, exclusive-territory extension, group size, intruder pressure and number of chemical-signal sites for each group during each season (dry and wet seasons). We also included in these calculations the estimates of territory size of giant-otter groups monitored during 2006 and 2007 by Leuchtenberger & Mourão (2008). We used ANCOVA models to estimate (1) the effects of territory size and season on the number of chemical-signal sites; (2) the effects of group size and season on territory size and (3) the effect of number of adult otters in neighboring groups and season on exclusive-territory size of groups. In all cases, we first checked the assumption of slope parallelism of ANCOVA by testing a preliminary model including the interaction term between the explanatory variables (Wilkinson, 2004). If the interaction term was not significant ($P<0.05$), we excluded it and ran the ANCOVA with interaction. If the interaction term was significant, we tested the simple effect of the continuous explanatory variable separately for each season.

Agonistic events were video recorded during the study period. We classified these events as "fights" when individuals of different groups fought or chased each other, and "warning vocalizations", when a group emitted agonistic vocalizations (e.g. screams and hahs, see Chapter 4) to another group or when invading the borders of neighboring territories. Since we did not observe enough agonistic events to make confident conclusions of seasonal patterns, we presented this data only for purposes of discussion.

We used the percentage overlap of total extent of the territory of a group during one season with the total territory extent from the previous season as an index of territory fidelity. Territory fidelity was estimated only for groups that were monitored in more than three months during each season. As giant otters in this area had been monitored in 2006 and 2007 by our team, we used the available data (Leuchtenberger & Mourão, 2008) to evaluate long-term changes in group territories. There was no siginificant relationship between estimated territory size and number of observations of the groups during the dry (P=0.102) or wet seasons (P=0.285). However, due to the small sample size (N<20 per season), territory estimates from some groups were excluded from analyses involving seasonality.

Results

The ten groups monitored had a mean of six individuals per group (2-15), totaling 77 individuals (20 females, 26 males and 31 indeterminate), which resulted in a linear density of 0.42 individuals/km. Almost all groups overlapped their territory borders with neighboring groups. Overlap ranged from 0 to 69% of linear extensions during both dry and wet seasons (Table 1).

The linear density of chemical-signal sites did not differ significantly between exclusive and overlapped territories ($F_{(1,27)} = 0.431$, $P = 0.517$) or seasons ($F_{(1,27)} = 0.802$, $P = 0.379$). There was no interaction between territory size and season in the ANCOVA analysis ($P = 0.899$) when predicting the number of chemical signal sites. The number of chemical-signal sites increased linearly with territory size ($\beta = 0.858$, $t = 4.884$, $P <0.001$), but did not differ between seasons ($t = -1.401$, $P = 0.185$).

Linear territories during the dry seasons ranged from 1.1 to 17.8 km ($N = 7$ groups, Table 1), excluding the estimates for two groups, which had few locations and one new group that was establishing its territory within the season, as that biased estimates of territory size. The wet linear territories ranged from 8.1 to 23.9 km ($N = 5$ groups), as some groups extended their former ranges into the flooded areas or artificial lakes beside stretches of the *Estrada Parque Pantanal* (EPP) road (Fig. 1). The extent of the exclusive territories varied from 1.1 to 12.7 km during the dry seasons and from 6.6 to 16.1 km during the wet seasons (Table 2). There was no interaction ($P = 0.67$) between group size and season, as explanatory variables of territory size. ANCOVA ($F_{(2,\ 13)} = 11.67$, $P = 0.001$, $R^2 = 0.64$) indicated that territory size increased linearly with group size ($\beta = 1.434$, $t = 4.356$, $P<0.001$) and was larger during high water ($\beta = 6.599$, $t = 2.910$, $P = 0.012$). The effects of the number of adult otters in neighboring groups interacted with the season ($t = 2.827$, $P = 0.015$) as explanatory variables of exclusive territory size. Therefore we examined its simple effects within each level of season. The exclusive territory size was linearly and negatively affected by the number of adult neighboring otters during the dry seasons ($\beta = -1.732$, $F_{(1,\ 8)} = 8.487$, $P = 0.019$, $r^2 = 0.52$), but not during the wet seasons ($F_{(1,4)} = 0.509$, $P = 0.515$).

Although most overlapped areas were not used simultaneously by more than one group, we witnessed 12 agonistic events between groups, which seemed to occur more likely at the boundaries (Fig. 1), including warning vocalizations (*N* = 7) and fights (*N* = 5). Most of the fights we saw occurred during dry periods, while the warning vocalizations were more frequent during floods, but the number of observations is too small to allow generalizations (Fig. 2).

Territory fidelity varied from 0 to 100% between seasons (Table 3). Three groups (G2, G9 and G12) changed their territories completely between seasons (Fig. 1). Group G8 was observed in the area only during the dry season of 2009. Group G10 expanded its territory from the wet season to the dry season of 2010 pushing group G1 up the Miranda River. Nevertheless, group G1 maintained 15% of its territory between the dry seasons of 2009 and 2010. Groups G1 and G3 have been observed in the study area since 2002 (Ribas, 2004) and group G4 established its territory in 2006 (Leuchtenberger & Mourão, 2008), with changes in territory location thereafter (Fig. 1). Group G2 was first observed in 2006, but the dominant male was substituted four times in the following two years (Leuchtenberger & Mourão, 2008). During the wet season of 2010, we sighted group G2 in the same site that the group used during the dry season of 2008.

Discussion

The linear density of 0.42 ind/km of river observed for the giant otters in the study area has been stable since the surveys conducted in 2002 in the same area (Ribas, 2004), reinforcing the suggestion that this population had achieved carrying capacity (Leuchtenberger & Mourão, 2008; Ribas *et al.*, 2012). This density is within the range reported for the Guyana, Suriname and the Amazon Basin, which varied from values as high as the 1-2 ind/km (Duplaix, 1980; Evangelista & Rosas, 2011) to about 0.2 ind/km (Laidler, 1984; Schenck, 1999). Otters may increase the intensity of territorial defense behaviors when at high densities (Erlinge, 1968; Laidler, 1984), and giant otter groups may defend the entire extent of their home ranges, even though some boundaries overlap (Duplaix, 1980).

In our study, some giant otter groups overlapped the boundaries of neighboring territories and both groups alternately scent-marked these areas, sometimes in the same day, which could have confounded the real limit of groups territories. Demarcation in overlapped territories has been considered as attempts of animals to expand their territories (Stamps & Krishnan, 1990; Doncaster & Macdonald, 1992; Adams, 2001). Some social species increase their investment in the defense of borders to maximize the chance of being detected by intruders (Kruuk *et al.*, 1984; Sillero-Zubiri & Macdonald, 1998; Zub *et al.*, 2003; Herr & Rosell, 2004). In our study, the total territory extent and the extent of exclusive territories were larger during the wet seasons than during the dry seasons. Furthermore, the number of giant otter chemical-signal sites was positively correlated with territory length in both seasons and the density of chemical-signal sites did not differ between overlapped and exclusive territories (this study, Leuchtenberger & Mourão, 2008), indicating that groups spend proportionally more time and energy to mark their territory as it increases in size. Although scent-marking is energetically expensive, giant-otter groups commonly forage throughout their entire territory every day, and may expend almost 10% of their daily active time in marking their territory (Chapter 1). For species such as *Lutra lutra*, inhabiting areas where flood-pulses occur within hours, scent-marks may signal priority of use of resources for other members of the group (Kruuk, 1992). However, for a species as cohesive as the giant otter, inhabiting areas with seasonal flood-pulses, the distribution of chemical signals throughout the territory may be related to defense and reduction of intrusion, since a sparsely marked territory could be considered a vacant area by neighboring groups (Sillero-Zubiri & Macdonald, 1998).

Territory size of giant otters was correlated with group size in both seasons, despite the increase in territory size during the wet season, which may suggest that larger groups increment their territories more during flooding, when resources are more dispersed. Although this relationship is not common for social carnivores living in heterogeneous habitat (Macdonald, 1983; Doncaster & Macdonald, 1992; Johnson *et al.*, 2001; Adams, 2001), this could be related to the need of larger groups to access more resources (Macdonald, 1983; Kruuk & Macdonald, 1985), as there is a relationship between metabolic needs and home range size of most carnivores (Gittleman & Harvey 1982; Grant et al 1992). The addition of individuals to the group may also improve defense capacity (Doncaster & Macdonald, 1992; Sillero-Zubiri & Macdonald, 1998; Mares *et al.*, 2012; Tallents *et al.*, 2012), favoring the acquisition of larger territories.

During the dry season, the extent of exclusive territories of giant otter groups was negatively related to the number of adults present in adjacent groups. The pressure of intruders may restrict the expansion of territories, and consequently exert a negative effect on exclusive-territory size (Stamps, 1990; Stamps & Krishnan, 1990; Wolf, 1993; Tallents *et al.*, 2012). However, there was no relationship between intruder pressure and exclusive-territory size during the wet season, probably because resources become widely distributed during floods, attenuating the pressure of neighboring groups with the decrease in density of otters along water bodies.

Fights between giant otter groups are highly vocal and may lead to severe injuries or death of individuals and the disintegration of the group (Schweizer, 1992; Mourão & Carvalho, 2001; Ribas & Mourão, 2004). In our study, agonistic events (fights and warning vocalizations) were common at the borders of territories and areas of territory overlap, and appeared to be more frequent during the dry season, while warning vocalizations were more frequent during the floods. Smaller groups seemed to avoid fights in overlap areas. We have witnessed cases of large groups invading the territory of smaller groups, which remained hidden in marginal swamps or ponds until the invaders left the area. However, hiding is more practicable at high water when there are many ways to avoid detection or to escape, which may account for the lower rate of fights between groups during the wet season. Agonistic encounters, as well as scent-marking, may constrain each group to its territory (White & Harris, 1994; Sillero-Zubiri & Macdonald, 1998). As scent-marking may inform intruders about the composition and identity of the group (Sillero-Zubiri & Macdonald, 1998; Rostain *et al.*, 2004; Brennan & Kendrick, 2006), the behavior of mixing feces and urine in communal latrines could be a strategy to hide the information about the size of the group, in order to make it more difficult for larger groups to identify weakly protected territories.

Territory fidelity ranged from 0 to 100% between seasons. Site familiarity may be a strategy to promote continuous access to key resources and enhance the owners' fitness (Stamps, 1995). Also, in seasonal environments, such as the Pantanal, the establishment of territories before important resources become available appears to help a group maintain its territory in the following seasons (Stamps & Krishnan, 1990; Adams, 1994). However, in these seasonal areas, the maintenance of territories could be difficult, as flooding can submerge marks and border limits, and allow access to new areas not yet settled. Despite these difficulties, in our study area, some groups maintained their territory for long periods (> 7 years), which demanded effort in marking and re-establishing their territories during the wet season.

Defense capacity apparently had an important role in territory maintenance of giant otter groups across seasons, and negative experiences as during fights may lead a group to abandon its territory. During the wet season of 2010, a larger group (G10) overlapped and ultimately took over the territory from group G1, which was forced to dislocate up river and settle a new area. Other groups apparently were forced to leave their high-quality territories and settle new ones in sub-optimal or marginal areas (Ribas *et al.*, 2012; this study). The shift of one group from the river to a marginal habitat (group G2) seems to have caused it to reduce in size, with the death of the cubs and the dispersal of the only subordinate. The reproductive success of giant otter alpha pairs maybe affected by their capacity to maintain a territory in a high-quality environment for a long time and by increasing the number of helpers in the group. Giant otter groups commonly increase in size through the philopatry of offspring (Duplaix, 1980). However groups with unrelated members were observed in the study area (Leuchtenberger & Mourão, 2008; Ribas, 2012), which may be an efficient strategy to improve the success of a giant otter groups and individual fitness.

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References

Adams, E. S. (1994). Settlement Tactics in Seasonally Territorial Animals: Resolving Conflicting Predictions. *Am. Nat.* **143**(5), 939-943.

Adams, E. S. (2001). Approaches to the study of territory size and shape. *Ann. Rev. Ecol. Syst.* **32**, 277-303.

Brennan, P. A. & Kendrick, M. K. (2006). Mammalian social odours: attraction and individual recognition. *Philos. T. Roy. Soc. B* **361**, 2061-2078.

Brown, J. L. & Orians, G. H. (1970). Spacing patterns in mobile animals. *Ann. Rev. Ecol. Syst.* **1**, 239-262.

Brown, J. L. (1982). Optimal group size in territorial animals. *J. Theor. Biol.* **95**, 793-810.

Carter, S. & Rosas, F. C. W. (1997). Biology and conservation of the giant otter *Pteronura brasiliensis*. *Mammal Rev.* **27**(1), 1−26.

Doncaster, C. P. & Macdonald, D. W. (1992). Optimum group size for defending heterogenous distributions of resources: A model applied to red foxes, *Vulpes vulpes*, in Oxford City. *J. theor. Biol.* **159,** 189-198.

Duplaix, N. (1980). Observations on the ecology and behavior of the giant otter *Pteronura brasiliensis* in Suriname. *Rev. Ecol. (Terre Vie)* **34**, 495-620.

Erlinge, S. (1968). Territoriality of the Otter *Lutra lutra* L. *Oikos* **19** (1): 81-98

Evangelista, E. & Rosas, F. C.W. (2011). The home range and movements of giant otters (*Pteronura brasiliensis*) in the Xixuaú Reserve, Roraima, Brazil, *IUCN Otter Spec. Group Bull.* **28**(A), 31-37.

Gittleman, J. L. & Harvey, P. H. (1982). Carnivore home-range size, metabolic needs and ecology. *Behav. Ecol. Sociobiol.* **10**(1), 57−63.

Gosling, L. M. & Roberts, S. C. (2001). Testing ideas about the function of scent marks in territories from spatial patterns. *Anim. Behav.* **62**, F7-F10.

Gosling, L. M. (1982). A reassessment of the function of scent marking in territories. *Z. Tierpsychol.* **60,** 89–118.

Grant, J. W. A., Chapman, C. A. & Richardson, K. S. (1992). Defended versus undefended home range size of carnivores, ungulates and primates. *Behav. Ecol. Sociobiol.* **31,** 149-161.

Groenendijk, J., Hayek, F., Duplaix, N., Reuther, C., Van Damme, P., Schenck, C., Staib, E., Wallace, R., Waldemarin, H., Notin, R., Marmontel, M., Rosas, F., de Mattos, G.E., Evangelista, E., Utreras, V., Lasso, G., Jacques, H., Matos, K., Roopsind, I. & Botello, J.C. (2005) Surveying and monitoring distribution and population trends of the giant otter (*Pteronura brasiliensis*) – Guidelines for a standardization of survey methods as recommended by the Giant Otter Section of the IUCN/SSC Otter Specialist Group. *Habitat* **16**, 1–100.

Hamilton, S. K., Sippel, S. J. & Melack, J. M. (1996). Inundation patterns in the Pantanal wetland of South America determined from passive microwave remote sensing. *Arch. Hydrobiol.* **137**, 1-23.

Herr, J. & Rossell, F. (2004). Use of space and movement patterns in monogamous adult Eurasian beavers (*Castor fiber*). *J. Zool., Lond.* **262**, 257–264

Kernohan, B. J., Gitzen, R. A. & Millspaugh, J. J. (2001). Analysis of animal space use and movements. In *Radio tracking and Animal Populations:* 125-166. Millspaugh, J. J. & Marzluff, J. M. (Eds). San Diego: Academic press.

Kruuk, H. (1992). Scent marking by otters *(Lutra lutra)*: signaling the use of resources. *Behav. Ecol.* **3**(2), 133-140

Kruuk, H., Gorman, M. & Leitch, A. (1984). Scent-marking with the subcaudal gland by the European Badger, *Meles meles* L. *Anim. Behav.* **32**, 899-907.

Kruuk, H. & Macdonald, D.W. (1985). Group territories of carnivores: empires and enclaves. In *Behavioural ecology: ecological consequences of adaptive behaviour*, 521-536. Sibly, R. M. & Smith, R. H. (Eds), Blackwell Scientific Publications, Oxford, UK.

Laidler, L. (1984). The behavioral ecology of the giant otter in Guyana. Master thesis, University of Cambridge.

Leuchtenberger, C. & Mourão, G. (2008). Social organization and territoriality of giant otters (Carnivora : Mustelidae) in a Seasonally Flooded Savanna in Brazil. *Sociobiology* **52**(2), 257-270.

Leuchtenberger, C. & Mourão, G. (2009). Scent-marking of giant otter in the Southern Pantanal, Brazil. *Ethology* **115**, 210-216.

Macdonald, D.W. (1983). The ecology of carnivore social behaviour. *Nature* **301**, 379–384

Maher, C. R. & Lott, D. F. (2000). A Review of ecological determinants of territoriality within vertebrate species. *Am. Midl. Nat.* **143**(1), 1-23.

Mares, R., Young, A. J. & Clutton-Brock, T. H. (2012). Individual contributions to territory defence in a cooperative breeder: weighing up the benefits and costs. *Philos. T. Roy. Soc. B.* http// rspb.royalsocietypublishing.org.

Mourão, G. & Carvalho, L. (2001). Canibalism among giant otters (*Pteronura brasiliensis*). *Mammalia* **6**(2), 225-227.

Powell, R. A. (2000). Animal home ranges and territories and home range estimators. In *Research techniques in animal ecology: controversies and consequences*, 65-110. Boitani, L. & Fuller, T. K. (Eds). Columbia University Press, New York.

Revilla, E. & Palomares, F. (2002). Spatial organization, group living and ecological correlates in low-density populations of Eurasian badgers, *Meles meles. J. Anim. Ecol.* **71**, 497–512.

Ribas, C. (2004). *Desenvolvimento de um programa de monitoramento em longo prazo das ariranhas (Pteronura brasiliensis) no pantanal brasileiro.* Master thesis. Federal University of Mato Grosso do Sul, Brazil.

Ribas, C. (2012). *Grau de parentesco e relações sociais entre grupos de ariranhas (Pteronura brasiliensis).* PhD thesis. Instituto Nacional de Pesquisas da Amazônia, Brazil.

Ribas, C. & Mourão, G. (2004). Intraspecific Agonism Between Giant Otter Groups. *IUCN Otter Spec. Group Bull.* **21**(2), 89-93.

Ribas, C., Damasceno, G., Magnusson, W., Leuchtenberger, C. and Mourão, G. (2012). Giant otters feeding on caiman: evidence for an expanded trophic niche of recovering populations. *Stud. Neotrop. Fauna E.* **47**(1), 19-23.

Rostain, R. R., Ben-David, M., Groves, P. & Randall, J. A. (2004). Why do river otters scent-mark? An experimental test of several hypotheses. *Anim. Behav.* **68,** 703–711.

Schenck, C. (1999). *Lobo de Rio (Pteronura brasiliensis). Presencia, uso del hábitat y protección en el Perú.* GTZ/INRENA, Lima, Peru.

Schweizer, J. (1992). *Ariranhas no Pantanal: Ecologia e comportamento de Pteronura brasiliensis*. Edibran-Editora Brasil Natureza Ltda, Curitiba, Paraná.

Sillero-Zubiri, C. & Macdonald, D.W. (1998) Scent-marking and territorial behaviour of Ethiopian wolves *Canis simensis*. *J. Zool.* **245**, 351–361.

Staib, E. (2005). Eco-Etología del Lobo de Río (*Pteronura brasiliensis*) en el Sureste del Perú. PhD thesis. Sociedad Zoológica de Francfort Perú.

Stamps, J.A. (1990). The effect of contender pressure on territory size and overlap in seasonally territorial species. *Am. Nat.* **135**(5), 614-632.

Stamps, J. A. (1995). Motor learning and the value of familiar space. *Am. Nat.* **146**(1), 41-58.

Stamps, J. A. & Krishnan, V. V. (1990). The effect of settlement tactics on territory sizes. *Am. Nat.* **135**(4), 527-546.

Stamps, J. A. & Krishnan, V. V. (1999). A learning-based model of territory establishment. *Q. Rev. Biol.* **74**(3), 291-318.

Tallents, L. A., Randall, D. A, Williams, S. D. & Macdonald, D. W. (2012). Territory quality determines social group composition in Ethiopian wolves *Canis simensis. J. Anim. Ecol.* **81**, 24–35.

Tomas, W., Borges, P. A. L., Rocha, H. J. F., Sá Filho, R., Kutchenski Junior, F. & Udry, T. V. (2000). Potencial dos Rios Aquidauana e Miranda, no Pantanal de Mato Grosso do Sul, para a conservação da ariranha (*Pteronura brasiliensis*). In *III Simpósio sobre Recursos Naturais e Sócio-econômicos do Pantanal: Os Desafios do Novo Milênio.* Corumbá, Brazil.

White, P.C.L. & Harris, S. (1994). Encounters between red foxes (*Vulpes vulpes*): implications for territory maintenance, social cohesion and dispersal. *J. Anim. Ecol.* **63**(2), 315-327.

Wilkinson, L. (2004). SYSTAT—Systems for Statistics. Version 11. Systat Software Inc, Chicago, Illinois.

Wolf, J. O. (1993). Why Are Female Small Mammals Territorial? *Oikos* **68**(2), 364-370.

Zub, K., Theuerkauf, J, Edrzejewski, B. J. I., Schmidt, K. & Alczyk, R. K. (2003). Wolf pack territory marking in the Bilaowieza Primeval Forest (Poland). *Behaviour* **140**, 635-648.

FIGURE LEGENDS

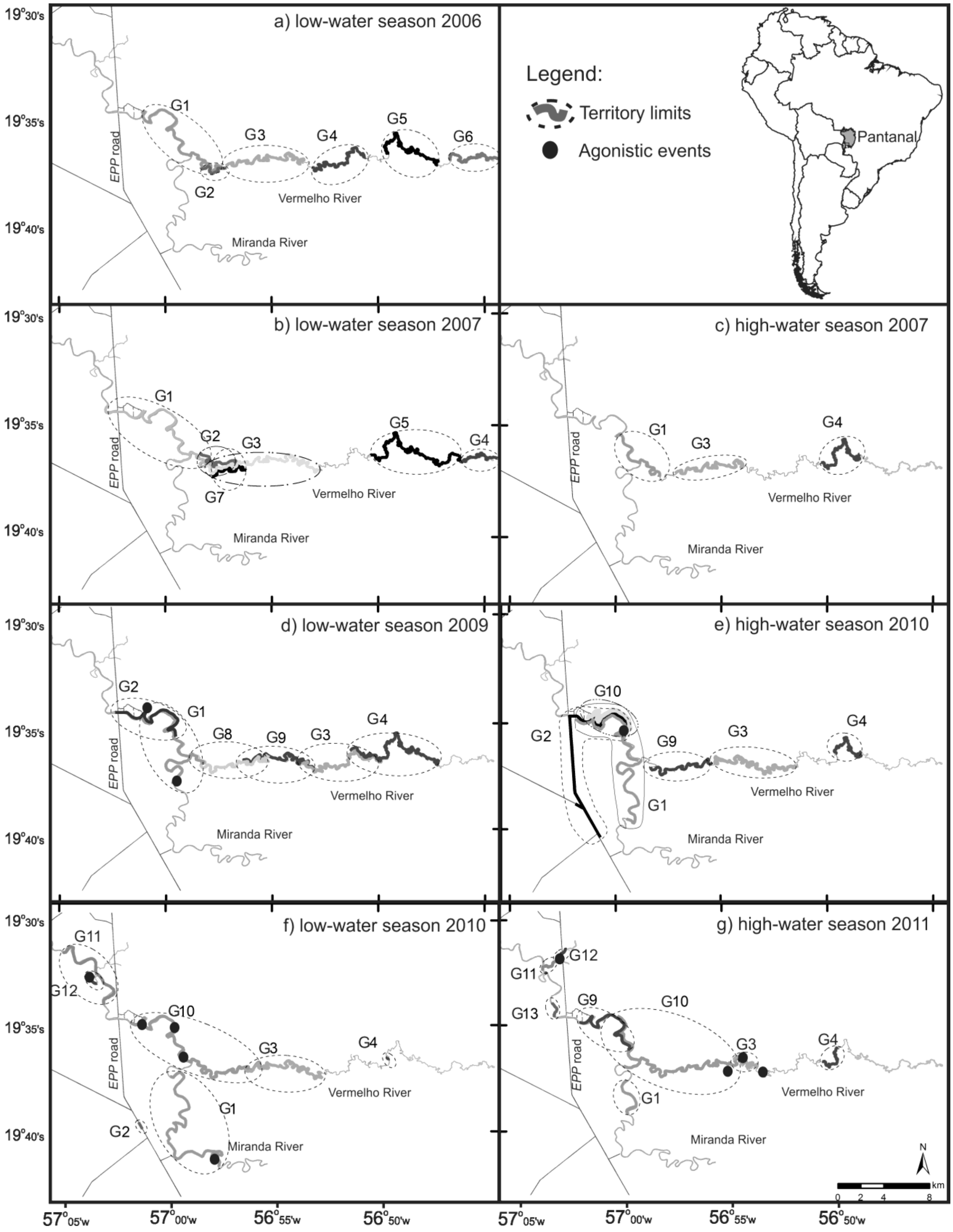

Figure 1. Territory extent of 13 giant otter groups (G1-G13) monitored between July 2006 and November 2007 (Leuchtenberger & Mourão 2008), and from June 2009 to June 2011 (this study), on the Miranda and Vermelho Rivers, in the southern Brazilian Pantanal. Parts a, b and c were modified from Leuchtenberger & Mourão 2008.

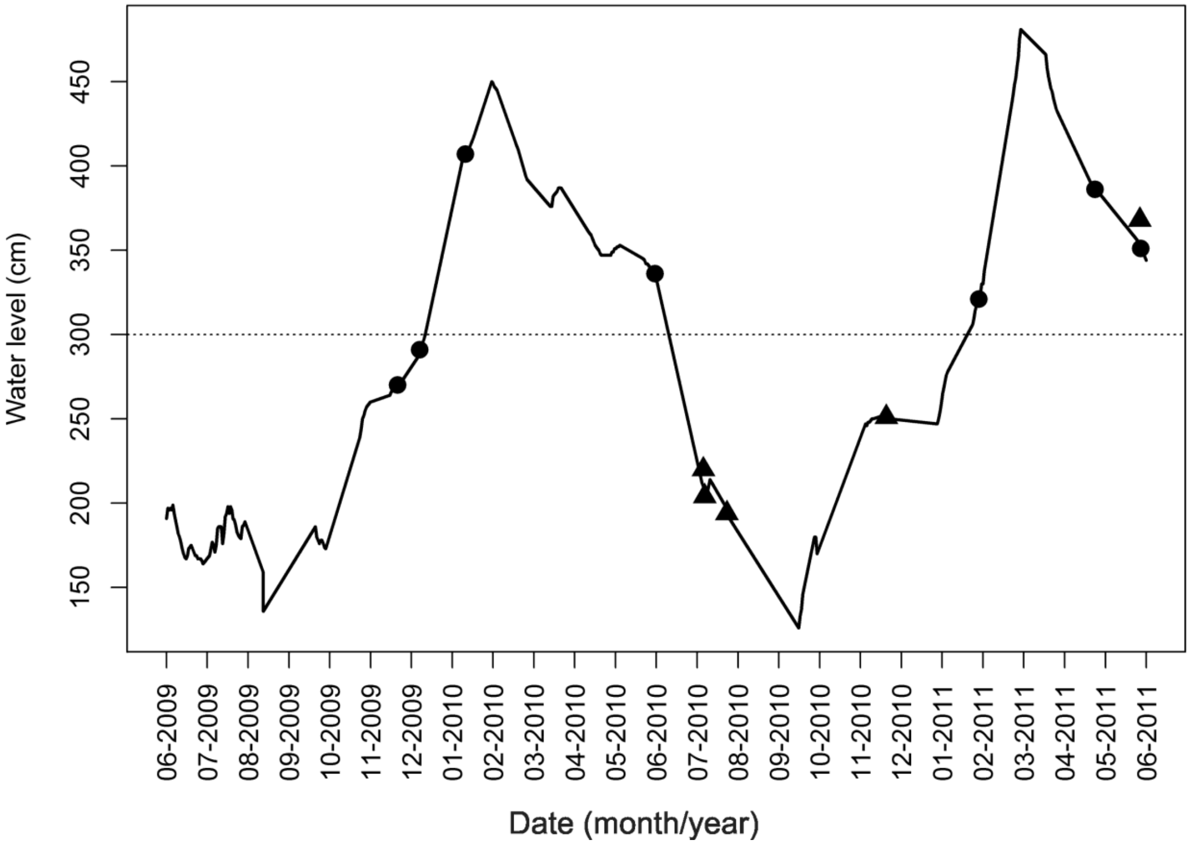

Figure 2. Water level in the Miranda River in the Brazilian Pantanal during the study. The dotted line indicates the limit between dry (river within its banks) and wet (floodplain inundation) seasons. Agonistic events between giant otters groups are indicated by triangles (fights) and circles (warning vocalizations).

TABLE LEGENDS

Table 1. Percentage of territories (in rows) overlapped by the neighboring group's territory (in columns) during each season (dry season of 2009, wet season of 2010, dry season of 2010, wet season of 2011) from June 2009 to June 2011, in the southern Pantanal, Brazil. Group size is indicated in parentheses beside the group ID. ("-" indicates the absence of the group in the study area, * territory estimated based on small number of locations, and not included in the analyses).

	Groups	G1	G2	G3	G4	G8	G9	G10	G11	G12	G13
Low-water 2009	G1 (8)	100	38.93	0	0	10.22	0	-	-	-	-
	G2 (3)	69.23	100	0	0	0	0	-	-	-	-
	G3 (5)	0	0	100	31.69	0	18.78	-	-	-	-
	G4 (7)	0	0	26.16	100	0	0	-	-	-	-
	G8 (8)	15.04	0	0	0	100	39.09	-	-	-	-
	G9 (6)	0	0	17.54	0	36.38	100	-	-	-	-
High-water 2010	G1 (8)	100	27.35	0	0	-	0	24.11	-	-	-
	G2 (3)	34.09	100	0	0	-	0	0	-	-	-
	G3 (3)	0	0	100	*	-	0	0	-	-	-
	G4 (7)	0	0	*	100	-	0	0	-	-	-
	G9 (3)	0	0	0	0	-	100	0	-	-	-
	G10 (9)	*	0	0	0	-	0	100	-	-	-
Low-water 2010	G1 (5)	100	0	0	0	-	-	0	0	0	-
	G2 (2)	0	100	0	0	-	-	0	0	0	-
	G3 (9)	0	0	100	*	-	-	16.79	0	0	-
	G4 (7)	0	0	*	100	-	-	0	0	0	-
	G10 (15)	0	0	10.36	0	-	-	100	0	0	-
	G11 (4)	0	0	0	0	-	-	0	100	*	-
	G12 (3)	0	0	0	0	-	-	0	*	100	-
High-water 2011	G1 (4)	100	-	0	0	-	0	0	0	0	0
	G3 (9)	0	-	100	*	-	0	*	0	0	0
	G4 (7)	0	-	*	100	-	0	0	0	0	0
	G9 (2)	0	-	0	0	-	100	48.31	0	0	*
	G10 (11)	*	-	6.86	0	-	19.21	100	0	0	0
	G11 (4)	0	-	0	0	-	0	0	100	*	*
	G12 (3)	0	-	0	0	-	0	0	18.26	100	0
	G13 (3)	0	-	0	0	-	*	0	*	0	100

Table 2. Territory total extent (TE, km) and exclusive territory (ET, km) of ten giant otter groups monitored by radio-telemetry (RT) and direct observations (DO), during four seasons (dry season of 2009, wet season of 2010, dry season of 2010, wet season of 2011), from June 2009 to June 2011, in the southern Pantanal, Brazil.

		Dry 2009		Wet 2010		Dry 2010		Wet 2011	
	Groups	TE	ET	TE	ET	TE	ET	TE	ET
RT	G2	10.5	3.0	21.4	13.1	0.7*	0.7*		
	G10			7*	0*	22.2**	19.9**	23.9	16.1
	G12					1.1	1.1	8.1	6.6
DO	G1	17.8[1]	9.1	23.1**[1]	15.8	20.1*[1]	20.1*	4.2*	4.2*
	G3	14.2[1]	7.3	14.8[1]	14.8	13.7[1]	11.4	4.9*[1]	4.9*[1]
	G4	17.2[1]	12.7	6.7*[1]	6.7	0.3*[1]	0.32*	4.1*[1]	4.1*[1]
	G8	12.1[1]	5.5						
	G9	13.0[1]	6.0	8.5*[1]	8.5			9.5	6.9
	G11					9.4*[1]	9.4*	1.8*[1]	1.8*[1]
	G13							1.6*[1]	1.6*[1]
	Median	13.6[1]	6.7	18.1	13.9	7.4	6.3	9.5	6.9

*Estimates should be considered with caution, as they are based on few locations (<20), ** There was an expansion and/or shift of territory, which may have lead to overestimated sizes, and these values were not used to calculate medians. [1]Chapter 2.

Table 3. Territory fidelity (% overlap of territories among seasons) of six giant otter groups between consecutive seasons (columns 1-3) and between same season (high- or dry) in different years (columns 4-5), monitored from June 2009 to June 2011, in the southern Pantanal, Brazil. Dry season = DS; wet season = WS.

Groups	DS2009-WS2010	WS2010-DS2010	DS2010-WS2011	DS2009-DS2010	WS2010-WS2011
G1	26.30	35.53		15.09	
G2	43.2	100		0	
G3	51.72	73.78	100	27.41	
G9					0
G10			71.09		
G12			0		

CAPÍTULO 4

Leuchtenberger, C.; Sousa-Lima; Magnusson. W. & Mourão, G. A sentence is more than the sum of its words: vocal repertoire of the giant otter. Manuscrito formatado para *Animal Behaviour*.

A sentence is more than the sum of its words: vocal repertoire of the giant otter

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Word count= 7965

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The giant otter (*Pteronura brasiliensis*) is a highly social species. Knowledge of its vocal repertoire is limited to qualitative descriptions and opportunistic recordings of sounds in specific contexts. The aim of this study was to describe, qualitatively and quantitatively, the vocal repertoire of giant otters in the Brazilian Pantanal and the distribution of call types across different behavioral contexts.We classified 15 basic sound types emitted in different behavioural contexts by otters of different ages. Cub calls and purrs were the most frequently emitted sounds. However, the vocal repertoire of giant otters comprises a continuum of sound types, with combinations, gradations and transitions that allow for a much larger repertoire than the 15 basic types, reflecting the complex and subtle communication system used by this social species. Not only for giant otters, but also for other social mammals, rather than defining subjective new sound types, it may be more productive to describe vocalisations in multivariate space and relate these coordinates to the presumed motivational states of the animals.

Keywords: communication, emission rate, *Pteronura brasiliensis*, social behaviour, vocalisation.

Animals communicate through different kinds of signals, which presumably increase their fitness (Bradbury & Vehrencamp 1998; Endler 2000; Wilson 2000). The content of signals may provide information on the status, mood, and identity of senders and may vary according to the behavioural context and the environment (Bradbury & Vehrencamp 1998). A way to understand the communication system of a species is to pool the sets of signals used to deal with different questions (Bradbury & Vehrencamp 1998; Lehner 1998). Different sound types within vocal repertoires are associated with different behavioural contexts in a wide range of species, including otters (e.g., Schassburger 1993; Sieber 1994; McShane et al. 1995; Wong et al. 1999).

The vocal repertoires of the social mustelids, such as sea otters (*Enhydra lutris*, McShane et al. 1995) and badgers (*Meles meles*, Wong et al. 1999), seem to be more complex, containing larger sets of sounds and compounds and graded signal structures than solitary species (*Mustela nivalis*, Huff & Price 1968; *Martes americana*, Belan *et al.* 1978; *Mustela eversamanni*, Farley et al. 1987; *Aonyx cinereus*, *Lutrogale perspicillata*, *Lontra canadensis*, Duplaix 1982, *Lutra lutra*, Gnoli & Prigioni 1995). Highly social species display more complex interactions and behaviours than solitary or non-social animals, which may adopt more complex communication systems (Bradbury & Vehrencamp 1998; McComb & Semple 2005; Roux et al. 2009). Some social species use of graded sounds and combinations, which increase the number of messages that can be transmitted and add to the complexity of their vocal repertoire (Schassburger 1993; Wilson 2000).

Giant otters live in cohesive groups of two to 20 individuals (Duplaix 1980; Leuchtenberger & Mourão 2008). Individuals in the group undertake almost all their daily activities together and frequently scent-mark the banks of water bodies to delineate their territories (Duplaix 1980, Leuchtenberger & Mourão 2009), and defending these areas from intruders with loud choruses (Duplaix 1980, Ribas & Mourão 2004). However, knowledge of the vocal communication of giant otters is limited to a few studies carried out with free-ranging animals in the Guyanas and Amazon Basins (Duplaix 1980; Staib 2005; Bezerra et al. 2010), observations of some captive animals originating from the Amazon and the Pantanal regions (Machado 2004), and a few spectrographic descriptions of sounds emitted by free-ranging animals in specific contexts in the Pantanal (Ribas & Mourão 2004; Leuchtenberger & Mourão 2009; Ribas et al. 2012). Despite the information provided by these studies, the vocal communication of this highly social species is poorly understood. In this study, we set out to document the vocal repertoire of giant otters in the Brazilian Pantanal and the distribution of call types across different behavioral contexts.

METHODS

The study was carried out in an area of the Pantanal, a large, seasonally flooded wetland covering approximately 160 000 km^2 located at low altitude (75-200 m a.s.l), near the geographic centre of South America (Mourão et al. 2010). The area is subject to a strong annual flood pulse (Alho 2008). The Paraguay River is the main river draining the region from north to south, and most of its tributaries flow from east to west, including the Miranda and Negro rivers (Fig. 1). We monitored five giant otter groups (G1, G2, G4, G10 and G12) monthly, from September 2009 to June 2011, along a stretch of the Miranda River (19°36'S, 57° 00'W) and its tributary, the Vermelho River (19^{o}34'S; 57^{o}01'W). We monitored another four groups (G17 – G20) in the Negro River (19^{o}35'S; 56 ^{o}11'W) in September 2009, June and September 2010, and June 2011. Each monthly field campaign lasted from 7 to 10 days. Most groups were located through the use of boat-based visual surveys, which were carried out in daylight hours (5:00-19:00h), but three groups were radio-tracked from November 2009 to June 2011 (G2, G10 and G12) as a part of a spatial ecology study (Chapter 2). Giant otters were captured and implanted with radio-transmitters using the methods described by Silveira et al. (2011, for more details see Chapter 2).

All handling and surgery procedures followed the guidelines of the American Society of Mammalogists for the use of wild mammals in research (Sikes et al. 2011) and were authorised under license n° 12 794/4 of the Brazilian Federal Environment Agency (IBAMA).

The locations of individuals, groups and signs of the species, such as dens and latrines, were registered with a global positioning system receptor (Garmin Etrex, Inc., Olathe, KS). Once located, the group was followed at a distance of 10 to 100 m, depending on the shyness and on the reaction of the group to the observer, to avoid disturbance. Whenever possible, the behaviours of individuals, their natural individualistic throat marks, and their sex were recorded using a high-definition camcorder (Canon HF-200) during the whole observation period. Images were analyzed to describe behaviour and identity of individuals. We also identified the hierarchy of individuals within the group through specific behaviours, such as by defense position and frequency of scent-marking or by the presence of lactation (for more details see Leuchtenberger & Mourão 2009). Sounds were recorded with a directional microphone (Sennheiser ME-66) connected to a digital Marantaz PMD-660 recorder (AIFF format, 16-bit resolution and 44.1 kHz sampling rate). Behavioural samples of visible individuals vocalising (senders) were filmed *ad libitum* (Altmann 1974), and the sounds were recorded concomitantly, from a maximum distance of 50 m.

We classified the senders into three age categories according to the system of Groenendijk et al. (2005): adults and sub-adults (>12 months), juveniles (6–12 months), and cubs (0–6 months). The behavioural context of the individual or group that vocalised was classified in the following manner: *i*) close contact (CC), when two or more members of the same group displayed affiliative contact; *ii*) grooming (GR), when individuals displayed self-grooming or groomed other members of the group; *iii*) swimming (SW), when moving through the area; *iv*) within den behaviour (DE), when cubs vocalised from within the den; *v*) scent-marking (SM), when the individuals were scent marking and/or defecating; *vi*) isolation (IS), when the individual was distant from the other members of the group and started to call looking around as if searching for other individuals; *vii*) begging (BE), when an individual solicited a prey item from another; *viii*) warning defense (WD), mainly when the individual caught a fish and/or was eating, he vocalized an advertisement sound to keep other otters away; *ix*) inquiry (IN), when individuals investigated something new in their environment, sometimes adopting a periscoping posture; *x*) alarmed (AL), when an individual was startled and its behaviour generated attention or led the other members of the group to escape; *xi*) intraspecific agonistic encounter (IA), when the individual or the group interacted negatively (physically or vocally) with a conspecific intruder; and *xii*) interspecific encounter (IE), when an individual or a group faced a caiman (*Caiman crocodilus yacare*).

The emission rate was estimated from the number of sounds emitted by all group members combined during each monitoring period. The average emission rate per individual was subsequently divided by the number of individuals present during the recording period. The monitoring interval was counted from the beginning of the visual detection of the group or individual at a maximum distance of 50 m until the end of observations, when they were lost form sight. The monitoring was restarted when the same or another individual or group was re-located during the same day. The emission rate of sounds emitted exclusively by a particular age category was calculated, normalising for the monitoring time in which that individual was present during the sampling. To determine emission rates, we only considered sounds recorded from six of the groups monitored (G1, G2, G10, G17, G18 and G20), because three groups (G4, G12 and G19) were very shy, which might have compromised our ability to approach without disturbing their normal behaviour. Even within the groups that we considered in our analyses, sounds clearly emitted in response to the presence of the observers were not used to estimate emission rates.

Acoustical analyses

Acoustic analyses were performed using Raven Pro 1.4 (Cornell Lab of Ornithology), applying the following settings for spectrograms and power spectra: Hanning window; FFT size = 1024 and 50% overlap. Sound parameters were measured in spectrograms, oscillograms and power spectra (Fig. 2) and were used to describe and/or compare vocalisations: (CD) call duration, (LF) lowest frequency of the sound, (HF) highest frequency of the sound, (PF) peak frequency of the entire sound, (Q3) 3rd quartile frequency, this value is computed automatically by the software and represents the frequency that divides the selection into two frequency intervals containing 75% and 25% of the energy in the selection, (PU) number of pulses (temporal units that repeat rhythmically) of the sound, (FI) initial frequency of F0 (for harmonic sounds) or of the peak frequency (for non-harmonic sounds), (FM) maximum frequency of F0 or PF, (FF) final frequency of F0 or PF, (FD) difference between the highest and the lowest frequency of F0 or PF, (D1) duration from the start of the vocalisation to the highest frequency value of F0 or PF, (D2) duration from the highest frequency of F0 or PF to the end of the vocalisation, and (PD) plateau duration (when the frequency of F0 or PF did not vary). The number of pulses was measured using oscillograms for sounds that presented stretches with regularly spaced pulses (e.g., coo-call, purr, snort, adult and cub growls, scream and scream-gurgle), and for sounds that presented a large number (>10) of pulses, we estimated the number of pulses by dividing the duration of pulsed stretches by the inter-pulse interval within that stretch. The sound parameters are presented as the mean and standard deviation (SD) of the mean or median and its respective ranges. Sound types were classified according to the species vocal description first elaborated by Duplaix (1980). Spectrogram and oscillogram figures were produced with R software using the function *spectro* in the package *seewave* (Sueur et al. 2008).

Statistical Analyses

All statistical analyses were undertaken using R 2.13 Software (R Foundation for Statistical Computing, 2011). The vocal repertoire of giant otters is derived from a continuum, with transitions, gradations and combinations among different sound types. However, based on 13 structural characteristics, we visually classified 15 discrete sound types. We then standardised the acoustic parameters by columns and rows using the *decostand* function with the *total* method in the Vegan package (Oksanen et al. 2008) and used a nested nonparametric multivariate permutational analysis of variance (PERMANOVA, age categories nested within sound types) to identify differences among sound types. We used the PERMANOVA analysis with 1000 permutations, which permutes the distance matrix (Manhattan method) of acoustic parameters, through the *adonis* function in the Vegan package.

A linear discriminant analysis (LDA) was carried out to estimate the distinctiveness between sound types, using the package MASS (Venables & Ripley 2002). We applied the first step of LDA with a sorted (training) subset of 50% of the data. The remaining (validation) subset of data was used to evaluate the accuracy of classification based on the equations derived from the training subset. The percentage of correctly classified cases indicates the effectiveness of discriminant function in distinguishing groups (vocalisation type). We only used four variables to estimate the LDA among sound types (PF, Q3, FD, PU), because the other variables did not conform to the linearity assumptions of the analysis.

Because some of the sound types were expected to be subdivided between age categories, we applied a PERMANOVA with 1000 permutations (*adonis,* Vegan package) to test for these differences. We then conducted a hierarchical clustering analysis taking into account these subdivisions. For this analysis, we used a Manhattan-distance matrix of the median values of the variables extracted from each sound type and the average linkage between groups (UPGMA). This analysis results in a dendrogram that represents the similarity between sound clusters (Wong et al. 1999).

A principal-coordinate analysis (PCoA) was carried out to ordinate the 13 acoustic variables of the 15 main sound types from the Manhattan-distance matrix. To avoid distortions of the configuration due to extreme points from the PCoA, we corrected 53.3% of the distances using the “extended” procedure available in the *stepacross* function from the package Vegan. We used a PERMANOVA (1000 permutations, *adonis,* Vegan package) to test whether the context associated with the emissions of sounds was statistically associated with the ordination of acoustic variables (*i.e.*, the first three axis of the PCoA).

RESULTS

The giant otter groups included 43 adults (20 males, 16 females and 7 unknown), 4 juveniles (2 male, 1 female and 1 unknown) and 25 cubs (1 male, 1 female and 23 unknown). During the study period, eight cubs became juveniles, and three of the juveniles became adults. Group size varied from 2 to 15 individuals, with an average of 6 individuals.

We recorded 6246 vocalisations during 112 hours of monitoring. The individual total emission rate was 11.4 sounds/h (Table 1), and the frequency of individual sound types varied from the infrequently emitted cub squeak (0.03 sounds/h) to the more frequent cub call (3.4 sounds/h). We included only 458 of the total recorded sounds for the vocal-repertoire analysis (379 from adults/sub-adults, 9 from juveniles and 70 from cubs), because most of the recordings overlapped with sounds from motor boats and/or vocalisations of other species or non-focal giant otters.

The vocal repertoire of giant otters was classified into 15 discrete sound types (PERMANOVA: $F_{14, 443}$= 130.66, R^2=0.81, P<0.001), of which seven were emitted only by adults and sub-adults; one, by juveniles and cubs; two, exclusively by cubs; and five, by all age categories. Linear discriminant analysis correctly classified 74% of the sound types. The first two discriminant functions explained 92% of the variance in sound variables. The number of pulses was the variable that contributed most to the first discriminant function, while the difference between the highest and the lowest frequency of F0 or PF (FD) was the most important variable in the second discriminant function.

Some of the main sounds could be subdivided into two types, depending on the age of the sender animal, resulting in a total of 19 distinct sounds (Fig. 3). The begging scream of adults/sub adults and cubs/juveniles differed (PERMANOVA: $F_{1,19}$=3.35, P=0.016), but it accounted for little of the variance in the data (R^2=0.15). The cub growl differed from adult growls (PERMANOVA: $F_{1,25}$=14.53, P<0.001), but the difference explained a relatively low proportion of the variance in the data (R^2=0.37), and as the cub sound could be classified aurally as a growl, we considered them to be the same sound type. The high scream of cubs and adults (PERMANOVA: $F_{1,12}$=0.78, P=0.536) did not differ, although the high scream of some adults had nonlinear components and the adult/sub-adult and cub screams also did not differ statistically (PERMANOVA: $F_{1, 27}$=1.35, P=0.232).

Vocal Repertoire

Coo. The coo is a discrete harmonic sound (Fig. 4a) vocalised with the mouth closed and was heard only at close range (to approximately 10 m). The average coo duration was 0.36 (SD= 0.11 s), with two harmonic parts or notes: an ascendant (D1: X + SD= 0.15 + 0.06 s, Table 2) in the beginning of the coo and a descendant segment (D2: X + SD= 0.07 + 0.03 s) at the end, interspersed by an interval of silence (PL: X + SD= 0.16 + 0.09 s). Pulses (PU: X + SD= 109.67 +

29.19 pulses) were visible in part or through the entire harmonic segment. The mean of F0 ranged from 0.27 (SD= 0.06) kHz to 0.52 (SD= 0.06) kHz, with an average peak frequency of 0.45 (SD= 0.05) kHz. *Context:* Coos were emitted at a rate of 1.1 sounds/h (Table 1). This chevron-shaped double-note sound was emitted mainly during close-contact episodes (51%, n=290), especially when adults were caring for cubs, but also during scent-marking events (26%, n=148). Adults cooed when they met during swimming (14%, n=80), sometimes touching their noses, and before changing their activity or leaving the site. Coos were also emitted during grooming sessions (9%, n=51).

Coo-hum. This low sound is emitted with the mouth closed, and it seems to be a combination of the coo (Fig. 4a) and the hum (Fig. 4d) sounds. The coo-hum is a harmonic sound with at least three visible harmonics and mean call duration 0.2 s (SD= 0.09 s, Fig. 4b), with pulses (PU: *X* +SD= 98.7 + 45.88 pulses) through the entire duration of the sequence or in segments of the sound. The F0 is frequency modulated and begins at a low frequency (F1: *X* + SD= 0.25 + 0.04 kHz), rising to a mean of 0.43 (SD= 0.08) kHz for a mean of 0.11 (SD =0.07) s and then decreasing towards the end of the sequence of continuous sound. *Context:* Adults vocalised coo-hums at a rate of 0.7 sounds/h (Table 1). Coo-hums were mainly emitted during close-contact events (72%, n=226), when individuals were swimming together (12%, n=38), grooming (9%, n=28) and scent marking (5%, n=16) and were emitted in behavioural contexts similar to those in which coos were produced. However, this sound was also emitted when an adult called other individuals, independent of their ages, to come out of the den (2%, n=6).

Coo-call. The coo-call is louder than coos and coo-hums, with an average duration of 0.44 (SD= 0.13) s, and is vocalised with the mouth partially closed. This sound seems to be a combination between the coo (Fig. 4a) and adult calls (Fig. 4j). It has an abrupt transition from an ascendant low-pitch harmonic and pulsed segment resembling a coo to a high-pitch bell-shaped frequency modulated harmonic sound similar to the adult call and then reverts back to a descendant pulsed sound at the end of the sound (Fig. 4c). The middle part of this sound may have a plateau (median of 0.03 s, ranging from 0.01 to 0.2 s) with a constant frequency (*X* + SD= 4.32 + 1.14 kHz). The minimum F0 average of the beginning and end segments were 0.26 (SD= 0.1) kHz and 0.34 (SD= 0.1) kHz, respectively. *Context:* Coo-calls were vocalised at a rate of 0.3 sounds/h (Table 1) when the animal appeared to be in an intense motivational state, mainly in close-contact events (64%, n=124). This sound was also used for calling to other members of the group (16%, n=31), as well as during scent-marking events (12%, n=23) and swimming (8%, n=15).

Hum. The hum is a low sound emitted with the mouth closed. It had at least five visible harmonics (Fig. 4d), lasting an average of 0.33 (SD= 0.19) s, with some segments of regular pulses (PU: *X* + SD= 80.4 + 48.2 pulses). The mean beginning frequency of F0 was 0.23 (SD= 0.04) kHz, which increased to a mean of 0.27 (SD= 0.07) kHz at the end of the sound. *Context:* The hum emission rate was 0.5 sounds/h (Table 1), and this sound was observed more frequently during affiliative close contacts (55%, n=123), followed by scent-marking events (21%, n=47) and grooming (19%, n=43). This type of sound was observed less often during swimming (5%, n=11). The hum was commonly produced in combination with purrs (hum-purr, Fig. 6a) and growls (hum-growl, Fig. 6b).

Purr. The purr is a low, harmonic and pulsed sound that is vocalised with the mouth closed and has a nasal quality (Fig. 4e). This sound had a call duration average of 0.54 (SD= 0.27) s and an average of 11.65 (SD= 5.25) pulses. The average value of F0 was 0.21 (SD= 0.01) kHz, and the peak frequency average (*X* + SD= 0.42 + 0.07 kHz) was concentrated on the second harmonic. *Context:* Purr was the most frequent vocalisation of adults, with an emission rate of 3 sounds/h (Table 1). This sound was emitted during similar behavioural contexts to coos and hums and was more frequently observed during close contact (52%, n=733). Gradations between the close contact coo, coo-hum and coo-call sounds were commonly combined with hums and purrs (Fig. 5c). Peters (2002) suggested that the term purr is not adequate for similar sounds observed in mustelids because it is not homologous to felid purring. However, considering the low amplitude and rhythmic characteristics of this sound and the behavioural context in which giant otters emitted purrs, we maintained this term in the species' vocal repertoire.

Growl. Growl is a low, harmonic and pulsed sound emitted with the mouth totally or partially closed and may present amplitude modulation along the signal, with increasing energy towards the end of the sound (Fig. 4f). The mean duration of this sound was 2.35 (SD= 1.71) s, and a high number of pulses (*X* + SD= 516.94 + 339.27 pulses) and high values of the 3rd quartile frequency (*X* + SD= 2.16 + 0.77 kHz) were observed. The mean values of minimum and maximum F0 frequency were 0.20 (SD= 0.03) kHz and 0.22 (SD= 0.04) kHz, respectively, with at least four visible harmonics at distances greater than 20 m and at least eight at closer range. *Context:* Adults growled at a rate of 0.3 sounds/h (Table 1). Growls were emitted mainly in warning and defense contexts (74%, n=107), when the vocalising individual was handling and eating a fish or it was directed toward another individual trying to steal it. While eating and growling, the individuals sometimes opened their mouths, producing a more intense sound with a slight increase in frequency. Startled individuals also growled as an alarm (24%, n=35) and during inter-specific encounters (2%, n=3) with caimans (*Caiman crocodilus yacare*).

Cub growl. The cub growl is a pulsed (PU: *X* + SD= 115.8 + 63.62 pulses) sound with harmonic interval (F1, F2, FM: *X* + SD= 0.22 + 0.01 kHz). The mean duration was 0.46 (SD= 0.25) s, with no frequency modulation. The peak frequency coincided with the second harmonic, with a mean value of 0.44 (SD= 0.02) kHz. *Context:* This sound was recorded from newborn cubs (1-3 months) inside the den at a rate of 0.1 sounds/h (Fig. 4g).

Snort. The snort is an explosive, noisy and pulsed sound, emitted during strong exhalations of air with the mouth partially open. While snorting in water, the animals commonly raised their throat out of the water (periscoping). Snorts had a call duration average of 0.27 (SD= 0.1) s and a mean of 6.55 (SD= 2.35) pulses. The average peak frequency was 1.47 (SD= 0.74) kHz, and 75% of the energy of the sound was concentrated in a mean frequency of 2.63 (SD= 0.67) kHz. Snorts can be emitted as a single note or in double bursts. The snort burst was often louder when the animal was startled and may serve to alert other members of the group. Five formants were visible along the spectrogram of the snorts (Fig. 4h). The snort was the second most emitted sound type observed (1.4 sounds/h, Table 1), vocalised by all age categories, including five-month-old cubs. *Context:* This sound was usually emitted during alarm situations (93%, n=726). Snorts were also emitted during intra-specific agonistic encounters (5%, n=39) between different groups and inter-specific events (2%, n=16) when the group faced caimans.

Hah. This noisy and atonal sound was produced by exhalation and/or inhalation (Fig. 4i). The hah is a short sound with mean duration of 0.16 (SD= 0.07) s and an average peak frequency of 1.56 (SD= 0.63) kHz. *Context:* Hahs were emitted mostly in low alarm situations in an inquiry context (100%, n=174). In conflict situations, groups may emit sequential hahs combined with snorts (Fig. 6d). Hahs were emitted at a rate of 0.3 sounds/h and can transition into either alarm or affiliative sounds.

Adult call. The adult call is a harmonic bell-shaped sound (Fig. 4j), vocalised with the mouth partially open. The mean call duration was 0.3 (SD= 0.1) s, with the plateau lasting from 0.01 to 0.26 s (Median= 0.05 s). At least two harmonics were visible with the peak frequency (X + SD= 4.42 + 1.51 kHz) restricted to the F0. The FI had a median value of 0.56 kHz (ranging from 0.217 to 4.15 kHz) and reached its highest value of 5.94 (SD= 1.42) kHz at approximately 0.14 (SD= 0.04) s. Adults emitted 0.2 adult calls/h (Table 1). *Context:* This sound was vocalised mainly when animals were calling to another member of the group (74%, n=120), which sometimes elicited a response from other individuals that called back with either calls or screams. During intra-specific agonistic encounters (21%, n=33) adult calls were emitted in combinations with screams and snorts. Adult calls were also emitted when individuals were startled (5%, n=8). The ending of this sound became harsher and noisier (Fig. 6e) or transitioned to a scream as the senders became more excited.

Adult scream. This harmonic sound, which may have a wavering quality, was emitted with the mouth open. This sound has some pulsed segments (X + SD= 466.35 + 202.72 pulses), a mean duration of 0.93 (SD= 0.41) s and at least eleven visible harmonics (Fig. 4l). The average value of F0 varied from 0.35 (SD= 0.06) kHz in the beginning of the signal to 0.43 (SD= 0.06) kHz at the end, with a high-frequency mean value of 0.48 (SD= 0.08) kHz. The peak frequency exhibited a mean of 1.56 (SD= 0.64) kHz. *Context:* This sound was emitted at a rate of 0.5 sounds/h (Table 1), mainly in situations where it apparently was used as a warning (47%, n=145) during fishing events. The individual that had caught a fish (especially if the fish was large) usually screamed with the prey in its mouth or in its forepaws. This sound was also emitted by giant otters that tried to steal prey caught by another group member, which was usually answered with growls. When the motivation of the individual sender appeared to be more intense, screams showed chaotic components towards the end of the signal (Fig. 6g) or the scream merged into a begging scream. Adult screams were also emitted when individuals called to each other (39%, n=121). For instance, individuals screamed to get cubs out from the den, or if an individual was not keeping up with the rest of the group during excursions, the individual may scream as a signal to wait up, which may be answered with other screams by individuals ahead of it. Moreover, individuals screamed (9%, n=28) when startled, apparently as an alarm for others. Screams may also become harsher in hostile situations, as during intra-specific agonistic encounters (5%, n=16) when almost all members of the group screamed in a chorus interspersed with abrupt calls (Fig. 6h).

Cub scream. This harmonic scream presented in pulsed segments (*X* + SD= 268.22 + 146.67 pulses) with a mean duration of 0.81 (SD= 0.44) s (Fig. 4m). Ten to 24 harmonics were visible. The mean frequency in the beginning of the F0 was 0.32 (SD= 0.07) s, rising to a maximum mean value of 0.37 (SD= 0.05) kHz and then decreasing to a mean value of 0.34 (SD= 0.05) kHz. *Context:* This scream was emitted by young cubs at a rate of 0.2 sounds/h from within the den.

Begging scream. This sound is derived from the adult scream but with a highly frequency modulated tonal component along parts of the signal or throughout the entire sound (Fig. 5a). The begging scream was produced by opening and closing the mouth when in high-intensity motivational states. The mean begging scream duration was 1.21 (SD= 1.03) s. The mean F0 frequency value was 0.39 (SD= 0.1) kHz in the beginning, rising to 0.49 (SD= 0.09) kHz and decreasing to a mean of 0.36 (SD= 0.09) kHz at the end of the sound. The peak frequency (PF: *X* + SD= 3.13 + 1.82 kHz) was higher than that for the adult scream because of the high modulation index of the tonal component that modulates this sound from a minimum PF of 1.17 (SD= 0.39) kHz to a maximum PF of 6 (SD= 1.32) kHz. *Context:* The begging scream was emitted at a rate of 0.3 sounds/h (Table 1) in a begging context during fishing events (58%, n=86) and during agonistic encounters (32%, n=48). Individuals sometimes screamed when scent marking (10%, n=15), probably in response to an intruder's scent.

Cub begging scream. This scream lasted a mean of 2.65 (SD= 1.39) s. The mean value of the F0 was 0.33 (SD= 0.03) kHz at the beginning of the sound, reaching a maximum value of 3.22 kHz (median of 0.48 kHz) and ending with an average frequency of 0.37 (SD= 0.04) kHz. The peak frequency was higher than that of the adult scream, with a mean value of 2.67 (SD= 0.87) kHz. The tonal component ranged from a minimum PF of 1.59 (SD= 0.07) kHz to a maximum of 5.69 (SD= 1.83) kHz. *Context:* Cub begging screams were emitted at a rate of 0.7 sounds/h, when begging for fish (n=155).

High scream. This harmonic scream was vocalised with the mouth open. The median call duration of adult high screams was 0.94 s (ranging from 0.36 to 2.25 s, Fig. 5b). Unlike the adult scream, the peak frequency values were found for F0. The start frequency of F0 ranged from 0.39 to 6.09 kHz, ascending to a mean frequency of 6.31 (SD= 1.05) kHz and decreasing to 3.02 (SD= 1.88) kHz at the end. This sound showed nonlinear phenomena, including subharmonics and biphonation at irregular time intervals. *Context:* High screams were heard only in five fishing events (emission rate= 0.1 sounds/h, n=25), when the adult begged for a fish from another group member. High screams were often combined in a continuous sequence with adult screams.

Cub high scream. This scream showed at least three visible harmonics (Fig. 5c) and was recorded from young cubs (1-3 months) within the den. The median duration of this scream was 0.46 s (ranging from 0.29 to 0.95 s). The F0 began at a frequency of 3.03 (SD= 1.71) kHz, ascended to a maximum frequency of 5.19 (SD= 1.96) kHz and then decreased to 2.83 (SD= 0.98) kHz towards the end. *Context:* This sound was emitted at a rate of 0.05 sounds/h and sometimes displayed a gradation distinct from cub screams (Fig. 6i).

Cub call. This high pitched and loud sound is emitted with the mouth open (Fig. 5d). Cub calls were frequency modulated with a mean duration of 0.35 (SD= 0.15) s and sometimes showed a plateau in frequency of variable intervals (median 0.03 s, ranging from 0 to 0.34 s). The mean F0 was 3.17 (SD= 2.12) kHz in the beginning, ascending to an average frequency of 8.83 (SD= 1.92) kHz, with a mean interval of 0.13, (SD= 0.06) s and then decreasing to a mean frequency of 5.54 (SD= 2.82) kHz. *Context:* Cub calls were the most frequent (Emission rate = 3.4 sounds/h) sounds, and they were vocalised by individuals ranging from 2 to 9 months of age (Table 1). This sound was mainly emitted when cubs were calling to others (59%, n= 811), typically when they were separated from the group. Cubs also used this type of sound to beg for fish (31%, n= 426) during fishing sessions. During more excited states, these calls may have a harsher ending (Fig. 6f) or merge into a longer and high-frequency modulated begging scream. Cubs also called when cared for by adults (10%, n=137) in close-contact events.

Scream-gurgle. The scream-gurgle is a harmonic sound with a mean duration of 1.01 (SD= 0.1) s. This sound begins with a pulsed scream (PU: *X* + SD= 227.17 + 33.89 pulses) and ascends to a high-frequency interval, comprising four to five bell-shaped frequency modulated parts interspersed by short screams (Fig. 5e). The scream part has a mean F0 value of 0.24 (SD= 0.03) kHz at the beginning of the sound and 0.33 (SD= 0.04) kHz at the end of the sound. The middle bell-shaped parts of this sound have a maximum F0 of 7.83 (SD= 0.9) kHz. The peak frequency value was found in the scream structure with a mean value of 0.75 (SD= 0.26) kHz. *Context:* Scream-gurgles were vocalised by young cubs inside the den at a rate of 0.1 sounds/h, and other cubs frequently vocalised screams and high screams in the background. All scream-gurgles were vocalised when the lactating female was in the den. On one occasion, the cubs were seen emitting scream-gurgles while suckling from the female, which was lying near the den entrance.

Squeak. This harmonic sound was recorded only from two-month-old cubs from one group, resulting in an emission rate of 0.03 sounds/h. The mean duration of squeaks was 0.44 (SD= 0.1) s, with a peak frequency of 8.38 (SD= 0.65) kHz (Fig. 5f). The mean frequency of F0 at the beginning of the sound was 0.52 (SD= 0.06) kHz, rising to an average maximum frequency of 0.72 (SD= 0.07) kHz. *Context:* This sound was vocalised during a close contact event, while adults were caring for cubs, emitting purrs, coos and hums in the background.

The PCoA analysis resulted in three axes that accounted for 56% of the variation among sounds types, with 27.7% of the variation represented by the first axis; 17.1%, by the second axis;

and 11.2%, by the third axis. Axis 1 had the highest loadings for the D2 (-0.686), D1 (-0.573) and PU (-0.536), and axis 2 had the highest loadings for FD (0.675), PU (-0.388) and PD (-0.328), while PU (0.377), D1 (-0.353) and FD (0.302) presented the highest loadings on the third axis (Fig. 7). The behavioural context of sound types was significantly associated with the ordination of acoustic variables provided by the three axes of the PCoA (PERMANOVA: $F_{6,451}$=121.7, R^2=0.62, P<0.001).

DISCUSSION

The vocal repertoire of giant otter groups in this study comprised 15 main sound types, usually emitted in different behavioural contexts. Inclusion of different age categories of the sender results in a total of 19 sound types. Duplaix (1980) described nine of these sounds qualitatively for giant otters from a locality in Suriname. Bezerra et al. (2010) presented acoustic measurements of five known sounds (snort, hah, scream, purr and cub call) emitted by five giant otters observed in the Jaú National Park, Amazonas, Brazil. Machado (2004) also identified nine sound types emitted by captive giant otters and free-ranging groups in the Balbina Hydroelectric reservoir in the Brazilian Amazon and suggested three new sounds recorded from captive giant otters (buck, humhum and a sound emitted by a resting adult female).

In our study, the purr was the sound that was most used by adults, followed by the snort, while the cub call was the most frequently emitted vocalisation by cubs. Purrs have been described in many mammal vocal repertoires (Peters 2002) and are commonly classified as an affiliative close-contact sound (Sieber 1984; Wong et al. 1999). Giant otters emitted purrs in intra-group close-contact events and when individuals were engaged in group activities, such as scent marking or swimming. The emission of purrs by giant otter groups in Suriname was rare, as Duplaix (1980) recorded this sound only when adults were caring for young cubs, which was replaced by hums and coos as cubs grew. However, Bezerra et al. (2010) recorded purrs vocalised by a giant otter group in the Amazon but did not mention hums or coos, which were relatively common in our study (emission rate, hum=0.5 sounds/h and coo=1.1 sounds/h). Snorts, hahs, adult screams and cub calls seem to be common vocalisations in the repertoire of giant otters, as they have been described by many authors (Duplaix 1980; Machado 2004; Staib 2005; Bezerra et al. 2010; this study). Variation in repertoire sizes as well as call-emission rates among giant otters from different localities may be a consequence of differences in environmental features, learning, or genetic variation among clades (Bradbury & Vehrencamp 1998; Wilson 2000).

The ability to detect rare sound types may be compromised by limited opportunities to witness specific behaviours, such as the newborn cub's squeaks recorded from young cubs by Duplaix (1980). Some sounds, such as the cub growl, scream-gurgle, scream, and high scream were first reported in the present study. Morales-Betancourt (2011) described a comfort sound that may refer to the scream-gurgle sound, which was emitted by a captive juvenile male before sleeping and performing a suckling-like movement. Tonal whistles were recorded once by Duplaix (1980) during an intra-group event in Suriname. Ribas & Mourão (2004) also mentioned whistles during an agonistic encounter between a giant otter group and a solitary male in the Pantanal, but the sound presented a harmonic structure, characteristic of adult calls, as we witnessed in five other agonistic encounters between giant otter groups.

The vocal repertoire of a species includes a variation of sounds, which may transmit a corresponding number of messages (Bradbury & Vehrencamp 1998). The giant otter snort is a sound type that is also found in the repertoire of other mammals (Sieber 1994; Wong et al. 1999) and that is commonly emitted in alarm situations. In giant otters, more energetic snorts (with increasing amplitude) cause an immediate response of group members, which usually run to the water and submerge. The atonal hah appears to mean an inquiry (Duplaix 1980), and it is similar to the hiss sound commonly vocalised in aggressive and fearful contexts by sea otters (McShane et al. 1995) and other mustelids (Huff & Price 1968; Farley et al. 1987; Wong et al. 1999). Screams and harmonic sounds are frequent in the repertoires of many species (McShane et al. 1995; Wong et al. 1999, Fitch et al. 2002), and they may provide identity information and have an important function in group cohesion, as they can be heard at great distances (McComb & Reby 2005). Some physical features of sounds, such as the presence of formants in the snorts and the fundamental frequency of harmonic sounds, can be considered an ‘honest’ indication of body size and individual identity (McShane et al. 1995; Sousa-Lima et al. 2002; Fitch et al. 2002; Taylor & Reby 2010), and they should be considered in studies of acoustic individuality in the species.

Nonlinear components, shown as chaotic structures, biphonations and subharmonics, were observed in adult screams and high screams. These acoustic phenomena originate from the intrinsic properties of the vibrating components of the larynx (Fitch et al. 2002; Tokuda et al. 2005) but may also be produced by the presence of systemic infection or diseases in the vocal tract (Riede et al. 1997). The presence of nonlinear components has been observed in many other mammalian vocalisations (Wilden et al. 1998; Riede et al. 2000; Fitch et al. 2002; Sousa-Lima et al. 2002; Blumstein et al. 2008; Riede et al. 2008) and may be a means of achieving individual recognition (McComb & Reby 2005). However, in some mammals, the presence of non-linearity in sounds may indicate the arousal state of individuals (*Marmota flaviventris*, Blumstein et al. 2008; *Ailuropoda melanoleuca*, Briefer et al. 2012; Stoeger et al. 2012).

The behavioural contexts of sound types were significantly associated with the acoustic variables. The main variables of the three axes of the PCoA were related to the duration and shape of the sound (D1, D2, FD) and the number of pulses (PU). According to Briefer et al. (2012), there is a positive relationship between arousal level and some acoustic variables, such as call duration, F0 range and F0 contour. This observation is consistent with the motivational structure (MS) model, which hypothesises that sounds vocalised in aggressive and hostile situations are low frequency and noisy and that sounds vocalised in fearful or friendly contexts are high frequency and tonal (Collias 1960; Morton, 1977; August & Anderson 1987). In the giant otter vocal repertoire, alarm, inquiry and warning sounds were noisier and occurred at lower frequency, while calls and some scream types were harmonic and had higher frequencies. In more excited motivational states, the endpoint of adult calls and screams becomes harsher and noisier, indicating a high degree of individual hostility, as suggested by Morton (1977). The harmonic coo sounds vocalised in close contacts changed from a lower amplitude coo with a silent interval to a combination coo-hum and, in a more excited state, to a coo-call with a high frequency interval, which may elicit proximity in affiliative contexts. Although there is much overlap between fearful and friendly contexts (August & Anderson 1987), the vocal repertoire of giant otters seems to be consistent with the MS hypothesis and may reflect the arousal state of individuals.

Transitions and gradations may increase the variability of sound combinations and convey more information than discrete signals (Wilson 2000). The vocal repertoire of giant otters can be classified as a continuum, presenting graded sounds that were common during affiliative close contacts and in more excited and agonistic events. The combination of sounds, as between the hum and the affiliative purr, or the hum with the aggressive growl, probably increases the amount of decodable information (Crockford & Boesch 2005). During agonistic encounters, adult screams became modulated and turned into abrupt calls generating a harsh and long chorus (Ribas & Mourão 2004; this study). During some excited fishing events, as well as during suckling, screams and cub calls graded to begging screams or high screams.

Giant otter vocal repertoires represent a good example of how communication is intrinsically linked with sociality (Pollard & Blummstein 2012). The presence of gradations and transitions in the vocal repertoire of giant otters reflect their high degree of sociality, as previously suggested (Duplaix 1980; 1982) and observed in other social mammals (*Canis lupus*, Schassburger 1993; *E. lutris*, McShane et al. 1995; Wilden et al. 1998; *M. meles*, Wong et al. 1999; *Pan troglodytes*, Crockford & Boesch 2005). The variety of sound types and possible combinations, as well as the function of nonlinear components in giant otter vocalisations, should be considered in future acoustic studies, as these components may indicate an important mechanism in the communication system of the species. Although giant otter vocalisations can be subjectively divided into a few dozen categories, they occupy almost all of the available multivariate space when analysed as continuous variables. Not only for giant otters, but also for other social mammals, rather than defining subjective new sound types, it may be more productive to describe vocalisations in multivariate space and relate these coordinates to presumed motivational states of the animals involved.

ACKNOWLEDGMENTS

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RESUMO

Ariranha (*Pteronura brasiliensis*) é uma espécie altamente social. O conhecimento de seu repertório vocal é limitado a descrições qualitativas e gravações oportunísticas de sons em contextos específicos. O objetivo deste estudo foi descrever, qualitativamente e quantitativamente, o repertório vocal de ariranhas no Pantanal Brasileiro e a distribuição dos tipos sonoros em diferentes contextos comportamentais. Nós classificamos 15 tipos sonoros básicos emitidos por ariranhas de diferentes idades, em diferentes contextos comportamentais. Chamados de filhotes e *purrs* foram os sons emitidos mais frequentemente. No entanto, o repertório vocal de ariranhas compreende um contínuo de tipos sonoros, com combinações, gradações e transições que proporcionam um repertório maior do que os 15 tipos básicos, refletindo o sistema de comunicação complexo usado por essa espécie social. Não apenas para ariranhas, mas também para outros mamíferos sociais, em vez de apenas definir novos tipos sonoros, pode ser mais produtivo descrever vocalizações em um espaço multivariado e relacionar essas coordenadas com o estado motivacional dos animais.

Keywords: comunicação, taxa de emissão, *Pteronura brasiliensis*, comportamento social, vocalisação.

REFERENCES

Alho, C. J. R. 2008. Biodiversity of the Pantanal: response to seasonal flooding regime and to environmental degradation. *Brazilian Journal of Biology*, **68**(4), 957-966.

Altmann, J. 1974. Observational study of behaviour: sampling methods. *Behaviour*, **49**, 227–267.

August, P. V. & Anderson, J. G. T. 1987. Mammal sounds and motivation-structural rules: A test of the hypothesis. *Journal of Mammalogy*, **68**(1), 1-9.

Belan, I.; Lehner, P. N. & Clark, T. 1978. Vocalizations of the American Pine Marten, *Martes americana*. *Journal of Mammalogy*, **59**(4), 871-874.

Bezerra, B. M.; Souto, A. S., Schiel, N. & Jones, G. 2010. Notes on vocalisations of giant otters in the flooded Igapó forests of Jaú National Park, Amazonas, Brazil. *Journal of Ethology*, **29**(1), 169-175.

Blumstein, D. T.; Richardson, D. T.; Cooley, L., Winternitz, J. & Daniel J.C. 2008. The structure, meaning and function of yellow-bellied marmot pup screams. *Animal Behaviour*, **76**, 1055-1064.

Bradbury, J. W. & Vehrencamp, S. L. 1998. *Principles of Animal Communication*. Massachusetts, Sinauer Associates Inc. Publishers. 882 p.

Briefer, E. F. 2012. Vocal expression of emotions in mammals: mechanisms of production and evidence. *Journal of Zoology*, http://dx.doi.org/10.1111/j.1469-7998.2012.00920.x.

Collias, N. E. 1960. An ecological and functional classification of animal sounds. *In: Animal sounds and communication* (Ed. By Lanyon, W.E. & Tavolga, W.N.), pp. 368-391, American Institute of Biological Sciences.

Crockford, C. & Boesch, C. 2005. Call combinations in wild chimpanzees. *Behaviour*, **142**(4), 397-421.

Duplaix, N. 1980. Observations on the ecology and behaviour of the giant river otter *Pteronura brasiliensis* in Surinam. *Review Ecologique (Terre Vie)*, **34**, 495–520.

Duplaix, N. 1982. Contribution à l'écologie et à l'éthologie de *Pteronura brasiliensis* (Carnivora, Lutrinae): Implications évolutives. PhD Thesis, Université Paris-Sud. 353 p.

Endler, J. A. 2000. Evolutionary implications of the interaction between animal signals and the environment. *In: Animal Signals: Signaling and Signal design in animal communication.* (Ed. By Espmark, Y.; Amundsen, T. & Rosenqvist, G.), pp. 11-46, Tapir Academic Press, Trondheim, Norway. 496 p.

Farley, S.D.; Lehner, P.N.; Clark, T. & Trost, C. 1987. Vocalizations of the Siberian ferret (*Mustela eversmanni*) and comparisons with other Mustelids. *Journal of Mammalogy*, **68**(2), 413-416.

Fitch, W. T.; Neubauer, J. & Herzel, H. 2002. Calls out of chaos: the adaptive significance of nonlinear phenomena in mammalian vocal production. *Animal Behaviour*, **63**, 407–418.

Gnoli, C. & Prigioni, C.1995. Preliminary study on the acoustic communication of captive otters (*Lutra lutra*). *Hystrix*, **7**(1-2), 289-296.

Groenendijk, J.; Hajek, F.; Duplaix, N.; Reuther, C.; Van Damme, P.; Schenk, C.; Staib, E.; Wallace, R.; Waldemarin, H.; Notin, R.; Marmontel, M.; Rosas, F. W. C.; Mattos De, G. E.; Evangelista, E.; Utreras, V.; Lasso, G.; Jaques, H.; Matos, K.; Roopsind, I. & Botello, J. C. 2005. Surveying and monitoring distribution and population trends of the giant otter (*Pteronura brasiliensis*). *Habitat*, **16**, 1-500.

Huff, N. & Price, E. O. 1968. Vocalizations of the least weasel, *Mustela nivalis*. *Journal of Mammalogy*, **49**(3), 548-550.

Lehner, P. N. 1998. Handbook of ethological methods. Garland STPM Press, London, 672 p.

Leuchtenberger C. & Mourão G. 2009. Scent-marking of giant otter in the Southern Pantanal, Brazil. *Ethology*, **115**, 210–216.

Leuchtenberger C. & Mourão G. 2008. Social organization and territoriality of giant otters (Carnivora: Mustelidae) in a seasonally flooded Savanna in Brazil. *Sociobiology*, **52**(2), 257-270.

Machado M. R. B. 2004. Bioacústica de ariranhas (*Pteronura brasiliensis*) (Carnivora: Mustelidae): discriminação vocal e repertório. Master Thesis, Instituto Nacional de Pesquisa da Amazônia.

McComb, K. & Reby, D. 2005. Vocal communication networks in large terrestrial mammals. In: *Animal Communication Networks.* (Ed. by P. McGregor). pp. 372-389. University Press.

McComb, K. & Semple, S. 2005. Coevolution of vocal communication and sociality in primates. *Biology Letters*, **1**, 381–385.

McShane L., Estes J. A., Riedman M. L., Staedler M. M. 1995. Repertoire, structure and individual variation of vocalisation in the sea otter. *Journal of Mammalogy*, **76**, 414–427.

Morales-Betancourt, D. 2011. Report of an adaptive reintroduction of a juvenile giant otter (*Pteronura brasiliensis*). *IUCN Otter Specialist Group Bulletin*, **28**(1), 23-33.

Morton, E. S. 1977. On the occurrence and significance of motivation-structural rules in some bird and mammal sounds. *American Naturalist*, **111**, 855–869.

Mourão, G.; Tomas, W. & Campos, Z. 2010. How much can the number of jabiru stork (Ciconiidae) nests vary due to change of flood extension in a large Neotropical floodplain? *Zoologia*, **27**(5), 751-756.

Oksanen, J.; Kindt, R.; Legendre, P.; O'Hara, B.; Simpson, G. L.; Solymos, P.; Stevens, M. H. H. & Wagner, H. 2008. The Vegan Package.

Peters, G. 2002. Purring sounds in mammals. *Mammal Review*, **32**(4), 245–271.

Pollard, K. A. & Blumstein, D. T. 2012. Evolving communicative complexity: insights from rodents and beyond. *Philosophical Transactions of The Royal Society B*, **367,** 1869–1878.

Ribas, C. & Mourão, G. 2004. Intraspecific agonism between giant otter groups. *IUCN Otter Specialist Group Bulletin*, **21**, 89–93.

Ribas, C.; Damasceno G.; Magnusson W.; Leuchtenberger C. & Mourão, G. 2012. Giant otters feeding on caiman: evidence for an expanded trophic niche of recovering populations. *Studies on Neotropical Fauna and Environment*, **47**(1), 19-23.

Riede, T.; Wilden, I & Tembrock, G. 1997. Subharmonics, biphonations, and frequency jumps-common components of mammalian vocalization or indicators for disorders. *Zeitschrift für Säugetier*, **62**(Suppl 2), 198–203.

Riede, T.; Herzel, H.; Mehwald, D.; Seidner, W.; Trumler, E.; Böhme, G. & Tembrock, G. 2000. Nonlinear phenomena in the natural howling of a dog-wolf mix. *The Journal of the Acoustical Society of America*, **108**, 1435–1442.

Riede, T.; Owren, M. J. & Arcadi, A. C. 2008. Nonlinear acoustics in pant hoots of common chimpanzees (*Pan troglodytes*): frequency jumps, subharmonics, biphonation, and deterministic chaos. *American Journal of Primatology*, **64**, 277–291.

Roux, A. L.; Cherry, M. I. & Manser, M. B. 2009. The vocal repertoire in a solitary foraging carnivore, *Cynictis penicillata*, may reflect facultative sociality. *Naturwissenschaften*, **96**, 575–584.

Schassburger, R. M. 1993. *Vocal communication in the Timber Wolf, Canis lupus, Linnaeus*. Paul Parey Scientific Publishers, Berlin, Germany.

Sieber, O. J. 1984. Vocal communication in raccoons (*Procyon lotor*). *Behaviour*, **90**(1/3), 80-113.

Silveira, L.; Furtado, M. M.; Rosas, F. C. W.; Silva, L. C.; Cabral, M. M. M.; Torres, N. M.; Sollmann, R.; Kouba, A. & Jácomo, A. T. A. 2011. Tagging giant otters (*Pteronura brasiliensis*) (Carnivora, Mustelidae) for radio-telemetry studies. *Aquatic Mammals*, **37**, 208-212.

Sousa-Lima, R.; Paglia, A. P. & Fonseca, G. A. B. da. 2002. Signature information and individual recognition in the isolation calls of Amazonian manatees, *Trichechus inunguis* (Mammalia: Sirenia). *Animal Behaviour*, **63**, 301–310.

Staib, E. 2005. Eco-etología del lobo de río (*Pteronura brasiliensis*) en el sureste del Perú. PhD Thesis – Sociedad Zoológica de Francfort Perú, 195 p.

Stoeger, A.; Baotic, A.; Li, D. & Charlton, B. D. 2012. Acoustic features indicate arousal in infant giant panda vocalisations. *Ethology*, **118**, 1–10.

Sueur, J.; Aubin, T. & Simonis, C. 2008. Seewave: a free modular tool for sound analysis and synthesis. *Bioacustics*, **18**, 213-216.

Taylor, A. M. & Reby, D. 2010. The contribution of source–filter theory to mammal vocal communication research. *Journal of Zoology*, **280**, 221–236.

Tokuda, I.; Riede, T. Neubauer, J.; Owren, M. & Herzel, H. 2005. Nonlinear analysis of irregular animal vocalizations *The Journal of the Acoustical Society of America*, **111**(6), 2908-2919.

Venables, W. N. & Ripley, B. D. 2002. *Modern applied statistics with S.* 4th edition. Springer, New York.

Wilden, I.; Herzel, H.; Peters, G. & Tembrock, G. 1998. Subharmonics, biphonation, and deterministic chaos in mammal vocalization. *Bioacoustics*, **9**, 171-196.

Wilson, E. 2000. *Sociobiology: The new synthesis*. 25th Aniversary ed. President and Fellows of Harvard College, USA. 697 p.

Wong, J.; Stewart, P. D. & MacDonald, D. W. 1999. Vocal repertoire in the European badger (*Meles meles*): structure, context, and function. *Journal of Mammalogy*, **80**, 570–588.

FIGURE LEGENDS

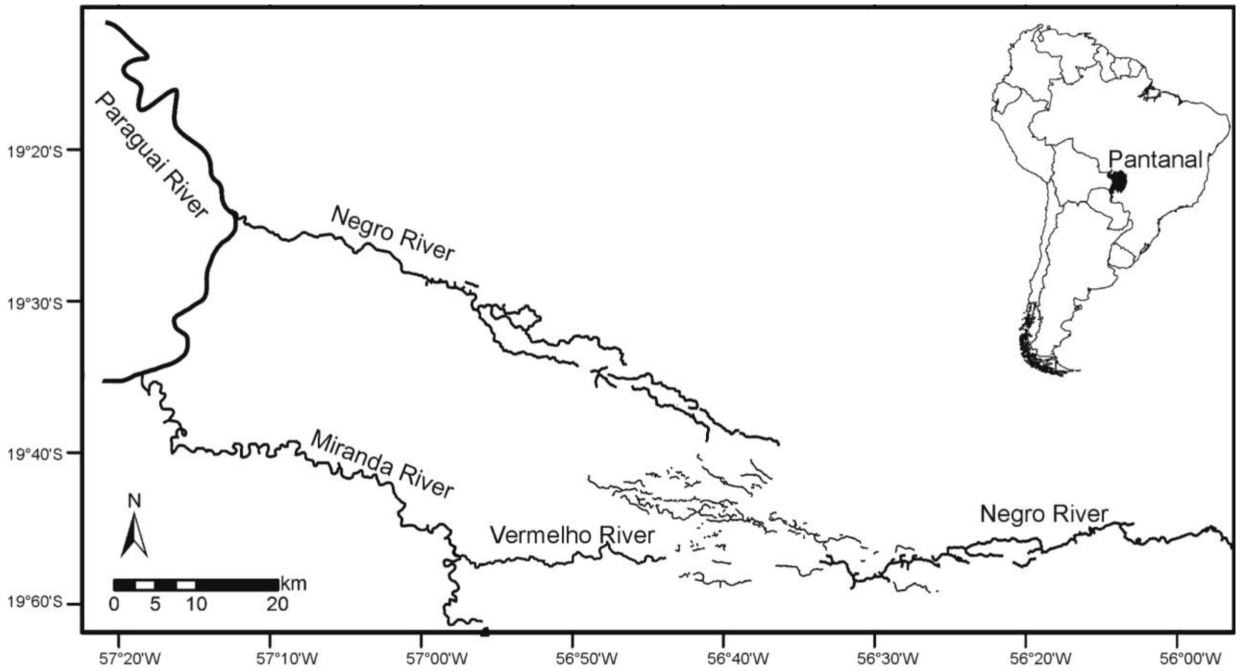


Figure 1. Map of the study area, presenting the Miranda and Vermelho Rivers, located in the Southern Pantanal in Brazil.

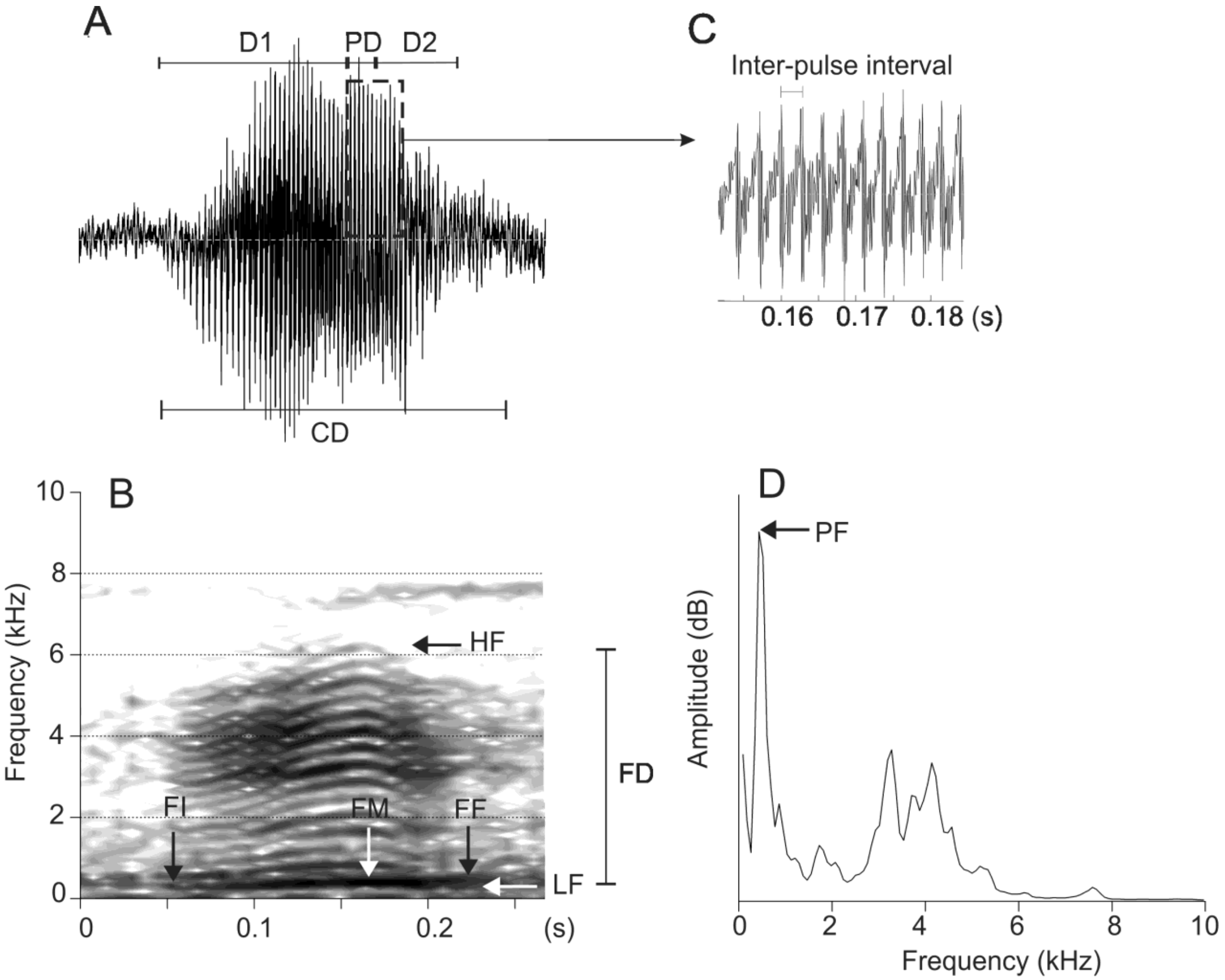


Figure 2. Measurements of acoustic parameters of a giant-otter coo-hum call: A) Oscillogram used to measure the total call duration (CD); the duration (D1) from the start of the vocalisation to the highest value of fundamental frequency (F0) or Peak frequency (PF); the duration (D2) from the highest frequency of F0 or PF to the end of the vocalisation; and the plateau duration (PD), when the frequency of F0 or PF did not vary. B) Spectrogram (winodw size 512) used to measure the lowest frequency (LF) of the sound; the highest frequency (HF) of the sound; the difference (FD) between HF and LF; the initial frequency (FI) of F0 or PF of the sound; final frequency (FF) of F0 or PF; and the maximum frequency (FM) of the FO or PF. C) Zoom view of a stretch of the oscillogram showing the measurement of the inter-pulse interval used to estimate the number of pulses of the sound. D) Power spectrum used to measure of the peak frequency (PF) of the selection.

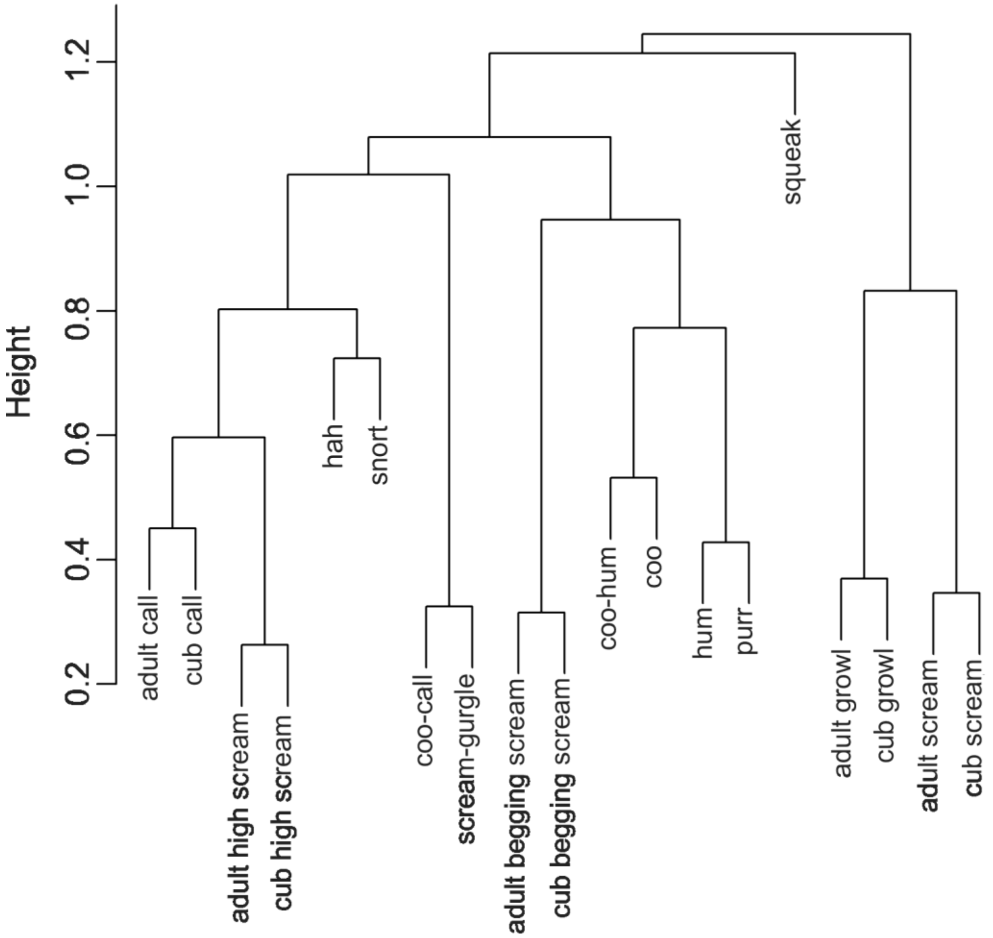


Figure 3. Dendrogram of the hierarchical-cluster relationship of the 19 sounds (N=458 vocalizations) emitted by giant otters distributed in 9 groups in the Southern Pantanal, from November 2009 to June 2011.

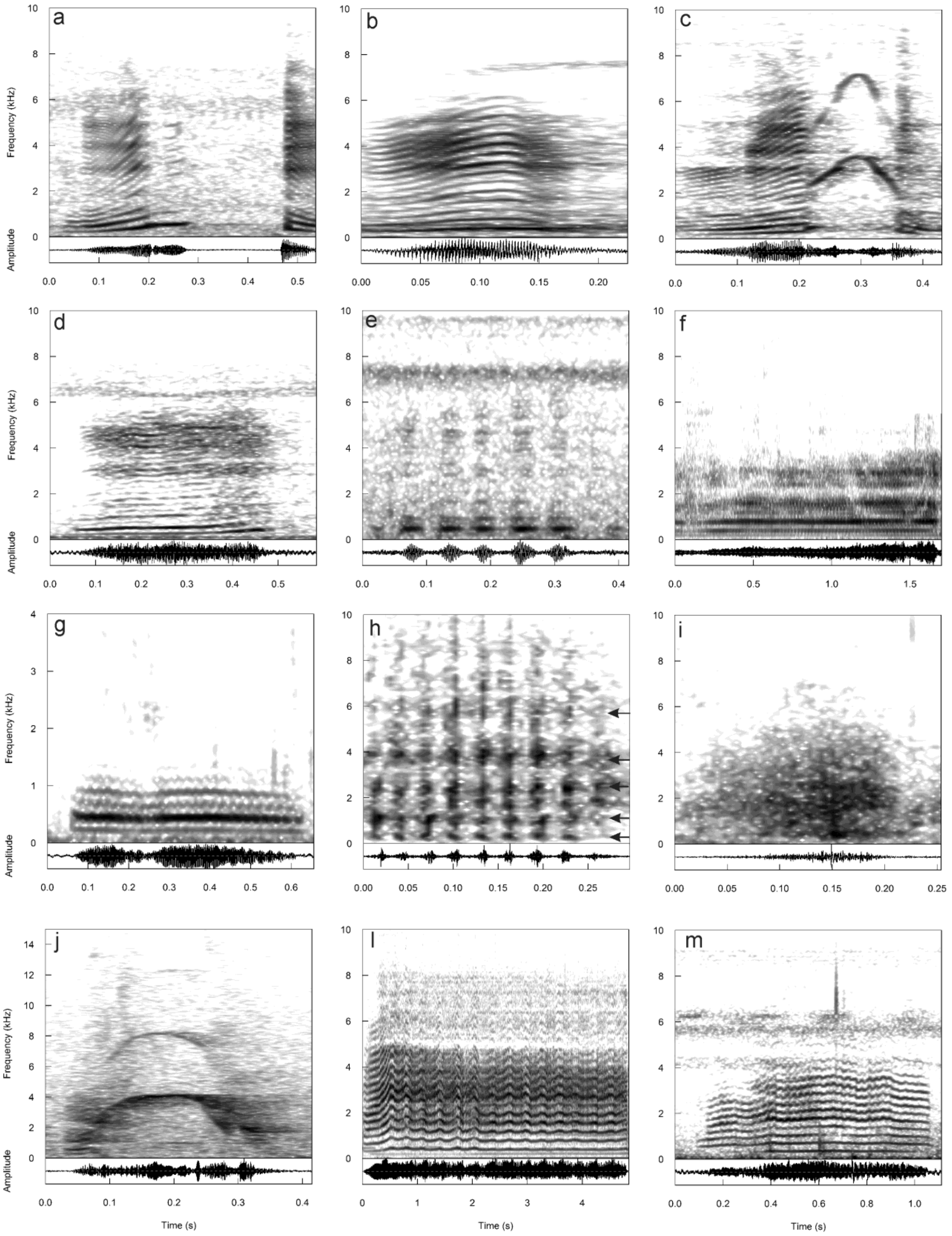

a
b
c
d
e
f
g
h
i
j
l
m
Frequency (kHz)
Amplitude
Time (s)
0 2 4 6 8 10
0 1 2 3 4
0 2 4 6 8 10 12 14
0.0 0.1 0.2 0.3 0.4 0.5
0.00 0.05 0.10 0.15 0.20
0.0 0.1 0.2 0.3 0.4
0.0 0.1 0.2 0.3 0.4 0.5
0.0 0.1 0.2 0.3 0.4
0.0 0.5 1.0 1.5
0.0 0.1 0.2 0.3 0.4 0.5 0.6
0.00 0.05 0.10 0.15 0.20 0.25
0.00 0.05 0.10 0.15 0.20 0.25
0.0 0.1 0.2 0.3 0.4
0 1 2 3 4
0.0 0.2 0.4 0.6 0.8 1.0

Figure 4. Spectrograms and oscillograms (bottom) of vocalisations emitted by giant otters in the southern Pantanal of Brazil: a) coo (FFT=1024), b) coo-hum (FFT=1024), c) coo-call (FFT=1024), d) hum (FFT=1024), e) purr (FFT=512), f) adult growl (FFT=512) , g) cub growl (FFT=512, note the scale difference in frequency), h) snort (FFT=512, arrows indicate formants), i) hah (FFT=512), j) adult call (FFT=512, note scale difference in frequency), l) adult scream (FFT=1024), and m) cub scream (FFT=1024).

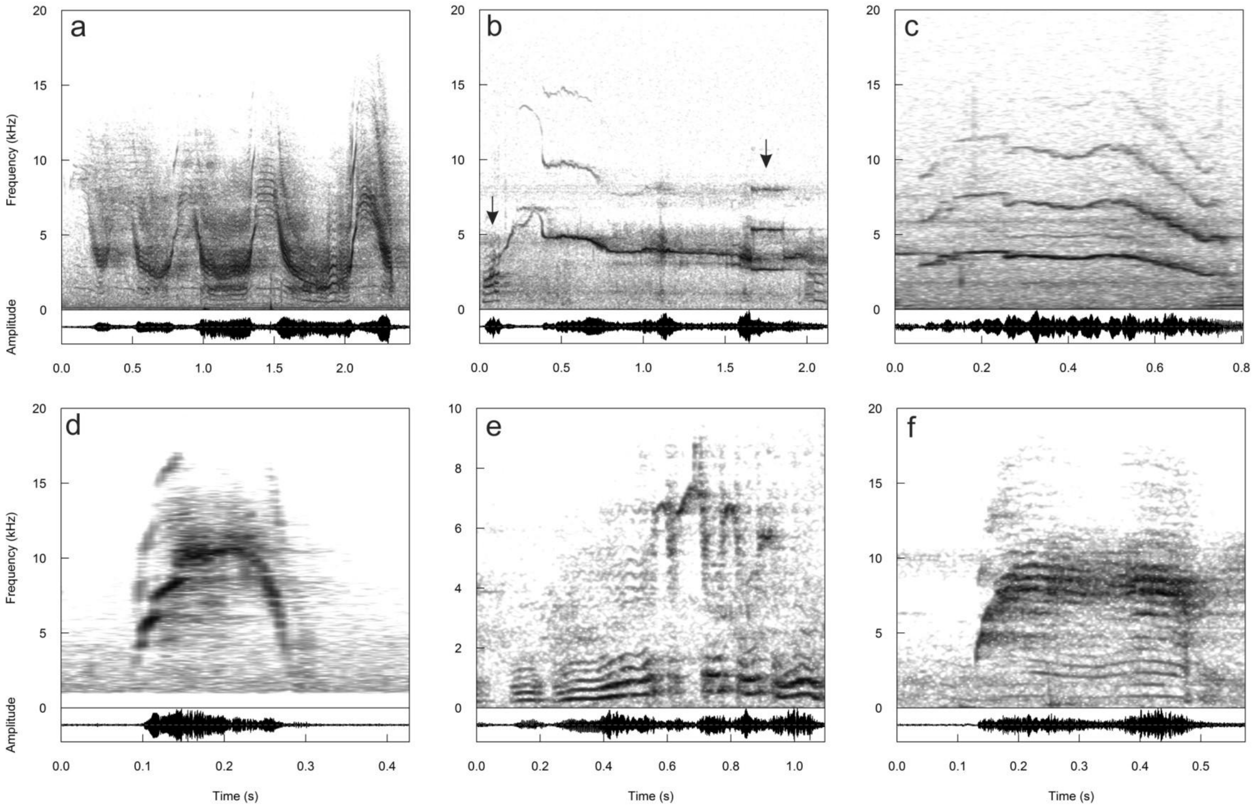


Figure 5. Spectrograms and oscillograms (bottom) of vocalisations emitted by giant otters in the southern Pantanal of Brazil: a) cub begging scream (FFT=1024), b) adult high scream (FFT=1024, arrows indicate subharmonics and a biphonation), c) cub high scream (FFT=1024), d) cub call (FFT=512), e) scream-gurgle (FFT=512, note the scale difference in frequency), and f) squeak (FFT=512).

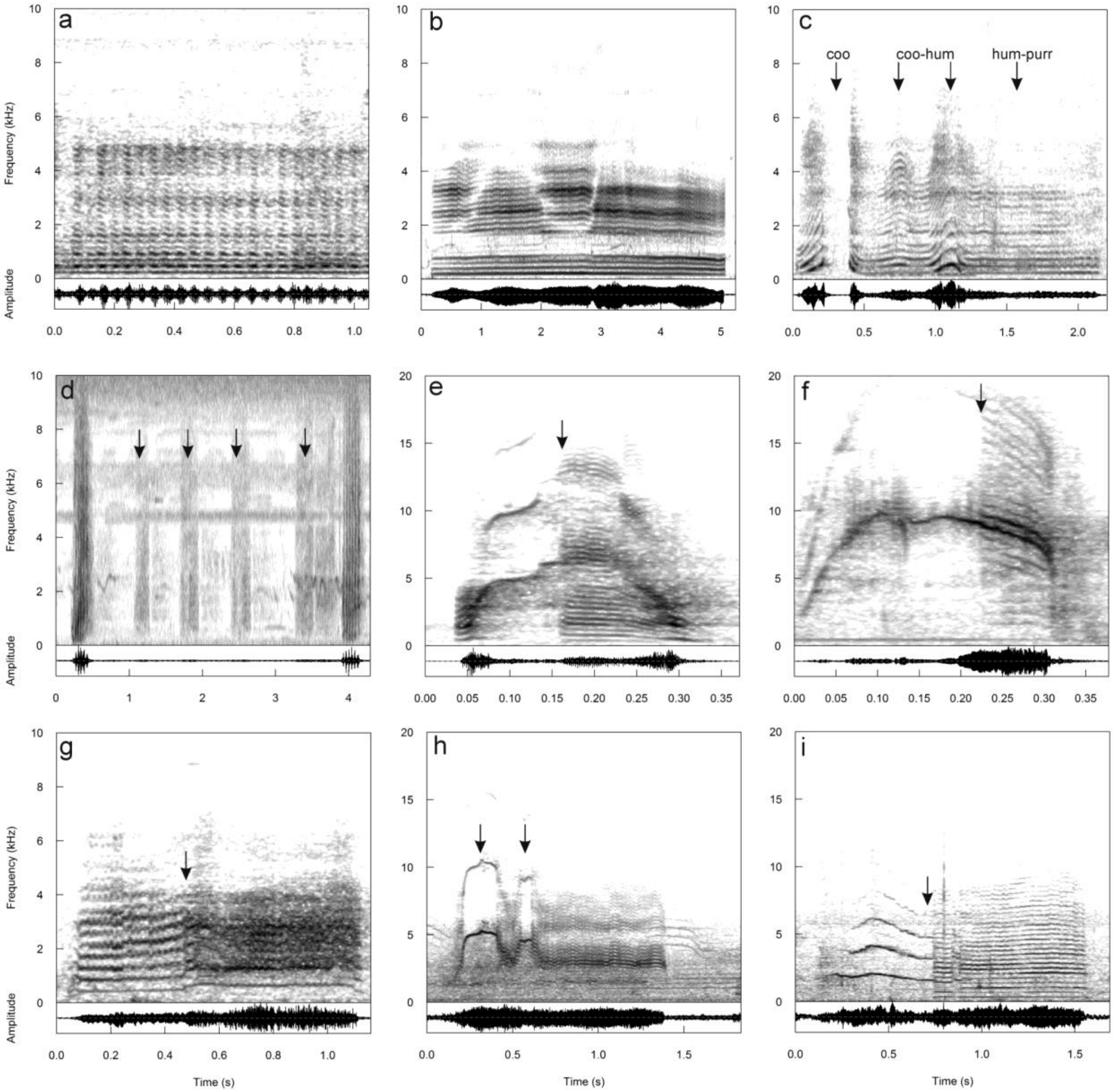
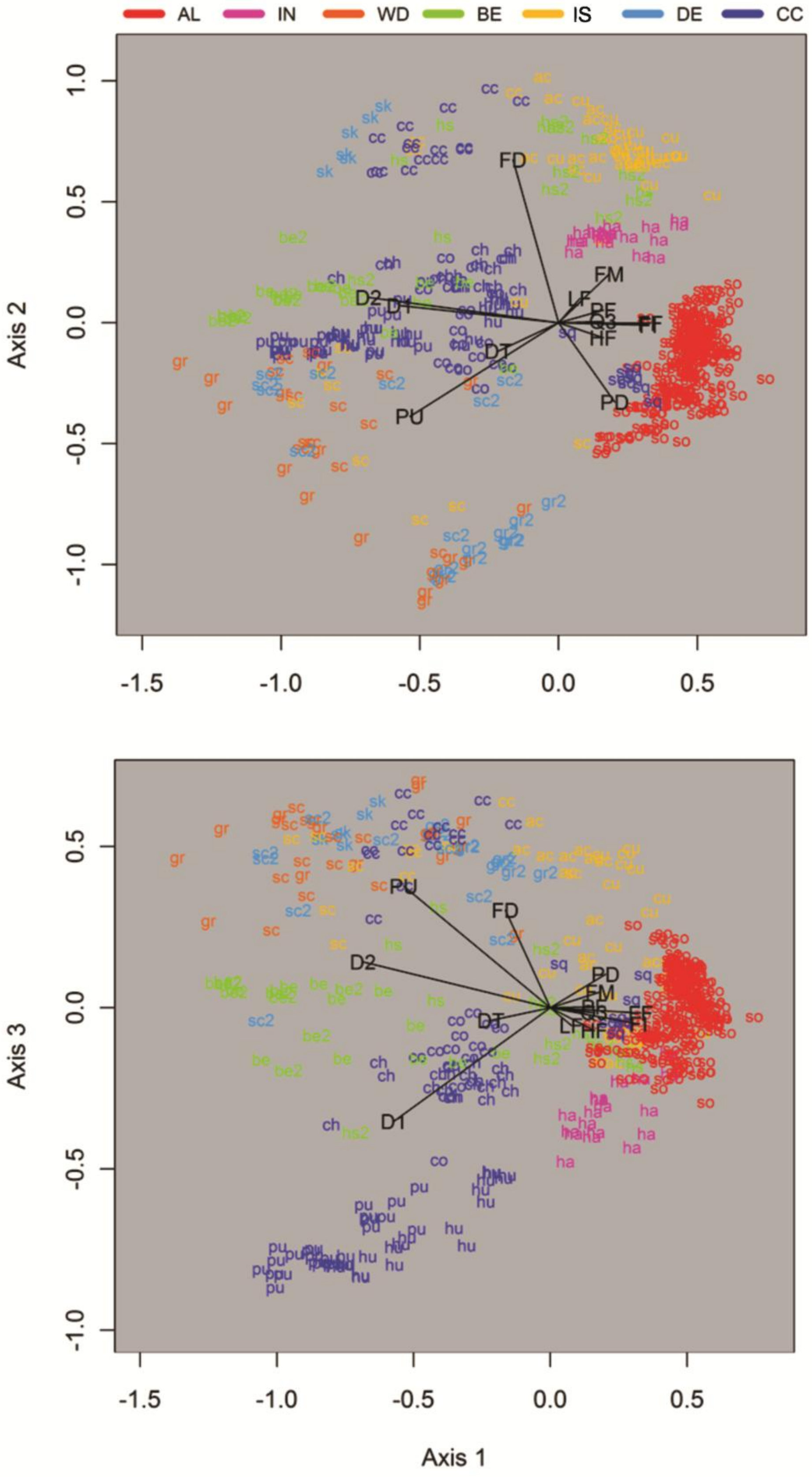


Figure 6. Spectrograms and oscillograms (bottom) of vocalisations emitted by giant otters in the southern Pantanal of Brazil: a) combination of hum and purr sounds (hum-purr, FFT=1024), b) combination of hum and growl sounds (hum-growl, FFT=1024), c) gradation among affiliative sounds (coo, coo-hum and hum-purr, FFT=1024), d) sequence of snort-hahs (indicated by arrows, FFT=512), e) adult call with a harsh, noisy ending (arrow indicates the transition, FFT=512), f) cub call with a harsh, noisy ending (arrow showing the transition, FFT=512), g) adult scream with a harsh, noisy ending (arrow indicates the transition, FFT=512), h) transition of adult calls

(arrows) and adult scream vocalised during an agonistic encounter (FFT=1024), and i) transition between cub high scream and cub scream (arrow indicates the transition, FFT=1024).


AL
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FD
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Figure 7. Biplots of the relationship between the first and second axes (a) and the first and third axes (b) of the principal coordinate analysis of 19 sound types vocalised by giant otters in different behavioural context (AL-alarm, IN-inquiry, WD-warning/defense, BE-begging, IS-isolation, DE-within den, CC-close contact) represented by different colours (see legend above the graphs). Small letters refer to the different sound types (co=coo, cc=coo-call, ch=coo-hum, hu=hum, pu=purr, gr=growl, gr2=cub growl, so=snort, ha=hah, ac=adult call, sc=adult scream, sc2=cub scream, be=adult begging scream, be2=cub begging scream, hs=adult high scream, hs2=cub high scream, cu=cub call, sk=scream-gurgle, sq=squeak), and the capital letters (in black) indicate the sound features analysed (CD=call duration, LF= lowest and HF=highest frequencies of the sound, PF=peak frequency of the entire sound, Q3=3rd quartile frequency, PU=number of pulses of the sound, FI=initial value of F0 (for harmonic sounds) or of the peak frequency (for non-harmonic sounds), FM=maximum value of F0 or PF, FF=final F0 or PF, FM=maximum frequency of F0 or PF, FD=difference between the highest and the lowest frequency of F0 or PF, D1=duration from the start of the vocalisation to the highest frequency value of F0 or PF, D2=duration from the highest F0 or PF to the end of the vocalisation, and PD=plateau duration (when F0 or PF did not varied)).

TABLES

Table 1. Individual emission rates (number of sounds/hour) and proportions of giant otter vocalisations given in different behavioural contexts (CC – close contact, GR – grooming, SW – swimming, DE – within the den, SM – scent-marking, IS – isolation, BE – begging, WD – warning/defense , IN – inquiry, AL – alarm, IA – intraspecific agonistic encounter, and IE – interspecific encounter by adults (A), subadults (S), juveniles (J) and cubs (C) from six groups. *N* is the number of sounds recorded, (groups) refers to the number of groups that presented that particular sound type in its repertoire.

				BEHAVIORAL CONTEXT (%)											
Sound	***N* (groups)**	**Age class**	**Sound/h**	**CC**	**GR**	**SW**	**DE**	**SM**	**IS**	**BE**	**WD**	**IN**	**AL**	**IA**	**IE**
1. Cub call	1388 (6)	J/C	3.4	10					59	31					
2. Purr	1523 (6)	A/S	3.0	52	15	12		21							
3. Snort	781 (6)	A/S/J/C	1.4										93	5	2
4. Coo	584 (6)	A/S	1.1	51	9	14		26							
5. Coo-hum	322 (6)	A/S	0.7	72	9	12		5	2						
6. Adult scream	310 (5)	A/S	0.5						39		47		9	5	
6.1. Cub scream	43 (5)	C	0.2				100								
7. Hum	235 (6)	A/S	0.5	55	19	5		21							
8. Coo-call	197 (6)	A/S	0.3	64		8		12	16						
9. Hah	174 (6)	A/S	0.3									100			
10. Adult begging scream	149 (4)	A/S	0.3					10		58				32	
10.1. Cub begging scream	155 (3)	J/C	0.7							100					
11. Growl	149 (5)	A/S	0.3								74		24		2
11.1. Cub Growl	12 (1)	C	0.1				100								
12. Adult call	148 (6)	A/S	0.2						74				5	21	
13. Scream-gurgle	25 (3)	C	0.1				100								
14. Adult high scream	25 (3)	A/S	0.1							100					
14.1. Cub high scream	11 (2)	J/C	0.05				100								
15. Squeak	15 (1)	C	0.03	100											
Total	6246		11.4												

Table 2. Descriptive statistics [*X* ±SD or median (minimum-maximum ranges)] of sound types emitted by giant otters from six groups monitored from September 2009 to June 2011 in the Southern Pantanal, Brazil. *N* represents the number of sounds used for acoustic measurements, and the number of giant otters groups included in analyses of each sound type is given in parentheses. (Sound – Co=coo, Cc=coo-call, Ch=coo-hum, Hu=hum, Pu=purr, Gr=growl, Gr2=cub growl, So=snort, Ha=hah, Ac=adult call, Sc=adult scream, Sc2=cub scream, Be=adult begging scream, Be2=cub begging scream, Hs=adult high-scream, Hs2=cub high-scream, Cu=cub call, Sk=scream-gurgle, Sq=squeak; Variables – CD=call duration, LF= lowest and HF=highest frequencies of the sound, PF=peak frequency of the entire sound, Q3=3rd quartile frequency, PU=number of pulses of the sound, FI=initial value of F0 (for harmonic sounds) or of the peak frequency (for non-harmonic sounds), FM=maximum value of F0 or PF, FF=final F0 or PF, FM=maximum frequency of F0 or PF, FD=difference between the highest and the lowest frequency of F0 or PF, D1=duration from the start of the vocalisation to the highest frequency value of F0 or PF, D2=duration from the highest F0 or PF to the end of the vocalisation, and PD=plateau duration (when F0 or PF did not varied), *temporal units in seconds (s), frequency units in kHz).

Call	*N*	CD	LF	HF	PF	Q3	PU	FI	FF	FM	FD	D1	D2	PD
Co	15	0.36 ±0.11	0.18 ±0.05	5.29 ±0.94	0.45 ±0.05	0.61 ±0.26	109.67 ±29.19	0.27 ±0.06	0.33 ±0.05	0.52 ±0.06	0.25 ±0.06	0.15 ±0.06	0.07 ±0.03	0.16 ±0.09
Cc	18	0.44 ±0.13	0.16 ±0.04	4.98 ±1.43	0.5 (0.3-4.09)	2.89 ±1.38	77.22 ±33.55	0.26 ±0.1	0.34 ±0.1	4.32 ±1.14	4.06 ±1.14	0.26 ±0.12	0.13 ±0.07	0.03 (0.01-0.2)
Ch	20	0.2 ±0.09	0.17 ±0.03	4.75 ±1.31	0.44 ±0.08	0.51 (0.39- 3.66)	98.7 ±45.88	0.25 ±0.04	0.27 ±0.06	0.43 ±0.08	0.18 ±0.08	0.11 ±0.07	0.08 ±0.04	0
Hu	20	0.33 ±0.19	0.09 ±0.07	4.84 ±1.18	0.43 ±0.08	0.62 (0.43-4.1)	80.4 ±48.2	0.23 ±0.04	0.26 ±0.06	0.27 ±0.07	0.04 ±0.07	0.26 ±0.14	0	0
Pu	23	0.54 ±0.27	0.09 ±0.07	2.35 ±1.76	0.42 ±0.07	0.52 (0.39-3.19)	11.65 ±5.25	0.21 ±0.01	0.21 ±0.01	0.21 ±0.01	0	0.54 ±0.27	0	0
Gr	17	2.35 ±1.71	0.12 ±0.04	3.75 ±0.8	0.39 (0.17-2.63)	2.16 ±0.77	516.94 ±339.27	0.2 ±0.03	0.2 ±0.04	0.22 ±0.04	0.02 (0-0.1)	0.1 (0-1.97)	0.13 (0-4.23)	1.05 (0 to 3.22)

Gr2	10	0.46 ±0.25	0.07 (0- 0.15)	1.29 ±0.17	0.44 ±0.02	0.47 ±0.01	115.8 ±63.62	0.22 ±0.01	0.22 ±0.01	0.22 ±0.01	0	0.00	0.00	0.37 (0.17-0.93)
So	197	0.27 ±0.1	0.16 ±0.04	8.70 ±1.29	1.47 ±0.74	2.63 ±0.67	6.55 ±2.35	1.47 ±0.75	1.77 ±0.81	1.47 ±0.74	0	0	0	0.27 ±0.1
Ha	11	0.16 ±0.07	0	4.38 ±0.55	1.56 ±0.63	2.31 ±0.54	1	1.43 ±0.49	1.03 ±0.67	2.07 ±0.23	0	0.16 ±0.07	0	0
Ac	15	0.3 ±0.1	0.75 ±0.86	5.94 ±1.47	4.42 ±1.51	4.96 ±0.86	1 ±0	0.56 (0.27-4.15)	1.87 ±1.32	5.94 ±1.42	4.33 ±1.95	0.14 ±0.04	0.09 ±0.05	0.05 (0.01-0.26)
Sc	20	0.93 ±0.41	0.22 ±0.09	6.57 ±2.22	1.56 ±0.64	2.60 ±0.95	466.35 ±202.72	0.35 ±0.06	0.43 ±0.07	0.48 ±0.08	0.12 ±0.09	0.27 ±0.22	0.29 ±0.26	0.23 (0-1.42)
Sc2	9	0.81 ±0.44	0.19 ±0.09	5.64 ±2.34	1.18 ±0.71	2.24 ±0.87	268.22 ±146.67	0.32 ±0.07	0.34 ±0.05	0.37 ±0.05	0.05 (0-0.22)	0.09 (0-1.1)	0.31 ±0.3	0.22 ±0.09
Be	12	1.21 ±1.03	0.13 ±0.11	6.91 ±1.52	3.13 ±1.82	4.15 ±1.1	1 ±0	0.39 ±0.1	0.36 ±0.09	0.49 ±0.09	0.1 (0-0.34)	0.25 ±0.19	0.96 ±0.92	0
Be2	9	2.65 ±1.39	0.17 ±0.08	7.76 ±1.67	2.67 ±0.87	3.69 ±1.04	1 ±0	0.33 ±0.03	0.37 ±0.04	0.48 (0.35-3.22)	0.43 (0.07-2.9)	0.43 ±0.34	2.22 ±1.38	0
Hs	4	0.94 (0.36-2.25)	1.41 ±1.26	6.61 ±1.17	4.04 ±1.91	4.68 ±1.33	1 ±0	3.15 (0.39-6.09)	3.02 ±1.88	6.31 ±1.05	3.12 ±2.69	0.22 ±0.13	0.63 (0.2-2.13)	0 (0-0.07)
Hs2	10	0.46 (0.29-0.95)	1.72 ±0.81	6.3 ±2.29	3.29 ±1.07	4.29 ±0.77	1 ±0	3.03 ±1.71	2.83 ±0.98	5.19 ±1.96	2.16 ±2.06	0.17 (0-0.64)	0.33 ±0.19	0
Cu	27	0.35 ±0.15	1.41 ±0.46	9.95 (7.7-13.92)	8.02 ±1.46	8.64 ±0.99	1 ±0	3.17 ±2.12	5.54 ±2.82	8.83 ±1.92	5.66 ±2.43	0.13 ±0.06	0.14 ±0.09	0.03 (0-0.34)
Sk	6	1.01 ±0.1	0.15 ±0.02	8.73 ±1.18	0.75 ±0.26	0.85 ±0.16	227.17 ±33.89	0.24 ±0.03	0.33 ±0.04	7.83 ±0.9	7.59 ±0.91	0.61 ±0.15	0.40 ±0.06	0
Sq	15	0.44 ±0.1	0	18.3 ±1.23	8.38 ±0.65	8.74 ±0.68	1 ±0	0.52 ±0.06	0.57 ±0.06	0.72 ±0.07	0.21 (0.06-0.8)	0.08 (0.06-0.1)	0.06 (0-0.24)	0.26 (0.2-0.5)

CAPÍTULO 5

Leuchtenberger, C.; Sousa-Lima R.; Ribas, C.; Magnusson, W. & Mourão, G. Acoustic variation in giant otter alarm calls. Manuscrito formatado para *Animal Behaviour*.

Acoustic variation in giant otter alarm calls

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Acoustic variations in animal calls may carry identity coding, which in social species may improve communication within and among groups, and may be useful to identify the sex of senders. Giant otters live in highly cohesive groups, which defend exclusive territories along water bodies, using acoustic and chemical signals. Snorts are harsh alarm calls, vocalised in threat contexts, which commonly elicit a reaction in the other members of the group. The aim of this study was to determine whether giant otter snorts vary across study areas, social groups, individuals, or sexes. Alarm calls emitted by twenty giant otters, composing eight different groups, were recorded from September 2009 to June 2011 in the Vermelho and Negro Rivers in the Pantanal. The sex and identity of individuals were determined. Acoustic parameters, as well as formant frequencies, were measured and analysed through acoustic softwares. Snort acoustic variables did not differ significantly among study areas. Snorts varied significantly among groups, individuals and between sexes, with highest discrimination between sexes. The frequency of formants (F1-F5) and formant dispersion (DF) potentially allow identity coding among groups, individuals and sexes. The higher discrimination of snort acoustic variation between sexes may be related to information on body size carried by formant frequencies and dispersion, indicating some sexual dimorphism in giant otters. Acoustic differences among groups and individuals are more likely to be learned, since we did not find correlation with genetic traits of some individuals.

Key-words: acoustic identity; formant frequency; *Pteronura brasiliensis*; sex discrimination; vocal communication.

Communication in social species occurs within a network of multiple potential senders and receivers (McComb & Reby 2005). In such systems, identity coding carried in vocal signals facilitates the coordination of individual activities and may improve the cohesion of groups (Janik & Slater 1998; Fitchel & Manser 2010). Acoustic variations are commonly determined by a mix of environmental and genetic influences (Bradbury & Vehrencamp 1998). However, some variation may also be learned and fixed through behaviour matching, which can create geographic variation in repertoires (Mitani et al. 1999; Collins & Terhune 2007; Delgado 2007), as well as group and individual coding (Weilgart & Whitehead 1997; Boughman 1998; Janik & Slater 1998; Sousa-Lima et al. 2002, 2008; McComb et al. 2003; Crockford et al. 2004).

Acoustic signals that carry individual or kin-group specificity must have a large number of distinguishable variants (Bradbury & Vehrencamp 1998). Frequency components of sounds, such as fundamental frequency and formants, are potential parameters to carry individual and social coding (Fitch & Hauser 1995; Rendall et al. 1996; Sousa-Lima et al. 2002, 2008; McComb et al. 2003; Fitch & Fritz 2006; Delgado 2007; Vannoni & Elligott 2007, 2008; Koren & Geffen 2011). Fundamental frequency is determined by the length and mass of vocal folds (Fitch 1997), which in some species seem to be related to body size, which is also useful to determine sex identity of senders (e.g. Sousa-Lima et al. 2008; Vannoni & Elligott 2008). However this correlation does not occur in all vertebrates (Fitch 1997) and acoustic variables related to the filter component of the vocal tract, such as formant frequencies (McComb & Reby 2005), are more likely to be an ‘honest’ indication of the sender’s body size (Fitch & Hauser 1995; Rendall et al. 1996; Charlton et al. 2011). In some species, the identity of sex and body size of senders may be a useful tool for sexual selection and/or determining the social status of individuals (Vannoni & Elligott 2008; Charlton et al. 2010).

Giant otters (*Pteronura brasiliensis*) live in highly cohesive groups formed by a dominant pair and up to 20 other related or unrelated individuals (Ribas 2012), which spend almost all their daily activities together (Duplaix 1980; Chapter 1). Groups defend exclusive territories along water bodies, which are patrolled daily by the whole group, and marked with acoustic and chemical signals (Duplaix 1980; Schweizer 1992; Leuchtenberger & Mourão 2009). Agonistic encounters between groups and solitaries have been observed, especially in the Pantanal (Schweizer 1992; Ribas & Mourão 2004; Leuchtenberger & Mourão 2009; Ribas et al 2012; Chapter 3), and may lead to serious injuries or the death of individuals. Therefore, kin recognition through communication within and among giant otter groups must be efficient to maintain cohesion and to avoid agonistic interactions.

Giant otters emit harsh snorts when alarmed and use a periscoping posture display, which commonly elicit a reaction in the other members of the group (Duplaix 1980). Snorts are broadband and pulsed calls, often showing five visible formants (Chapter 4). Considering that alarm signals are likely to have individual traits in social species (Pollard 2011), we analyzed if giant otter snorts show acoustic variations between two study areas, among social groups and among individuals. We also tested if acoustic traits of snorts of males and females are distinguishable.

METHODS

The Pantanal is a seasonally flooded plain of approximately 160 000 km^2, of which 80% may be flooded from November to March, the extent depending on the rainfall that year (Hamilton et al. 1996). We monitored giant otters in two areas, approximately 61 km distant, in the Southern Pantanal. The first study area was located in the Vermelho River (19^{o}34'S; 57^{o}01'W), a stretch of the Miranda River (19°36'S, 57° 00'W) and water bodies along the

Estrada-Parque Pantanal (EPP) road. The second study area included the middle stretch of the Negro River (19^{o}35'S; 56 ^{o}11'W). The two areas are connected through a wide swamp, which drained waters from the Negro River to the Vermelho River (Fig. 1).

Alarm calls from four groups (G1, G2, G10 and G12) were recorded monthly from September 2009 to June 2011 in the Vermelho River area. In the Negro River we recorded sounds from four giant otter groups (G17, G18, G19 and G20) during the months of September 2009, June and September 2010 and June 2011. Monthly monitoring lasted from 7 to 10 days, and was undertaken during daylight hours (5-19 h). Most groups were located opportunistically, but three groups (G2, G10 and G12) were radio-tagged and monitored in different periods from November 2009 to June 2011 (Chapter 2).

The sex of individuals was identified through observation of their genitals when they were on land and their identity was confirmed by their individually-distinctive natural throat marks. The behaviour of individuals was recorded by a high-definition camcorder (Canon HF-200) and the hierarchy of individuals in the group was inferred as described by Leuchtenberger & Mourão (2009). The territorial limits of each giant otter group were estimated through the location of active latrines and dens (see Chapter 3). Once located, the group was followed at a distance of 10 to 100 m that did not disturb their behaviour. We considered only snorts vocalised in response to the observer, excluding those snorts that resulted in the chasing of another individual or the entire group. Sounds were recorded at a maximum distance of 50 m with a directional microphone (Sennheiser, ME-66) connected to a digital Marantaz PMD-660 recorder (AIF format, 16-bit resolution and 44.1 kHz sampling rate).

Acoustical analyses

Acoustic measurements were carried out using oscillograms and power spectra generated with Raven Pro 1.4 (Cornell Lab of Ornithology), using the following settings: Hanning window;

FFT size = 1024 and 50% overlap. We measured the following call properties to analyze snorts: (CD) call total duration, (PF) peak frequency of the entire call, (Q3) 3rd quartile frequency and (PU) the number of pulses (temporal units that repeat rhythmically) of the call.

Additionally, snort formant frequencies (Fig. 2) were estimated using Linear Predictive Coding analysis (LPC) through the command “To Formant (burg)” in Praat 5.3.12 software (P. Boersma & D. Weenink, University of Amsterdam, Amsterdam, The Netherlands). We carried out two LPC analyses on each snort, to better detect the frequency of first formant (F1). The first LCP was carried out using the following settings: time step 0.01s, number of formants 1, maximum formant 400– 500 Hz and window length 0.02 s, to measure the frequencies of F1. The second LPC analysis was carried out to measure the frequencies of formants 2 to 5 (F2 - F5), using the following settings: time step 0.01 s, number of formants: 4, maximum formant 5500–7500 Hz, window length 0.02 s. We measured the formant dispersion (DF) following the methods of Fitch (1997).

Statistical Analyses

All statistical calculations were performed with the R 2.13 Software (The R Foundation for Statistical Computing). The acoustic parameters were standardized by columns using the *decostand* function with the *total* method in the package Vegan (Oksanen et al. 2008). A principal-component analysis (PCA) was carried out to ordinate acoustic variables. Components with eigenvalues greater than the mean were selected. A nested nonparametric multivariate analysis of variance (PERMANOVA, function *adonis* from the package Vegan), with 1000 permutations, was used to test for differences in standardized acoustic parameters between study areas (nested within groups), among giant otter groups (nested within study areas), among individuals and between sexes (nested within group).

A linear discriminant analysis (LDA) was carried out to estimate the distinctiveness between acoustic variables of snorts, using the package MASS (Venables & Ripley 2002). The first step of LDA was carried out with a sorted subset of 50% of the total data set of the standardized acoustic parameters. The remaining subset of data was used to attest the predictions based on the equations generated by the first classification. The percentage of correctly classified cases indicates the effectiveness of the discriminant function in identifying group. For performing LDA among snorts, we included only the acoustic variables (PU, PF, Q3, F5, DF) that presented higher loadings in the PCA and conform to the linearity assumptions of the analysis.

We tested whether the snort traits of groups were correlated with the distance between groups, by measuring the median of standardized snort features for each group and computing the Euclidean distance matrix between all possible dyads of groups. Then we computed the distance matrix between the centres of the territories of groups (Leuchtenberger & Mourão 2008) and applied the Mantel test to estimate the correlation between the two matrix, using the package ade4 (Thioulouse et al. 1997).

Biological samples were collected from six individuals (aqu, exc, ris, pal, wil, pig; Table 1) inhabiting the Vermelho and Miranda Rivers as part of a larger study on genetic questions about the groups inhabiting this area (Ribas 2012). These data provided information on genetic relationships among individuals, and this matrix was compared with a Euclidean matrix of snort traits of respective senders with a Mantel test.

For each of the acoustic variables of snorts, we measured the total coefficient of variation (CVtot) considering the overall mean (X) and the respective standard deviation (SD) by the equation CVtot=100% × (SD/X). We also calculated the coefficient of variation (CVi) of each of these variables at four different levels: within study areas (CVi_{are}), within giant otter groups (CVi_{gro}), within individuals (CVi_{ind}) and within sex (CVi_{sex}), using the mean (Xi) and the standard deviation (SDi) of each variable within levels. We then determined the potential of individual identity coding (PIC) of each parameter by CVtot/mean CVi. Parameters with PIC value greater than 1 may be used for individual recognition since intra-individual variability is smaller than inter-individual variability (Robisson et al. 1993). The formant frequencies and dispersion of formants were compared between females and males and the differences were tested with ANOVA.

RESULTS

The giant otter groups we studied included 36 adults (19 males, 15 females and 2 not identified), 4 juveniles (2 male, 1 female and 1 not identified) and 24 cubs (1 male, 1 female and 21 not identified). Group size varied from 2 to 15 individuals, with an average of 6. We recorded snorts from 8 adult males (5 dominant and 3 subordinate) and 12 adult females (6 dominant and 6 subordinate) (Table 1).

The PCA analysis resulted in three axes that accounted for 79% of the variation among snorts (first axis=47%, second axis=18% and third axis=14%). The frequency of the second to the fifth formants and dispersion of formants had the highest loadings (F2=2.41, F3= 2.63, F3= 2.64, F5 = 2.67, DF=2.62) on the first component. The second component had the highest loadings for Q3 (-3.61) and PF (-3.45), while PU (-3.6) and CD (-3.22) had the highest loadings on the third component. Standardized snort variables did not differ significantly among study areas (PERMANOVA: $F_{1,\ 195}$=0.26, P=0.87). Snorts varied significantly amongst groups, nested within study areas (PERMANOVA: $F_{7,\ 189}$=4.479, P=0.001, R^2=0.14) and there was significant variation in snorts amongst individuals (PERMANOVA: $F_{19,\ 177}$=7.61, P=0.001, R^2=0.45) and between sexes (PERMANOVA: $F_{1,\ 195}$=31.926, P=0.001, R^2=0.14), nested within groups. However there was high overlap of call traits among giant otter groups and individuals (Fig. 3). The similarity of snorts traits between dyads of groups was not correlated with the straight line (euclidean) distance between the centres of their territories (Mantel test: r_{obs}= 0.014, P=0.297). Also, snort traits were not correlated with genetic relationships among individuals (Mantel test: r_{obs}<0.001, P=0.541). The discriminant function analysis weakly distinguished among groups (32%) and individual (25%) snorts, but classified correctly 77% of the snorts grouped by sex. The first discriminant function explained 100% of the variance of snorts between sex and the most important variables for discrimination were by F5 and DF.

All acoustic parameters presented PIC (potential for individual identity coding) values between 1 and 2, but the frequency of formants (F1-F5) and DF (formant dispersion) presented the higher values considering group, individual and sex levels of acoustic variation (Table 2). Females presented higher frequencies of formants and higher formant dispersion than males (Table 3).

DISCUSSION

Geographic variation in mammal calls is commonly attributed to differences in acoustic habitat features, cultural behaviour and genetic diversity among populations (Mitani et al. 1999; Collins & Terhune 2007; Delgado 2007; Trephy & Hik 2010). Giant otter snort traits did not differ significantly between study areas. The areas are relatively close (61 km) and they are connected by a swamp, whose drainage is enhanced by seasonal flooding and may allow frequent flux of individuals between the sites, as found for the population of Vermelho and Miranda Rives and Estrada Parque Pantanal in a area of approximately 52 km (Ribas 2012). Therefore, geographic variation in giant otter snorts may be more likely to occur among areas that have been isolated for a long time (Machado 2004; Pickles et al. 2011).

There was significant variation in snorts among giant otter groups and individuals, although the discriminations of these sounds were weak and there was no strict separation within these groups. Snort variation among neighboring groups and individuals may result from vocal learning (Weilgart & Whitehead 1997; Boughman 1998; Janik & Slater 1998; Sousa-Lima et al. 2002, 2008; Crockford et al. 2004) and genetic variation (Sousa-Lima et al. 2002, 2008; Rendell et al. 2012). However the absence of correspondence between the acoustic parameters measured in snorts and genetic traits of some senders may indicate that variations in this type of sound are more likely achieved by vocal learning. Considering the cohesion of giant otter groups, vocal learning could evolve through the intense social interactions among individuals (Fitchel & Manser 2010). Nevertheless, the high degree of genetic relationship among giant otter groups of the Vermelho and Miranda Rivers (Ribas 2012) indicates a high exchange of individuals among groups, which may dilute differences (Boughman 1998).

The main function of alarm sounds is to inform about predation risk (Blumstein 1999) and individual discrimination through alarm signals may have an adaptive value (Pollard 2011; Hare 1998; Blumstein & Daniel 2004; Matrosova et al. 2011). Social species are expected to have more individualistic alarm signals (Pollard 2011), since the recognition of alarm calls of group members may inform a more imminent threat than calls from more distant conspecifics (Hare 1998). However contact calls and loud screams, which can be heard over large distances, may be more likely to carry identity coding than alarm calls (Charrier et al. 2001; McComb & Reby 2005), as observed in screams of sea otters (McShane et al. 1995). Furthermore, the use of other modalities of signals, such as scent-marks, plays an important role in individual identity in mustelids (e.g. Palphramand & White 2007; Oldham & Black 2009) and these multi-modal signals may enhance the communication of identity among giant otter groups (Bradbury & Vehrencamp 1998; Leuchtenberger & Mourão 2009). Although giant otter snorts commonly elicit a reaction in other individuals (Duplaix 1980; Chapter 3), the potential function of this call in carrying identity coding must be further tested by playback experiments.

Giant otter-snorts differed significantly between sexes. The distinctiveness of potential mates is commonly accessed through acoustic source filter traits, which may indicate the hormonal status of senders and their phenotypic characteristics (Sousa-Lima et al. 2002, 2008; Vannoni & Elligott 2008; Charlton et al. 2010). The frequencies and dispersion of formants were the parameters most likely to encode group, individual and sex discrimination in giant otter snorts. These acoustic traits are determined by the filter component of the vocal tract (Fitch 1997; McComb & Reby 2005) and play important roles in size estimation and individual recognition in mammals (Fitch 1997; Fitch & Fritz 2006; Vanoni & McElligott 2007). Since formants are an 'honest' indication of body size, some species identify potential mates through the formant frequencies of the sender's calls (Vannoni & Elligott 2008; Charlton et al. 2010), and this may also be an important cue to potential mates in giant otters.

Giant-otter-male snorts had lower formant dispersion and lower frequencies at the fifth formants than female snorts. Considering giant otter's vocal tract as a uniform tube, the negative correlation between formant dispersion and vocal tract length (Fitch 1997) suggests that adult males have larger vocal tracts than adult females, which may also correspond to larger body sizes (Fitch 1997; Reby & McComb 2003; Sanvito et al. 2007; Charlton et al. 2009; Charlton et al. 2011). Although some authors have suggested that giant otter adult males have larger body size and wider necks than adult females (Duplaix 1980; Carter & Rosas 1997), Rosas et al. (2009) did not record significant differences in body measurements of captive males (average of 163 cm and 22.5 kg, N=11) and females (average of 162 cm and 28.8 kg, N =4). However, measurement of three adult males captured for radio-telemetry procedures in Pantanal (Chapter 2) presented higher values (171-183 cm total body length and 29.5-32.9 kg of total weight) than those presented by Rosas et al. (2009). These values may be an indication of geographic variation in body structure between individuals in the Pantanal and in Amazonia (Carter & Rosas 1997) or the differences may just be due to the vagaries of sampling. If sexual dimorphism exists in giant otters, broadcasting body size through snorts may provide a tool for sexual selection in the species. The next step in testing this hypothesis is to correlate senders' vocal tract length with body size, which will clarify the function of formants in discriminating sex and physical characteristics among giant otters.

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RESUMO

Variações acústicas em vocalizações de animais podem carregar codificações de identidade, as quais em espécies sociais podem melhorar a comunicação dentro e entre grupos, e pode ser útil para identificar o sexo dos emissores. Ariranhas vivem em grupos altamente coesos, que defendem territórios exclusivos ao longo dos corpos d'água, usando sinais acústicos e químicos. Bufos são sinais de alarme estridentes, vocalizados em contextos de pergio, os quais geralmente provocam uma reação em outros membros do grupo. O objetivo deste estudo foi determinar se bufos de ariranhas variam entre áreas de estudo, grupos sociais, indivíduos e entre sexos. Sons de alarme emitidos por vinte ariranhas, compondo oito grupos diferentes, foram gravados entre Setembro de 2009 e Junho de 2011 nos rios Vermelho e Negro no Pantanal. O sexo e identidade dos indivíduos foi determinado. Parâmetros acústicos, assim como as frequências formantes, foram medidos e analisados através de programas acústicos. Variáveis acústicas dos bufos não diferiram entre áreas de estudo. Bufos variaram significativamente entre grupos, indivíduos e entre sexos, apresentando uma discrminação maior entre sexos. A frequência dos formantes (F1-F5) e a dispersão dos formantes (DF) potencialmente permitem a codificação de identidade entre grupos, indivíduos e sexos. A alta discriminação da variação acústica dos bufos entre sexos pode estar relacionada com a informação do tamanho corporal transmitida pela frequência e dispersão dos formantes, indicando algum dimorfismo sexual em ariranhas. Diferenças acústicas entre grupos e indivíduos são mais propensos a serem aprendidas, uma vez que nós não encontramos correlação com as caracteríticas genéticas de alguns indivíduos.

Key-words: dentidade acústica; frequência formante; *Pteronura brasiliensis*; discriminação de sexo; comunicação vocal.

REFERENCES

Blumstein, D. T. 1999. Alarm calling in three species of marmots. *Behaviour*, **136**, 731-757.

Blumstein, D. T. & Daniel, J. C. 2004. Yellow-bellied marmots discriminate between the alarm calls of individuals and are more responsive to calls from juveniles. *Animal Behaviour*, **68**, 1257–1265.

Boughman, J. W. 1998. Vocal Learning by Greater Spear-Nosed Bats. *Biological Sciences*, **265**(1392), 227-233.

Bradbury, J. W. & Vehrencamp, S. L. 1998. *Principles of Animal Communication*. Massachusetts, Sinauer Associates Inc. Publishers. 882 pp.

Carter, S. & Rosas, F. C. W. 1997. Biology and Conservation of the Giant Otter *Pteronura brasiliensis*. *Mammal Review,* **27**, 1-26.

Charlton, B. D.; Zhihe, Z. & Snyder, R. J. 2009. The information content of giant panda, *Ailuropoda melanoleuca,* bleats: acoustic cues to sex, age and size. *Animal Behaviour,* **78**, 893–898.

Charlton, B. D.; Zhile, Z. & Snyder, R. J. 2010. Giant pandas perceive and attend to formant frequency variation in male bleat. *Animal Behaviour,* **79**, 1221-1227.

Charlton, B. D.; Ellis, W. A. H.; McKinnan, A. J.; Cowin, G. J.; Brumm, J.; Nolsson, K. & Fitch W. T. 2011. Cues to body size in the formant spacing of male koala (*Phascolarctos cinereus*) bellows: honesty in an exaggerated trait. *The Journal of Experimental Biology*, **214**, 3414-3422.

Charrier, I.; Jouventin, P.; Mathevon, N. & Aubin, T. 2001. Individual identity coding depends on call type in the South Polar skua *Catharacta maccormicki*. *Polar Biology,* **24**, 378-382.

Collins, K. T. & Terhune, J. M. 2007. Geographic variation of Weddell seal (Leptonychotes weddellii) airborne mother–pup vocalisations. *Polar Biology,* **30**, 1373–1380.

Crockford, C.; Herbinger, I.; Vigilant, L. & Boesh, C. 2004. Wild chimpanzees produce group-specific calls: a case for vocal learning? *Ethology*, **110**, 221—243.

Delgado, R. A. Jr. 2007. Geographic Variation in the Long Calls of Male Orangutans (*Pongo* spp.). *Ethology*, **113**, 487–498.

Duplaix, N. 1980. Observations on the ecology and behaviour of the giant river otter *Pteronura brasiliensis* in Surinam. *Review Ecologique (Terre Vie)*, **34**, 495–520.

Fitch, W. T. & Hauser, M. D. 1995. Vocal production in nonhuman primates: Acoustics, physiology, and functional constraints on 'honest' advertisement. *American Journal of Primatology*, **37**, 191–219.

Fitch, W. T. 1997. Vocal tract length and formant frequency dispersion correlate with body size in rhesus macaques. *Journal of the Acoustical Society of America*, **102**, 1213-1222.

Fitch, W. T. & Fritz, J. B. 2006. Rhesus macaques spontaneously perceive formants in conspecific vocalizations. *Journal of the Acoustical Society of America*, **120**, 2132-2141.

Fitchel, C. & Manser, M. 2010. Vocal communication in social groups. In: *Animal Behaviour*: *Evolution and Mechanisms, Part I,* (Ed. by P. Kappeler), pp. 29-54. Springer Berlin Heidelberg.

Hamilton, S. K.; Sippel, S. J. & Melack, J. M. 1996. Inundation patterns in the Pantanal wetland of South America determined from passive microwave remote sensing. *Archives of Hydrobiology*, **137**, 1-23.

Hare, J. F. 1998. Juvenile Richardson's ground squirrels, *Spermophilus richardsonii*, discriminate among individual alarm callers. *Animal Behaviour*, **55**, 451–460.

Janik, V. & Slater, P. J. B. 1998. Context-specific use suggests that bottlenose dolphin signature whistles are cohesion calls. *Animal Behaviour*, **56**, 829-838.

Koren, L. & Geffen, E. 2011. Individual identity is communicated through multiple pathways in male rock hyrax (*Procavia capensis*) songs. *Behavioral Ecology and Sociobiology*, **65**, 675–684.

Leuchtenberger, C. & Mourão, G. 2008. Social organization and territoriality of giant otters (Carnivora: Mustelidae) in a seasonally flooded savanna in Brazil. *Sociobiology*, **52**, 257-270.

Leuchtenberger, C. & Mourão, G. 2009. Scent-marking of giant otter in the Southern Pantanal, Brazil. *Ethology*, **115**, 210–216.

Machado, M. R. B. 2004. *Bioacústica de ariranhas (Pteronura brasiliensis) (Carnivora: Mustelidae): discriminação vocal e repertório.* MSc thesis, Universidade Federal do Amazonas and Instituto Nacional de Pesquisa da Amazônia, Amazonas, Brazil.

Matrosova, V. A.; Blumstein, D. T.; Volodin, I. A. & Volodina, E. V. 2011. The potential to encode sex, age, and individual identity in the alarm calls of three species of Marmotinae. *Naturwissenschaften*, **98**, 181–192.

McComb, K.; Reby, D.; Baker, L.; Moss, C. & Sayialel, S. 2003. Long-distance communication of acoustic cues to social identity in African elephants. *Animal Behaviour*, **65**, 317–329.

McComb, K. & Reby, D. 2005. Vocal communication networks in large terrestrial mammals. In: *Animal Communication Networks.* (Ed. by P. McGregor). pp. 372-389. University Press.

McShane, L.; Estes, J. A.; Riedman, M. L. & Staedler, M. M. 1995. Repertoire, structure and individual variation of vocalisation in the sea otter. *Journal of Mammalogy*, **76**, 414–427.

Mitani, J. C.; Hunley, K. L. & Murdoch, M. E. 1999. Geographic variation in the calls of wild chimpanzees: a reassessment. *American Journal of Primatology* **47,** 133–151.

Oksanen, J.; Kindt, R.; Legendre, P.; O'Hara, B.; Simpson, G. L.; Solymos, P.; Stevens, M. H. H. & Wagner, H. 2008. *The Vegan Package*.

Oldham, A. & Black, J. M. 2009. Experimental tests of latrine use and communication by river otters. *Northwestern Naturalist*, **90**(3), 207-211.

Palphramand, K. & White, P. C. L. 2007. Badgers, *Meles meles*, discriminate between neighbour, alien and self scent. *Animal Behaviour*, **74,** 429-436.

Pickles, R. S. A; Groombridge, J. J.; Zambrana Rojas, V. D.; Van Damme, P.; Gottelli, D.; Kundu, S.; Ariani, C. V.; Iyenar, A. & Jordan, W. C. 2011. Evolutionary history and identification of conservation units in the giant otter, *Pteronura brasiliensis*. *Molecular Phylogenetics and Evolution*, 1:12.

Pollard, K. A. 2011. Making the most of alarm signals: the adaptive value of individual discrimination in an alarm context. *Behavioral Ecology*, **22**(1), 93-100.

Reby, D. & McComb, K. 2003. Anatomical constraints generate honesty: acoustic cues to age and weight in the roars of red deer stags. *Animal Behaviour*, **65**, 519–530.

Rendall, D.; Rodman, P.S. & Emond, R.E. 1996. Vocal recognition of individuals and kin in free-ranging rhesus monkeys. *Animal Behaviour*, **51**, 1007–1015.

Rendell, L.; Mesnick, S. L.; Dalebout, M. L.; Burtenshaw, J. & Whitehead, H. 2012. Can genetic differences explain vocal dialect variation in sperm whales, *Physeter macrocephalus*? *Behavioral Genetics*, **42,** 332-343.

Ribas, C. & Mourão, G. 2004. Intraspecific agonism between giant otter groups. *IUCN Otter Specialist Group Bulletin*, **21**, 89–93.

Ribas, C.; Damasceno, G.; Magnusson, W.; Leuchtenberger, C. & Mourão, G. 2012. Giant otters feeding on caiman: evidence for an expanded trophic niche of recovering populations. *Studies on Neotropical Fauna and Environment*, **47,** 19-23.

Ribas, C. 2012. Grau de parentesco e relações sociais entre grupos de ariranhas (*Pteronura brasiliensis*). PhD thesis. Instituto Nacional de Pesquisas da Amazônia. 105pp.

Robisson, P.; Aubin, T. & Bremond, J-C. 1993. Individuality in the voice of the Emperor Penguin *Aptenodytes forsteri*: adaptation to a noisy environment. *Ethology*, **94**(4), 279-290.

Rosas, F. C. W.; da Rocha, C. S.; Mattos, G. E. de & Lazzarini, S. M. 2009. Body Weight-Length Relationships in Giant Otters (*Pteronura brasiliensis*) (Carnivora, Mustelidae). *Brazilian Archievs of Biology and Technology,* **52**(3), 587-591.

Sanvito, S.; Galimberti, F. & Miller, E. H. 2007. Vocal signalling of male southern elephant seals is honest but imprecise. *Animal Behaviour*, **73**, 287-299.

Schweizer, J. 1992. *Ariranhas no Pantanal: Ecologia e comportamento da Pteronura brasiliensis.* Edibran-Editora Brasil Natureza Ltda, Curitiba, Paraná.

Sousa-Lima, R.; Paglia, A. P. & Fonseca, G. A. B. da. 2002. Signature information and individual recognition in the isolation calls of Amazonian manatees, *Trichechus inunguis* (Mammalia: Sirenia). *Animal Behaviour*, **63**, 301-310.

Sousa-Lima R., Paglia A. P. & Fonseca G. A. B. da. 2008. Gender, age, and identity in the isolation calls of Antillean manatees (*Trichechus manatus manatus*). *Aquatic Mammals*, **34**(1), 109-122

Thioulouse, J.; Chessel, D.; Doledec, S. & Olivier J. M. 1997. Ade-4: a multivariate analysis and graphical display software. *Statistics and Computing*, **7**, 75–83.

Trephy, S. A. & Hik, D. S. 2010. Variation in pika (Ochotona collaris, O. princeps) vocalizations within and between populations. *Ecography*, **33**, 784-795.

Vannoni, E. & McElligott, A. G. 2007. Individual acoustic variation in fallow deer (*Dama dama*) common and harsh groans: a source-filter theory perspective. *Ethology,* **113,** 223–234.

Vannoni, E. & McElligott, A. G. 2008. Low frequency groans indicate larger and more dominant fallow deer (*Dama dama*) males. **Plos One**, **3**(9), 1-8.

Venables, W. N. & Ripley, B. D. 2002. *Modern applied statistics with S.* 4th edition. Springer, New York.

Weilgart, L. & Whitehead, H. 1997.Group-specific dialects and geographical variation in coda repertoire in South Pacific sperm whales. *Behavioral Ecology and Sociobiology*, **40,** 277-285.

FIGURE LEGENDS

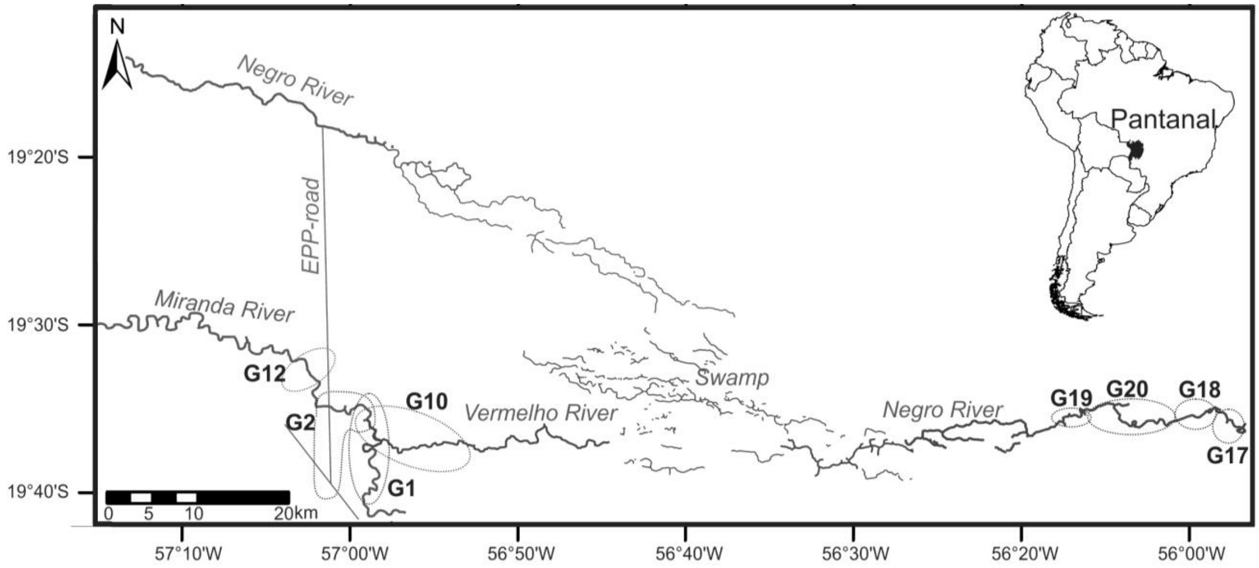

Figure 1. Map of the study area showing the limits of linear territories (dot ellipsis) of eight giant otter groups (G1, G2, G10, G12, G17 – G20) monitored from September 2009 to June 2011 in the Southern Pantanal of Brazil.

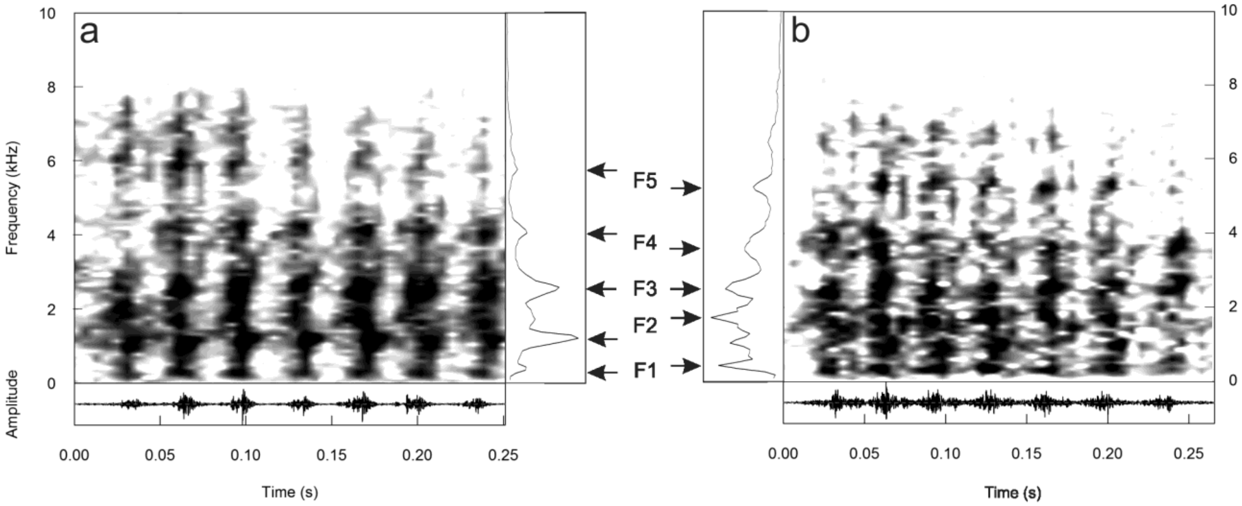

Figure 2. Spectrogram and oscillogram (bottom) of snorts vocalized by a giant otter dominant female (a) and a dominant male (b). Arrows indicate the five formants (F1-F5) that present higher energy in the frequency spectrum.

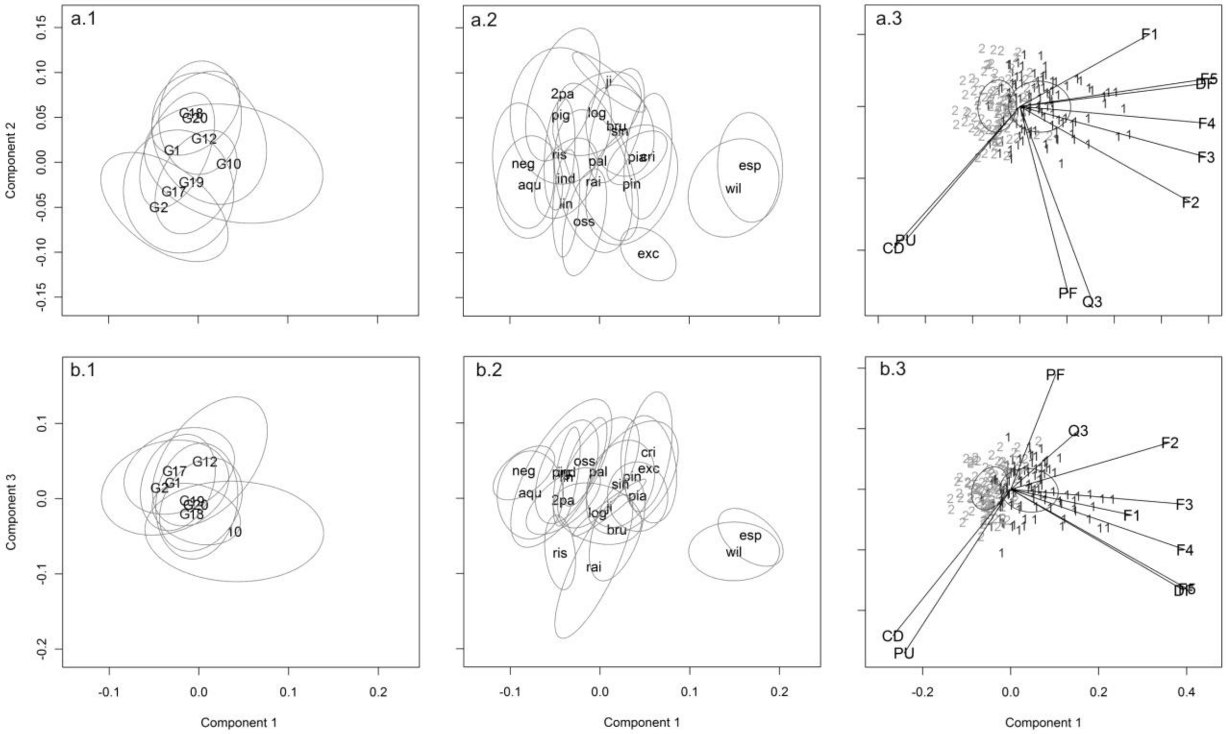

Figure 3. Biplot of the relationship (a) between the first and second components and (b) between the first and third components of the PCA of 197 snorts emitted by 20 giant otters distributed in 8 giant otter groups, monitored from September 2009 to June 2011 in the Southern Pantanal. The biplots are presented in relation to three grouping factors: 1) giant otter groups (G1, G2, G10, G12, G17 – G20); 2) individuals (see Table 1 for the identity code of individuals); 3) sex (1=Female, 2=Male). Ellipses represent standard deviation of factors. The single numbers and names represent the centroid of the sample of each group and individual, respectively. Arrows in a.3 and b.3 indicate the loadings of acoustic variables (CD=call duration, PU=number of pulses, PF=peak frequency, Q3=3rd quartile frequency, F1-F5=frequency of formants and DF=formant dispersion).

TABLES

Table 1. Number of snorts recorded from giant otters living in 8 groups (Group ID=G1, G2, G10, G12, G17-G20) located in the Miranda (Mir), Vermelho (Ver), EPP road (EPP) and Negro (Neg) Rivers in the Southern Pantanal, Brazil. Additional information of each individual are presented as sex (M=male, F=female), hierarchical status (D=dominant, S=subordinate) and group size, which varied during the study period.

ID	Snorts (*N*)	Sex/Hierarchical status	Group ID	Group Size	Location
ji	4	FS	G1	5 - 8	Mir
ind	10	MS			
aqu	16	MD	G2	3	Mir/EPP
exc	7	FD			
pal	10	MD	G10	9 - 15	Mir/Ver
wil	7	FS			
esp	9	FS			
ris	18	MS			
pig	6	MD	G12	2 - 3	Mir/EPP
cri	8	FD			
oss	11	FD	G17	5 - 9	Neg
pin	10	FS			
neg	10	MS			
log	11	FD	G18	4 - 8	Neg
lin	12	MD	G19	3	Neg
rai	5	FD			
pia	10	FS			
2pa	10	MD	G20	6 - 9	Neg
bru	11	FD			
sin	12	FS			

Table 2. Coefficient of variation (CV) average (±SD) and potential for individual identity coding (PIC) of ten acoustic parameters (CD – call duration, PU – number of pulses, PF – peak frequency, Q3F – 3rd quartile frequency, F1-F5 – frequency of formants 1-5 and DF – formant dispersion) measured from 197 snorts vocalized by 20 giant otters (8 males and 11 females) distributed in 8 groups localized two study areas in the Southern Pantanal, Brazil. CV and PIC are presented within study areas (CVi_{are}, PIC_{are}), among groups (CVi_{gro}, PIC_{gro}), among individuals (CVi_{ind}, PIC_{ind}), between sex (CVi_{sex}, PIC_{sex}) and the total coefficient of variation (CVtot).

Parameter	CVi_{are}	CVi_{gro}	CVi_{ind}	CVi_{sex}	CVtot	PIC_{are}	PIC_{gro}	PIC_{ind}	PIC_{sex}
CD	35.52 ±0.96	35.39 ±11.68	31.17 ±13.72	33.56 ±5.03	35.54	1	1	1.14	1.06
PU	35.93 ±1.8	35.23 ±11.06	33.67 ±11.56	34.79 ±3.47	35.86	1	1.02	1.07	1.03
PF	50.37 ±2.23	50.3 ±13.61	45.92 ±17.36	50.49 ±1.6	50.34	1	1	1.1	1
Q3F	25.39 ±2.42	23.63 ±4.52	21.21 ±7.2	24.3 ±0.49	25.39	1	1.08	1.2	1.04
F1	11.05 ±1.44	9.93 ±2.93	7.19 ±2.25	9.52 ±0.59	11.1	1	1.12	1.54	1.17
F2	17.3 ±3.48	15.9 ±3.64	11.51 ±3.85	14.6 ±0.21	17.44	1	1.1	1.52	1.2
F3	13.47 ±3.04	11.88 ±4.04	8.4 ±3.51	11.5 ±3.84	13.84	1.03	1.17	1.65	1.2
F4	12.93 ±3.54	10.39 ±3.04	7.2 ±2.27	10.59 ±3.55	13.41	1.04	1.29	1.86	1.27
F5	9.15 ±2.85	7.51 ±1.81	5.2 ±1.52	7.57 ±1.37	9.31	1.02	1.24	1.79	1.23
DF	9.44 ±3.01	7.72 ±1.9	5.56 ±1.66	7.94 ±1.38	9.6	1.02	1.25	1.73	1.21

Table 3. Results of the differences (ANOVA) between the snort formant frequencies (F1-F5) and formant dispersion (DF) of giant otter females and males. Mean and standard deviation (SD) are given in Hz.

	ANOVA		Females		Males	
	$F_{1,195}$	P	Mean	SD	Mean	SD
F1	66.017	<0.001	0.37	0.04	0.33	0.03
F2	80.926	<0.001	1.38	0.2	1.14	0.17
F3	51.856	<0.001	2.56	0.36	2.25	0.2
F4	75.926	<0.001	3.96	0.52	3.43	0.28
F5	84.095	<0.001	5.63	0.48	5.08	0.34
DF	75.671	<0.001	1.32	0.12	1.19	0.08

SÍNTESE

Ariranhas são sociais e se alimentam principalmente de peixes (Duplaix, 1980, Rosas et al. 1999). A espécie se orienta visualmente para capturar suas presas, o que parece limitar sua atividade ao período diurno (Duplaix, 1980; Schweizer, 1992; Kruuk, 2006). Neste estudo, utilizando o método de rádio-telemetria e armadilhas fotográficas, observamos que grupos de ariranhas apresentam um padrão de atividade crepuscular e diurno no Pantanal, com picos de saída da loca no início da manhã (06:00 h) e de entrada na loca no final do dia (16:00 a 19:00 h), como observado por outros autores (Duplaix, 1980; Schweizer, 1992). No entanto, 31% das atividades registradas por armadilhas fotográficas ocorreram durante a noite. A maioria dos registros noturnos correspondeu a eventos individuais, que podem estar associados com a passagem do alimento através do trato digestivo (Carter *et al.*, 1999), comportamento territorial, risco de predação e disponibilidade de presas próximo à loca.

Apesar do crescente conhecimento sobre ariranhas desde o estudo pioneiro de Duplaix (1980), informações sobre ecologia espacial têm sido restritas a observações diretas realizadas durante a estação seca. Neste estudo apresentamos estimativas de área de vida de três grupos de ariranhas adquiridas através de rádio-telemetria, que variaram entre 0.1 e 2.3 km^2 (LoCoh 98%) na estação seca e de 3.6 a 7.9 km^2 na estação chuvosa. Mudanças sazonais no tamanho da área de vida têm sido observadas para muitos carnívoros (Curtis & Zaramody, 1998; Dillon & Kelly, 2008; Valenzuela & Ceballos, 2000), incluindo lontras (Blundell *et al.*, 2000), e parecem estar fortemente relacionadas com a disponibilidade de recursos. O aumento de área de vida observada neste estudo é similar ao estimado por Utreras *et al.* (2005) na Amazônia do Equador e parece estar associado à dispersão de peixes nas áreas alagadas, como sugerido por (Duplaix, 1980). Enquanto que a disponibilidade de barrancos para a construção de locas e latrinas não foi um fator limitante, já que alguns grupos utilizaram vegetação emergente como refúgio durante o pico de inundação.

A fidelidade à área de vida entre estações variou de 0 a 87%, já que durante a estação chuvosa dois grupos monitorados com rádio-telemetria abandoram a área utilizada durante a seca e dispersaram para a planície inundada. Mudanças na disponibilidade de características da paisagem podem induzir mudanças nos padrões de seleção de habitat (Arthur *et al.*, 1996).

Grupos de ariranhas foram seletivos em relação ao uso de elementos da paisagem durante a estação seca. No entanto, eles foram menos seletivos durante a estação chuvosa. Considerando que a disponibilidade de alimento é um fator importante na seleção de habitat da espécie (Duplaix, 1980), a dispersão de peixes para áreas alagadas pode afetar a movimentação dos grupos, que passam a se deslocar mais imprevisivelmente ao longo do ambiente a procura de alimento para maximizar o ganho energético, como esperado para animais que utilizam estratégias de forrageamento ótimo (Schoener, 1971).

O tamanho da área de vida de carnívoros geralmente apresenta uma relação positiva com as necessidades metabólicas dos animais (Gittleman & Harvey, 1982). De acordo com essa relação, ariranhas apresentam uma área de vida menor do que esperada para uma espécie com uma dieta estritamente carnívora. Isto sugere que ariranhas dependem de uma base de presas grande e densa, relativos a um habitat saudável. Como a produtividade de peixes está ligada com o pulso de inundação em ambientes sazonais (Welcomme 1985; 1990), a manutenção de flutuações hidrológicas anuais deve ser considerada uma prioridade para a conservação de uma espécie vulnerável, que tem peixes como sua presa principal. Esta é uma preocupação particularmente importante para ariranhas no Pantanal, devido aos mais de 70 projetos hidrelétricos e outros 44 em fase de contrução na Bacia do Rio Paraguai (Mourão *et al.*, 2010), que deverão promover mudanças drásticas no pulso de inundação desta grande planície inundável.

Territorialidade implica em custos e benefícios, que geralmente são afetados pela abundância e previsibilidade de alimento no tempo e espaço (Macdonald, 1983). Neste estudo, grupos de ariranhas defenderam territórios ao longo das estações secas e chuvosas e alguns grupos sobrepuseram os limites de seus territórios com grupos vizinhos. Embora algumas espécies dispendem um maior esforço em defender partes do território que são mais requisitadas por competidores (Kruuk *et al.*, 1984; Sillero-Zubiri & Macdonald, 1998; Zub *et al.*, 2003; Herr & Rosell, 2004), a densidade de sinais químicos não foi significativamente diferente entre as áreas sobrepostas e exclusivas dos territórios. No entanto, o número de sinais químicos foi positivamente relacionado ao tamanho do território, o que pode ser uma estratégia para reduzir a invasão de intrusos, já que territórios marcados esparsamente podem ser considerados como uma área vaga para o estabelecimento de grupos vizinhos (Sillero-Zubiri & Macdonald, 1998).

O tamanho da extensão total do território foi maior durante as estações chuvosas do que durante as estações secas e esteve correlacionado positivamente com o tamanho do grupo em ambas as estações. Embora essa relação não seja comum para carnívoros socias em ambientes heterogêneos (Macdonald, 1983; Doncaster & Macdonald, 1992; Johnson *et al*., 2001; Adams, 2001), este resultado pode estar relacionado com as necessidades metabólicas dos grupos, uma vez que grupos maiores necessitariam acessar mais recursos (Macdonald, 1983; Kruuk & Macdonald, 1985). Mas essa relação também pode ser um efeito da capacidade de defesa, uma vez que grupos maiores teriam a capacidade de defender territórios maiores. Durante a estação seca, o tamanho do território exclusivo foi relacionado negativamente com o número de adultos presentes em grupos adjacentes, como observado para outras espécies (Stamps, 1990; Stamps & Krishnan, 1990; Wolf, 1993; Tallents *et al*., 2012). No entanto, na estação chuvosa não observamos relação entre a pressão de intrusos e o tamanho dos territórios exclusivos, provavelmente por que os recursos estão mais amplamente distribuídos neste período, atenuando a pressão de grupos vizinhos com a diminuição da densidade de ariranhas ao longo dos corpos d'água. Dessa forma, os resultados indicam que a capacidade de defesa exece um papel importante na manutenção de territórios de grupos de ariranhas ao longo das estações, o que pode afetar o sucesso reprodutivo dos casais dominantes.

Ariranhas vivem em grupos coesos, que realizam a maioria das atividades diárias em conjunto (Duplaix, 1980; Leuchtenberger & Mourão, 2008) e dessa forma necessitam de um complexo sistema de comunicação para manter as relações sociais dentro e entre os grupos. O repertório vocal da espécie representou um contínuo, com transições e gradações que aumentam a complexidade do sistema de comunicação da espécie. Classificamos 15 tipos sonoros distintos emitidos em diferentes contextos comportamentais, que estiveram significativamente associados com a ordenação das variáveis acústicas. Embora haja muita sobreposição entre contextos de medo e afiliativos (August & Anderson, 1987), o repertório vocal de ariranhas parece estar de acordo com o modelo de estrutura motivacional (Morton, 1977) e reflete o estado motivacional dos indivíduos.

A principal função dos sons de alarme é informar sobre o risco de predação (Blumstein, 1999) e a discriminação individual através de sinais de alarme pode ter um valor adaptativo (Hare, 1998; Blumstein & Daniel, 2004; Matrosova *et al.*, 2011; Pollard, 2011). Espécies sociais podem apresentar individualidade em sinais de alarme (Pollard, 2011), uma vez que o reconhecimento de sons de alarme de membros do grupo pode informar um perigo mais eminente do que sons de indivíduos mais distantes (Hare, 1998). Ariranhas vocalizam sons de alarme (*snorts*), que geralmente resultam em uma reação nos demais membros do grupo e, dessa forma, são sinais potenciais para transmitir informações individuais (Bezerra *et al*., 2010). Neste estudo, *snorts* não foram significativamente distintos entre as áreas de estudo, mas discriminaram significativamente entre grupos sociais e indivíduos, sendo que a discriminação foi mais forte entre fêmeas e machos. A frequência e a dispersão dos formantes foram as variáveis acústicas com maior potencial para codificar identidade de grupo, indivíduos e sexos. Estas características acústicas são determinadas por componentes do trato vocal denominadas de filtro (Fitch 1997, McComb & Reby, 2005) e têm uma importante função na estimativa de tamanho e reconhecimento individual em mamíferos (Fitch, 1997; Fitch & Fritz, 2006; Vanoni & McElligott, 2007). A correlação negativa entre a dispersão dos formantes e o comprimento do trato vocal (Fitch, 1997) sugere que machos adultos de ariranhas têm tratos vocais maiores do que fêmeas adultas, o que pode também corresponder a maiores tamanhos corporais. Dessa forma, *snorts* poderiam ser uma importante ferramenta para seleção de potenciais parceiros reprodutivos na espécie. No entanto, a discriminação de identidade de grupos, indivíduos e entre sexos deve ser testada com experimentos de play-back, além das correlações entre trato vocal e dispersão de formantes, para confirmar a função dos formantes na discriminação sexual e de características físicas entre ariranhas.

REFERÊNCIAS BIBLIOGRÁFICAS

Adams, E.S. 1994. Settlement Tactics in Seasonally Territorial Animals: Resolving Conflicting Predictions. *American Naturalist,* 143(5): 939-943.

Adams, E.S. 2001. Approaches to the study of territory size and shape. *Annual Review of Ecology and Systematics,* 32: 277-303.

Aebischer, N.J.; Robertson, P.A. & Kenward, R.E. 1993. Compositional analysis of habitat use from animal radio-tracking data. *Ecology,* 74(5): 1313−1325.

Alho, C.J.R. 2008. Biodiversity of the Pantanal: response to seasonal flooding regime and to environmental degradation. *Brazilian Journal of Biology,* 68(4): 957-966.

Altmann, J. 1974. Observational study of behaviour: sampling methods. *Behaviour,* 49: 227–267.

Anoop, K.R. & Hussain, S.A. 2004. Factors affecting habitat selection by smooth-coated otters (*Lutra perspicillata*) in Kerala, India. *Journal of Zoology,* 263:417–423.

Arthur, S.M.; Manly, B.F.J.; McDonald, L.L. & Garner, G.W. 1996. Assessing habitat selection when availability changes. *Ecology,* 77(1):215-227.

Aschoff, J. 1966. Circadian activity pattern with two peaks. *Ecology,* 47:657-662.

August, P.V. & Anderson, J.G.T. 1987. Mammal sounds and motivation-structural rules: A test of the hypothesis. *Journal of Mammalogy,* 68(1), 1-9.

Belan, I.; Lehner, P.N. & Clark, T. 1978. Vocalizations of the American Pine Marten, Martes Americana. *Journal of Mammalogy,* 59 (4), 871-874.

Bezerra, B.M.; Souto, A.S., Schiel, N. & Jones, G. 2010. Notes on vocalisations of giant otters in the flooded Igapó forests of Jaú National Park, Amazonas, Brazil. *Journal of Ethology,* 29(1), 169-175.

Blumstein, D.T. & Daniel, J.C. 2004. Yellow-bellied marmots discriminate between the alarm calls of individuals and are more responsive to calls from juveniles. *Animal Behaviour,* 68: 1257–1265.

Blumstein, D.T. 1999. Alarm calling in three species of marmots. *Behaviour,* 136:731-757.

Blumstein, D.T.; Richardson, D.T.; Cooley, L., Winternitz, J. & Daniel J.C. 2008. The structure, meaning and function of yellow-bellied marmot pup screams. *Animal Behaviour,* 76: 1055-1064.

Blundell, G.M.; Maier, J.A.K. & Debevec, E.M. 2001. Linear home ranges: effects of smoothing, sample size, and autocorrelation on kernel estimates. *Ecological Monographs,* 71(3):469−489.

Blundell, G.M.; Bowyer, R.T.; Ben-David, M.; Dean, T.A. & Jewett, S.C. 2000. Effects of food resources on spacing behavior of river otters: does forage abundance control home-range size?. *In*: Eiler, J.H.; Alcorn, D.J. & Neuman, M.R. (Eds). *Proceedings of the Fifteenth International Symposium on Biotelemetry*. International Society of Biotelemetry, Wageningen, Netherlands. p. 325-333.

Boughman, J.W. 1998. Vocal Learning by Greater Spear-Nosed Bats. *Biological Sciences*, 265(1392): 227-233.

Bradbury, J.W. & Vehrencamp, S.L. 1998. *Principles of Animal Communication.* Massachusetts, Sinauer Associates Inc. Publishers. 882 pp.

Brennan, P.A. & Kendrick, M.K. 2006. Mammalian social odours: attraction and individual recognition. *Philosophical Transactions of The Royal Society B,* 361: 2061-2078.

Briefer, E.F. 2012. Vocal expression of emotions in mammals: mechanisms of production and evidence. *Journal of Zoology,* http://dx.doi.org/10.1111/j.1469-7998.2012.00920.x.

Brown, J.L. 1982. Optimal group size in territorial animals. *Journal Theoretical Biology*, 95: 793-810.

Brown, J.L. & Orians, G.H. 1970. Spacing patterns in mobile animals. *Annual Review of Ecology and Systematics,* 1: 239-262.

Callenge, C. 2006. The package “adehabitat” for the R software: A tool for the analysis of space and habitat use by animals. *Ecological Modelling,* 197:516–519.

Callenge, C. & Dufour A.B. 2006. Eigenanalysis of selection ratios from animal radio-tracking data. *Ecology,* 87 (9): 2349–2355.

Carter, S.K.; Rosas, F.C.W.; Cooper, A.B. & Cordeiro-Duarte, A.C. 1999. Consumption rate, food preferences and transit time of captive giant otter *Pteronura brasiliensis*: Implications for the study of wild populations. *Aquatic Mammals* 25(2):79-90.

Carter, S. & Rosas F.C.W. 1997. Biology and conservation of the giant otter *Pteronura brasiliensis*. *Mammal Review,* 27(1):1−26.

Charlton, B.D.; Ellis, W.A.H.; McKinnan, A.J.; Cowin, G.J.; Brumm, J.; Nolsson, K. & Fitch, W.T. 2011. Cues to body size in the formant spacing of male koala (*Phascolarctos* *cinereus*) bellows: honesty in an exaggerated trait. *The Journal of Experimental Biology*, 214: 3414-3422.

Charlton, B.D.; Zhihe, Z. & Snyder, R.J. 2009. The information content of giant panda, *Ailuropoda melanoleuca*, bleats: acoustic cues to sex, age and size. *Animal Behaviour*, 78: 893–898.

Charlton, B.D.; Zhile, Z. & Snyder, R.J. 2010. Giant pandas perceive and attend to formant frequency variation in male bleat. *Animal Behaviour*, 79: 1221-1227.

Charrier, I.; Jouventin, P.; Mathevon, N. & Aubin, T. 2001. Individual identity coding depends on call type in the South Polar skua *Catharacta maccormicki*. *Polar Biology*, 24: 378-382.

Collias, N.E. 1960. An ecological and functional classification of animal sounds. *In:* Lanyon, W.E. & Tavolga, W.N (Eds). *Animal sounds and communication.* American Institute of Biological Sciences. p. 368-391.

Collins K.T. & Terhune J.M. 2007. Geographic variation of Weddell seal (*Leptonychotes weddellii*) airborne mother–pup vocalizations. *Polar Biology*, 30:1373–1380.

Crockford C., Herbinger I., Vigilant L. & Boesh C. 2004. Wild chimpanzees produce group-specific calls: a case for vocal learning? *Ethology*, 110: 221-243.

Crockford, C. & Boesch, C. 2005. Call combinations in wild chimpanzees. *Behaviour*, 142 (4): 397-421.

Curtis, D. J. and Zaramody, A. 1998. Group size, home range use, and seasonal variation in the ecology of *Eulemur mongoz*. *International Journal of Primatology*, 19 (5):811-835.

Daly, M.; Behrends, P.R.; Wilson, M.I. & Jacobs, L.F. 1992. Behavioral modulation of predation risk: moonlight avoidance and crepuscular compensation in a nocturnal desert rodent, *Dipodomys merriami*. *Animal Behaviour*, 44:1-9.

De Solla, S.R.; Bonduriansky, R. & Brooks, R.J. 1999. Eliminating autocorrelation reduces biological relevance of home range estimates. *The Journal of Animal Ecology*, 68(2):221−234.

Delgado, R.A.Jr. 2007. Geographic variation in the long calls of male orangutans (*Pongo* spp.). *Ethology*, 113: 487–498.

Dillon, A. & Kelly, M.J. 2008. Ocelot home range, overlap and density: comparing radio telemetry with camera trapping. *Journal of Zoology*, 275:391–398.

Doncaster, C.P. & Macdonald, D.W. 1992. Optimum group size for defending heterogenous distributions of resources: A model applied to red foxes, *Vulpes vulpes*, in Oxford City. *Journal of Theoretical Biology*, 159: 189-198.

Duplaix N. 1980. Observations on the ecology and behavior of the giant river otter *Pteronura brasiliensis* in Suriname. *Revue Ecologique (Terre Vie)* 34: 496-620.

Duplaix, N. 1982. Contribution à l'écologie et à l'éthologie de *Pteronura brasiliensis* (Carnivora, Lutrinae): Implications évolutives. PhD Thesis, Université Paris-Sud. 353 pp.

Duplaix, N. 2004. Guyana giant otter project: 2002-2004 research results. Oceanic Society. San Francisco, California, USA**:** 44 p. http://www.giantotterresearch.com/articles/OCEANIC_SOCIETY_Guyana_Project_Report_2002-2004.pdf

Endler, J. A. 2000. Evolutionary implications of the interaction between animal signals and the environment. *In:* Espmark, Y.; Amundsen, T. & Rosenqvist, G. (Eds). *Animal Signals: Signaling and Signal design in animal communication.* Tapir Academic Press, Trondheim, Norway. p. 11-46.

Erlinge, S. 1967. Home range of the otter *Lutra lutra* L. in southern Sweden. Oikos 18(2):186−209.

Erlinge, S. 1968. Territoriality of the Otter *Lutra lutra* L. *Oikos* 19 (1): 81-98

Evangelista, E. & Rosas, F.C.W. 2011a. The home range and movements of giant otters (*Pteronura brasiliensis*) in the Xixuaú Reserve, Roraima, Brazil, *IUCN Otter Specialist Group Bulletin*, 28(A):31−37.

Evangelista, E. & Rosas, F.C.W. 2011b. Breeding behavior of giant otter (*Pteronura brasiliensis*) in the Xixuaú Reserve, Roraima, Brazil. *IUCN Otter Specialist Group Bulletin*, 28(A):5−10.

Farley, S.D.; Lehner, P.N.; Clark, T. & Trost, C. 1987. Vocalizations of the Siberian ferret (*Mustela eversmanni*) and comparisons with other Mustelids. *Journal of Mammalogy*, 68(2): 413-416.

Fitch, W.T. & Hauser, M.D. 1995. Vocal production in nonhuman primates: Acoustics, physiology, and functional constraints on ‘honest’ advertisement. *American Journal of Primatology*, 37; 191–219.

Fitch, W.T. 1997. Vocal tract length and formant frequency dispersion correlate with body size in rhesus macaques. *Journal of Acoustic Society of America*, 102 (2): 1213-1222.

Fitch, W. T.; Neubauer, J. & Herzel, H. 2002. Calls out of chaos: the adaptive significance of nonlinear phenomena in mammalian vocal production. *Animal Behaviour*, 63: 407–418.

Fitch, W.T. & Fritz, J.B. 2006. Rhesus macaques spontaneously perceive formants in conspecific vocalizations. *Journal of Acoustic Society of America*, 120(4): 2132-2141.

Fitchel, C. & Manse,r M. 2010. *Vocal communication in social groups* Animal Behaviour: Evolution and Mechanisms, Part I, Pages 29-54.

Garcia de Leaniz, C.; Forman, D.W.; Davies, S. & Thomson, A. 2006. Non-intrusive monitoring of otters (*Lutra lutra*) using infrared technology. *Journal of Zoology*, 270: 577-584.

Gerell, R. 1969. Activity patterns of the mink *Mustela vison* Schreber in southern Sweden. *Oikos* 20:451-460.

Getz, W.M. & Wilmers C.C. 2004. A local nearest-neighbor convex-hull construction of home ranges and utilization distributions. *Ecography*, 27: 489−505.

Gittleman, J.L. & Harvey, P.H. 1982. Carnivore home-range size, metabolic needs and ecology. *Behavioral Ecology and Sociobiology*, 10(1): 57−63.

Gnoli, C. & Prigioni, C.1995. Preliminary study on the acoustic communication of captive otters (*Lutra lutra*). *Hystrix*, 7(1-2): 289-296.

Gómez, J.R.; Jorgenson, J.P. & Valbuena, R. 1999. Report on the rehabilitation and release of two giant river otter (*Pteronura brasiliensis*) pups in the Bita river (Vichada, Colombia). *IUCN Otter Specialist Group Bulletin*, 16(2): 86-89.

Gompper, M.E. & Gittleman, J.L. 1991. Home range scaling: intraspecific and comparative trends. *Oecologia*, 87(3): 343-348.

Gosling, L.M. & Roberts, S.C. 2001. Testing ideas about the function of scent marks in territories from spatial patterns. *Animal Behaviour*, 62: F7-F10.

Gosling, L.M. 1982. A reassessment of the function of scent marking in territories. *Zeitschrift für Tierpsychologie*, 60: 89–118.

Grant, J.W.A.; Chapman, C.A. & Richardson, K.S. 1992. Defended versus undefended home range size of carnivores, ungulates and primates. *Behavioral Ecology and Sociobiology*, 31: 149-161.

Groenendijk, J.; Hajek, F.; Duplaix, N.; Reuther, C.; Van Damme, P.; Schenk, C.; Staib, E.; Wallace, R.; Waldemarin, H.; Notin, R.; Marmontel, M.; Rosas, F.W.C.; Mattos De, G.E.; Evangelista, E.; Utreras, V.; Lasso, G.; Jaques, H.; Matos, K.; Roopsind, I. & Botello, J.C. 2005. Surveying and monitoring distribution and population trends of the giant otter (*Pteronura brasiliensis*). *Habitat*, 16: 1-500.

Hamilton, S.K.; Sippel, S.J. & Melack, J.M. 1996. Inundation patterns in the Pantanal wetland of South America determined from passive microwave remote sensing. *Archiv für Hydrobiologie*, 137:1−23.

Hare, J.F. 1998. Juvenile Richardson’s ground squirrels, *Spermophilus richardsonii*, discriminate among individual alarm callers. *Animal Behaviour*, 55: 451–460.

Herr, J. & Rossell, F. 2004. Use of space and movement patterns in monogamous adult Eurasian beavers (*Castor fiber*). *Journal of Zoology, London*, 262: 257–264

Hijmans, R.J. & van Etten, J. 2010. Raster: package for reading, writing, and manipulating raster (grid) type geographic (spatial) data. http://cran.r-project.org/web/packages/raster/index.html.

Humphrey, S. R. & Zinn, T. L. 1982. Seasonal habitat use by river otters and everglades mink in Florida. *The Journal of Wildlife Management*, 46: 375–381

Huff, N. & Price, E. O. 1968. Vocalizations of the least weasel, *Mustela nivalis*. *Journal of Mammalogy*, 49(3): 548-550.

Ivlev, V.S. 1961. *Experimental ecology of the feeding of fishes*. Yale University Press, New Haven, Connecticut, USA.

Janik, V. & Slater, P.J.B. 1998. Context-specific use suggests that bottlenose dolphin signature whistles are cohesion calls. *Animal Behaviour*, 56: 829-838.

Johnson, D.H. 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61(1): 65−71.

Kean, E.F.; Müller, C.T. & Chadwick, E.A. 2011. Otter scent signals age, sex, and reproductive status. *Chemical Senses*, 36: 555-564.

Keitt, T.H.; Bivand, R.; Pebesma, E. & Rowlingson, B. 2010. Rgdal: bindings for the geospatial data abstraction library. R package version 0.6-24. http://CRAN.R-project.org/package=rgdal

Kernohan, B.J.; Gitzen, R.A. & Millspaugh, J.J. 2001. Analysis of animal space use and movements. *In:* Millspaugh, J. J. & Marzluff, J. M. (Eds). *Radio tracking and Animal Populations*. San Diego: Academic press. p. 125-166.

Kleiman, D.G. 1989. Reintroduction of captive mammals for conservation. *BioScience*, 39(3):152−161.

Koren, L. & Geffen, E. 2011. Individual identity is communicated through multiple pathways in male rock hyrax (*Procavia capensis*) songs. *Behaviroal Ecology and Sociobiology*, 65: 675–684.

Krebs, J.R., and Davies, N.B. 1997. *Behavioural ecology: an evolutionary approach*. 4th ed. Oxford, UK: Blackwell.

Kruuk, H. 1992. Scent marking by otters *(Lutra lutra)*: signaling the use of resources. *Behavioral Ecology*, 3(2): 133-140

Kruuk, H. 2006. *Otters: Ecology, behavior and conservation*. Oxford University Press Inc., New York.

Kruuk, H. & Macdonald, D.W. 1985. Group territories of carnivores: empires and enclaves. *In:* Sibly, R. M. & Smith, R. H. (Eds). *Behavioural ecology: ecological consequences of adaptive behavior*. Blackwell Scientific Publications, Oxford, UK. p. 521-536.

Kruuk, H.; Gorman, M. & Leitch, A. 1984. Scent-marking with the subcaudal gland by the European Badger, *Meles meles* L. *Animal Behaviour*, 32: 899-907.

Laidler L. 1984. *The behavioral ecology of the giant otter in Guyana*. Master dissertation, University of Cambridge.

Lehner, P.N. 1998. *Handbook of ethological methods*. Garland STPM Press, London, 672 pp.

Leuchtenberger, C & Mourão, G. 2009. Scent-marking of giant otter in the Southern Pantanal, Brazil. *Ethology*, 115:210–216.

Leuchtenberger C. & Mourão G. 2008. Social organization and territoriality of giant otters (Carnivora: Mustelidae) in a seasonally flooded Savanna in Brazil. *Sociobiology*, 52 (2): 257-270.

Lewin-Koh, N.J., et al. 2009. Maptools: Tools for reading and handling spatial objects. R package version 0.7-29. http://CRAN.R-project.org/package=maptools

Lim, N.T.L. & Ng, P.K.L. 2008. Home range, activity cycle and natal den usage of a female Sunda pangolin *Manis javanica* (Mammalia: Pholidota) in Singapore. *Endangered Species Research,* 4: 233-240.

Lima, dosS.D. 2009. *Ocorrência de ariranhas Pteronura brasiliensis (Carnivora: Mustelidae) e interferências antrópicas à espécie no lago Amanã, Reserva de Desenvolvimento Sustentável Amanã, Amazonas.* Dissertação de Mestrado. Fundação Universidade Federal do Amapá. 58pp.

Lima, D. dos S.; Marmontel, M. & Bernard, E. 2012. Site and refuge use by giant river otters (*Pteronura brasiliensis*) in the Western Brazilian Amazonia. *Journal of Natural History*, 46(11-12): 729−739.

Lode T. 1995. Activity pattern of polectas *Mustela putorius* L. in relation to food habits and prey activity. *Ethology*, 100: 295-308.

Macdonald, D.W. 1983. The ecology of carnivore social behaviour. *Nature*, 301: 379−384.

Macdonald, S.M., and Mason, C.F. 1983. Some factors influencing the distribution of otters (*Lutra lutra*). *Mammal Review*, 13:1–10.

Machado, M.R.B. 2004. *Bioacústica de ariranhas (Pteronura brasiliensis) (Carnivora: Mustelidae): discriminação vocal e repertório*. Dissertação de Mestrado, Instituto Nacional de Pesquisa da Amazônia. 94pp.

Maher, C.R. & Lott, D.F. 2000. A review of ecological determinants of territoriality within vertebrate species. *The American Midland Naturalist*, 143(1):1−23.

Mares, R.; Young, A.J. & Clutton-Brock, T.H. 2012. Individual contributions to territory defence in a cooperative breeder: weighing up the benefits and costs. *Philosophical Transactions of The Royal Society B,* (http// rspb.royalsocietypublishing.org) Acesso: 10/07/2012.

Matrosova, V.A.; Blumstein, D.T.; Volodin, I.A. & Volodina, E.V. 2011. The potential to encode sex, age, and individual identity in the alarm calls of three species of Marmotinae. *Naturwissenschaften,* 98:181–192.

McComb, K.; Reby, D.; Baker, L.; Moss, C. & Sayialel, S. 2003. Long-distance communication of acoustic cues to social identity in African elephants. *Animal Behaviour*, 65: 317–329.

McComb, K. & Reby, D. 2005. Vocal communication networks in large terrestrial mammals. *In* McGregor, P. (Eds). *Animal communication networks*. Cambridge University Press. p 372-389.

McComb, K. & Semple, S. 2005. Coevolution of vocal communication and sociality in primates. *Biology Letters*, 1: 381–385.

McShane, L.; Estes, J.A.; Riedman, M.L. & Staedler, M.M. 1995. Repertoire, structure and individual variation of vocalisation in the sea otter. *Journal of Mammalogy*, 76: 414–427.

Medina-Vogel, G.; Kaufman, V. S.; Monsalve, R. & Gomez, V. 2003. The influence of riparian vegetation, woody debris, stream morphology and human activity on the use of rivers by southern river otters in *Lontra provocax* in Chile. *Oryx*, 37(4):422−430.

Melquist, W. E. & Hornocker, M.G. 1983. Ecology of river otters in west Central Idaho. *Wildlife Monographs*, 83:1-60.

Mitani, J.C.; Hunley, K.L. & Murdoch, M.E. 1999. Geographic variation in the calls of wild chimpanzees: a reassessment. *American Journal of Primatology*, 47:133–151.

Morales-Betancourt, D. 2011. Report of an adaptive reintroduction of a juvenile giant otter (*Pteronura brasiliensis*). *IUCN Otter Specialist Group Bulletin*, 28 (1): 23-33.

Morton, E.S. 1977. On the occurrence and significance of motivation-structural rules in some bird and mammal sounds. *American Naturalist*, 111: 855–869.

Mourão, G. & Carvalho, L. 2001. Canibalism among giant otters (*Pteronura brasiliensis*). *Mammalia* 6(2): 225-227.

Mourão, G.; Tomas, W. & Campos, Z. 2010. How much can the number of jabiru stork (Ciconiidae) nests vary due to change of flood extension in a large Neotropical floodplain? *Zoologia*, 27(5):751−756.

Oksanen, J.; Kindt, R.; Legendre, P.; O’Hara, B.; Simpson, G. L.; Solymos, P.; Stevens, M. H. H. & Wagner, H. 2008. The Vegan Package.

Oldham, A. & Black, J.M. 2009. Experimental tests of latrine use and communication by river otters. *Northwestern Naturalist*, 90(3): 207-211.

Ottaviani, D., Cairns, S.C.; Oliverio, M. & Boitani, L. 2006 Body mass as a predictive variable of home-range size among Italian mammals and birds. *Journal of Zoology*, 269: 317–330.

Palphramand, K. & White, P.C.L. 2007. Badgers, *Meles meles*, discriminate between neighbour, alien and self scent. *Animal Behaviour*, 74: 429-436.

Perrin, M. R., and C.Carugati. 2000. Habitat use by the cape clawless otter and the spotted-necked otter in the KwaZulu-Natal Drakensberg, South Africa. *South African Journal of Wildlife Research*, 30(3):103−113.

Peters, G. 2002. Purring sounds in mammals. *Mammal Review*, 32 (4), 245–271.

Pickles, R.; Zambrana, V.; Jordan, B.; Hoffmann-Heap, I.; Salinas, A.; Groombridge, J. & Damme, P.V. 2011. An evalutaion of the utility of camera traps in monitoring giant otter populations. *IUCN Otter Specialist Group Bulletin,* 28:39-45.

Pickles, R.S.A; Groombridge, J.J.; Zambrana Rojas, V.D.; Van Damme, P.; Gottelli, D.; Kundu, S.; Ariani, C.V.; Iyenar, A. & Jordan, W.C. 2011. Evolutionary history and identification of conservation units in the giant otter, *Pteronura brasiliensis*. *Molecular Phylogenetics and Evolution*, 1:12.

Pollard, K.A. 2011. Making the most of alarm signals: the adaptive value of individual discrimination in an alarm context. *Behavioral Ecology*, 22(1): 93-100.

Pollard, K.A. & Blumstein, D.T. 2012. Evolving communicative complexity: insights from rodents and beyond. *Philosophical Transactions of The Royal Society B*, 367: 1869–1878.

Powell, R. A. 2000. Animal home ranges and territories and home range estimators. Pp. 65-110 *In*: Boitani, L. & Fuller, T.K. (Eds). *Research techniques in animal ecology: controversies and consequences*. Columbia University Press, New York.

Ralls K. & Siniff D.B. 1990. Time budget and activity patterns in California sea otters. *The Journal of Wildlife Management* 54:251-259.

Reby D. & McComb K. 2003. Anatomical constraints generate honesty: acoustic cues to age and weight in the roars of red deer stags. *Animal Behaviour,* 65: 519–530.

Renard, D. & Bez, N. 2005. *RGeoS: geostatistical package. R package. Version 2.1.* Centre de Géostatistique, Ecole des Mines de Paris, Fontainebleau, France.

Rendall, D.; Rodman, P.S. & Emond, R.E. 1996. Vocal recognition of individuals and kin in free-ranging rhesus monkeys. *Animal Behaviour,* 51: 1007–1015

Rendell, L.; Mesnick, S.L.; Dalebout, M.L.; Burtenshaw, J. & Whitehead, H. 2012. Can genetic differences explain vocal dialect variation in sperm whales, *Physeter macrocephalus*? *Behavior Genetics*, 42: 332-343.

Revilla, E. & Palomares, F. 2002. Spatial organization, group living and ecological correlates in low-density populations of Eurasian badgers, *Meles meles. Journal of Animal Ecology,* 71: 497–512.

Reynolds, T.D. & Laundre, J.W. 1990. Time intervals for estimating pronghorn and coyote home ranges and daily movements. *The Journal of Wildlife Management,* 54(2): 316−322.

Ribas, C. 2012. *Grau de parentesco e relações sociais entre grupos de ariranhas (Pteronura brasiliensis).* PhD thesis. Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil. 105pp.

Ribas, C.; Damasceno, G.; Magnusson, W.; Leuchtenberger, C. & Mourão, G. 2012. Giant otters feeding on caiman: evidence for an expanded trophic niche of recovering populations. *Studies on Neotropical Fauna and Environment*, 47: 19-23.

Ribas, C. & Mourão, G. 2004. Intraspecific agonism between giant otter groups. *IUCN Otter Specialist Group Bulletin*, 21: 89–93.

Ribas, C. 2004. *Desenvolvimento de um programa de monitoramento em longo prazo das ariranhas (Pteronura brasiliensis) no pantanal brasileiro.* Dissertação de Mestrado. Universidade Federal do Mato Grosso do Sul, Campo Grande, Brazil. 68pp.

Riede, T.; Herzel, H.; Mehwald, D.; Seidner, W.; Trumler, E.; Böhme, G. & Tembrock, G. 2000. Nonlinear phenomena in the natural howling of a dog-wolf mix. *The Journal of the Acoustical Society of America*, 108: 1435–1442.

Riede, T.; Owren, M.J. & Arcadi, A.C. 2008. Nonlinear acoustics in pant hoots of common chimpanzees (*Pan troglodytes*): frequency jumps, subharmonics, biphonation, and deterministic chaos. *American Journal of Primatology*, 64: 277–291.

Riede, T.; Wilden, I & Tembrock, G. 1997. Subharmonics, biphonations, and frequency jumps-common components of mammalian vocalization or indicators for disorders. *Zeitschrift für Säugetier*, 62 (Suppl 2): 198–203.

Robisson, P.; Aubin, T. & Bremond, J-C. 1993. Individuality in the voice of the Emperor Penguin *Aptenodytes forsteri*: adaptation to a noisy environment. *Ethology*, 94 (4): 279-290

Rooney, S.M.; Wolfe, A. & Hayden, T. J. 1998. Autocorrelated data in telemetry studies: time to independence and the problem of behavioural effects. *Mammal Review*, 28(2): 89–98.

Rosas, F.C.W.; Zuanon, J.A.S. & Carter, S.K. 1999. Feeding ecology of the giant otter, *Pteronura brasiliensis*. *Biotropica*, 31: 502-506.

Rosas, F.C.W.; Waldemarin, H. & Mattos, G.E.de. 2008. *Pteronura brasiliensis* (Zimmermann, 17880). pp. 800-801. *In*: Machado, A.B.M.; Drummond G.M. & Paglia A.P. (Eds). *Livro Vermelho da Fauna Brasileira Ameaçada de Extinção*. 1a Ed. Belo Horizonte: Ministério do Meio Ambiente - Fundação Biodiversitas.

Rosas, F.C.W.; da Rocha, C.S.; Mattos, G.E.de & Lazzarini, S.M. 2009. Body weight-length relationships in giant otters (*Pteronura brasiliensis*) (Carnivora, Mustelidae). *Brazilian Archievs of Biology and Technology*, 52 (3): 587-591.

Rostain, R.R.; Ben-David, M.; Groves, P. & Randall, J.A. 2004. Why do river otters scent-mark? An experimental test of several hypotheses. *Animal Behaviour*, 68: 703-711.

Roux, A.L.; Cherry, M.I. & Manser, M.B. 2009. The vocal repertoire in a solitary foraging carnivore, *Cynictis penicillata*, may reflect facultative sociality. *Naturwissenschaften*, 96: 575–584.

Ruiz-Olmo, J.; Margalida, A. & Batet, A. 2005. Use of small rich patches by Eurasian otter (*Lutra lutra* L.) females and cubs during the pre-dispersal period. *Journal of Zoology*, 265: 339–346.

Samuel, M.D.; Pierce, D.J. & Garton, E.O. 1985. Identifying areas of concentrated use within the home range. *Journal of Animal Ecology*, 54(3): 711−719.

Sanvito, S.; Galimberti, F. & Miller, E.H. 2007. Vocal signalling of male southern elephant seals is honest but imprecise. *Animal Behaviour*, 73: 287 299.

Schassburger, R.M. 1993. *Vocal communication in the Timber Wolf, Canis lupus, Linnaeus*. Paul Parey Scientific Publishers, Berlin, Germany.

Schenck, C. 1999. *Lobo de Rio (Pteronura brasiliensis). Presencia, uso del hábitat y protección en el Perú.* GTZ/INRENA, Lima, Peru.

Schoener, T.W. 1971. Theory of Feeding Strategies. *Annual Review of Ecology and Systematics*, 2: 369−404

Schweizer, J. 1992. *Ariranhas no Pantanal: Ecologia e comportamento de Pteronura brasiliensis*. Edibran-Editora Brasil Natureza Ltda, Curitiba, Paraná.

Servheen, C. & Klaver, R. 1983. Grizzly bear dens and denning activity in the Mission and Rattlesnake Mountains, Montana. *Bears: Their Biology and Management*, 5: 201-207.

Sieber, O.J. 1984. Vocal communication in raccoons (*Procyon lotor*). *Behaviour*, 90(1/3): 80-113.

Sikes, R.S.; Gannon, W.L. & the Animal Care and Use Committee of the American Society of Mammalogists. 2011. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *Journal of Mammalogy*, 92: 235-253.

Sillero-Zubiri, C. & Macdonald, D.W. 1998. Scent-marking and territorial behaviour of Ethiopian wolves *Canis simensis*. *Journal of Zoology,* 245, 351–361.

Silveira, L.; Furtado, M.M.; Rosas, F.C.W.; Silva, L.C.; Cabral, M.M.M.; Torres, N.M.; Sollmann, R.; Kouba, A. & Jácomo, A.T.A**.** 2011. Tagging giant otters (*Pteronura brasiliensis*) (Carnivora, Mustelidae) for radio-telemetry studies. *Aquatic Mammals*, 37: 208-212.

Sousa-Lima, R.; Paglia, A. P. & Fonseca, G.A.B.da. 2002. Signature information and individual recognition in the isolation calls of Amazonian manatees, *Trichechus inunguis* (Mammalia: Sirenia). *Animal Behaviour*, 63: 301-310.

Sousa-Lima, R.; Paglia, A.P. & Fonseca, G.A.B.da. 2008. Gender, age, and identity in the isolation calls of Antillean manatees (*Trichechus manatus manatus*). *Aquatic Mammals*, 34(1): 109-122

Souza, J.D.de. 2004. *Estudos ecológicos da ariranha, Pteronura brasiliensis (Zimmermann, 1780) (Carnivora: Mustelidae) no Pantanal Mato-Grossense*. Dissertação de Mestrado, Universidade Federal do Mato Grosso, Brazil. 97pp.

Stabler, B. 2003. Shapefiles, version 0.3. R package. http://cran.r-project.org.

Staib, E. 2005. *Eco-Etología del Lobo de Río (Pteronura brasiliensis) en el Sureste del Perú*. Tese de Doutorado. Sociedad Zoológica de Francfort Perú.

Stamps, J.A. 1990. The effect of contender pressure on territory size and overlap in seasonally territorial species. *The American Naturalist,* 135(5): 614-632.

Stamps, J.A. 1995. Motor learning and the value of familiar space. *The American Naturalist*, 146(1): 41−58.

Stamps, J.A. & Krishnan, V.V. 1990. The effect of settlement tactics on territory sizes. *The American Naturalist*, 135(4): 527-546.

Stamps, J.A. & Krishnan, V.V. 1999. A learning-based model of territory establishment. *The Quarterly Review of Biology*, 74(3): 291-318.

Stevens S.S. & Serfass T.L. 2008. Visitation patterns and behavior of nearctic river otters (*Lontra canadensis*) at latrines. *Northeastern Naturalist,* 15:1-12.

Stoeger, A.; Baotic, A.; Li, D. & Charlton, B. D. 2012. Acoustic features indicate arousal in infant giant panda vocalisations. *Ethology,* 118: 1–10.

Sueur, J.; Aubin, T. & Simonis, C. 2008. Seewave: a free modular tool for sound analysis and synthesis. *Bioacustics*, 18: 213-216.

Tallents, L.A.; Randall, D.A.; Williams, S.D. & Macdonald, D.W. 2012. Territory quality determines social group composition in Ethiopian wolves *Canis simensis. Journal of Animal Ecology,* 81: 24–35.

Taylor, A.M. & Reby, D. 2010. The contribution of source–filter theory to mammal vocal communication research. *Journal of Zoology*, 280: 221–236.

Terry, A. M. R.; Peake, T. M. & McGregor, P. K. 2005. The role of vocal individuality in conservation. *Frontiers in Zoology*, 2:10.

Thioulouse, J.; Chessel, D.; Doledec, S. & Olivier, J.M. 1997. Ade-4: a multivariate analysis and graphical display software. *Statistics and Computing*, 7: 75–83.

Tokuda, I.; Riede, T. Neubauer, J.; Owren, M. & Herzel, H. 2005. Nonlinear analysis of irregular animal vocalizations *The Journal of the Acoustical Society of America*, 111(6): 2908-2919.

Tomas, W.; Borges, P.A.L.; Rocha, H.J.F.; Sá Filho, R.; Kutchenski Junior, F. & Udry, T.V. 2000. Potencial dos Rios Aquidauana e Miranda, no Pantanal de Mato Grosso do Sul, para a conservação da ariranha (*Pteronura brasiliensis*). *In: III Simpósio sobre Recursos Naturais e Sócio-econômicos do Pantanal: Os Desafios do Novo Milênio.* Corumbá, Brazil.

Trephy, S.A.& Hik, D.S. 2010. Variation in pika (*Ochotona collaris*, *O. princeps*) vocalizations within and between populations. *Ecography,*, 33: 784-795.

Utreras, V. & Pinos, L. 2003. Camera trap use for studying giant otters (*Pteronura brasiliensis*) in the Yasuní Biosphere Reserve, Ecuadorian Amazon. *IUCN Otter Specialist Group Bulletin*, 20:12-13.

Utreras, V.B.; Suárez, E.R.; Zapata-Ríos, G.; Lasso, G. & Pinos, L. 2005. Dry and rainy season estimations of giant otter, *Pteronura brasiliensis*, home range in the Yasuní National Park, Ecuador. *The Latin American Journal of Aquatic Mammals*, 4 (2):1–4.

Valenzuela, D. & Ceballos, G. 2000. Habitat Selection, Home Range, and Activity of the White-Nosed Coati (*Nasua narica*) in a Mexican Tropical Dry Forest. *Journal of Mammalogy*, 81(3): 810−819.

Vannoni, E. & McElligott, A.G. 2007. Individual acoustic variation in fallow deer (*Dama dama*) common and harsh groans: a source-filter theory perspective. *Ethology*, 113: 223–234.

Vannoni, E. & McElligott, A.G. 2008. Low frequency groans indicate larger and more dominant fallow deer (Dama dama) males. *Plos One*, 3(9): 1-8.

Venables, W.N. & Ripley, B.D. 2002. *Modern applied statistics with S.* 4th edition. Springer, New York.

Wantzen, K.M.; Machado, F.deA.; Voss, M.; Boriss, H. & Junk, W.J. 2002. Seasonal isotopic shifts in fish of the Pantanal wetland, Brazil. *Aquatic Sciences*, 64:239–251.

Weilgart, L. & Whitehead, H. 1997.Group-specific dialects and geographical variation in coda repertoire in South Pacific sperm whales. *Behavioral Ecology and Sociobiology*, 40: 277-285.

Welcomme, R.L. 1985. *River fisheries.* FAO Fish. Technical Paper, 262.

Welcomme, R.L. 1990. Status of fisheries in South American rivers. *Interciência*, 15(6): 337−345.

White, P.C.L. & Harris, S. 1994. Encounters between red foxes (*Vulpes vulpes*): implications for territory maintenance, social cohesion and dispersal. *Journal of Animal and Ecology*, 63(2): 315-327.

Wilden, I.; Herzel, H.; Peters, G. & Tembrock, G. 1998. Subharmonics, biphonation, and deterministic chaos in mammal vocalization. *Bioacoustics*, 9: 171-196.

Wilkinson, L. 2004. *SYSTAT—Systems for Statistics. Version 11*. Systat Software Inc, Chicago, Illinois.

Wilson, E. 2000. *Sociobiology: The new synthesis*. 25th Aniversary ed. President and Fellows of Harvard College, USA. 697pp.

Winemiller, K.O. & Jepsen, D.B. 1998. Effects of seasonality and fish movement on tropical river food webs. *Journal of Fish Biology*, 53A: 267–296.

Wolf, J.O. 1993. Why Are Female Small Mammals Territorial? *Oikos*, 68(2): 364-370.

Wong, J.; Stewart, P.D. & MacDonald, D.W. 1999. Vocal repertoire in the European badger (*Meles meles*): structure, context, and function. *Journal of Mammalogy*, 80: 570–588.

Zielinski, W.J. 1988. The influence of daily variation in foraging cost on the activity of small carnivores. *Animal Behaviour*, 36: 239-249.

Zub, K., Theuerkauf, J, Edrzejewski, B. J. I., Schmidt, K. & Alczyk, R. K. 2003. Wolf pack territory marking in the Bilaowieza Primeval Forest (Poland). *Behaviour*, 140: 635-648.

APÊNDICE I

Studies on Neotropical Fauna and Environment
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ORIGINAL ARTICLE

To each his own taste: latrines of the giant otter as a food resource for vertebrates in Southern Pantanal, Brazil

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Pteronura brasiliensis feeds mainly on fish and uses communal latrines for territorial marking. The aim of this study was to identify the vertebrate species associated with latrines of giant otters and which species use the feces as a food resource. From December 2010 to June 2011, we positioned camera traps in front of 21 latrines of six different giant otter groups in 24 h cycles monthly. We registered 29 vertebrate species at latrines. Latrines seem to be used as a frequent food resource for some species. Studies of giant otter diets should take into account possible changes in relative abundance of prey items due to consumption of feces.

Pteronura brasiliensis se alimenta principalmente de peixes e utiliza latrinas para marcação territorial. O objetivo deste estudo foi identificar as espécies de vertebrados associadas a latrinas de ariranhas e as espécies que utilizam as fezes como fonte de recurso. De dezembro de 2010 a junho de 2011, posicionamos armadilhas fotográficas em frente a 21 latrinas de seis grupos de ariranhas distintos, mensalmente em ciclos de 24 h. Registramos 29 espécies de vertebrados em latrinas. Latrinas parecem ser utilizadas como um recurso freqüente por algumas espécies. Estudos sobre dieta de ariranhas devem considerar a possibilidade de alterações na abundância relativa dos itens de presas.

Keywords: coprophagy; diet; feces removal; giant otter; scent-mark; Brazil

Introduction

Animal excrement represents an important resource for some vertebrate species (Rowland 1975). Coprophagous species benefit by acquiring microorganisms from feces that improve the digestion of some chemical components of their diet (Giovannetti 1982). Feces can also provide various nutrients and may be an important food source during periods of food scarcity (Livingston et al. 2005; Solano-Ugalde 2005).

Pteronura brasiliensis (Zimmermann 1780) lives in family groups that are spatially organized in territories along rivers, lakes and streams (Carter & Rosas 1997; Leuchtenberger & Mourão 2008). Giant otters feed mainly on fish and groups use communal latrines and other scent stations to mark their territories (Duplaix 1980; Leuchtenberger & Mourão 2009). Latrine samples are often used to evaluate the diet of the species (e.g. Rosas et al. 1999; Ribas et al. 2012). However, removal of feces by other species can bias studies based on feces composition (Livingston et al. 2005; Norris & Michalski 2010). The aim of this study was to identify the vertebrate species associated with latrines of giant otters, and determine which species use the spraints as a food source.

Materials and methods

The study area covered a 36-kilometer longitudinal stretch of the Miranda and Vermelho Rivers (19°36′ S, 56°44′ W), in the southern Pantanal of Brazil, using camera traps positioned in front of giant otter latrines. We only considered observations when the latrine contained fresh feces. From December 2010 to June 2011, we positioned camera traps (® Bushnell Trophy Cam 8MP, Overland Park, KS, USA) in front of 21 latrines of six different giant otter groups, for 2–9 days in 24 h cycles. The average straight line (Euclidian) distance among latrines was 7.8 km, ranging from 0.1 to 25.8 km.

Camera traps were programmed to take three sequential pictures at 15 s intervals, which allowed us to observe the behavior of most visitors. To increase independence between records, only photos taken 30 minutes apart were included in the analysis. This resulted in 93 camera-days and 584 independent photos.

We calculated the dissimilarity in the species assemblages of visitors to each latrine with the Bray–Curtis distance. To examine if the composition of visitors was correlated with the Euclidian distance

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Table 1. Species photographed by camera traps at *Pteronura brasiliensis* latrines on the Miranda and Vermelho Rivers in the Brazilian Pantanal between December 2010 and June 2011. (Trophic guild: FRU = frugivorous, HER = herbivorous, DET = detritivorous, MOE = molluscovorous, INS = insectivorous, CAR = carnivorous, PIS = piscivorous, OMN = omnivorous).

		Records by camera trap							
Species	Trophic guild	December 2010	January 2011	February 2011	March 2011	April 2011	May 2011	June 2011	Total
Reptiles									
Alligatoridae									
Caiman crocodilus yacare	CAR						1		1
Iguanidae									
Iguana iguana	HER	19	4	12			13	5	53
Teiidae									
Tupinambis merianae	OMN		1	1					2
Ameiva ameiva	INS		1						1
Birds									
Ardeidae									
Tigrisoma lineatum	OMN			5	2		2		9
Anatidae									
Cairina moschata	OMN				1				1
Cathartidae									
Coragyps atratus	DET						2		2
Falconidae									
Caracara plancus	OMN			3	13	12	15		43
Cracidae									
Ortalis canicollis	OMN	6	1	1	1	69	10	7	95
Crax fasciolata	OMN			1	13	10	15	3	42
Pipile pipile	OMN					14	1		15
Rallidae									
Aramides cajanea	OMN	5	1	7	17	5	11	38	84
Aramidae									
Aramus guarauna	MOE				8	2			10
Columbidae									
Leptotila rufaxilla	FRU	6	2	4	3	33	11	1	60
Columba picazuro	FRU						1	1	2
Alcedinidae									
Chloroceryle americana	PIS						1		1
Ceryle torquata	PIS					1			1
Tyrannidae									
Pitangus sulphuratus	OMN		1				3		4
Furnariidae									
Furnarius leucopus	INS	15	7	1	5	4	15	1	48
Furnarius rufus	INS	2			5	11	17	1	36
Turdidae									
Turdus rufiventris	OMN				2	3	11	1	17
Turdus leucomelas	OMN						2		2
Mammals									
Dasyproctidae									
Dasyprocta azarae	HER				18	1			19
Didelphidae									
Philander opossum	INS-OMN						3		3
Dasypodidae									
Dasypus novemcinctus	OMN				2				2
Cervidae									
Mazama gouazoubira	HER						1		1
Canidae									
Cerdocyon thous	OMN					16			16
Felidae									
Leopardus pardalis	CAR					10			10
Panthera onca	CAR			2			2		4
Total records		53	18	37	90	191	137	58	584
Effort (trap-days)		7	4	11	8	17	32	14	93
Latrine sampled (*n*)		3	2	4	2	3	7	5	22

between latrines, we used the Mantel Test (with 1000 permutations). We evaluated the proportion of records in which individuals of some species were registered eating feces in relation to the total of independent photos taken for each species during sampling. We also investigated the relationship between visitation rate of vertebrates (number of independent photos per hour) per latrine and the rate of records of giant otters defecating per latrine. All analyses were undertaken with the R software, using the package ade4 (Dray & Dufour 2007).

Results

We identified 29 vertebrate species visiting latrines. The species composition was not correlated to the distance among latrines (Mantel test, $r_{\text{obs}} = 0.003$, $p = 0.458$). Most species registered were birds ($n = 18$), mammals ($n = 7$) and reptiles ($n = 4$) (Table 1). Species most frequently photographed were chaco chachalaca (*Ortalis canicollis*; $n = 95$), grey-necked wood rail (*Aramides cajanea*; $n = 84$), grey-fronted dove (*Leptotila rufaxilla*; $n = 60$), green iguana (*Iguana iguana*; $n = 53$), pale-legged hornero (*Furnarius leucopus*; $n = 48$), southern caracara (*Caracara plancus;* $n = 43$) and bare-faced curassow (*Crax fasciolata*; $n = 42$), which comprised 72.8% of the photographic records. The median visitation rate was 0.29 photos/h, ranging from 0.03 to 1.74 photos/h, which was not correlated with the giant otter defecation rate ($r_{\text{pearson}} = -0.076$, $n = 21$). However, latrines were more frequently visited during daylight hours (median = 0.4 photos/h, range 0.06–3.17) than at night (median = 0.005 photos/h, range 0–0.19).

We identified nine species that definitely ate feces at latrines (Table 2). The chaco chachalaca (Figure 1a), the southern caracara, the green iguana and the grey-necked wood rail (Figure 1b) were present at more than six latrines through almost the entire period of the study, and in more than 16% of their visits they were recorded eating feces. Yacare caiman (*Caiman crocodilus yacare*; Figure 1c), crab-eating fox (*Cerdocyon thous*; Figure 1d), black vulture (*Coragyps atratus*) and ocelot (*Leopardus pardalis*; Figure 1e) were recorded only at one latrine each during the high-water season, which extends from February to June (Table 1). The insectivorous-omnivorous gray four-eyed opossum (*Philander opossum*) was registered foraging at two latrines only in one month during the high-water season, but it was not possible to observe if feces were consumed (Figure 1f).

Discussion

The species composition of visitors was not related to the distance between latrines. In general, giant otters built latrines < 2 m from the water on the banks of the rivers or oxbow lakes (Lima et al. 2012) and therefore the potential visitors should be the same, independent of the longitudinal position of the latrine along the river. Most of the species were diurnal and the visitation rate was not correlated with the rate of giant otter defecation. This result suggests that the main resource obtained from latrine contents may remain at the latrines for long periods, or that most species use the latrines opportunistically, and not primarily to eat feces.

Some species, such as gray brocket deer (*Mazama gouazoubira*), nine-banded armadillo (*Dasypus novemcinctus*) and azara's agouti (*Dasyprocta azarae*) were not seen eating feces and their visits may not be related to the presence of latrines. Latrines seem to have an important role in giant otter chemical communication and they have a strong smell that is obvious to humans (Leuchtenberger & Mourão 2009). Scents may attract predators (Rosell & Sanda 2006), and the presence of jaguars, potential predators of giant otters (Carter & Rosas 1997), may have been because they were in search of otters rather than feces.

Table 2. Total number of photographic registers of vertebrate species that visited latrines of giant otters and the number of records (%) that each species was registered eating feces, between December 2010 and June 2011 in the Southern Pantanal, Brazil.

Species	Total of records	Records eating (%)	Latrines visited
Ortalis canicollis	95	15 (16)	14
Aramides cajanea	84	16 (19)	14
Iguana iguana	53	15 (28)	12
Caracara plancus	43	16 (37)	6
Crax fasciolata	42	5 (12)	7
Cerdocyon thous	16	2 (12)	1
Leopardus pardalis	10	1 (10)	1
Caiman crocodilus yacare	1	1 (100)	1
Coragyps atratus	2	1 (50)	1

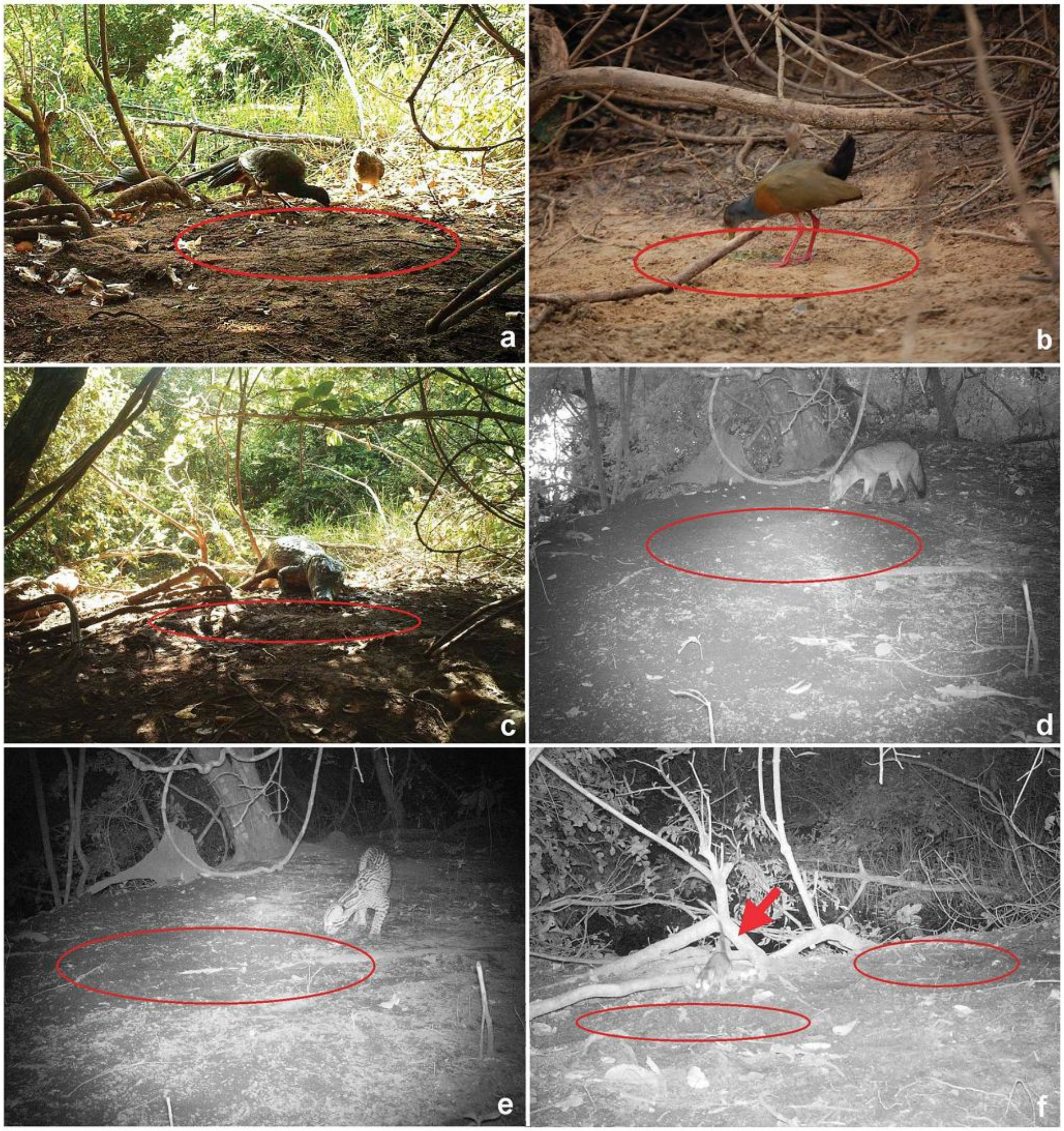


Figure 1. (Color online) Species registered foraging at latrines (ellipses) of *Pteronura brasiliensis* on the Miranda and Vermelho Rivers, Brazilian Pantanal: a, chaco chachalaca (*Ortalis canicollis*); b, grey-necked wood rail (*Aramides cajanea*); c, yacare caiman (*Caiman crocodilus yacare*); d, crab-eating fox (*Cerdocyon thous*); e, ocelot (*Leopardus pardalis*); f, gray four-eyed opossum (*Philander opossum* (arrow)).

Giant otter latrines may provide food for some species, such as the chaco chachalaca, the southern caracara, the green iguana and the grey-necked wood rail, since they foraged at these sites during most of the daytime sampling period. Coprophagy on giant otter feces by the green iguana might provide microorganisms to digest some plant chemicals ingested by this herbivore species, and may also represent a calcium source (Campos et al. 2011). The consumption of fish bones as a calcium supplement has been observed in the seed-eating white-winged crossbill (*Loxia leucoptera*), which forages on feces of North American otters (*Lontra canadensis*; Gallant 2004). Bare-faced curassow have also been reported as consuming soil rich in salt (del Hoyo 1994), which may also be found in giant otter feces. Insects are normally present on latrines and can attract insectivorous and omnivorous species. However, fresh feces may also have other uses, since the rufous hornero (*Furnarius rufus*) commonly builds its nests with fresh feces (Rowland 1975).

Some carnivores, as well as giant otters, consume their prey rapidly and portions of soft tissues can remain within the feces, which may represent an important source of protein for some species mainly during periods of food scarcity, as reported for grey-necked wood rail and Virginia opossum (*Didelphis virginiana*) (Livingston et al. 2005; Solano-Ugalde 2005). In our study, some species were seen eating from latrines only during the high-water season, when food availability is generally lower in the Pantanal (Alho et al. 2011).

Together with weather and temporal effects, the use of giant otter latrines as a food source by some species may change the relative occurrence of prey remnants at latrines. Therefore, studies of giant otter diets based on latrine surveys should be interpreted carefully, especially for questions related to relative prey abundance. Bias could be minimized by restricting collections to freshly deposited feces, before they have a chance to be eaten by coprophagous species.

Acknowledgments

We thank CNPq/Universal (n 476939/2008-9) and The Rufford Small Grants Foundation (Grant 88.08.09) for financial support. Embrapa/Pantanal, Barranco Alto Farm and the Federal University of Mato Grosso do Sul provided logistical support. CNPq provided scholarships for CL and CR. Sidnei Benício, Procópio de Almeida and Waldomiro de L. e Silva assisted in the field. Alessandro P. Nunes and Fernando Tizianel helped us with the taxonomic identification of birds. Luiz Gustavo R. O. Santos and Carlos A. Zucco helped with data analysis.

References

Alho CJR, Camargo G, Fisher E. 2011. Terrestrial and aquatic mammals of the Pantanal. Braz J Biol. 71(1):297–310.

Campos Z, Leuchtenberger C, Desbiez ALJ, Mourão G. 2011. *Iguana iguana* (Green iguana). Coprophagy. Herpetol Rev. 42(4):604–605.

Carter SK, Rosas FCW. 1997. Biology and conservation of the giant otter *Pteronura brasiliensis*. Mamm Rev. 27(1):1–26.

del Hoyo J. 1994. Family Cracidae. New world vultures to guineafowl. In: del Hoyo J, Elliott A, Sargatal J, editors. Handbook of the Birds of the World, Vol. 2. Barcelona: Lynx Edic. p. 310–363.

Dray S, Dufour AB. 2007. The ade4 package: implementing the duality diagram for ecologists. J Stat Softw. 22(4):1–20.

Duplaix N. 1980. Observations on the ecology and behavior of the giant river otter *Pteronura brasiliensis* in Suriname. Rev Ecol. (Terre Vie). 34:496–620.

Gallant D. 2004. White-winged crossbills obtain forage from river otter feces. Wilson Bull. 116(2):181–184.

Giovannetti PM. 1982. Effect of coprophagy on nutrition. Nutr Res. 2:335–349.

Leuchtenberger C, Mourão G. 2008. Social organization and territoriality of giant otters (Carnivora: Mustelidae) in a seasonally flooded savanna in Brazil. Sociobiology. 52(2):257–270.

Leuchtenberger C, Mourão G. 2009. Scent-marking of giant otter in the Southern Pantanal, Brazil. Ethology. 115:210–216.

Lima D dos S, Marmontel M, Bernard E. 2012. Site and refuge use by giant river otters (*Pteronura brasiliensis*) in the Western Brazilian Amazonia. J Nat Hist. 46(11–12):729–739.

Livingston TR, Gipson PS, Ballard WB, Sanchez DM, Krausman PR. 2005. Scat removal: a source of bias in feces- related studies. Wildlife Soc B. 33(1):172–178.

Norris D, Michalski F. 2010. Implications of faecal removal by dung beetles for scat surveys in a fragmented landscape of the Brazilian Amazon. Oryx. 44(3):455–458.

Ribas C, Damasceno G, Magnusson W, Leuchtenberger C, Mourão G. 2012. Giant otters feeding on caiman: evidence for an expanded trophic niche of recovering populations. Stud Neotrop Fauna E. 47(1):19–23.

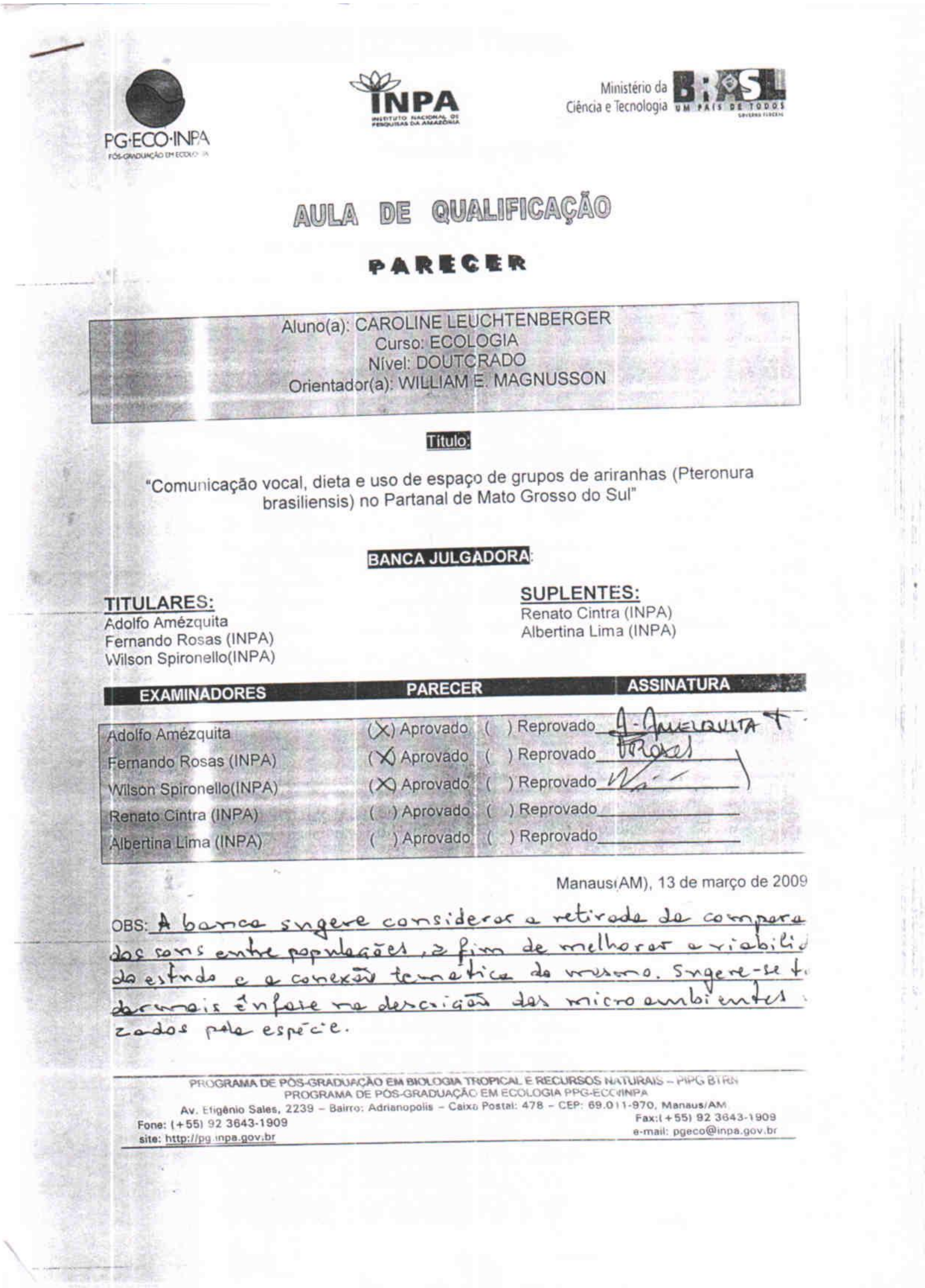
Rosas FCW, Zuanon JAS, Carter SK. 1999. Feeding ecology of the giant otter, *Pteronura brasiliensis*. Biotropica. 31(3): 502–506.

Rosell F, Sanda JI. 2006. Potential risks of olfactory signaling: the effect of predators on scent marking by beavers. Behav Ecol. 17: 897–904.

Rowland JT. 1975. Some ecological aspects of animal excrement. The Am Biol Teach. 37(3):154–157.

Solano-Ugalde A. 2005. Observaciones de coprofagismo por parte de *Aramides cajanea* (Rallidae: Aves) en el Refugio de Vida Silvestre Curú, Puntarenas. Zeledonia. 9(1):33–34.

APÊNDICE II



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Ministério da Ciência e Tecnologia
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GOVERNO FEDERAL

AULA DE QUALIFICAÇÃO

PARECER

Aluno(a): CAROLINE LEUCHTENBERGER
Curso: ECOLOGIA
Nível: DOUTORADO
Orientador(a): WILLIAM E. MAGNUSSON

Título:

"Comunicação vocal, dieta e uso de espaço de grupos de ariranhas (Pteronura brasiliensis) no Partanal de Mato Grosso do Sul"

BANCA JULGADORA:

TITULARES:
Adolfo Amézquita
Fernando Rosas (INPA)
Wilson Spironello(INPA)

SUPLENTES:
Renato Cintra (INPA)
Albertina Lima (INPA)

EXAMINADORES	PARECER		ASSINATURA
Adolfo Amézquita	(X) Aprovado	( ) Reprovado	A. AMEZQUITA
Fernando Rosas (INPA)	(X) Aprovado	( ) Reprovado	FRosas
Wilson Spironello(INPA)	(X) Aprovado	( ) Reprovado	
Renato Cintra (INPA)	( ) Aprovado	( ) Reprovado	
Albertina Lima (INPA)	( ) Aprovado	( ) Reprovado	

Manaus(AM), 13 de março de 2009

OBS: A banca sugere considerar a retirada da compara
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do estudo e a conexão temática do mesmo. Sugere-se t
dar mais ênfase na descrição dos microambientes
zados pela espécie.

PROGRAMA DE PÓS-GRADUAÇÃO EM BIOLOGIA TROPICAL E RECURSOS NATURAIS – PIPG BTRN
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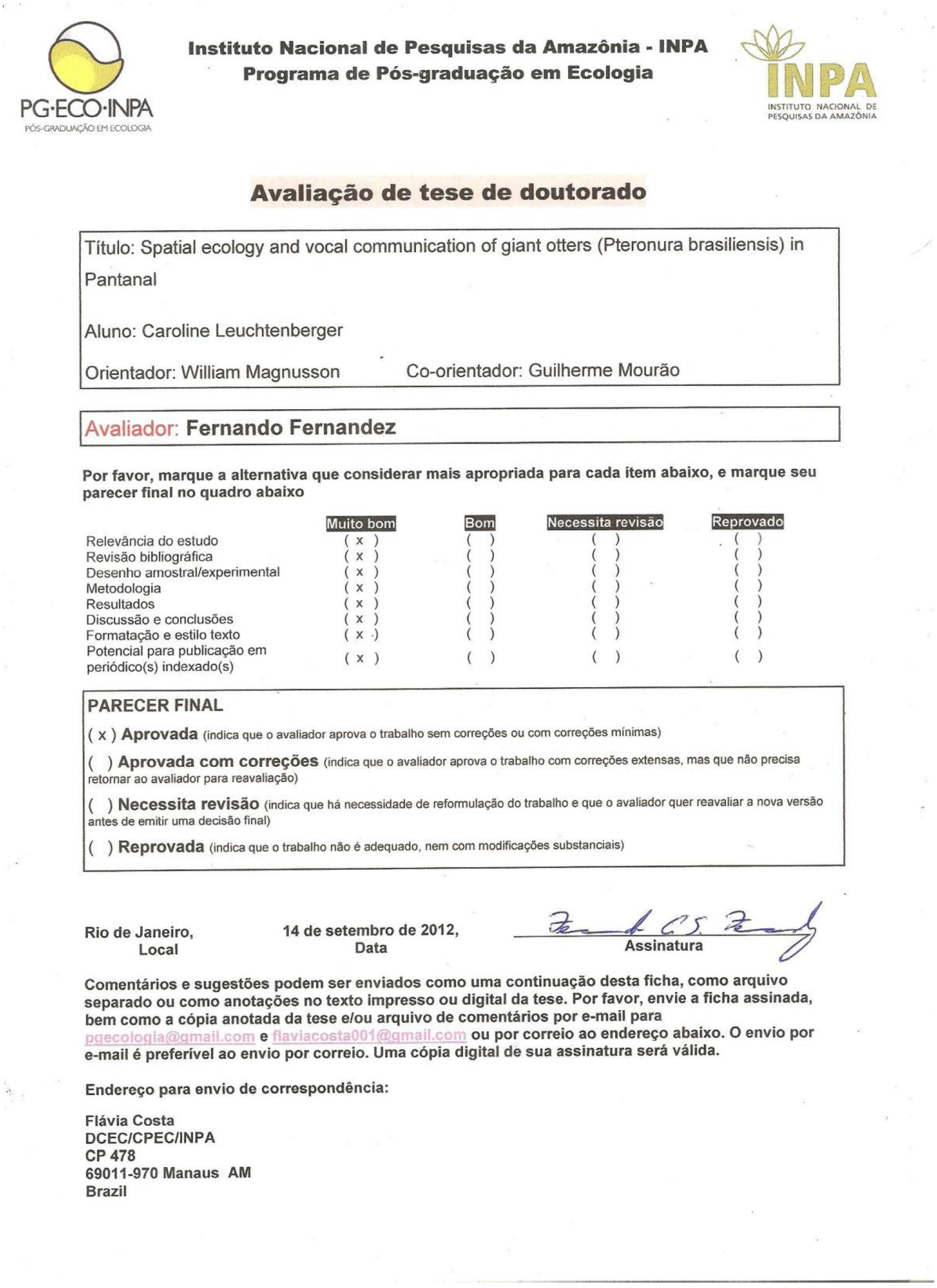
APÊNDICE III



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Avaliação de tese de doutorado

Título: Spatial ecology and vocal communication of giant otters (Pteronura brasiliensis) in Pantanal

Aluno: Caroline Leuchtenberger

Orientador: William Magnusson Co-orientador: Guilherme Mourão

Avaliador: **Fernando Fernandez**

Por favor, marque a alternativa que considerar mais apropriada para cada ítem abaixo, e marque seu parecer final no quadro abaixo

	Muito bom	Bom	Necessita revisão	Reprovado
Relevância do estudo	(x)	( )	( )	( )
Revisão bibliográfica	(x)	( )	( )	( )
Desenho amostral/experimental	(x)	( )	( )	( )
Metodologia	(x)	( )	( )	( )
Resultados	(x)	( )	( )	( )
Discussão e conclusões	(x)	( )	( )	( )
Formatação e estilo texto	(x)	( )	( )	( )
Potencial para publicação em periódico(s) indexado(s)	(x)	( )	( )	( )

PARECER FINAL

(x) **Aprovada** (indica que o avaliador aprova o trabalho sem correções ou com correções mínimas)

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( ) **Necessita revisão** (indica que há necessidade de reformulação do trabalho e que o avaliador quer reavaliar a nova versão antes de emitir uma decisão final)

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Rio de Janeiro, **14 de setembro de 2012,**
Local **Data** **Assinatura**

Comentários e sugestões podem ser enviados como uma continuação desta ficha, como arquivo separado ou como anotações no texto impresso ou digital da tese. Por favor, envie a ficha assinada, bem como a cópia anotada da tese e/ou arquivo de comentários por e-mail para pgecologia@gmail.com e flaviacosta001@gmail.com ou por correio ao endereço abaixo. O envio por e-mail é preferível ao envio por correio. Uma cópia digital de sua assinatura será válida.

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APÊNDICE IV

Instituto Nacional de Pesquisas da Amazônia - INPA
Programa de Pós-graduação em Ecologia

Avaliação de tese de doutorado

Título: Ecologia espacial e comunicação vocal de ariranhas (*Pteronura brasiliensis*) no Pantanal

Aluno: CAROLINE LEUCHTENBERGER

Orientador: William Magnusson Co-orientador: Guilherme Mourão

Avaliador: **Mario Cohn-Haft**

Por favor, marque a alternativa que considerar mais apropriada para cada ítem abaixo, e marque seu parecer final no quadro abaixo

	Muito bom	Bom	Necessita revisão	Reprovado
Relevância do estudo	( )	(x)	( )	( )
Revisão bibliográfica	(x)	( )	( )	( )
Desenho amostral/experimental	(x)	( )	( )	( )
Metodologia	(x)	( )	( )	( )
Resultados	(x)	( )	( )	( )
Discussão e conclusões	(x)	( )	( )	( )
Formatação e estilo texto	(x)	( )	( )	( )
Potencial para publicação em periódico(s) indexado(s)	(x)	( )	( )	( )

PARECER FINAL

(x) **Aprovada** (indica que o avaliador aprova o trabalho sem correções ou com correções mínimas)

( ) **Aprovada com correções** (indica que o avaliador aprova o trabalho com correções extensas, mas que não precisa retornar ao avaliador para reavaliação)

( ) **Necessita revisão** (indica que há necessidade de reformulação do trabalho e que o avaliador quer reavaliar a nova versão antes de emitir uma decisão final)

( ) **Reprovada** (indica que o trabalho não é adequado, nem com modificações substanciais)

Manaus, AM, **15 nov 2012**, ____________________

Local **Data** **Assinatura**

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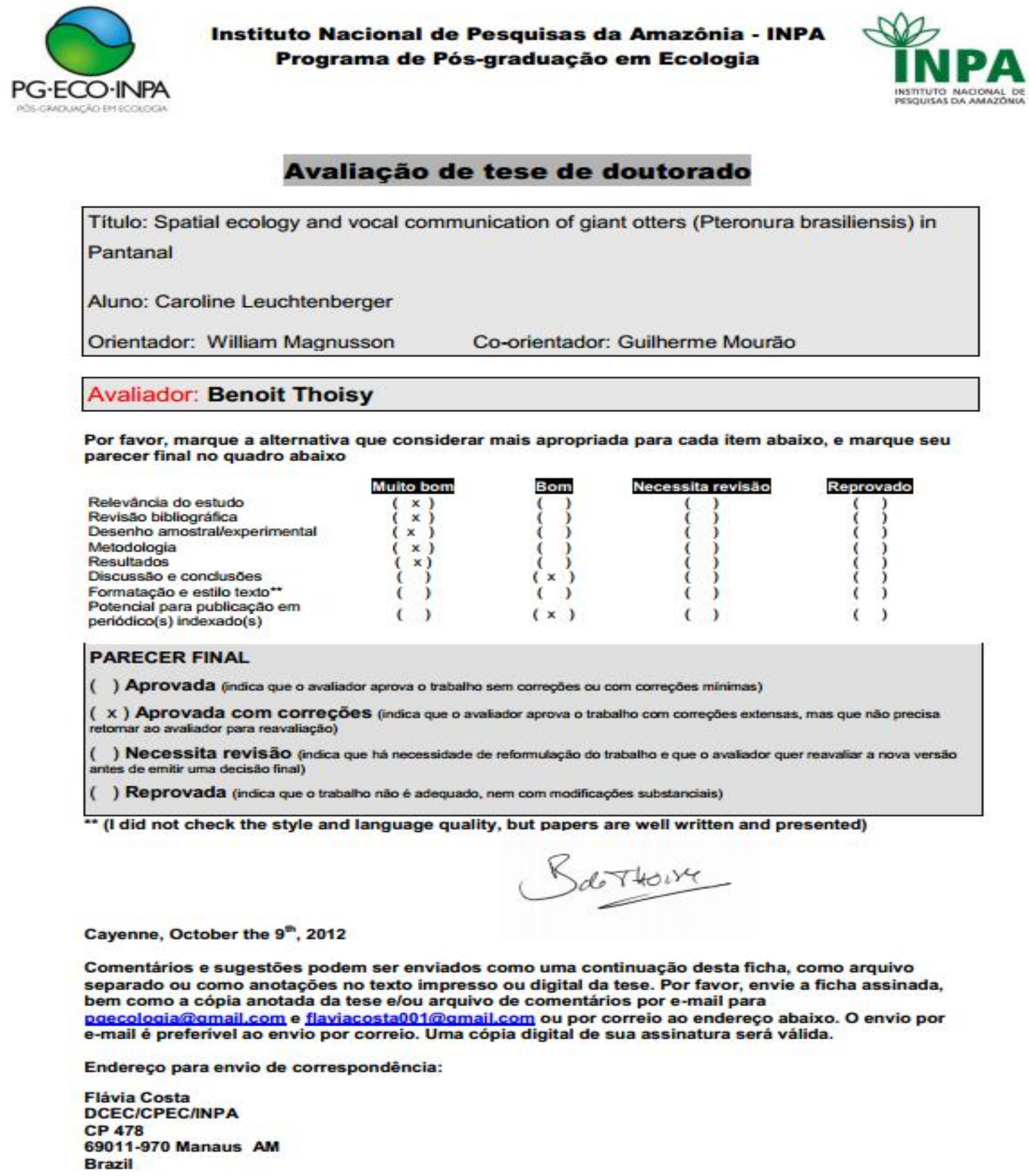
APÊNDICE V



Instituto Nacional de Pesquisas da Amazônia - INPA
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Avaliação de tese de doutorado

Título: Spatial ecology and vocal communication of giant otters (Pteronura brasiliensis) in Pantanal

Aluno: Caroline Leuchtenberger

Orientador: William Magnusson Co-orientador: Guilherme Mourão

Avaliador: **Benoit Thoisy**

Por favor, marque a alternativa que considerar mais apropriada para cada item abaixo, e marque seu parecer final no quadro abaixo

	Muito bom	Bom	Necessita revisão	Reprovado
Relevância do estudo	(x)	( )	( )	( )
Revisão bibliográfica	(x)	( )	( )	( )
Desenho amostral/experimental	(x)	( )	( )	( )
Metodologia	(x)	( )	( )	( )
Resultados	(x)	( )	( )	( )
Discussão e conclusões	( )	(x)	( )	( )
Formatação e estilo texto**	( )	( )	( )	( )
Potencial para publicação em periódico(s) indexado(s)	( )	(x)	( )	( )

PARECER FINAL

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(x) **Aprovada com correções** (indica que o avaliador aprova o trabalho com correções extensas, mas que não precisa retornar ao avaliador para reavaliação)

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**** (I did not check the style and language quality, but papers are well written and presented)**

Cayenne, October the 9th, 2012

Comentários e sugestões podem ser enviados como uma continuação desta ficha, como arquivo separado ou como anotações no texto impresso ou digital da tese. Por favor, envie a ficha assinada, bem como a cópia anotada da tese e/ou arquivo de comentários por e-mail para pgecologia@gmail.com e flaviacosta001@gmail.com ou por correio ao endereço abaixo. O envio por e-mail é preferível ao envio por correio. Uma cópia digital de sua assinatura será válida.

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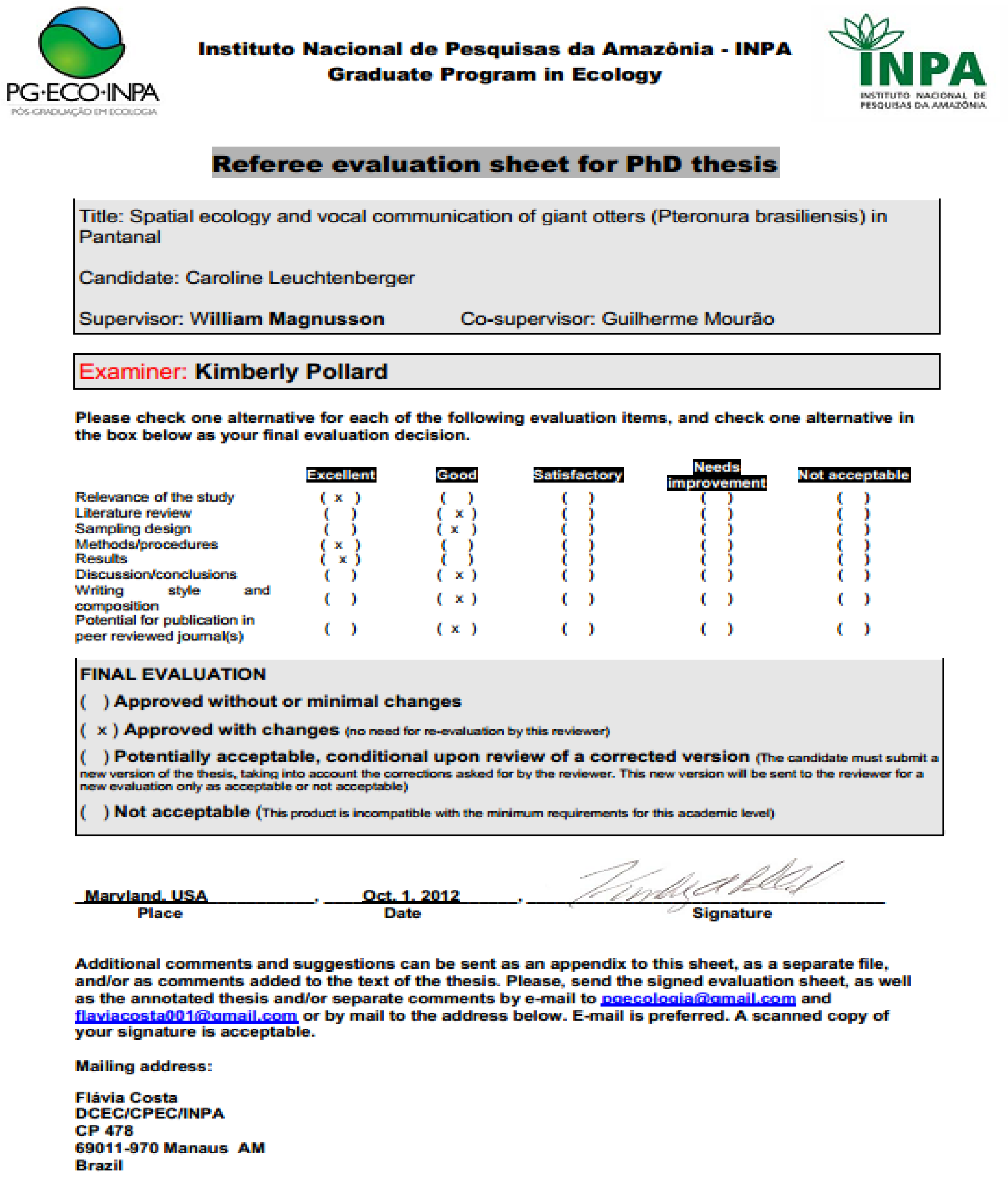
APÊNDICE VI



Instituto Nacional de Pesquisas da Amazônia - INPA
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Referee evaluation sheet for PhD thesis

Title: Spatial ecology and vocal communication of giant otters (Pteronura brasiliensis) in Pantanal

Candidate: Caroline Leuchtenberger

Supervisor: **William Magnusson** Co-supervisor: Guilherme Mourão

Examiner: **Kimberly Pollard**

Please check one alternative for each of the following evaluation items, and check one alternative in the box below as your final evaluation decision.

	Excellent	Good	Satisfactory	Needs improvement	Not acceptable
Relevance of the study	(x)	( )	( )	( )	( )
Literature review	( )	(x)	( )	( )	( )
Sampling design	( )	(x)	( )	( )	( )
Methods/procedures	(x)	( )	( )	( )	( )
Results	(x)	( )	( )	( )	( )
Discussion/conclusions	( )	(x)	( )	( )	( )
Writing style and composition	( )	(x)	( )	( )	( )
Potential for publication in peer reviewed journal(s)	( )	(x)	( )	( )	( )

FINAL EVALUATION

( ) **Approved without or minimal changes**

(x) **Approved with changes** (no need for re-evaluation by this reviewer)

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Maryland, USA, Oct. 1, 2012,

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Additional comments and suggestions can be sent as an appendix to this sheet, as a separate file, and/or as comments added to the text of the thesis. Please, send the signed evaluation sheet, as well as the annotated thesis and/or separate comments by e-mail to pgecologia@gmail.com and flaviacosta001@gmail.com or by mail to the address below. E-mail is preferred. A scanned copy of your signature is acceptable.

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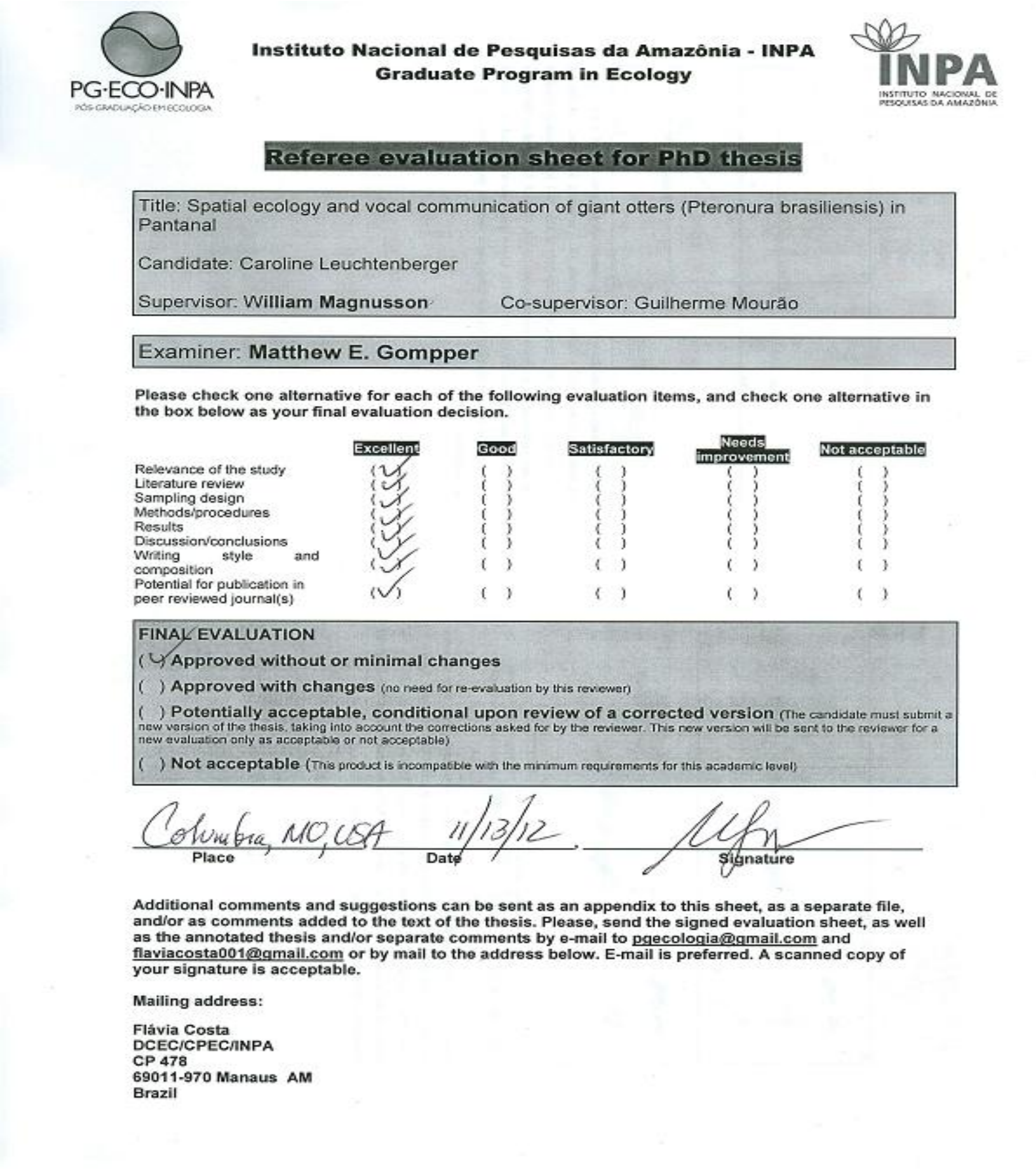
APÊNDICE VII



Instituto Nacional de Pesquisas da Amazônia - INPA
Graduate Program in Ecology

Referee evaluation sheet for PhD thesis

Title: Spatial ecology and vocal communication of giant otters (Pteronura brasiliensis) in Pantanal

Candidate: Caroline Leuchtenberger

Supervisor: **William Magnusson** Co-supervisor: Guilherme Mourão

Examiner: **Matthew E. Gompper**

Please check one alternative for each of the following evaluation items, and check one alternative in the box below as your final evaluation decision.

	Excellent	Good	Satisfactory	Needs improvement	Not acceptable
Relevance of the study	(✓)	( )	( )	( )	( )
Literature review	(✓)	( )	( )	( )	( )
Sampling design	(✓)	( )	( )	( )	( )
Methods/procedures	(✓)	( )	( )	( )	( )
Results	(✓)	( )	( )	( )	( )
Discussion/conclusions	(✓)	( )	( )	( )	( )
Writing style and composition	(✓)	( )	( )	( )	( )
Potential for publication in peer reviewed journal(s)	(✓)	( )	( )	( )	( )

FINAL EVALUATION

(✓) **Approved without or minimal changes**

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( ) **Potentially acceptable, conditional upon review of a corrected version** (The candidate must submit a new version of the thesis, taking into account the corrections asked for by the reviewer. This new version will be sent to the reviewer for a new evaluation only as acceptable or not acceptable)

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Columbia, MO, USA 11/13/12

Place **Date** **Signature**

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APÊNDICE VIII

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ATA DA DEFESA PÚBLICA DA TESE DE DOUTORADO DO PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA DO INSTITUTO NACIONAL DE PESQUISAS DA AMAZÔNIA

Aos 13 dias do mês de dezembro do ano de 2012, às 14:00 horas, na sala de aula do Programa de Pós Graduação em Entomologia – PPG ENT/INPA, reuniu-se a Comissão Examinadora de Defesa Pública, composta pelos seguintes membros: o(a) Prof(a). Dr(a). **Marina Anciães**, do Instituto Nacional de Pesquisas da Amazônia – INPA, o(a) Prof(a). Dr(a). **Wilson Roberto Spironello**, do Instituto Nacional de Pesquisas da Amazônia – INPA/TEAM e o(a) Prof(a). Dr(a). **Vera Maria Ferreira da Silva**, do Instituto Nacional de Pesquisas da Amazônia – INPA, tendo como suplentes o(a) Prof(a). Dr(a). Fernando César Weber Rosas, do Instituto Nacional de Pesquisas da Amazônia – INPA e o(a) Prof(a). Dr(a). Renato Cintra, do Instituto Nacional de Pesquisas da Amazônia - INPA, sob a presidência do(a) primeiro(a), a fim de proceder a argüição pública do trabalho de **TESE DE DOUTORADO** de **CAROLINE LEUCHTENBERGER**, intitulado "Ecologia espacial e comunicação vocal de ariranhas (*Pteronura brasiliensis*) no Pantanal", orientado pelo(a) Prof(a). Dr(a). William Ernest Magnusson, do Instituto Nacional de Pesquisas da Amazônia – INPA e co-orientado pelo(a) Prof(a). Dr(a). Guilherme de Miranda Mourão, da Empresa Brasileira de Pesquisa Agropecuária – EMBRAPA.

Após a exposição, o(a) discente foi argüido(a) oralmente pelos membros da Comissão Examinadora, tendo recebido o conceito final:

☑ APROVADO(A) ☐ REPROVADO(A)
☑ POR UNANIMIDADE ☐ POR MAIORIA

Nada mais havendo, foi lavrada a presente ata, que, após lida e aprovada, foi assinada pelos membros da Comissão Examinadora.

Prof(a).Dr(a). Marina Anciães ______
Prof(a).Dr(a). Wilson Roberto Spironello ______
Prof(a).Dr(a). Vera Maria Ferreira da Silva ______

______
Coordenação PPG-ECO/INPA