
PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA E BIODIVERSIDADE

**ANIMAL MOVEMENT, SOCIAL INTERACTIONS AND
MUTUALISM IN BRAZILIAN ECOSYSTEMS**

MILENE AMÂNCIO ALVES EIGENHEER

Tese apresentada ao Instituto de Biociências do Câmpus de Rio Claro, Universidade Estadual Paulista, como parte dos requisitos para obtenção do título de Doutora em Ecologia e Biodiversidade.

Maiο - 2018

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Orientador: Prof. Dr. Milton Cezar Ribeiro

Co-orientador: Prof. Dr. Mauro Galetti Rodrigues

Rio Claro-SP

2018

591.5
E34a Eigenheer, Milene Amâncio Alves
Animal movement, social interactions and mutualism in
Brazilian ecosystems / Milene Amâncio Alves Eigenheer. -
Rio Claro, 2018
97 f. : il., figs., gráfs., tabs.

Tese (doutorado) - Universidade Estadual Paulista,
Instituto de Biociências de Rio Claro
Orientador: Milton Cezar Ribeiro
Coorientador: Mauro Galetti Rodrigues

1. Ecologia animal. 2. Movimentação animal. 3.
Movement ecology. 4. Social behavior. 5. Seed dispersal. 6.
Landscape ecology. I. Título.

CERTIFICADO DE APROVAÇÃO

TÍTULO DA TESE: Animal movement, social interactions and mutualism on Brazilian ecosystems

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Rio Claro, 20 de abril de 2018

Para meu melhor amigo e parceiro de vida, André.

Para meus pais, Pedro e Eunice.

Agradecimentos

Primeiramente agradeço as agências financiadoras relacionadas a esse trabalho. À CAPES pela Bolsa Regular de Doutorado e ao programa CAPES/PDSE pelo financiamento do meu Doutorado Sanduíche junto à Wageningen University (Holanda). Ao SCCS Miriam Rothschild Travel Bursary Programme pelo financiamento no meu período junto a Swansea University (País de Gales) e ao DAAD (Deutscher Akademischer Austauschdienst) pela bolsa e auxílio durante a minha visita ao Max Planck Institute for Ornithology. Também agradeço à FAPESP (Processo 2013/50421-2) que contribuiu para o desenvolvimento desse trabalho em diversos momentos.

Uma tese não é um doutorado. O que nós vivemos e nos tornamos nesse período nos faz doutores. E eu sou muito grata por tudo o que vivi e fiz. E muitas pessoas fazem parte disso. Nem todas serão citadas aqui, mas sou grata a cada um que encontrei no meu caminho. Obrigada!

Agradeço ao meu orientador, Dr. Milton Cezar Ribeiro, que foi muito mais que um orientador. Foi um amigo e um ponto forte nos momentos de dificuldade. Miltoninho (e Keila e crianças), me espelho muito em vocês e no modo como vocês desenvolvem suas vidas e o lab. Muito obrigada, não só pela orientação, mas pela amizade e apoio nos momentos mais difíceis. Ao meu co-orientador, Dr. Mauro Galetti Rodrigues, que me ajudou no desenvolvimento das ideias de praticamente toda a minha tese e me deu ótimas oportunidades de trabalho. Sou muito grata.

Aos meus colaboradores – Ao Dr. Rogério Cunha de Paula, por compartilhar seus dados e todo o seu conhecimento por esses animais maravilhosos que são os lobos guarás. Sou muito grata por essa parceria. À Carly Vinne, Mariana Madeira e Leandro Silveira por compartilhar seus dados incríveis sobre dispersão de sementes e pela confiança no meu trabalho.

To my co-supervisors abroad – To Dr. Frank van Langevelde (Wageningen University) for all the support, patience and good energy. I learned so much about good science with you and everyone in Research Ecology Group. To Dr. Luca Börger (Swansea University) for the help with statistical analysis and support to my period in Swansea. To Dr. Kamran Safi for receive me in an amazing lab with a great team, besides for all the advices. I'm grateful to you all. Thank you.

Aos professores, funcionários e amigos do Departamento de Ecologia, em especial a Cristina Antunes, sempre tão prestativa e fofa! Ao pessoal da biblioteca e da sessão de pós, em especial à Ivana, uma pessoa incrível que sempre faz tudo para deixar nossas vidas mais fáceis! Obrigada pessoal, vocês são incríveis!

À equipe do Laboratório de Ecologia Espacial e Conservação (LEEC) e Movement Ecology Group. Que orgulho fazer parte desse time! Aprendi coisas com cada um de vocês e agradeço muito a presença de vocês na minha vida. Um agradecimento mais que especial aos alunos que eu orientei: Mitra Katherina Ferreira, Camila de Fátima Priante

Bernardo, Stephanie Marucci de Souza e Yuri Benko Brenninkmeijer. Vocês me ajudaram a descobrir o meu maior prazer e são parte da cientista que eu me tornei. Muito obrigada!

Aos amigos! Vocês são pessoas tão maravilhosas e que me enriquecem tanto! À Mariana Diniz, minha irmã de alma, que mesmo à distância sempre teve ótimos conselhos e palavras de amor. À Nara Vogado, que sempre se manteve presente, ajudou a cuidar da minha Pê quando eu não pude e sempre emana energia positiva. À Eliana Gressler, que mantém seu lugarzinho no meu coração (e no dos gatos) não importa onde estejamos. À Joana Bezerra, um dos maiores presentes que a Holanda me trouxe e que vou levar pra toda a vida. À Bianca Nadai, que além de ser família, meu bebezinho e uma princesa, também é uma das minhas melhores amigas e pontos de apoio.

Ao meu clube da Luluzinha leeciano, minhas role models, pepitas e musas - Renata Muylaert, Camila Bernardo, Paula Carolina Montagnana, Natalia Stefanini, Julia Assis, Patrícia Kerches Rogeri, Julia Oshima, Claudia Kanda, Vanessa Bejarano, Rafaela Silva (também conhecida como minha irmã gêmea) e Danielle Ribeiro. Não tenho palavras para explicar o quanto vocês são fundamentais na minha vida. Amo muito vocês! Obrigada por todas as aventuras, nacionais e internacionais.

To all my Brazilian and International friends, so many important and amazing people on my journey. A big thank you/obrigada to Tom Arkwright (my maned wolf brother XD); Vanille Kaarakainen (the sweetest person ever); Mariana Artur (minha drama queen favorita); Paulo Ribeiro, Anna Patrícia Florentino e Nilma Oliveira (que saudades das nossas jantinhas! vocês são incríveis); Shenglai Yin and Jente Ottenburghs (banana time! Best persons to share a work room XD); Jamir do Prado Junior (saudades dos cafés!); Eliezer Ramos (de Swansea pra vida!); Teja Curk and Helder Santos (#myukulelefriends XD); Martina Scacco (amazing dance partner) and Stefano (great problem listener, hahaha); Danai Papageorgiou (and also Dimitri and Aida, best Greek family); Erik and Jonne Kleyheeg (Dutch friends, wow!); Yachang Cheng (best noodle cook ever!); Lukas Gautshi (just thank you, you know!); Berger Medeiros (obrigada por todo o chocolate e por achar meu livro favorito!!!); Bernardo Niehbur (+ Dani e Gal, família maravilhosa!); and Joost Stevens (Dank je wel, altijd). I'm lucky to have so many amazing people in my life.

To the best housemates that I would dream! Naira C. de Moura and Giovani Arieira (Wageningen); Emma-Louise Cole, Carly Green and Joe Baxter (Swansea); Reyes Sallas, Alberto Pastorino and Ettore Camerlenghi (Moggingen); Mitra Ferreira, Patrícia Rogeri, Beatriz Telles e André Eigenheer (Rio Claro) – Thank you all for make me feel at home, doesn't matter where ♥.

Muitos amigos me apoiaram na fase final, mas algumas pessoas foram fundamentais quando eu estava muito muito muuuuito cansada e com tantas preocupações na cabeça: André Eigenheer, Tom Arkwright, Julia Assis, Karl Mokross e Rafaela Silva. Obrigada. Quem tem amigos tem tudo mesmo =)

À minha família: Eunice e Pedro, melhores pais que eu poderia pedir; Luciano e Junior, irmãos e parceiros de jornada; Kedmann e Fabiana, cunhadas queridas. Um agradecimento mais que gigante pros meus sobrinhos, que me ajudaram a me manter uma “criança adulta” (frase da Mari): Mateus, Isabelli, Mariana e Nicolli. Para o outro lado da família, minha sogra Ana Maria e minha cunhada e cunhado Ariana e Rodrigo, vocês são maravilhosos. Obrigada família. Amo vocês.

O maior agradecimento é pro meu parceiro, melhor amigo e exemplo de pessoa boa: André Eigenheer, você é parte essencial disso tudo. Se não fosse você eu teria desencanado lá atrás. Obrigada por segurar as pontas nos momentos difíceis, por me consolar nos dias difíceis, por encontrar novas receitas, por cuidar de mim e dos nossos filhos de quatro patas, por discutir ecologia e por ser amigo dos meus amigos. Obrigada por me consolar no choro, por segurar a minha mão nos momentos bons e difíceis, por topar experiências diferentes e por ser um Capitão América. Você é a minha pessoa favorita no mundo. Essa tese também é sua! Te amo, sempre.

Obrigada a todos. Sou muito sortuda mesmo.



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Resumo

O movimento de organismos é uma das características mais importantes da vida na Terra e um componente crucial para quase todos os processos ecológicos e evolutivos, ligando a ecologia de organismos, populações, comunidades e ecossistemas. Exemplos de processos dependentes de movimento incluem dispersão e migração, o que pode ter impactos em dispersão de sementes, regeneração de plantas e fluxo gênico. Movimentos são determinados por interações entre o estado interno dos indivíduos e o ambiente externo, dependendo de habilidades sensoriais dos animais. Nosso objetivo neste estudo foi desenvolver uma melhor compreensão da ecologia do movimento e suas consequências no comportamento animal e dispersão de sementes. Nós desenvolvemos três capítulos: uma revisão sobre desafios e perspectivas em ecologia do movimento no Brasil; um estudo sobre estruturas sociais de lobos guará (*Chrysocyon brachyurus*) em um mosaico de áreas protegidas e fragmentadas; e um outro estudo onde testamos o papel de dois canídeos frugívoros (lobo guará e cachorro do mato - *Cerdocyon thous*) na dispersão de sementes e distribuição espacial de *Solanum lycocarpum*. Nesta tese nós mostramos a importância da ecologia do movimento, assim como suas consequências no comportamento social de animais e na dispersão de sementes. Utilizando dados espaciais nós descobrimos mais sobre a ecologia de importantes espécies presentes na América do Sul, assim como suas interações animal-animal e animal-planta.

Abstract

The movement of organisms is one of the most important characteristics of life on Earth and is a crucial component of almost all ecological and evolutionary processes, linking the ecology of organisms, populations, communities and ecosystems. Examples of movement-dependent processes include dispersion and migration, which can have impacts on seed dispersal, plant regeneration and gene flow. Movements are determined by feedback interactions between the internal state of individuals and the external environment, conditional on the animal's movement and sensory abilities. In this study we aim at developing a better comprehension on movement ecology and its consequences on animal behavior and seed dispersal. We developed three chapters: a review about challenges and perspectives of movement ecology in Brazil; a study on social structure of maned wolves (*Chrysocyon brachyurus*) living in a mosaic of protected and fragmented areas; and another study where we tested the role of two canid frugivores (maned wolves and crab-eating foxes – *Cerdocyon thous*) on the seed dispersal and spatial distribution of *Solanum lycocarpum*. In this thesis we showed the importance of movement ecology, as well as its consequences on social behavior and seed dispersal. Using spatial data we could discover more about the ecology of important species present in South America, as well as their interactions animal-animal and animal-plant.

General Introduction

The movement of organisms is one of the most important characteristics of life on Earth and is a crucial component of almost all ecological and evolutionary processes, linking the ecology of organisms, populations, communities and ecosystems (Nathan *et al.*, 2008; Jeltsch *et al.* 2013). Research on movement ecology has progressed in recent decades, driven by advances in analytical techniques and technologies that acquire and quantify movement (Holyoak *et al.* 2008; Nathan *et al.* 2008; Kays *et al.* 2015).

Examples of movement processes include dispersion and migration, which can have impacts on seed dispersal, plant regeneration and gene flow (Nathan *et al.*, 2008; Kays *et al.*, 2015). These movement processes act over a great variety of spatial-temporal scales (Hundertmark, 1998; Nathan *et al.*, 2008; Niebuhr *et al.*, 2015; da Silveira, 2016; Molin *et al.*, 2017).

Movements are determined by feedback interactions between the internal state of individuals and the external environment, conditional on the individual's movement and sensory abilities (Nathan *et al.* 2008). A key component of the external environment is other individuals (conspecifics and non), affecting, for example, competition for food, mate search, predator-prey interactions, hence comprehending it is an important step to understand social and mating systems (Emlen & Oring, 1977; Clutton-Brock, 1989) and for the conservation of species and areas (Delgado *et al.* 2014, Kays *et al.*, 2015; Spiegel *et al.*, 2016).

The presence of conspecifics – other individuals of the same species - can thus influence individual movement patterns, and the attraction or avoidance by individuals depends on the benefits and costs of this association (Bode *et al.*, 2012; Delgado *et al.* 2014). Solitary animals usually prefer avoiding interactions with conspecifics and show limited sociality (Logan & Sweanor, 2001; Dammhahn & Kappeler, 2009). However, solitary species may interact with conspecifics in some moments of their life cycle, like to rear cubs, mate, or defend a territory (Sandell, 1989; Elbroch *et al.* 2015, 2017).

Another important aspect related to the interaction between the movement of animals and the external environment are the ecological processes, as pollination and seed dispersal (Kremen *et al.* 2007; Mitchell *et al.* 2015). Several facets played by frugivores have been highlighted to favor plant fitness. Removing seeds from the high mortality zone near the maternal plant, increasing germination rate, moving the seeds to favorable sites, and promoting gene flow via seed dispersal are some of the few direct

examples of how frugivores increase the chances of plant's survival (Herrera, 1985; Jordano *et al.*, 2007). This is particularly important in tropical regions, where most of the plant species are dispersed by animals (Almeida-Neto *et al.*, 2008).

Frugivore canids often consume large amounts of fruit and may be responsible for the seed shadow of many animal-dispersed plant species, however their role as seed-dispersers remains relatively unexplored. These species generate seed rain patterns that capture their foraging and post-feeding movements, therefore, sites chosen for patrolling or territorial marking receives a disproportionate number of seeds (Jordano *et al.*, 2007; González-Varo *et al.*, 2013). Canids are important seed dispersers for fruits of the Cerrado vegetation—a Brazilian like savanna— as they do not possess physiological adaptations for digesting cellulose. As seeds pass through the canids gut largely intact – they exhibit limited mastication during consumption—seed damage rates are low (Juarez & Marinho-Filho, 2002).

The maned wolf is a South American canid, with a broad diet which comprises fruits, small rodents, insects etc (Dietz, 1984; Santos *et al.*, 2003). The species is considered a vulnerable species at risk of extinction due to a drastic reduction and fragmentation of its original habitat (IBAMA 2003). The maned wolf is closely associated with *Solanum lycocarpum*, a conspicuous plant in the Cerrado, where it occurs in natural areas, pastures, and in natural remnants scattered within agricultural landscapes. Fruits of *S. lycocarpum* are an important food source and are reported to make up between 3.4% and 53.5% of total occurrence in maned wolf scat samples (Bueno & Motta-Junior, 2004, 2009; Juarez & Marinho-Filho, 2002; Motta-Junior & Martins, 2002; Santos *et al.*, 2003; Silva & Talomoni, 2003). Besides maned wolves, the crab-eating fox (*Cerdocyon thous*), the hoary fox (*Lycalopex vetulus*) and the tapir (*Tapirus terrestris*) disperse *Solanum* seeds (Dalponte & Lima, 1999; Juarez & Marinho-Filho, 2002; Bueno & Motta-Junior, 2004; Jácomo *et al.* 2004).

The social system of the maned wolf is based on monogamous breeding pairs, but little is known about their social behavior or landscape use. Dietz (1984) and Jácomo *et al.* (2009) contend that maned wolves are solitary animals that interact occasionally, especially during the mating season. However, these studies were conducted using VHF radiotelemetry technology, which obtain sparse and less accurate data when compared with modern global positioning systems (GPS). In addition, many of VHF data are collected during the day, which limits some analysis of movement behavior ecology. In fact, Bandeira de Melo *et al.* (2007) studied the social behavior of

three maned wolves – a couple and a juvenile female – using GPS for six months and found a strong interaction between the couples and high tolerance of both adults with the juvenile.

Paula (2016) showed in his study that maned wolves living in the Serra da Canastra National Park comprised couples sharing the same territories. However, the overlap between the home range of individuals cannot be considered a complete measure of interactions between individuals, as overlap does not provide any information about the intensity of interactions (Atwood & Weeks, 2003) and the presence of dynamic interactions between individuals. For more complete information, it is necessary to obtain data on the spatio-temporal location of both individuals of a potentially interacting pair ('dyad') of individuals (Mace & Waller, 1997).

The general aim of this thesis searches a better comprehension of movement ecology and its consequences on behavior and seed dispersal. The thesis is divided into three chapters:

1 - Challenges and perspectives of movement ecology research in Brazil – a systematic review where we describe the recent scientific research on movement ecology in Brazil, as well as its main topics, challenges and perspectives.

2 - Coordinated movements of maned wolves (*Chrysocyon brachyurus*) in protected and fragmented landscapes – a study that focus on the social structure of maned wolves (*Chrysocyon brachyurus*) living inside a national park and its surrounding fragmented area, in Brazil.

3 - Effects of frugivores canids on the seed dispersal and spatial distribution of *Solanum lycocarpum* in a Brazilian savanna – a study where we test the role of two canid frugivore species – maned wolf (*Chrysocyon brachyurus*) and crab-eating fox (*Cerdocyon thous*) – on the seed dispersal and spatial distribution of *Solanum lycocarpum*. We also assess the importance of this fruit to the canid species in habitats where less plant resource is available.

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Chapter 1

Challenges and perspectives of movement ecology research in Brazil

To be submitted to Austral Ecology

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KEYWORDS: Animal movement; GPS collar; Radiotelemetry; Movement analysis; Movement tracking.

Abstract

The recent progress in movement ecology research was driven by technological advances that facilitated the quantification and analysis of movement. Here we describe the recent scientific research on movement ecology in Brazil, as well as its main topics, challenges and perspectives. To assess it, we performed a literature survey spanning the last 30 years of movement ecology in Brazil and analyzed responses of a questionnaire completed by attendees that took place at the I Movement Ecology Brazil Workshop, in 2015. We found a rapid increase in movement ecology research in Brazil, with a total of 310 studies, 51% published since 2010. Most of the publications and workshop participants are from the southeastern region, showing a bias favoring the richest and most populous regions of the country. We describe the most studied taxa, topics of research and technologies, most studied biomes and challenges confronting Brazilian scientists. We propose collaborations among different lines of study and interdisciplinary research centers, besides recommend more education beyond the technical aspects of this area of research towards the development of competent and well-rounded scientists. Access to technology without bureaucracy, the growth of Brazilian tracking equipment companies, enhancement of national and international research networks and partnerships among biological and statistical sciences are some factors that will shape the autonomy of Brazilian researchers working in movement ecology. The main suggestion for the future directions is the exploration of organism movement data should integrate biomechanical, cognitive and optimality paradigms with movement-related ecological processes such as predation and seed dispersal.

Introduction

Movement is a key process to understand and link the ecology of organisms, populations, communities and ecosystems (Jeltsch et al. 2013). Understanding the movement of organisms is also important for conservation and socioeconomic applications such as diseases mitigation (Fèvre et al. 2006; Fuller et al. 2012), assessment of ecosystem services as pollination and seed dispersal (Kremen et al. 2007; Mitchell et al. 2015), ecophysiology (Williams et al. 2014; Altimiras and Anderson 2016), and dispersal of alien and native species in context of climate change and worldwide habitat loss (Trakhtenbrot et al. 2005).

Research on movement ecology has progressed in recent decades, driven by advances in analytical techniques and technologies that acquire and quantify movement (Holyoak et al. 2008; Nathan et al. 2008; Kays et al. 2015). Nathan et al. (2008) proposed a framework to classify the basic components describing the movement of organisms into the following conceptual categories: navigation capacity, internal state, motion capacity, movement path and external factors. This framework enabled a novel understanding of ecological and social dynamics, and it inspired innovative research perspectives within movement ecology (Nathan et al. 2008; Jeltsch et al. 2013; Baguette et al. 2014) by assessing why, when, how and where the movement of organisms occurs and the environmental variables that influence it.

Our aim is to evaluate the recent scientific research in movement ecology at Brazil, as well as its main topics, obstacles and perspectives. Also, we wish to identify and describe the kind of question asked by researchers, which were the study systems and methodologies (biome, organism, technologies used). The analysis was performed with a data survey based on a 30-year literature review, questionnaires filled by the participants of the I Movement Ecology Brazil (I MEB) Workshop in 2015, and discussions that occurred during the meeting.

Movement Ecology Brazil Workshop

The I Movement Ecology Brazil Workshop (I MEB) took place in September 2015 and aimed share experiences on the state of the art and new perspectives in this area of science. The I MEB meeting gathered 99 researchers from 32 Brazilian and 2 Argentinean institutions from the academic, government and environmental consultancy sectors. Twenty one studies were presented by posters, and the content included a wide

spectrum of topics such as the use of various ecological modeling techniques, the testing of new technologies, and the practical applications of movement ecology data.

All attendees answered in their event registration, an online questionnaire survey about their research group, the main challenges in their studies and other information reflecting important aspects of movement ecology research in Brazil (Supplementary Material 1). Here, we have synthesized these information and the discussions promoted at I MEB. We emphasize that it is just a sample of this scientific field in Brazil, but we believe that these results and conclusions reflect the movement ecology research that is being done in the country.

Literature survey

Movement ecology in Brazil was first studied by Cunningham and Reid (1932), who described movement by birds on a naturally heterogeneous landscape at the estuary of the Amazon River. Research on this topic was rarely conducted in Brazil in the following decades (Davis 1945; Best et al. 1981), but around 1990s the interest in movement ecology started to increase (Figure 1).

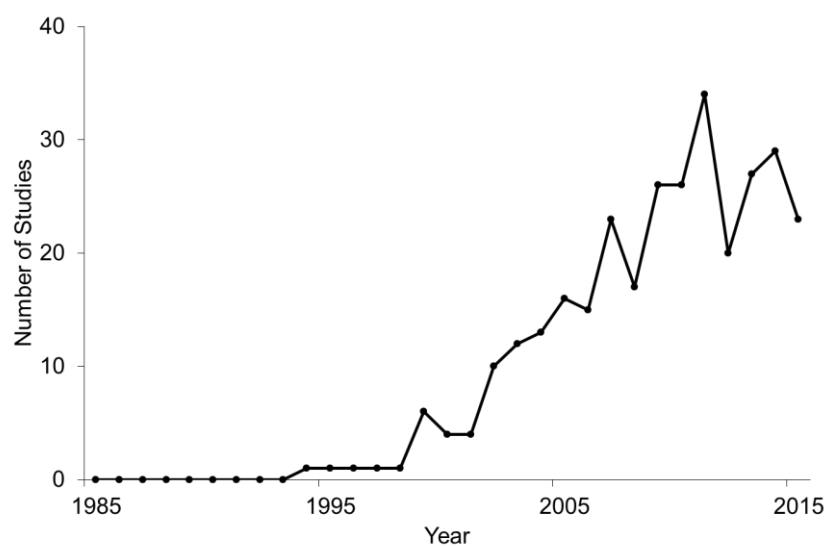


Figure 1. Quantity of indexed studies related to animal movement research done in Brazil over the last 30 years (1985-2015; Source: Web of Science). The number of studies started to increase since 1999. We searched the topics “movement* ecolog* Brazil”; “animal* movement* Brazil”; “animal* track* Brazil”, “telemetry Brazil”; and “model* movement* Brazil”. Also, the keywords “movement* ecolog*”, “simulat* OR model*”, and “random search* AND Lévy”, were searched for with “Brazil” in the address field.

To a better comprehension of this rising interest, we conducted a search of movement ecology research in Brazil over 30 years (1986-2015) through the scientific

citation index “Web of Science”[®] (WoS), using the keywords “movement* ecolog* Brazil”; “animal* movement* Brazil”; “animal* track* Brazil”; “telemetry Brazil”; and “model* movement* Brazil”. To include the literature related to simulation and modeling produced in the national institutions, we also included the keywords “movement* ecolog*”; “simulat* OR model*”; and “random search*” OR “Lévy”, with “Brazil” in the address field. The studies found were filtered and only those with a focus on movement (according to Holyoak et al. 2008) were kept (Supplementary Material 2).

Data compilation

To localize the scientific production on movement ecology in Brazil, we recorded the location of the institution of the first author for each study found in the literature (either the state if inside Brazil, or the country if abroad) and the MEB participants. In case the first author was from a foreign institution, we checked whether there was collaboration with Brazilian institutions. To complete that information, we also recorded the biome where the studies were carried (since many studies are made in an ecosystem far from the authors’ institutions), for both MEB participants and the literature review. Biomes were classified in the following categories: Amazon, Atlantic Forest, Caatinga, Cerrado, Pantanal, Pampas, Marine (organisms living in the Ocean or in estuary ecosystems), Multiple (in case of studies developed in more than one biome or studying animal migration beyond the borders of Brazil), and NA (simulation studies without a focus biome). Studies with freshwater organisms were classified according to the biome where they were located.

To understand which kind of ecological question has been asked, we used data on the classification that MEB attendees made on their research, regarding which components of the movement ecology framework proposed by Nathan et al. (2008) were related to their studies. Following the same method, we also classified the studies found in the literature review in one or more of these components. The classification followed the same methodology used by Holyoak et al. (2008), with the difference that we classified whether the components were present in the study approach, instead of the links between components.

We also identified, from both MEB participants research and in the literature survey, the taxonomic group studied and the technologies used in the studies. This was employed to a broader comprehension of the most studied organisms, as well as which

technologies and tools have been used to answer movement ecology questions. To a clearer result we calculate the percentages of each answer and classification in relation to the total of studies for both MEB questionnaire and the literature survey. Finally, our discussion on the challenges and perspectives in the area is based on the discussions that occurred at the I MEB, the answers of the participants to these topics in the questionnaires and the patterns found in the literature survey.

Movement ecology in Brazil: 30 years of growing research

The results of the literature survey showed that this topic of research has been steadily increasing in Brazil since 1999 – an average rate of 15.8% per year. A total of 310 studies were gathered, 51% of which were published since 2010. In the I MEB, the focus the participants' studies ranged from topics related directly to movement, as space use, foraging, and migration, to broader topics such as population dynamics, animal behavior and seed dispersal. Fifty six people (56.5%) of the participants declared they had explicit questions about movement ecology as principal aims of their studies.

The interest in the theme probably arose from the possibilities of ecological questions that may be answered with an increasing amount of movement data possible due to the recent technological tracking advances and their popularization (Kays et al. 2015), such as GPS devices, the most used by the workshop participants. Most studies using this technology focused on conservation, use of space, home range metrics and animal behavior. Ninety two per cent of these studies were conducted in large part by non-governmental organizations and public institutions.

Where is movement ecology being produced?

Despite the recent increase in movement ecology research in Brazil, this area is still incipient, with few specific working groups claiming to discuss and deal directly with movement ecology. The 6 institutions with proper movement ecology research groups present at I MEB were UNESP Rio Claro, UFRJ, UFMS-Campo Grande, USP-São Carlos and UFPR (Figure 2).

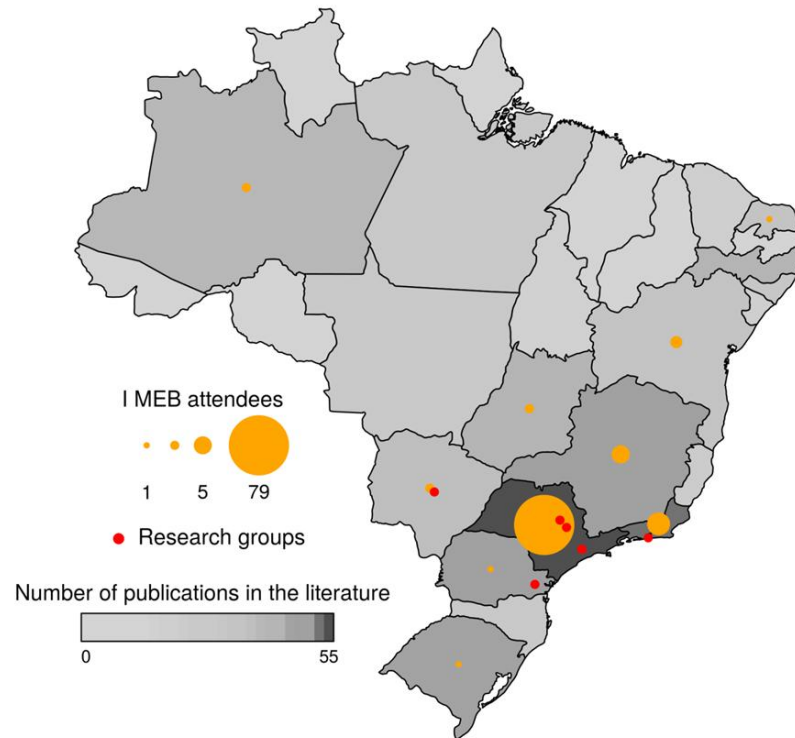


Figure 2. Map representing movement ecology research in Brazil. The grey tons indicate the quantity of publications in Web of Science (WoS) per state; the red dots indicate the location of the research groups present at I MEB (UNESP Rio Claro, UFRJ, UFMS-Campo Grande, USP-São Carlos, UFPR and UFOP), and the orange circles indicate the location of the I MEB attendees.

Most participants of the I MEB were from institutions located in southern and southeastern Brazil (87 participants, 88%). The articles published in the period 1986–2015, which we gathered from the literature review, showed similar results – from the 229 studies whose first authors were from Brazilian institutions (~74% of all studies), 149 (65%) were conducted from researchers linked to institutions located only in five states in southern and southeastern Brazil (São Paulo, Rio de Janeiro, Minas Gerais, Paraná and Rio Grande do Sul, in a rank order of production). These results shows that the country’s scientific production on movement ecology is biased in favor of the richest and most populous regions of Brazil (IBGE, 2017), as other authors have already pointed out regarding scientific production in all research areas in Brazil (Albuquerque et al. 2002; Silva and Simões 2004).

Another important consideration is that 26% (81 studies) of all studies from the literature review have foreigners as first authors (58% or 47 of them from USA and UK), and 54% (44 studies) of these studies involve collaboration with Brazilian institutions (which means that 37 of these studies, or 12% of all studies, are authored by

foreigners without collaboration with Brazilians). However, 38 of the 50 most cited articles have Brazilians as first or co-authors, which means that around 76% of the high impact scientific production in movement ecology in Brazil is made within the country.

Topic of research in Movement Ecology Framework

The 56 participants of the I MEB Workshop that develop their studies focused on movement were asked to classify their own research based on the components of the Movement Ecology Framework from Nathan et al. 2008 — internal state, motion capacity, navigation capacity, movement path and external factors. We included the additional aspect “consequences of movement”, which relates to ecological processes that result from movement, such as pollination, seed dispersal, predation–prey interaction and population dynamics (see the modifications to the framework, suggested by Jeltsch et al. 2013).

The most studied components reported by attendees were movement paths (n=30, 53.5%) and external factors (n=27, 48.2%). On the other hand, few studies involved motion capacity of organisms (n=8, 14.2%), internal states (n=10, 17.8%) and navigation capacity (n=14, 25%). Around 26.7% (n=15) of the studies were linked with the “consequences of movement” component (Figure 3). We made the same classification to studies of the literature survey. The main components studied were motion capacity (n=273, 88%), external factors (n=230, 74%) and movement path (n=202, 65%). The components less studied was internal state (n=122, 39%), navigation capacity (n=74, 24%) and consequences of movement (n=68, 22%). We found significant differences when comparing the literature surveys and the questionnaires answers ($\chi^2=29.2$, $df=5$, $p<0.001$).

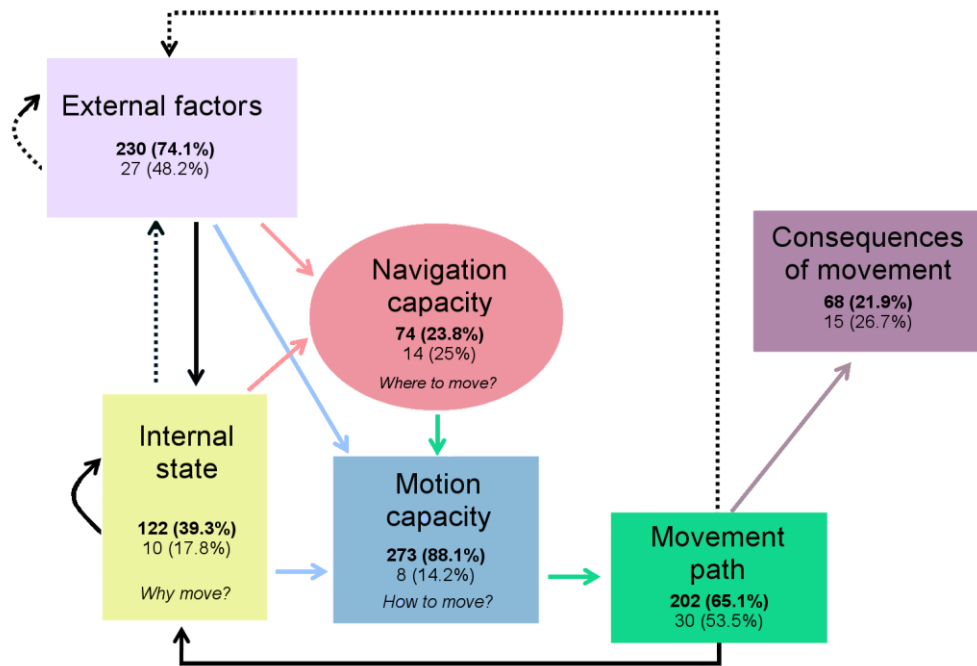


Figure 3. Classification of research conducted by studies in the literature survey (in bold font) and for the I MEB attendees (in regular font) based on the “movement ecology framework” (Nathan et al. 2008) and on the additional component “consequences of movement” (related to ecological process such as pollination, seed dispersal and predation).

The MEB participants had more answers related to internal state, less with external factor and a small increase on consequences of movement’ studies. These results corroborate the revision presented by Holyoak et al. (2008), who showed that most of the studies have been trying to describe movement patterns, their correlations with environmental variables, and to correlate it with conservation issues. Studies of motion capacity, internal state motivation and navigation capacity require scientific techniques or scales that need integration with other areas of knowledge such as physics, neurosciences and physiology, and crossing these disciplinary boundaries is still a challenge (Holyoak et al. 2008). The disproportionality in the research investment among those different areas that compose the movement ecology paradigm could delay the real understanding that movement effects play in important questions where the context is composed by ecological, behavioral and evolutionary components.

Biomes

Another topic that we explored in the survey was in which biomes the participants were developing their research. Because most participants were from institutions located in southeastern Brazil, and this region is predominantly in areas of Atlantic Forest and Cerrado, those biomes were also the most studied according to the answers of the questionnaires (n=22, 39.3%; and n=16, 28.6%; respectively). Other important biomes such as Marine (n=6, 10.7%) the Amazon (the largest rainforest on Earth, n=4, 7.1%), Caatinga (the largest tropical semiarid area in the world, with strong seasonality, n=1, 1.8%) and Pantanal (one of the most important wetlands and freshwater systems, n=1, 1.8%) was poorly explored for the participants of the I MEB (Alho et al. 1988, Moro et al. 2016). Four studies (7.1%) were being conducted in multiples biomes and two (3,6%) were not related with any biome. There was no mention of studies focused on the Pampas, even though it is a threatened ecosystem (Figure 4).

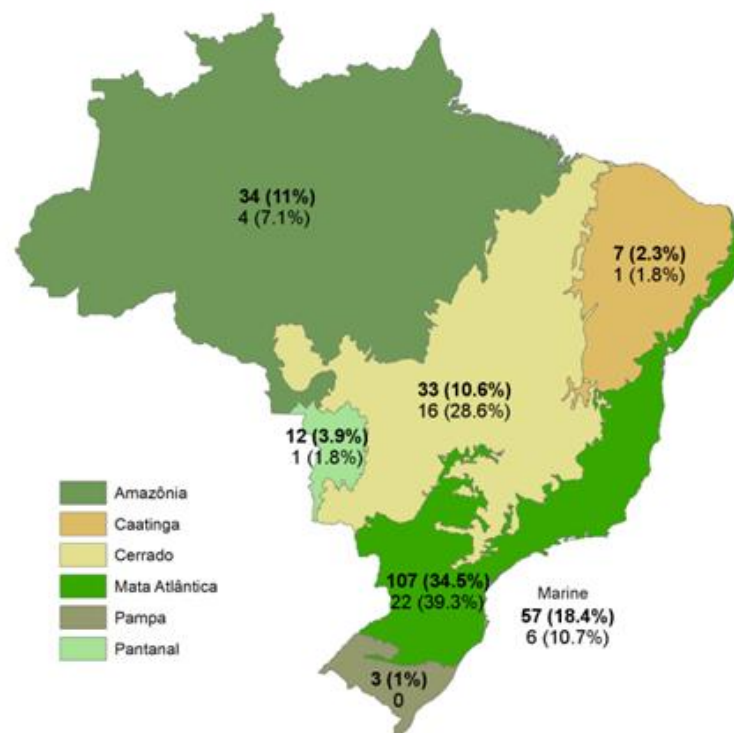


Figure 4. Quantity (number and percentage) of studies that were developed per biome in the literature survey (in bold font) and for the I MEB attendees (in regular font).

To the literature survey we found that one hundred seven (34.5%) of the studies was conducted in areas of Atlantic Forest, 57 (18.4%) in Marine biome, 34 (11%) in Amazon, 33 (10.6%) in Cerrado as well as simulations (n=33, 10.6%). These biomes

less studied were Pampas (n=3, 1%), Caatinga (n=7, 2.3%) and Pantanal (n=12, 3.9%). Twenty four studies (7.7%) were conducted in two or more biomes.

We also found differences when comparing the literature survey and the questionnaire answers ($\chi^2=17.6$, $df=8$, $p=0.02$), especially about more studies on Biomes Cerrado to participants of the I MEB. As well as the biomes mostly studied are reflecting the regions where participants of the I MEB live and study, the results also are related to other two important facts. Some biomes are harder to reach since logistic and costs to travel to and explore remote areas are more expensive, consequently these areas are less studied. Also, financial sources to research projects in Brazil are not uniformly distributed through the whole territory, with bigger investments in the southeastern region and most of the centers where movement research is being developed currently are placed in this region (Sidone et al. 2016, Chiarini et al. 2014).

Study taxa

The literature survey showed most studies were performed with mammals (n=128 studies, 41.3%) and birds (n=50, 16.1%) as their focus, followed by fishes (n=41, 13.2%), reptiles (n=30, 9.7%), simulated species (n=28, 9%), invertebrates (n=21, 6.8%), plants (n=7, 2.3%) and amphibians (n=3, 1%). One study (0.3%) compared movement patterns across a range of different taxa, as well as any taxa (n=1, 0.3%). We observed similar results among the MEB workshop attendees whose study focus was movement and mammals (n=32, 57.1%) or birds (n=16, 28.6%). Overall however, there patterns were different between the literature and the I MEB ($\chi^2=53.4$, $df=9$, $p < 0.001$). The questionnaires revealed an increased interest in amphibians, compared to the literature results (n=6, 10.7%), what can be related to the recent development of small telemetry devices (Pittman et al. 2014, Kays et al. 2015), besides a better integration between ecology and physiology researchers. Fishes and invertebrates constituted each one 7.1% (n=4) of study subjects, respectively. Plants (n=3, 5.4%), simulated species (n=3, 5.4%), and reptiles (n=2, 3.6%) received the least interest from I MEB workshop attendees. Nine participants (16.1%) are working in multiple taxa (Figure 5).

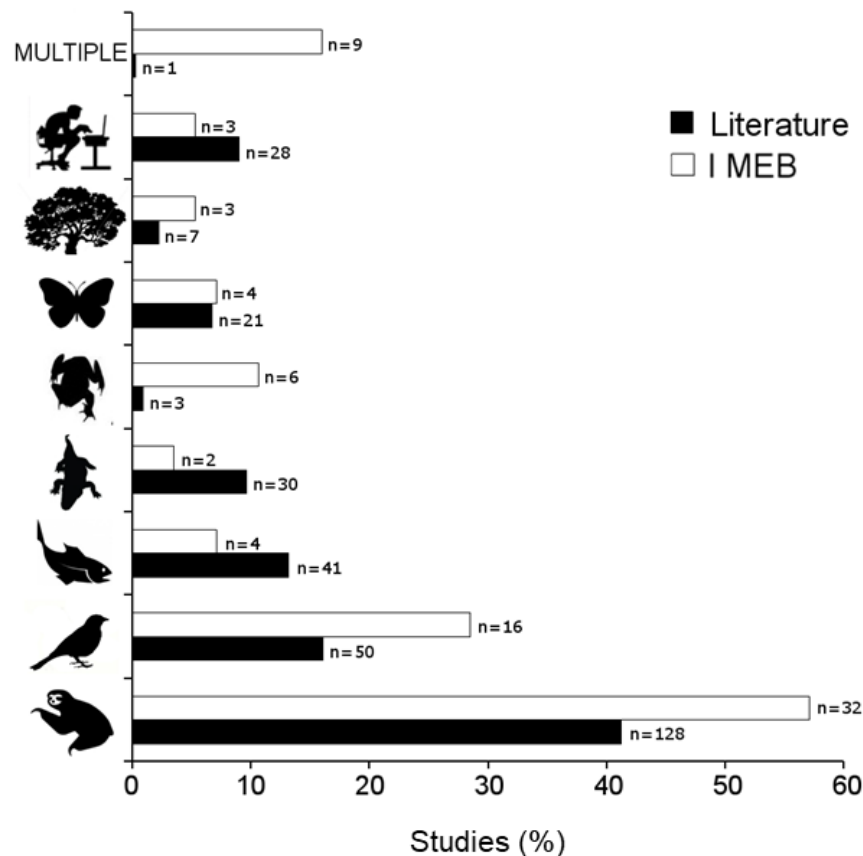


Figure 5. Quantity (number and percentage) of studies per taxon, according to the literature survey (black) and the I MEB attendees (white). The taxa groups, from bottom to top, are mammals, birds, fishes, reptiles, amphibians, invertebrates, plants, simulated species and multiple taxa.

The studied taxa scenario is in accordance with the revision made by Holyoak et al. (2008) for the movement ecology literature worldwide, where mammals, birds, and fish were the study taxa for which the percentage of studies focusing specifically on movement was higher ($n=55$, 59% of the articles). Furthermore, the patterns that influence the most studied taxonomic groups are also dependent of the places where research groups are working in with the thematic of movement ecology. In this specific case, understanding that the access to technology is also important to explain why vertebrates with bigger biomass were the most studied groups. Track equipment is generally expensive and as more technology is demanded to build smaller devices, the prices of equipment to monitor and transmit movement information for small organisms are higher (Bridge et al. 2011, Kays et al. 2015).

Technologies

The literature survey revealed that the main technologies associated with movement ecology studies are VHF telemetry (n=71 studies, 22.9%), mark-recapture (n=67, 21.6%) and modeling (n=48, 15.5%). In this study, modeling means that simulations were used in spatially explicit models based on the literature or pre-existing data bank information. GPS is featured in less than 9% (n=26) of studies, while 12.6% of the reviewed studies used other techniques (spool-and-line, geolocators, acoustic-based telemetry, accelerometers, isotopes, and genetic tools) and 16.5% used none technologies (direct observation accounted for 29 studies, or 9.4%, and the other ones did not measure movement directly). In contrast, the main technologies used by I MEB Workshop attendees were GPS telemetry (n=26, 46.4% of participants whose research focus was movement ecology), followed by VHF telemetry (n=20, 35.7%) and modeling (n=8, 14.3%). Other techniques were used in approximately 28.6% of the participants, while about 14.3% of them reported not to use technologies. No participants used isotopes to track the movement of organisms (Figure 6).

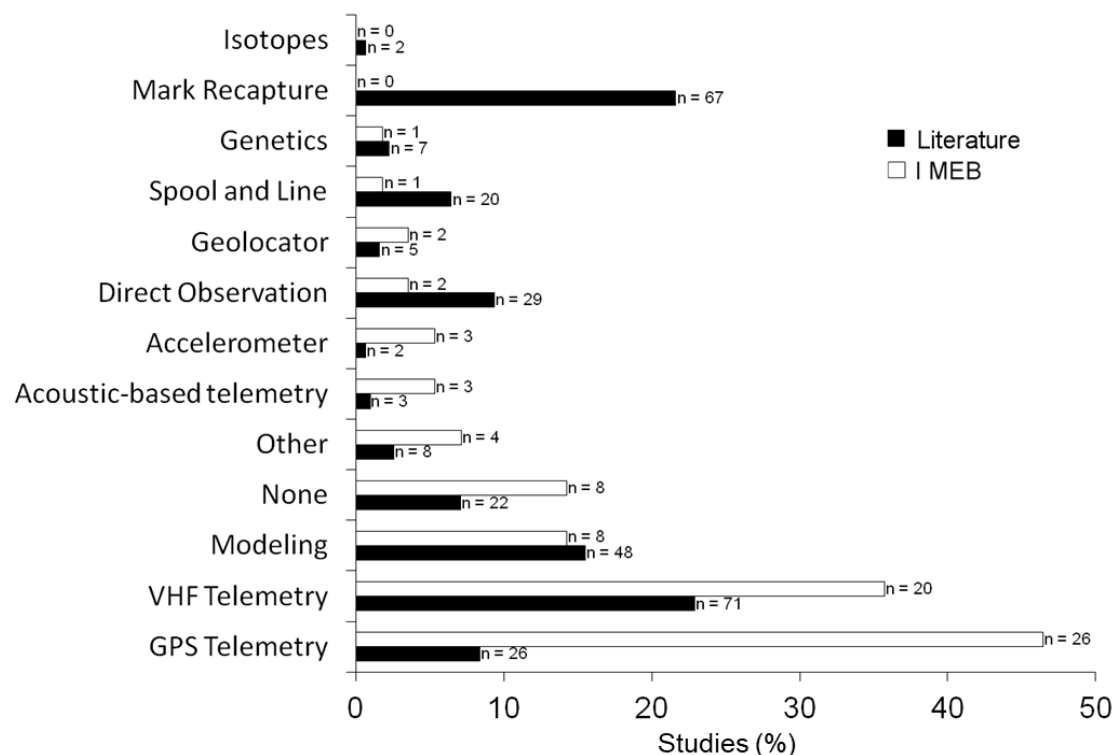


Figure 6. Quantity (number and percentage) of technologies' tools used to measure/acquire movement data, according to the literature survey (black) and the I MEB (white).

We observed differences between the results for the literature survey and the I MEB Workshop ($\chi^2=65.3$, d.f.=12, $p < 0.001$), evident mainly because of the percentage of studies using mark-recapture, much greater in the literature, and because of the elevated frequency of studies with GPS tracking in the I MEB. These differences were expected, given that the literature survey comprised 30 years of movement ecology research in Brazil and the I MEB gathered researchers that still developing their studies - and the technology that researchers use tends to change as equipment and techniques develop. An interesting trend that can be observed in our results comparing the literature review in the last 30 years with the event result in 2015 is the gradually increase in the use of GPS tracking equipment and decrease of VHF. Although the battery duration of VHF devices is usually larger and the prices still lower, the use of GPS tracking equipment is getting more attractive to researchers since more options are available in the market and technology is being improved to lighter devices.

We also found differences comparing the studies using genetic tools (greater in literature than in I MEB Workshop), what can be related with a low integration between researchers working on movement ecology and genetics in Brazil. Other big difference was on studies on simulations, what probably is a reflection of most of participants on I MEB was researchers and students of areas more related to ecology, and not directly involved with math and physics.

Big data, big challenges

New technologies also entail a new challenge: the large amount of data provided by high temporal resolution of movement trajectories (Kays et al. 2015). Dealing with this kind of information requires specific knowledge to organize process and analyze large quantities of data as well as incorporate and correlate all the available environmental spatial information, which is also becoming more developed and dynamic. This may explain why data analysis was the main challenge reported by the research participants in our survey (Figure 7). This is an expected result, since most movement ecologists are specialists in environmental sciences, while the analysis in this kind of studies requires broader knowledge of math, statistics and physics.

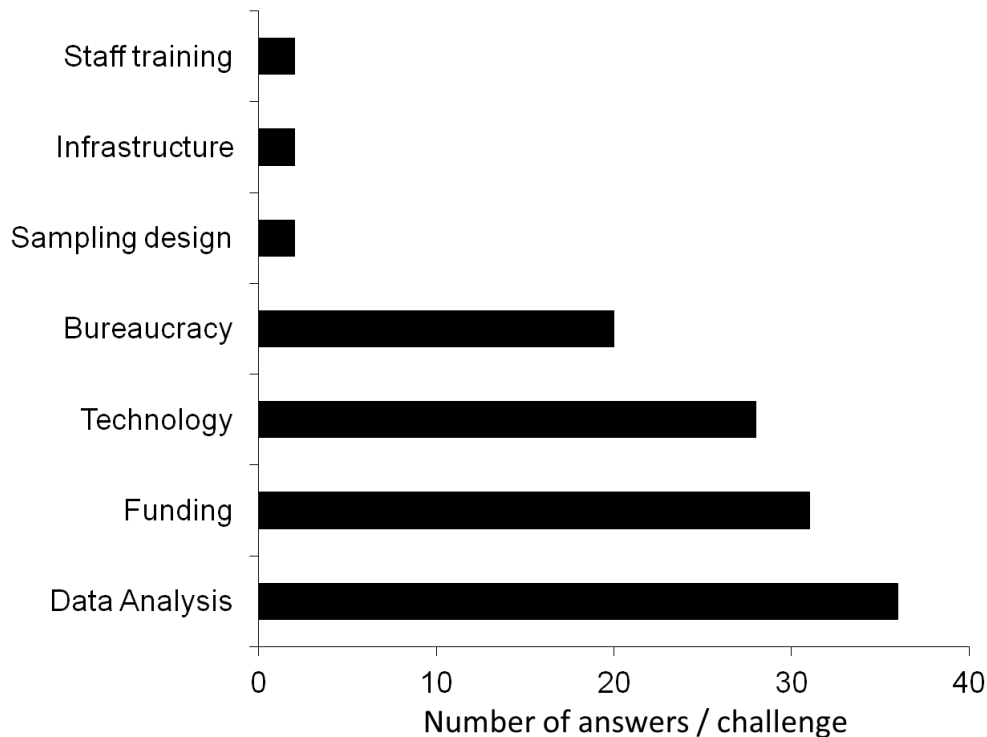


Figure 7. Quantity of answers per challenge of working in movement ecology indicated by the I MEB attendees.

The literature review and the MEB questionnaires presented nearly 15% of studies being developed using simulations, and many other also used complex statistical techniques to analyze data, as it is common in movement ecology (Kays et al. 2015). However, a great part of these studies (25 out of 48 studies, 52%) are developed exclusively inside Physics and Mathematics departments (without authors from biology or ecology departments), which indicates a difficulty in developing studies that integrate knowledge and tools from ecology and mathematics.

On the last years, some institutions in Brazil are providing interdisciplinary trainings, like the Southern-Summer School on Mathematical Biology (IFT, Universidade Estadual Paulista) and the Hierarchical Modeling Workshop (Gonçalo Ferraz's Lab, Universidade Federal do Rio Grande do Sul). These initiatives provide not just a deeper knowledge in methods and analyses, but also a better integration between researchers and students of different fields on science.

New technologies: little money and excessive bureaucracy

The I MEB survey showed that new technologies such as accelerometers and acoustic telemetry are starting to be used; however, we found no mention of innovative

methods such as animal-mounted cameras or implanted electronics that obtain information about physiological parameters. This is a reflection of the challenges described by the interviewed Brazilian researchers - scientific funding and bureaucracy involved in importing equipment were cited as the second and fourth greatest challenges, respectively (Figure 7). The newest technologies that acquire real-time data or information on animal physiology and behavior are expensive, and funding for science in Brazil is proportionally low - around 50% less than top research countries like USA and Germany (data from 2013; World Bank Group, 2016) – and is being reduced since 2013 by Brazilian Federal Government (Angelo, 2017).

These technological and bureaucratic challenges may also partly explain the bias towards studying larger animals such as mammals and birds, which can be tracked more easily than other organisms whether by GPS devices or more common technologies such as radio-telemetry and camera traps. The development of smaller devices is one priority on the field of movement ecology - allowing an increase on studies with small species respecting their weight limit (usually 5%), facilitating the fixation of the equipment and avoiding adverse effects on animal behavior (O'Mara et al. 2014, Kays et al. 2015, Marvin et al. 2016, Lameris & Kleyheeg, 2017).

A need for national technology development

Few Brazilian companies currently manufacture tracking equipment (e.g. Trapa® and Tigrinus®). Researchers interested in using such equipment must import them and usually pay in US dollars, the value of which is three times higher on average than the Brazilian Real. In addition, such devices must be adapted to different climatic environments and often present problems related to batteries, durability and resistance. Researchers opting for such wildlife tracking technologies face a common situation: the inevitable bureaucracy and high taxation when ordering devices or sending them for maintenance or repairs.

For these reasons, some researchers have been developing alternative low-cost methods to study animal movement, such as the adapted GPS harness system from Zucco and Mourão (2009), or using methods that are less accurate but more affordable like direct observation (Paulo and Lopes 2014, Garrone Neto and Uieda 2012) and mark recapture (Barreto-Lima et al. 2013). We identified a great need for cheaper and national technology development to stimulate and assist the movement ecology of the Brazilian rich biodiversity.

Ethical issues on animal tracking

Another issue widely discussed during the event is the ethical aspects of marking animals with tracking equipment. The main questions concerned the right of biologists to anesthetize or euthanize animals during field work and the necessity of a veterinarian, the payment of whom would increase field work costs. On the other hand, the presence of a veterinary specialist in wildlife can be essential for monitoring the vital parameters of animals or acting in cases of a veterinary emergency.

In Brazil this discussion started when the Biology Federal Council created a resolution 301/2012 that discussed the rights of biologist in wildlife handling. It includes capturing, containment, marking, release and collection of the animal specimen or to obtain samples of biological material, besides the rights to use anesthesia when necessary. In 2013 the Veterinary Federal Council started a lawsuit against the 301/2012 resolution claiming that biologist did not have the necessary training to execute anesthetic procedures in wild animals. Although the resolution 301/2012 is still valid, veterinaries and most biologists working in movement monitoring that express their view during the I MEB discussions, support the presence of a veterinary during capturing and anesthesia procedures.

It was also discussed that the specific training to capture, anesthetize and monitor wild animals is necessary for both biologists and veterinaries. With the increase of the accessibility to acquire GPS tracking devices and more use of anesthetics it is important to promote the integration of common research interests between both professionals. This could be a promising and necessary alternative to reduce costs and risks for the health of animals during capture and handling procedures.

Data: to share or not to share?

Another issue raised in the discussions was a resistance to integrating and sharing data among researchers in the country. Data sharing through movement ecology databases, such as MoveBank® (Wikelski and Kays, 2016) and ZoaTrack® (Dwyer et al. 2015), would save unnecessary investments and risks of injury inherent in capture procedures and fitting animals with tracking devices. Data integration and accessibility could also favor large-scale research and ecological investigation of interspecific relations.

Hot topics in I MEB

During the I MEB, 21 studies were presented by poster, and the content included a wide spectrum of topics such as the use of various ecological modeling techniques, the testing of new technologies, and the practical applications of movement ecology data (the abstracts are available on-line - <http://www.leec.eco.br/en/meb.html>). All the studied species were vertebrates, four studies (19%) applied the knowledge obtained through animal movement monitoring to better comprehend seed dispersal and only one study (5%) focused on migration. Seventy-six percent of the studies (n=14) were in areas suffering some anthropic impact such as forest fragmentation or river barriers, reflecting the current scenario of native habitat loss in most natural areas (Haddad et al. 2015). These studies are just a sample of all the movement ecology research being produced in Brazil, but they can be considered as representative of this field of study at the national level.

We know where we are; but where are we going?

The information gathered here on the scientific production within movement ecology in Brazil over the last 30 years and on the results and discussions of the I MEB Workshop inspires some questions about the role of Brazil in understanding its ecosystems from the movement ecology perspective. The technological challenges and the lack of nationally manufactured equipment, as well as the difficulties in analyzing complex and often large sets of movement data, are in part a reflex of the disciplinary character of Brazilian research institutions.

These challenges can be overcome through national and international collaborations among science fields and interdisciplinary research centers and institutes related to movement ecology. Furthermore, a comprehensive and multidisciplinary foundation at undergraduate and graduate research education institutions in Brazil (which are the main scientific producers in the country) would contribute to the formation of competent and well-rounded researchers. These professionals would be able to develop new ideas and ecological questions, planning and conducting the collection and analysis of data, and writing projects and science skillfully. Access to technology without bureaucracy, the growth of Brazilian companies that develop tracking equipment, enhanced research networks and partnerships are some necessary factors that will shape the autonomy of Brazilian researches working in the field of movement ecology.

There is still a need to link the mechanisms, processes and causes that influence movement in nature, to shape better ecological questions and to understand the consequences of movement for conservation. Specific capacitating training for wildlife veterinarians and biologists interested in handling wild animals would be an important development in Brazil. This kind of training is currently uncommon in the country despite the importance of dealing with animals in ways that guarantee safety for both the monitored species and the researcher during capture and monitoring procedures.

The main suggestion for the future directions in movement ecology research in Brazil is to explore organism movement data without forgetting the guiding principles, i.e. the underlying ecological questions. When this scientific field emerged, studies were often describing movement patterns, or they sought to understand very specific questions pertinent to related fields of knowledge such as the biomechanical, cognitive and optimality paradigms (Nathan et al. 2008). However, now it is time to move beyond researching animal movement for its own sake and integrate patterns and specific questions with ecological processes involved in movement itself, such as predation, pollination and seed dispersal. Further exploration on how movement facilitates natural forest restoration, ecosystem services and other phenomena could advance conservation policy planning and implementation.

ACKNOWLEDGMENTS

Authors would like to acknowledge to Trapa Câmera, Programa de Pós-Graduação em Zoologia and Programa de Pós-Graduação em Ecologia e Biodiversidade at UNESP Rio Claro. We also thank M. King, a native English speaker from Canada, for proofreading the manuscript.

FUNDING: This work was supported by Fundação de Amparo a Pesquisa do Estado de São Paulo (grant numbers 2013/50421-2, 2014/23132-2 and 2014/24291-4), CAPES and CNPQ (grant number 161089/2014-3).

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Supplementary Material - Alves-Eigenheer et al. Challenges and perspectives of movement ecology research in Brazil

Supplementary Material 1.Results of the online questionnaire survey filled by the 99 attendees of I MEB including information about their research group, main challenges and other information related to movement ecology in Brazil.

Available at: https://github.com/LEEClab/Movement_Ecology_Brazil_1985-2015.

Supplementary Material 2.The scientific articles that were acquired in the Web of Science research to evaluate 30 years of production (1985-2015) within the movement ecology in Brazil.

Available at: https://github.com/LEEClab/Movement_Ecology_Brazil_1985-2015.

Supplementary Material 3. Metadata file explaining the organization and structure of Supplementary Materials 1 and 2.

Description of the results of the I MEB questionnaires

The table with the results of questionnaires filled by the I Movement Ecology Brazil Workshop participants is organized in Excel format (.xls). It presents the following columns:

1. Participant: number identifying the participant (participant identification was omitted).
2. Affiliation_institution_Brazilian_state: Brazilian state of the institution with which the participants are affiliated.
3. Area_of_study: discipline of study of the participant (e.g., Ecology, Physiology, Physics)
4. Institution: Institution of affiliation of the participants.
5. Movement_ecology_group_in_institution: Is there a research group with focus on movement ecology at you institution? [Yes, No].
6. Works_with_movement: Do the focus of the participants' research is on movement ecology? [Yes, No].
7. When_started_to_work_with_movement: date when the participant started to work with movement ecology.
8. Type_of_research: Type of research. Categories: Theoretical, Applied, Both.
9. Taxon: Group whose movement was studied.

Categories: amphibians, birds, fish, invertebrates, mammals, multiple (in case of many taxon being studied in the same study), plants, reptiles, simulations (in case the study was performed without a focus in a specific taxon).

10. Biome_standardized: Brazilian biome of the study.

Categories: Amazon, Atlantic Forest, Caatinga, Cerrado, Marine, Multiple (in case of more than one biome or studies about animal migration that included Brazil), Pampas, Pantanal. Rivers and lakes were included in the biomes they were part of.

11. Level_study: Ecological level focused on the study.

Categories: Individual, Population, Community, Landscape, Ecosystem (or multiple options).

12. Components_mov_ecology_framework: classification of the participants' research within the movement ecology framework from Nathan et al. (2008), according to themselves – a list of components related to their research.

13. Technologies_used: technologies used in the participants' study.

Categories: Accelerometer, Acoustic-based telemetry, Direct Observation, Genetics, Geolocator, GPS Telemetry, Isotopes, Mark Recapture, Modeling (in case of simulations or any study without field collection), None (studies that did not record movement path and did not use technologies), Other, Spool and Line, and VHF Telemetry.

14. Challenges: greatest challenges the participants had while performing their research.

Data and code

The data and the code for analyzing the state of the art of Movement Ecology in Brazil, from the literature and I MEB data, are available on Github:

https://github.com/LEEClab/Movement_Ecology_Brazil_1985-2015.

Description of the results of the literature survey on Movement Ecology in Brazilian

The table with the results of the literature survey on movement ecology in Brazil, performed through the scientific citation index “Web of Science®”, is organized in Excel format (.xls). It presents the following columns:

1. Title: title of the study (e.g. article or book chapter).

Variables classified by the authors:

2. Techonology_used: technologies used in the study.

Categories: Accelerometer, Acoustic-based telemetry, Direct Observation, Genetics, Geolocator, GPS Telemetry, Isotopes, Mark Recapture, Modeling (in case of simulations or any study without field collection), None (studies that did not record

movement path and did not use technologies), Other, Spool and Line, and VHF Telemetry.

3. *Tecnology_detailed*: the same as “*Technology_used*”, but without standardization and with more details for some studies (such as “Other”).
4. *Author_affiliations_Brazilian_state*: Brazilian State abbreviation of the affiliation of the first author of the study. In case the first author was not affiliated with a Brazilian institution, the country of his/her institution was recorded.
5. *Foreign_collaboration_Brazilian_state*: Brazilian State abbreviation of the affiliation of a collaborator in Brazil, in case the first authors were not affiliated with a Brazilian institution. When there were collaborators from different institutions, only one of them was recorded at random. “NO” represents no collaborations with researchers in Brazil.
6. *Taxon*: Group whose movement was studied.

Categories: amphibians, birds, fish, invertebrates, mammals, multiple (in case of many taxon being studied in the same study), plants, reptiles, simulations (in case the study was performed without a focus in a specific taxon).

7. *Biome_standardized*: Brazilian biome of the study.

Categories: Amazon, Atlantic Forest, Caatinga, Cerrado, Marine, Multiple (in case of more than one biome or studies about animal migration that included Brazil), Pampas, Pantanal. Rivers and lakes were included in the biomes they were part of.

8. *Biome_detailed*: the same as “*Biome_standardized*”, but with the detailed biomes in case the study was developed in more than one.

Classification of components within the movement ecology framework from Nathan et al. (2008).

The components were classified as present (1) or absent (0) of the focus of the study. The classification followed Holyoak et al. (2008), but we classified the presence of components in the studies instead of their links.

9. *External_factors*: External factor component.
10. *Internal_state*: Internal state component.

11. Navigation_capacity: Navigation capacity component.
12. Motion_capacity: Motion capacity component.
13. Movement_path: Movement path component.
14. Consequences_of_movement: Component regarding consequences of movement (sensu Jeltsch et al., 2013).

Variables identifying the study:

15. Authors: list of authors of the study.
16. Journal: name of the Journal or book where the study was published.

It includes 139 journal/books (see the list below).

17. Year_of_publication.
18. Volume.
19. Issue.
20. Initial_page and End_page (or Article_number in case of online publications).
21. DOI: Digital Object Identifier.
22. Citations: number of citations from the publication of the study until 2015.
23. Mean_citations_per_year: average number of citations per year, from the publication of the study until 2015.

The studies were published in the following journals and books:

Acta Scientiarum Biological Sciences, Acta Theriologica, Amazoniana-Limnologia et Oecologia Regionalis Systemae Fluminis Amazonas, American Journal of Primatology, American Naturalist, Anais da Academia Brasileira de Ciências, Animal Behaviour, Animal Biology, Animal Conservation, Annales Zoologici Fennici, Antarctic Science, Aquatic Living Resources, Aquatic Mammals, Auk, Austral Ecology, Biodiversity and Conservation, Biological Conservation, Biology Letters, Biota Neotropica, Biotropica, Bird Conservation International, Boletim do Museu de Biologia Mello Leitão Nova Série, Brazilian Journal of Biology, Brazilian Journal of Oceanography, Brazilian Journal of Physics, Bulletin of The British Ornithologists' Club, Canadian Journal of Zoology-Revue Canadienne de Zoologie, Chelonian Conservation and Biology, Ciência Rural, Community Ecology, Computers and Biomedical Research, Computers and Electronics in Agriculture, Conservation Biology, Conservation Genetics, Copeia, Deep-

Sea Research Part I-Oceanographic Research Papers, Dispersal, Individual Movement and Spatial Ecology: A Mathematical Perspective, Ecological Complexity, Ecological Modelling, Ecological Monographs, Ecology, Ecology and Conservation of Grassland Birds of The Western Hemisphere, Ecology and Evolution, Ecology Letters, Ecology of Freshwater Fish, Ecotropica, Ecotropica-Bonn, Emerging Infectious Diseases, Endangered Species Research, Entomologia Experimentalis et Applicata, Environmental Biology of Fishes, Environmental Management, Estuarine Coastal and Shelf Science, Ethology Ecology & Evolution, European Journal of Wildlife Research, Europhysics Letters, Fisheries Management and Ecology, Fisheries Research, Florida Entomologist, Folia Primatologica, Forest Ecology and Management, Frontiers in Plant Science, Functional Ecology, Geographical Review, Herpetological Bulletin, Herpetological Journal, Herpetological Review, Iheringia Serie Zoologia, International Journal of Primatology, Journal of Animal Ecology, Journal of Applied Ichthyology, Journal of Arachnology, Journal of Cetacean Research and Management, Journal of Field Ornithology, Journal of Fish Biology, Journal of Herpetology, Journal of Mammalogy, Journal of Medical Entomology, Journal of Natural History, Journal of Ornithology, Journal of Physics A-Mathematical and Theoretical, Journal of Raptor Research, Journal of The Marine Biological Association of The United Kingdom, Journal of The Royal Society Interface, Journal of Tropical Ecology, Journal of Wildlife Management, Journal of Zoology, Landscape Ecology, Mammalia, Mammalian Biology, Mammal Review, Marine Biodiversity Records, Marine Biology, Marine Biology Research, Marine Ecology Progress Series, Marine Mammal Science, Marine Turtle Newsletter, Mastozoologia Neotropical, Memorias do Instituto Oswaldo Cruz, Methods in Ecology and Evolution, Molecular Ecology, Molecular Phylogenetics and Evolution, Nature, Naturwissenschaften, Nauplius, Neotropical Biology and Conservation, Neotropical Ichthyology, Oecologia, Ornitologia Neotropical, Oryx, Peerj, Phyllomedusa, Physica A-Statistical Mechanics and its Applications, Physical Review E, Physical Review Letters, Physics of Life Reviews, Plos Computational Biology, Plos Neglected Tropical Diseases, Plos One, Preventive Veterinary Medicine, Proceedings of The Royal Society B-Biological Sciences, Revista Brasileira de Biologia, Revista Brasileira de Entomologia, Revista Brasileira de Ornitologia, Revista Brasileira de Zoologia, Revista Brasileira de Zootecnia-Brazilian Journal Of Animal Science, Revista de Biologia Tropical, River Research and Applications, Salamandra, Scientific Reports, Studies on Neotropical Fauna and Environment, Subterranean

Biology, Transactions of the American Fisheries Society, Waterbirds, Wildlife Research, Wildlife Society Bulletin, Wilson Bulletin, Wilson Journal Of Ornithology, Zoologia.

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Chapter 2

Coordinated movements of maned wolves (*Chrysocyon brachyurus*) in protected and fragmented landscapes

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Cezar Ribeiro, Luca Börger**

Keywords: Dynamic Interactions, Social Behavior, Animal movement, Landscape.

Abstract

The contact between conspecifics is one of the most important events in animal lives. However, little attention has been dedicated to comprehend sociability of solitary species. Our study focuses on the social structure of maned wolves living inside a protected national park and the surrounding fragmented area around, in Brazil. Our objective is a better understanding about social behavior between dyads of maned wolves (couples, neighbors and strangers). We hypothesized that (a) sociability between conspecifics is higher between couples, intermediate between neighbors and lower with strangers; (b) protected and fragmented areas influence the sociability of conspecifics. We assessed the contacts between pairs using pairwise distances over time and dynamic interactions analyses. Our results indicate that maned wolves are solitary, but present interactions between couples, besides a high tolerance between spatially contiguous neighbors and few interactions between strangers. We also found that dyads in human-altered landscapes interact more than individuals living in protected areas. No evidence on influence of conspecifics on the direction of movement of others was recorded; however the displacements are related between dyads, indicating similar patterns on movement. Maned wolves are a solitary species, but present our results are a evidence for a degree of sociality between couples and neighbors of territory. The landscape use within the home range of maned wolves can influence the length of the pairwise distances, which therefore reflects the impact of human-dominated areas on behavior and movement of this important species. We recommend more studies on sociability of solitary animals and their social interactions, which may improve planning and conservation of the species and their occupied habitats.

Introduction

The movement of organisms is one of the most important characteristics of life on Earth and is a crucial component of almost all ecological and evolutionary processes, linking the ecology of organisms, populations, communities and ecosystems (Nathan *et al.*, 2008; Jeltsch *et al.* 2013). Examples of movement processes include dispersion and migration, which can have impacts on seed dispersal, plant regeneration and gene flow (Nathan *et al.*, 2008; Kays *et al.*, 2015). These movement processes act over a great variety of spatial-temporal scales (Hundertmark, 1998; Nathan *et al.*, 2008; Niebuhr *et al.*, 2015; da Silveira, 2016; Molin *et al.*, 2017).

Movements are determined by feedback interactions between the internal state of individuals and the external environment, conditional on the individual's movement and sensory abilities (Nathan *et al.* 2008). A key component of the external environment are other individuals (conspecifics and non), affecting for example competition for food, mate search, predator-prey interactions, hence comprehending it is an important step to understand social and mating systems (Emlen & Oring 1977 Science; Clutton-Brock review mammalian mating systems) and for the conservation of species and areas (Delgado *et al.* 2014, Kays *et al.*, 2015; Spiegel *et al.*, 2016). Animal movements can be affected by these interactions in two ways: (i) static interactions, whereby the movements of one individual are affected by the presence of another individual in the same area, even if not at the same time; and (ii) dynamic interactions, which refer to an effect of the presence of a conspecific at the same time and place as the focal individual. 'Dynamic interactions' is thus a broad term to define inter-dependent movements between two or more individuals present at the same time in a certain area (MacDonald *et al.* 1980; Long, 2015).

Long (2015) defines five types of movement patterns related to dynamic interactions: a) Proximity or contact: interaction that occurs when two or more individuals encounter each other; b) Attraction/Avoidance: movement in direction to or away from the other individual; c) Coordination: movement influenced by another individual which can be assessed independently of the distance between both animals; d) Leadership/Following: when the movement of one individual precedes that of the other one; and e) Grouping: coordinated movement of more than two individuals.

The presence of conspecifics – other individuals of the same species - can thus influence individual movement patterns, and the attraction or avoidance by individuals depends on the benefits and costs of this association (Bode *et al.*, 2012; Delgado *et*

al.2014). Gregarious animals use cooperative social strategies to live together, sharing benefits and responsibilities, like defense against predators, shared parenting and collective decision (Kappeler & van Schaik, 2002; Strandburg-Peshkin, 2018). On the other side, solitary animals usually prefer avoiding interactions with conspecifics and show limited sociality (Logan & Sweanor, 2001; Dammhahn & Kappeler, 2009). However, solitary species may interact with conspecifics in some moments of their life cycle, like to rear cubs, mate, or defend a territory (Sandell, 1989).

Carnivores are mainly solitary species – 179 of 247 species avoid conspecifics most of time, maintaining separate territories in space or time, except during mating season or territorial disputes (Sandell, 1989; Hunter, 2011; Kleiman & Eisenberg, 1973). However, depending on the availability of resources, solitary carnivore species present tolerance to other conspecific individuals (Elbroch *et al.*, 2017). Conspecific tolerance may actually be fundamental for the survival of species in areas of high anthropogenic pressure, *e.g.* when habitat fragmentation force individuals into small habitat fragments (Woodroffe & Ginsberg, 1998; Elbroch *et al.*, 2017). Accordingly, Tucker *et al.* (2018) showed that in areas with high human footprint, carnivores has smaller median displacements (3.3 ± 1.4 km median 10-day displacement distance, compared to 6.9 ± 1.3 km displacement distances of animals in preserved areas). Sociality and conspecific interactions, especially movement interactions, between solitary species have however been less studied than for social species and hence the former constitutes the aim of this study. For this we used the maned wolf (*Chrysocyon brachyurus*), a solitary Brazilian canid as a model species.

The maned wolf is a South American carnivore, have a broad diet which comprises fruits, small rodents, insects etc (Dietz, 1984; Santos *et al.*, 2003). The species is considered a vulnerable species at risk of extinction due to a drastic reduction and fragmentation of its original habitat (IBAMA 2003). The social system of the maned wolf is based on monogamous breeding pairs, but little is known about their social behavior or landscape use. Dietz (1984) and Jacomo *et al.* (2009) contend that maned wolves are solitary animals that interact occasionally, especially during the mating season. However, these studies were conducted using VHF radiotelemetry technology, which obtain sparse and less accurate data when compared with modern GPS systems. , and In addition, many of VHF data are collected during the day, which limits some analysis of movement behavior ecology. In fact, Bandeira de Melo *et al.* (2007) studied the social behavior of three maned wolves – a couple and a juvenile

female – using global positioning systems (GPS) for six months and found a strong interaction between the couples and high tolerance of both adults with the juvenile.

Paula (2016) showed in his study that maned wolves living in the Serra da Canastra National Park comprised couples sharing the same territories. However, the overlap between the home range of individuals cannot be considered a complete measure of interactions between individuals, as overlap does not provide any information about the intensity of interactions (Atwood & Weeks, 2003) and the presence of dynamic interactions between individuals. To obtain a more complete information, it is necessary to obtain data on the spatio-temporal location of both individuals of a potentially interacting pair ('dyad') of individuals (Mace & Waller, 1997).

In this study we aimed to understand the social structure of maned wolves living inside a protected national park and the surrounding fragmented area around it, in Brazil. The overall objective of this study was to obtain a better understanding of the social behavior, specifically dynamic movement interactions, between dyads of maned wolves. We quantified dynamic movement interactions between "couples", spatially contiguous "neighbors", and "strangers" [non-neighboring individuals separated by home range of a spatially contiguous neighbor do both individuals]. We hypothesized that (a) sociability between conspecifics is higher between couples, intermediate between neighbors and lower with strangers; (b) protected and fragmented areas influences the sociability with conspecifics. We intended to (i) quantify the social interactions (encounters, coordinated movements) of maned wolf pairs; and (ii) compare movements and interactions of pairs inside and outside protected areas.

Methods

Study area

The Serra da Canastra National Park (SCNP, Brazil) is a protected area, located at coordinates 20°20'S / 46°38'W and covering an area of 2000 km². The natural vegetation formations of the regions are typical of the Cerrado Biome, especially grasslands (Coutinho, 2000). The surrounding areas are heavily altered by human activities, with exotic grasses for dairy cattle feed, agriculture and coffee and pine plantation. The region is also used for non-regulated ecological tourism activities, especially in the SCNP area (Paula, 2016). The total area, which comprises part of SCNP and surrounding areas, is about 3000km².

GPS data collection

The maned wolf GPS data were collected on 13 adult individuals by R.C. de Paula from ICMBio (license SISBIO/ICMBio 11124). Six males and seven females were captured between 2007 to 2015 using live traps baited with cooked chicken and sardines, sedated, and equipped with GPS-collars programmed to record one location every 1 to 4 hours, depending on the individual (Table 1); the collars recorded locations between 2 months to over 2 years (Figure 1). Paula (*personal communication*) registered birth of pups from the females studied – Rose in July 2014; Lais in May/June 2007; and Tay in May/June 2008.

Table 1. Information on the 13 maned wolves monitored with GPS-collars between 2007 and 2015. ID is the identification of each individual; if they were part of a couple the letters are equal; HR is the home range estimation at 95% of confidence interval. This information is adapted from Paula (2016).

Id	Sex	Area of occurrence	Couple	N. days of data collection	N. locations	HR (95%)
Amadeo	male	Park / Transition	A	461	3514	118.3 4
Bolt	male	Park	C	547	12917	145.5 7
Gamba	male	Park / Transition	B	98	562	43.37
Henry	male	Farms	none	250	1451	40.45
Jurema	female	Farms	E	510	2846	40.58
Laís	female	Park / Transition	A	433	3726	106.1 8
Loba	female	Park / Transition	none	563	2317	93.85
Luna	female	Farms	D	295	5775	31.12
Miro	male	Farms	D	382	2687	41.28
Nilde	female	Farms	none	59	618	44.23
Rose	female	Park	C	356	8527	93.20
Samurai	male	Farms	E	86	496	49.44
Tay	female	Park / Transition	B	841	8760	31.50

Data organization

We convert the original coordinates from latitude and longitude in decimal degrees to UTM Zone 23S to facilitate metric distance calculations. We incorporated

this information into a new data frame that includes also date and ID information. After this step, we removed all the lines with no information in any of this fields (we miss 129 locations). We organized this data in 13 lists, one to each individual.

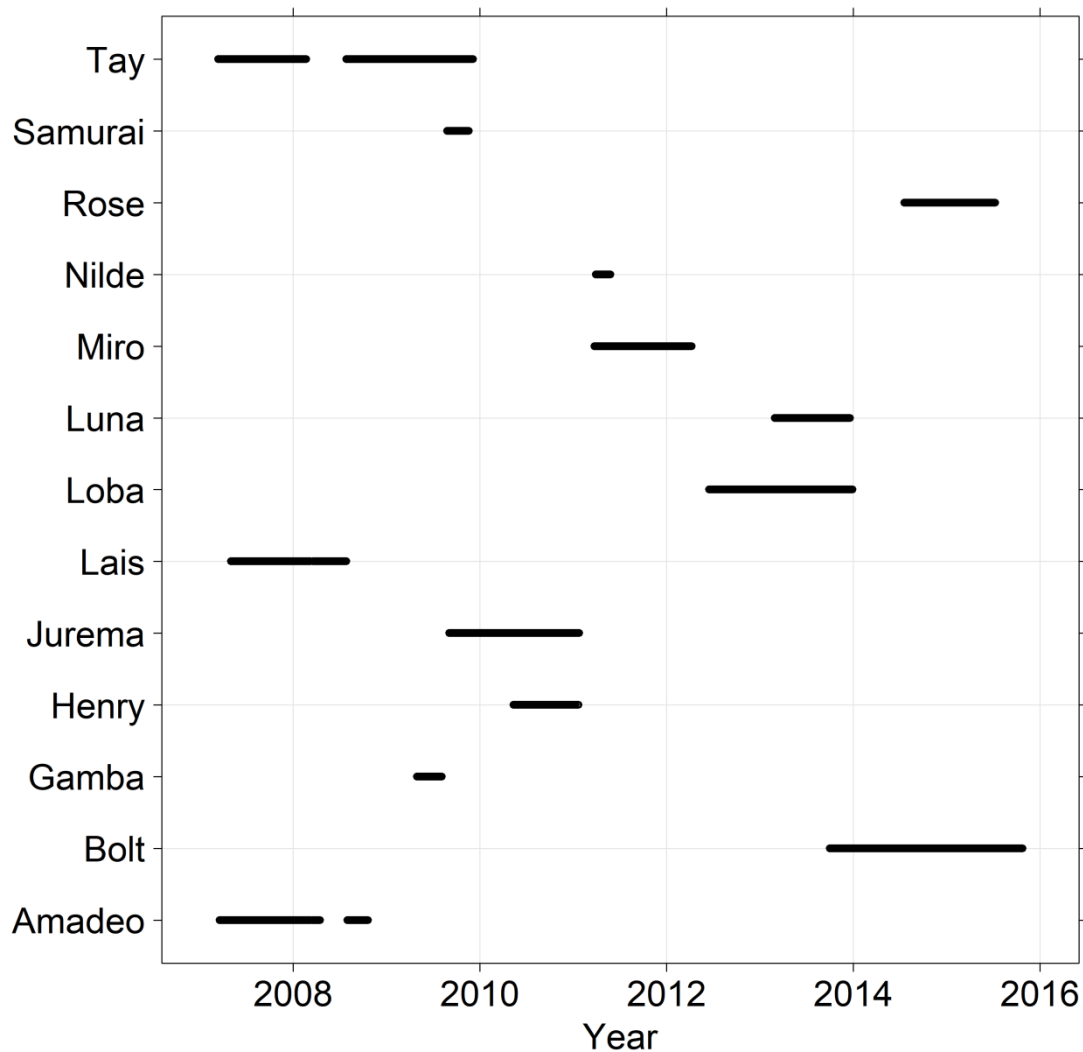


Figure 1. Period of study of the 13 individuals of maned wolf analyzed on this study. The x axes indicate the years (from 2007 to 2015) and the y axes shows the different individuals.

We created subsets between dyads of individuals spatially related with data collected at the same period, which includes 12 different individuals – unfortunately the individual “Luna” had no temporal match with other individuals spatially related (couple, neighbors or strangers). This information, as well as the data range between both individuals of each dyad, is available in Table 2. We also provide information about the area where each dyad was located (Park to SCNP, Farms to the fragmented and no protected region and Transition, to areas between Park and Farms).

Table 2. Maned wolf dyads organized by their relationship (Couple, neighbors and stranger). For each dyad we report the area of occurrence and the data range between the individual pairs.

Relationship	Dyad	Area	Data range
Couple	Bolt/Rose	Park	29/07/2014 to 10/07/2015
	Amadeo/Lais	Park/Transition	05/05/2007 to 04/04/2008
	Samurai/Jurema	Farms	03/09/2009 to 19/11/2009
	Gamba/Tay	Park/Transition	30/04/2009 to 05/08/2009
Neighbors	Amadeo/Tay	Park/Transition	20/03/2007 to 20/10/2008
	Lais/Tay	Park/Transition	01/05/2009 to 19/02/2010
	Loba/Bolt	Park	01/10/2013 to 29/12/2013
Strangers	Jurema/Henry	Farms	12/05/2010 to 22/01/2011
	Miro/Nilde	Farms	30/03/2011 to 27/05/2011

Data analysis

For each dyad of maned wolves we first selected the data occurring at the same days. These data were used to quantify the movements, and hence pairwise distances, step by step of both individuals at the same time. We first graphically represented the distribution of pairwise distances for each dyad using kernel density curves. Then we used generalized additive models (GAMs) to analyze the change in pairwise distances over time, allowing for non-linear relationships. GAMs are an extension of generalized linear models (GLM), and use a link function to relate the mean of the response variable with a smoothed non-parametric function of the explanatory variables (Guisan *et al.*, 2009; Zurr *et al.*, 2009).

To further analyses the interactions between the dyads, we used the dynamic interaction index analysis (Di-index), which can identify coincidental movement pattern between two individuals in certain segment of time, even though without considering physical proximity (Long and Nelson, 2013). The Di-index presents 3 main outputs (Figure 2) – the global Di measures the overall interaction in a set of movement segments; the Azimuth, which is related to the cosine of the angle between two individuals (positive values = same direction, negative values = opposite directions); and the Displacement, which measures interactions in the length of distance moved (therefore no presents negative results, just neutral, close to zero; or positive, close to 1). The main advantage of this method is that it splits the components of interactions – displacement and azimuth – thereby allowing to obtain a better comprehension of

interactions between individuals (Figure 2). Besides, the method allows weighting by time (useful in the case of missing fixes) and/or distance (interesting when the animal alternates between movement modes with longer and shorter movements).

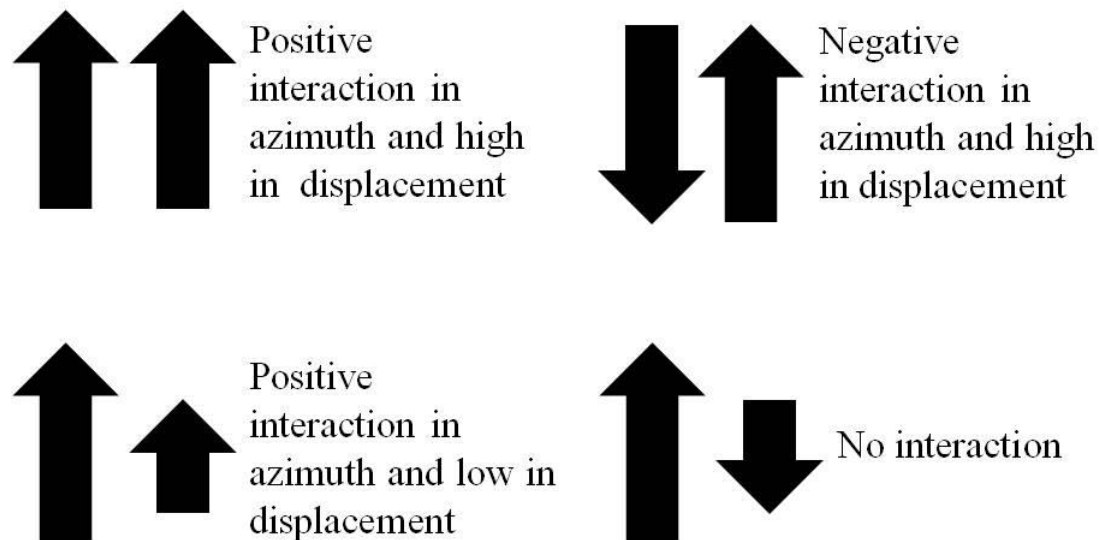


Figure 2. Diagram of movement properties (azimuth and displacement) that can be found analyzing interactions between two individuals using the DI-Index (Adapted from Long & Nelson, 2013).

We used the function *GetSimultaneous* from package *wildlifeDI* (Long, 2014) to identify the right amount of time to be considered for each segment per pair. It varies between each dyad and depends on the periodicity of data collection. All the analysis was run time weighed. The GAM and Di-index analyses were applied to all the animals that showed temporal match in the location data, including couples, neighbors and strangers. The statistical analysis were conducted in R 3.3 (R Development Team, 2017), using the *adehabitatLT* (Calenge, 2006), *mgcv* (Wood, 2018) and *wildlifeDI* (Long, 2014) packages.

Results

The distribution of pairwise distances clearly differed between couples, neighbours and strangers (Figure 3; see also Supplementary Material 2 for the minimum, maximum, median and mean values for all the dyads). Pairwise distances differed also within couples - the animals living inside the park showed larger distances, followed by the couple Amadeo and Lais, which lived on the edge between the park and

the non protected area. The other two couples present a similar pattern, with biggest distances smaller than 10 kilometers.

The neighbors present distances varying from less than one to more than 20 kilometers. When the neighbors were two females (Lais and Tay) this distance was smaller. The strangers present similar patterns, with distances varying from around 3 to 18 kilometers.

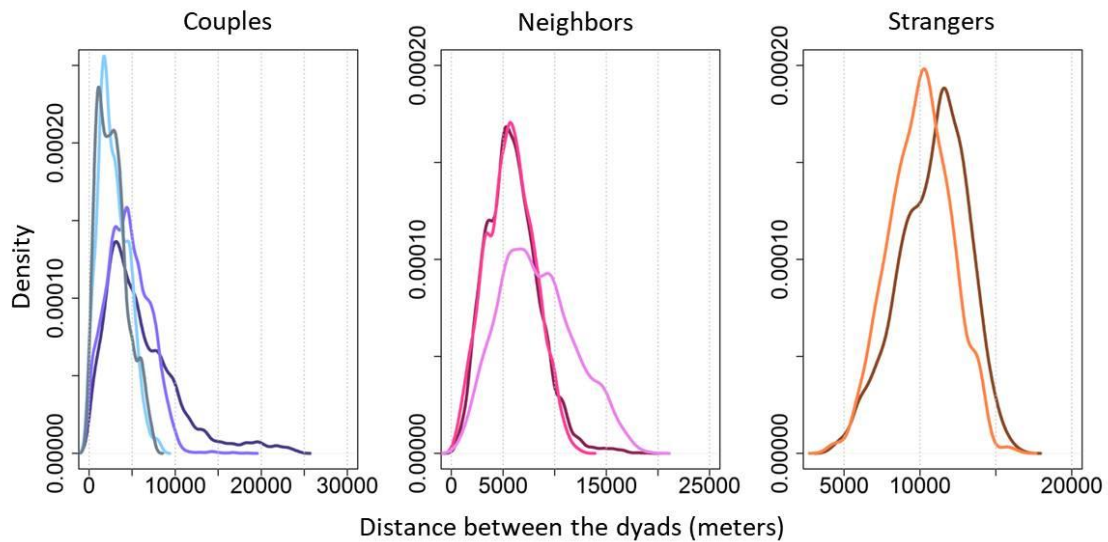


Figure 3. – Kernel density plots of the distribution of pairwise distances in meters between the dyads studied. The x axes indicate the distance between each individual of a dyad and the y axes indicates the density (distribution) of the pairwise distance values.

We further depict the distribution of pairwise distances using boxplots (Figure 4), which further reiterates the increase in pairwise distances from couples to neighbors to strangers.

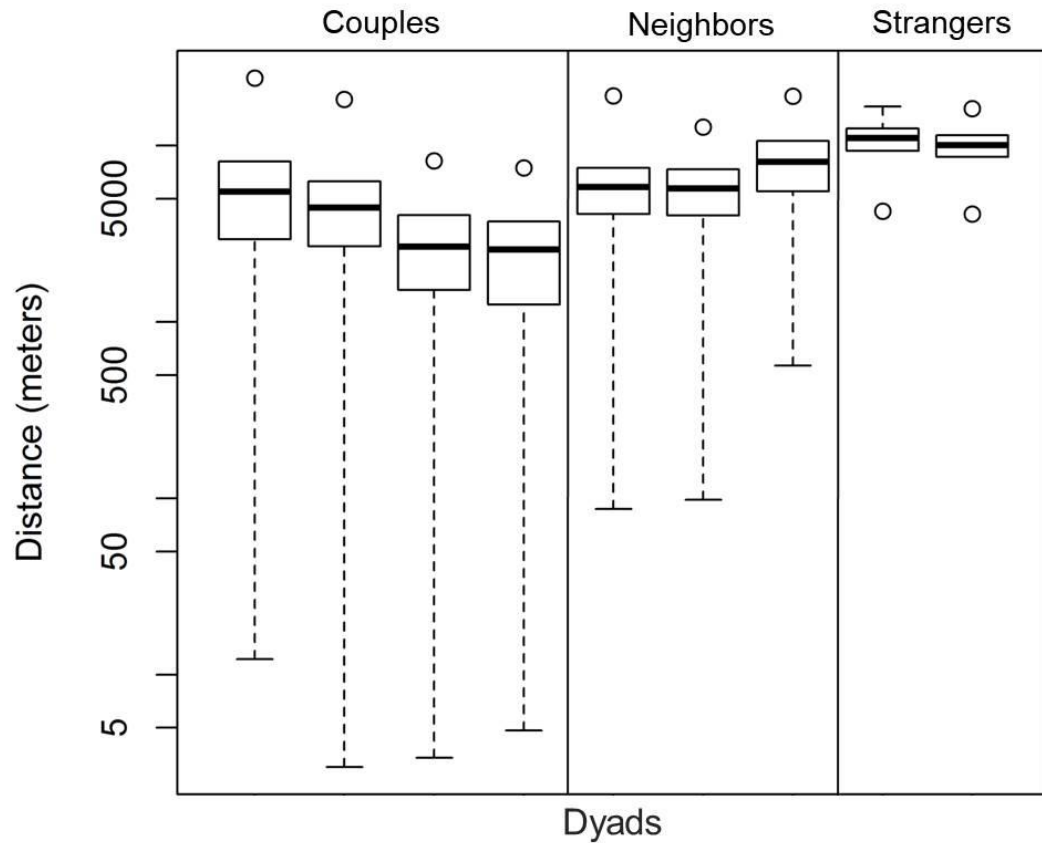


Figure 4. Distance in meters between concurrent locations of each dyad. Each box represent one dyad - Couples (Bolt/Rose, Amadeo/Lais, Samurai/Jurema and Gamba/Tay), neighbors (Amadeo/Tay, Lais/Tay and Loba/Bolt) and strangers (Jurema/Henry and Miro/Nilde), respectively. The x axes indicate the different dyads. The y axes is in logarithmic scale and indicates the distance in meters.

Given the large variance in pairwise distances, it was not possible to easily discern patterns in the plots of the raw pairwise distance values over time (Figure 5; Supplementary Material 3), hence we used GAM models to extract the shape of temporal variation of pairwise distances.

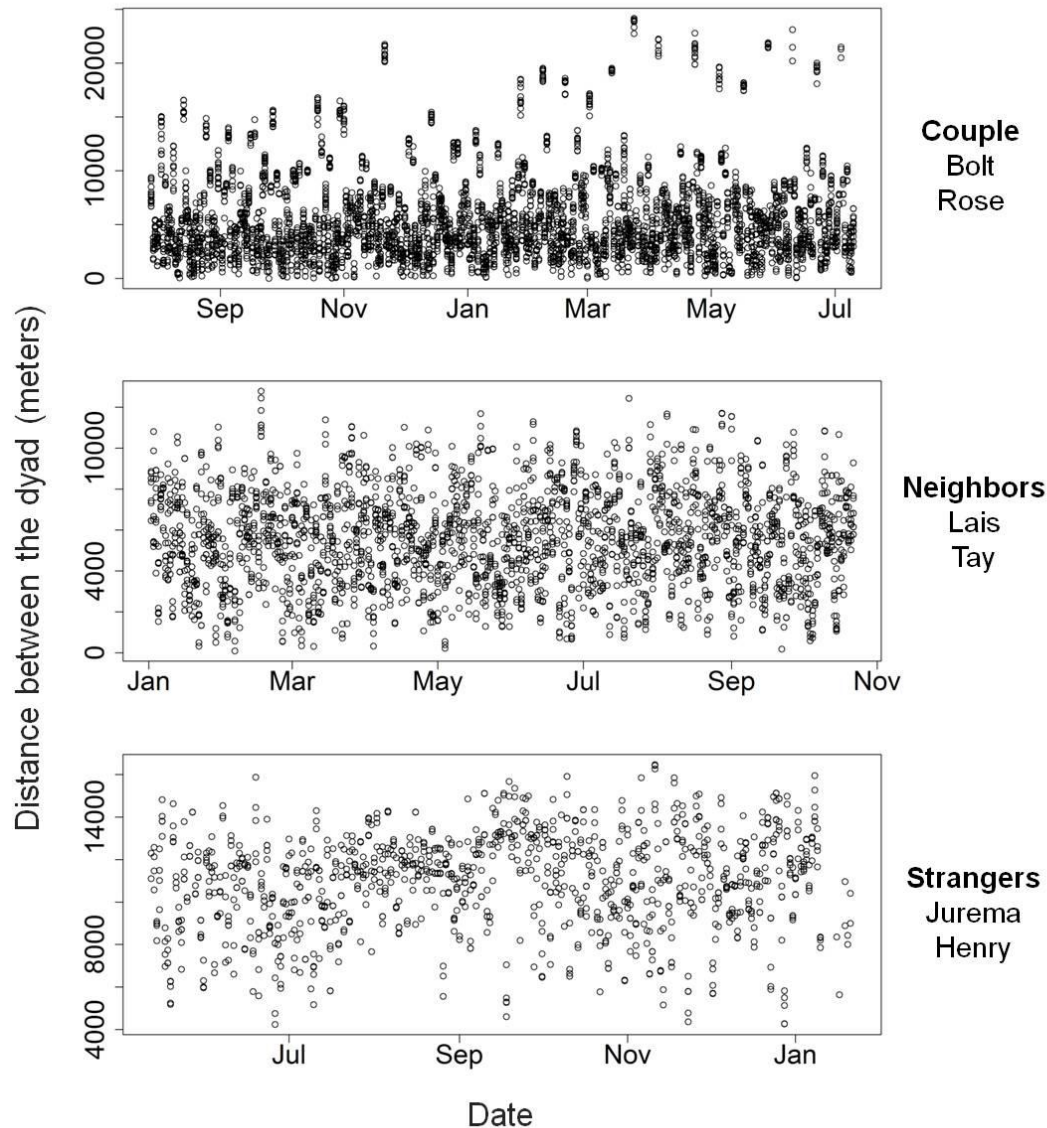


Figure 5. – Distance between the dyads over the period of study: Couple (Bolt and Rose), Neighbors (Lais and Tay) and Strangers (Samurai and Jurema). The y axes indicates the distance between each dyad (in meters) and the x axes indicate the period (months) with a overlap of data collection to the individuals of a dyad. The axes are different to each group.

The results of the generalized additive models (GAMs) showed that there was a significant temporal variation in pairwise distances ($p < 0.001$) for all the dyads studied. To exemplify we shows the plot the GAM distances over all the period of study for the same dyads of each group showed before (couple - Bolt/Rose, neighbors - Lais/Tay and strangers - Jurema/Henry; Figure 6). Similar plots to the other dyads are available at Supplementary Material 4.

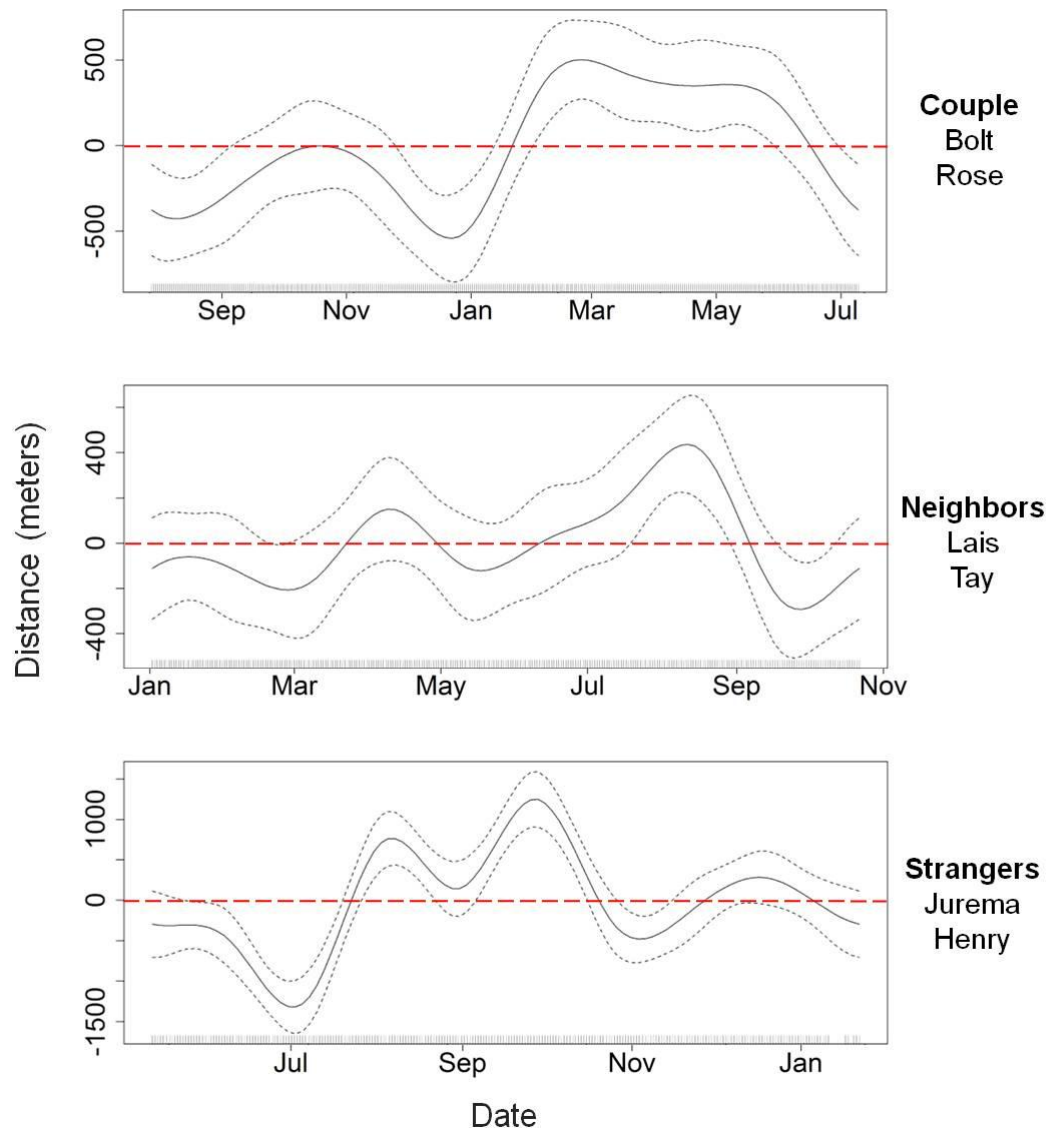


Figure 6. Distance in meters between the dyads over the period of study: Couple (Bolt and Rose), Neighbors (Lais and Tay) and Strangers (Samurai and Jurema). The red line on y axes indicates the mean of the distance between the dyads and the values above and under the red line indicates how much the values are different of the mean. The x axes indicate the period (months) with an overlap of data collection to the individuals of a dyad. The axes are different to each dyad.

Focusing on the couples, pairwise distances shorter than 300 meters were present during all the year, independent of the mating or pup rearing season. However, distances shorter than 50 meters were mainly restricted to these seasons, except for the couple Samurai and Jurema (Figure 7).

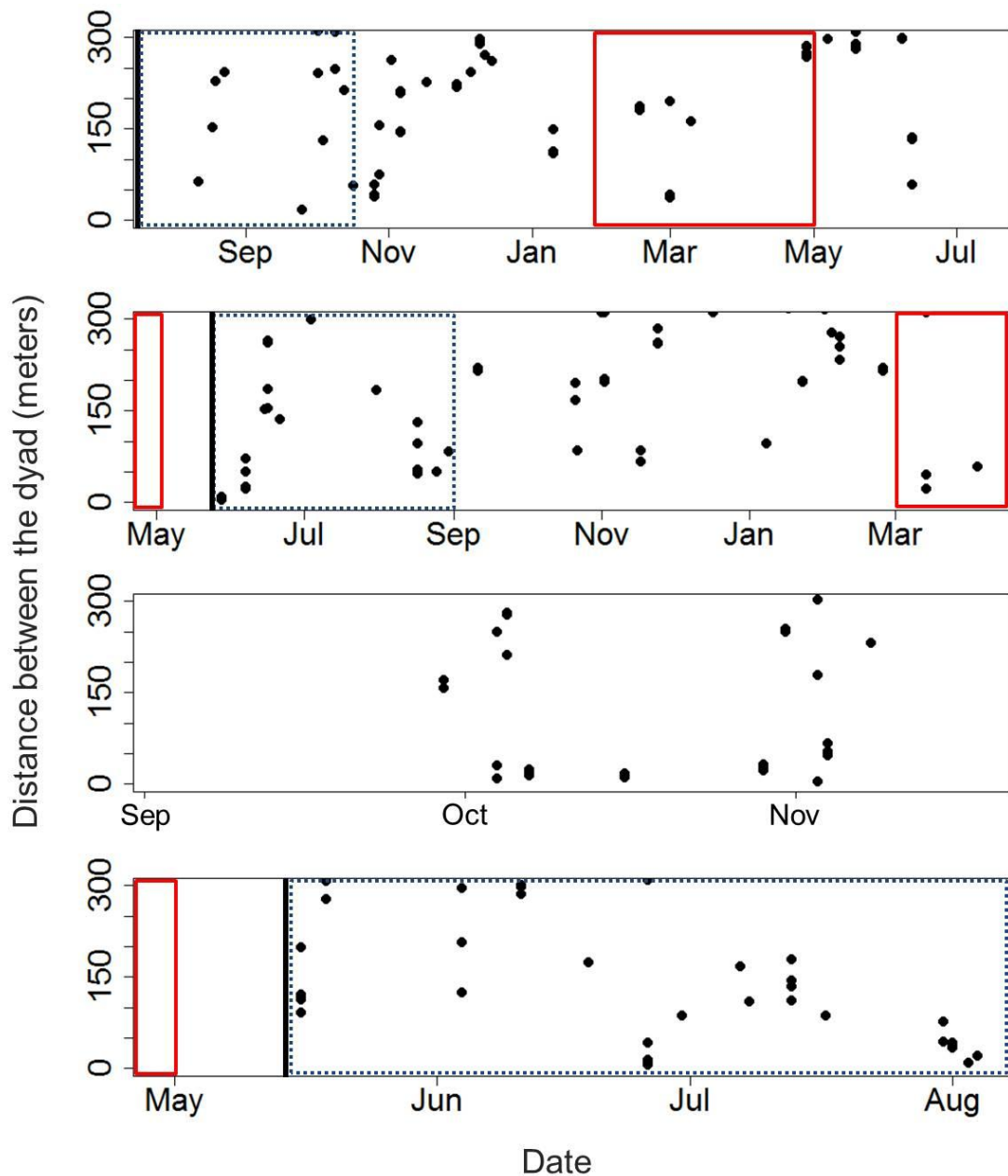


Figure 7. Distance in meters between the couples over the period of study: Bolt/Rose, Amadeo/Lais, Samurai/Jurema and Gamba/Tay. The red box indicates the mating season, the black line indicates the date of birth of a dependent pup (*Paula – personal communication*), and the blue and dashed box indicates the three first months of the pup rearing season. The y axes indicate the pairwise distances of each couple and the x axes indicate the period (months) with a overlap of data collection to both individuals of each dyad. The axes are different for each dyad.

The results of the global dynamic index are presented on table 3. The results for the Azimuth show a weak influence on the angle between the studied dyads, independent of their status. However, the Displacement presents a higher value (>0.6)

for all the dyads, except the couple Bolt and Rose and the strangers Luna and Bolt. The highest values were for neighbors, and to the strangers Jurema and Henry.

Table 3. Results of global dynamic index to all the dyads studied. The displacement has the range between 0 (no interaction) and 1 (positive interaction). The azimuth has a range between -1 (opposing directions) and 1 (same orientations). The Di global is a result of the interaction between the azimuth and the displacement. The Di global has a range between -1 and 1. The bold values indicates stronger interactions.

		Displacement	Azimuth	Global
Couples	Bolt/Rose	0.48	0.02	0.02
	Amadeo/Lais	0.66	0.05	0.06
	Samurai/Jurema	0.65	0.04	0.03
	Gamba/Tay	0.60	0.09	0.08
Neighbors	Amadeo/Tay	0.68	0.12	0.12
	Lais/Tay	0.77	0.04	0.04
	Loba/Bolt	0.86	-0.04	-0.04
Strangers	Jurema/Henry	0.75	0.00	0.00
	Miro/Nilde	0.53	-0.03	-0.01

Discussion

Contact between conspecifics is one of the most important occurrences within an animal life (Kays *et al.*, 2015). Little attention has been directed towards understanding the sociability of solitary species; however studies have found more interactions than expected in several groups, including carnivores (Atwood & Weeks, 2003, Dalerum, 2007; Elbroch *et al.* 2015, 2017).

The results of our study indicate that although maned wolf couples overlap territories, tending to be a temporal difference in territory occupation. Couples present large variations in pairwise distances, which may be a reflection of two related aspects – the size of their home range, as well as the area where they live. Paula (2016) found a strong correlation between the presence of protected areas and the size of the home range for the same individuals analyzed within the current study. In addition to this, we found the minimum, mean and maximum distances to decrease significantly for animals living inside the SCNP when moving in direction of the fragmented areas. All the

couples present short pairwise distances, which was expected as Paula (2016) had found a strong overlap of home ranges (static interaction) between these pairs.

Couples present pairwise distances shorter than 300 meters throughout the year, independently of the season. However, distances shorter than 50 meters were registered mainly during mating and birthing seasons (with the unique exception being the pair living entirely within the fragmented areas – Samurai/Jurema – that were observed in closer proximity to one another in October/November). During the rearing season, the distances varied considerably, but the couples were frequently close to each other. This result agrees with Bandeira de Melo *et al.* (2009) study on a wild maned wolf couple, where they identify the individuals as closer during the period of pup rearing, with the male possibly provisioning food to the female and partaking in territorial marking.

Bandeira de Melo *et al.* (2007) found a high sociability between the couple that frequently rest together, which indicates short pairwise distances. However, our results agree with Dietz (1984) and Jácomo *et al.* (2009) who found a limited sociability between individuals, with few direct interactions in the non-reproductive seasons. It can be an efficient strategy to defend the territories during non-reproductive seasons as both individuals can protect the territories; whereas during the months of pup rearing, the female can provide the main parental care (Bandeira de Melo, 2009) while the male undergoes limited interactions, but promotes the pups/female feeding and protection, in addition to territorial defense.

The neighbors present 2 subgroups, with Amadeo/Tay and Lais/Tay presenting smaller mean distances (at around 5.8 kilometers) than Loba/Bolt (with a mean of 8.3 kilometers). The minimum distances show that the second subgroup possibly never interacts directly, even never getting closer than 0.5 kilometers at one point. The first subgroup present minimum distances shorter than 100 meters in different moments per dyad, indicating a high tolerance between individuals which may be a consequence of lower resource availability. In theory, solitary carnivores should only interact during the reproductive season or in territorial disputes (Hunter, 2011), however, several authors have found evidence that canids share their space and interact more frequently on areas with temporal or spatial variation in critical resources, like food or cover (Atwood & Weeks, 2003; Baker *et al.* 2000).

The dyad Lais/Tay, comprising of two females, presents a looser distribution on their pairwise distances, exhibiting distances less than 1000 meters across the entire year. The months that their pairwise distances exceeded 600 meters for several weeks

were during the pup rearing period (May-October). Furthermore, the maximum distances between this dyad represent the smallest maximum distances of all the neighbors, being around 6 kilometers shorter than the other two dyads, perhaps indicating a higher tolerance between females sharing territory borders. This tolerance could be a consequence of individuals living in a stable territory for a long time, prompting repeated interactions between the same animals (Elbroch *et al.*, 2015, 2017).

The two dyads of strangers present similar patterns, whereby the pair never enters proximity of less than four kilometers of one another, with a mean of around 10 kilometers of distance apart. Although none of the couples or neighbors were registered in the same point, that would indicate a direct interaction, it does not indicate no direct contact. The gap between data collection was from 1 to 4 hours, depending on the dyad, and this closer interaction could have occurred during this time.

The results of the DI-Index analysis show a weak influence of the azimuth to all the dyads, which indicates that one individual is not influencing the direction of movement of the other. However, the displacement provides high values for all the dyads, with the exception of the couple, as well as the strangers living inside the park (Bolt/Rose and Luna/Bolt) who present an interaction just marginally lower. This result indicates that the maned wolves are not affected directly by the movement of their spatial pairs, but instead present similar patterns of movement. This result supports the findings of Paula (2016) who did not find significant differences in the step lengths of the same individuals studied in protected and non-protected areas or between males and females. Atwood (2006) also did not find difference in interactions of seventeen dyads of coyotes between protected and non-protected areas, however, the author highlights that this may be a product of the low sample size used. Although several authors have created theories and methods to assess animal interactions (Bertrand *et al.*, 1996; Kenward *et al.*, 1993; Long & Nelson, 2013; Minta, 1992; Spielgel *et al.* 2016), this area is still new and little is known about how to assess the interactions between wild species (Long, 2015).

Several studies have indicated that human influence may alter maned wolf behavior. Péron *et al.* (2017) showed that maned wolves can change their periodicity accordingly to human presence, which can help them persist in fragmented areas. Paula (2016) shows that movement and home ranges are affected by anthropic effects, with smaller areas of use in fragmented habitats than for the individuals living inside the

park. Tucker *et al.* (2018) study also suggests a high anthropic effect on movement of several species, including the maned wolf.

Within the current study we assess the interactions between dyads of maned wolves using pairwise distances and dynamic interaction methods. The pairwise distances in fragmented areas are shorter than in protected areas, which may have implications on the dispersion of diseases between individuals and increase the chances of agonistic interactions between wolves or wolves and humans. The dyads of the couples overlap territories spatially, but not temporally. The couples have more interactions during mating and pup rearing season, but they can be at short distances during the entire year. A high tolerance between individuals can be exhibited by neighbors can also be inferred, and in relation to the dynamic interactions, we found no evidence for the influence of conspecifics on the direction of movement. However, the displacements are related between dyads, indicating similar patterns of movement.

Our study indicates that maned wolves are solitary, but presents some interactions between couples and a high tolerance between spatially contiguous neighbors and thus provides evidence for a degree of sociality. The landscape use within the home range of maned wolves can influence the length of the pairwise distances, which therefore reflects the impact of human-dominated areas on behavior and movement of this important species. Although maned wolves are a solitary species, we recommend more studies about their social interactions, which may improve planning and conservation of the species and their occupied habitats.

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Supplementary Material - Alves-Eigenheer et al. Coordinated movements of maned wolves (*Chrysocyon brachyurus*) in protected and fragmented landscapes

Supplementary Material 1.Script of all the analysis realized to this study on R 3.4.3

```

# Script Social Behaviour Dyads
# Milene Alves-Eigenheer
# Rogerio Cunha de Paula
# Milton Ribeiro
# Mauro Galetti
# Luca Borger

#Loading workspace and packages
setwd("\\_Your_Dir")
if(!require(adehabitatLT)) install.packages("adehabitatLT", dep=T);library(adehabitatLT)
if(!require(move)) install.packages("move", dep=T); library(move)
if(!require(rgdal)) install.packages("rgdal", dep=T); library(rgdal)
if(!require(wildlifeDI)) install.packages("wildlifeDI", dep=T); library(wildlifeDI)
if(!require(dplyr)) install.packages("dplyr", dep=T); library(dplyr)
if(!require(foreign)) install.packages("foreign", dep=T); library(foreign)
if(!require(mgcv)) install.packages("mgcv", dep=T); library(mgcv)
if(!require(date)) install.packages("date", dep=T); library(date)
if(!require(bbmle)) install.packages("bbmle", dep=T); library(bbmle)
if(!require(png)) install.packages("png", dep = T); library(png)
if(!require(xlsx)) install.packages("xlsx", dep=T); library(xlsx)
if(!require(png)) install.packages("png", dep = T); library(png)

#Load data -
mw_original <- read.table("MW_original.csv", header = T, sep = ";")

# Converting coordinates (lat-long --> utm)
xy<- cbind(mw_original$location.long, mw_original$location.lat)
# Convert it to UTM coordinates (in units of meters)
xy2 <- project(xy, "+proj=utm +datum=WGS84 +zone=23 +south +ellps=WGS84
+towgs84=0,0,0")
colnames(xy2)<-c("x","y")
head(xy2)
mw<- data.frame(xy2, mw_original$timestamp, mw_original$individual.local.identifier)
colnames(mw)<-c("x","y","timestamp","id")
head(mw)

# Removing NAs from my data bank and reorganizing
mw<-mw[complete.cases(mw),]
mw<- data.frame(mw$x, mw$y, mw$timestamp, mw$id)
colnames(mw)<-c("x","y","timestamp","id")

```

```

# Agrupping by id using lists
ind_list <- split(mw, mw$id)
amadeo<-ind_list[[1]]
bolt<-ind_list[[2]]
gamba<-ind_list[[3]]
henry<-ind_list[[4]]
jurema<-ind_list[[5]]
lais<-ind_list[[6]]
loba<-ind_list[[7]]
luna<-ind_list[[8]]
miro<-ind_list[[9]]
nilde<-ind_list[[10]]
rose<-ind_list[[11]]
samurai<-ind_list[[12]]
tay<-ind_list[[13]]

# Couples: Amadeo + Lais, Tay + Gamba, Samurai + Jurema, Bolt + Rose
# Neighbors: Amadeo + Tay, Lais + Tay
# Dyads: Tay + Samurai, Tay + Jurema, Jurema + Henry, Miro + Nilde
#           Loba + Luna, Loba + Bolt, Luna + Bolt

#####
##### GAM #####
#####

#####
##### ind_Y + ind_X #####
#####

# Converting data Ind_Y/julian days
ind_Y$yearmonthday<-as.numeric(paste(substr(ind_Y$timestamp,7,10),
      substr(ind_Y$timestamp,4,5),substr(ind_Y$timestamp,1,2),sep=""))
ind_Y$year<-as.numeric(substr(ind_Y$timestamp,7,10)) #year
ind_Y$month<-as.numeric(substr(ind_Y$timestamp,4,5)) #month
ind_Y$day<-as.numeric(substr(ind_Y$timestamp,1,2)) #day
ind_Y$julian<-mdy.date(ind_Y$month, ind_Y$day, ind_Y$year)

# Converting data Ind_X/julian days
ind_X$yearmonthday<-as.numeric(paste(substr(ind_X$timestamp, 7, 10),
      substr(ind_X$timestamp,4,5),substr(ind_X$timestamp,1,2),sep=""))
ind_X$year<-as.numeric(substr(ind_X$timestamp,7,10))
ind_X$month<-as.numeric(substr(ind_X$timestamp,4,5))
ind_X$day<-as.numeric(substr(ind_X$timestamp,1,2))
ind_X$julian<-mdy.date(ind_X$month, ind_X$day, ind_X$year)

# plotting to see the overposition
ind_X$couple=0

```

```

ind_Y$couple=1
plot(couple~julian, data=ind_Y, ylim=c(0,1), xlab="Date", ylab="",
      main="Periodicity of locations")
points(couple~julian, data=ind_X, col="red")

# Subsetting both at the same period
ind_Y.subset<-subset(ind_Y, select=c(couple,julian,yearmonthday, y, x))
ind_X.subset <-subset(ind_X, select=c(couple,julian,yearmonthday, y, x))
data.ind_Y.ind_X<-data.frame(rbind(ind_Y.subset, ind_X.subset))

#order by data
data.ind_Y.ind_X.ord<-data.ind_Y.ind_X[order(data.ind_Y.ind_X$julian) ,]
data.ind_Y.ind_X.ord$posicao<-1:nrow(data.ind_Y.ind_X.ord)

# Subsetting the clumped data
## female
ind_X.ini <- min(subset(data.ind_Y.ind_X.ord, couple==0)$posicao)
ind_X.fim <- max(subset(data.ind_Y.ind_X.ord, couple==0)$posicao)
## male
ind_Y.ini <- min(subset(data.ind_Y.ind_X.ord, couple==1)$posicao)
ind_Y.fim <- max(subset(data.ind_Y.ind_X.ord, couple==1)$posicao)
##initial and final to both
ind_Y.ind_X.ini <- max(ind_X.ini, ind_Y.ini)
ind_Y.ind_X.fim <- min(ind_X.fim, ind_Y.fim)

## ordenaded junction
data.ind_Y.ind_X.ord.match = subset(data.ind_Y.ind_X.ord,
                                   posicao>=ind_Y.ind_X.ini)
data.ind_Y.ind_X.ord.match = subset(data.ind_Y.ind_X.ord.match,
                                   posicao<=ind_Y.ind_X.fim)

## junction of both with x and y
data.ind_Y.ind_X.ord.match$y <-as.numeric(data.ind_Y.ind_X.ord.match$y)
data.ind_Y.ind_X.ord.match$x<-as.numeric(data.ind_Y.ind_X.ord.match$x)
data.ind_Y.ind_X.ord.match$julian<-
                                   as.numeric(data.ind_Y.ind_X.ord.match$julian)

# Ploting the earlier steps
cols=c("red", "black")
ind_Y.ind_X.junction<-plot(couple~as.Date(julian, origin="2007-05-04"),
                           data=data.ind_Y.ind_X.ord.match, ylim=c(0,1),
                           col=data.ind_Y.ind_X.ord.match$couple+1,
                           main="Ind_X + Ind_Y")
legend("bottomright", legend=c("Ind_Y", "Ind_X"),col=cols, cex=1.5, bty="n", lwd=3,
      lty=1)

ind_Y.ind_X.junction.overlap<-plot(y~x, data=data.ind_Y.ind_X.ord.match,
                                   col=data.ind_Y.ind_X.ord.match$couple+1,

```

```

pch=19, main="GPS points Ind_X + Ind_Y")

## female
ind_X_before_y<-0
ind_X_before_x<-0
##male
ind_Y_before_y<-0
ind_Y_before_x<-0

ind_Y.cum<-NULL
ind_X.cum<-NULL
pair.ind_Y.ind_X.dist<-NULL

### Calculating the distances plotting the movement of the individuals
mov.ind_Y.ind_X<-
for (i in 1:nrow(data.ind_Y.ind_X.ord.match))
{
plot(y~x, data=data.ind_Y.ind_X.ord.match, col="grey60", cex=0.1)
aux<-data.ind_Y.ind_X.ord.match [i,]
if (length(ind_Y.cum)>0)
if (length(ind_X.cum)>0)
points(y~x, data=aux, pch=19, col=aux$couple+1, cex=2.3)
if (aux$couple==1)
{
ind_Y_before_y<-aux$y
ind_Y_before_x<-aux$x
ind_Y.cum<-data.frame(rbind(ind_Y.cum, aux))
}
if (aux$couple==0)
{
ind_X_before_y<-aux$y
ind_X_before_x<-aux$x
ind_X.cum<-data.frame(rbind(ind_X.cum, aux))
}
points(ind_Y_before_x, ind_Y_before_y, pch=19, col=1, cex=2.3)
points(ind_X_before_x, ind_X_before_y, pch=19, col=2, cex=2.3)
pair.ind_Y.ind_X.dist<-c(pair.ind_Y.ind_X.dist,
sqrt((ind_Y_before_y-ind_X_before_y)^2 +
(ind_Y_before_x-ind_X_before_x)^2) )
}

pair.ind_Y.ind_X.dist.fim<-subset(pair.ind_Y.ind_X.dist,
pair.ind_Y.ind_X.dist<30000)

# Data range
range(as.Date(data.ind_Y.ind_X.ord.match$julian, origin="1960-01-01"))

```



```
# plot pairwise distances over time. Given the way pair.dist is calculated, take only first
part, as it is repeated for each of the two individuals
```

```
femDats.ind_Y.ind_X <- which(data.ind_Y.ind_X.ord.match$couple==0)
```

```
# Plotting GAM distribution of the distances between individuals
```

```
gam.ind_X.ind_Y<-
  gam(pair.ind_Y.ind_X.dist.fim[femDats.ind_Y.ind_X]~s(data.ind_Y.ind_X
    .ord.match$julian[femDats.ind_Y.ind_X] ,bs="cc"))
summary(gam.ind_X.ind_Y)
plot(gam.ind_X.ind_Y, residuals=FALSE, main="GAM Ind_X - Ind_Y",
xlab="Date", cex.lab=2,cex.axis=2)
residuals(gam.ind_X.ind_Y)
```

```
# plotting distances in all the year
```

```
plot(pair.ind_Y.ind_X.dist.fim[femDats.ind_Y.ind_X] ~
  as.Date(data.ind_Y.ind_X.ord.match$julian[femDats.ind_Y.ind_X],
  origin="1960-01-01"), main="Distances over the period Ind_X + Ind_Y",
  cex.lab=2,cex.axis=2,xlab="Date", ylab="Distance (meters)")
```

```
# plotting shorter distances in all the year
```

```
plot(pair.ind_Y.ind_X.dist.fim[femDats.ind_Y.ind_X] ~
  as.Date(data.ind_Y.ind_X.ord.match$julian[femDats.ind_Y.ind_X],
  origin="1960-01-01"), main="Distances over the period Ind_X + Ind_Y",
  cex.lab=2,cex.axis=2,xlab="Date", ylab="Distance (metters)",
  ylim=c(0,300), pch=20, cex=2)
```

```
### Do the same to all the dyads (couples, neighbors and strangers)
```

```
#### # Kernel Density Plots
```

```
c1<-density(pair.ind_Y.ind_X.dist.fim) # returns the density data
plot(c1, lwd=3, col="slateblue4", xlim=c(0,30000),ylim=c(0,0.000250),
  cex.lab=2,cex.axis=2, xlab="Distance between the Dyad (metters)",
  ylab="Density", main="")
abline(v=seq(0,30000,5000), col='grey', lty='dotted')
legend("topright", legend=c("Ind_Y / Ind_X"), col=c("slateblue4"),
  lty=1:1, lwd=3, cex=2, box.lwd = 0,box.col = "white",bg = "white")
```

```
# Boxplot graphs to summarize results
```

```
bp1<-summary(pair.ind_Y.ind_X.dist.fim)
sd(pair.ind_Y.ind_X.dist.fim)
boxplot(bp1, #(bp2,bp3...bpn #depending on how much dyads will be analyzed
  xlab="Dyads", ylab="Distance (meters)", log="y")
axis(1,labels=c("Ind_Y / Ind_X"))
```

```
#####
##### DI-INDEX #####
#####
setwd("\\_Your_Dir")
if(!require(adehabitatLT)) install.packages("adehabitatLT", dep=T);library(adehabitatLT)
if(!require(rgdal)) install.packages("rgdal", dep=T); library(rgdal)
if(!require(wildlifeDI)) install.packages("wildlifeDI", dep=T); library(wildlifeDI)
if(!require(dplyr)) install.packages("dplyr", dep=T); library(dplyr)
if(!require(foreign)) install.packages("foreign", dep=T); library(foreign)
if(!require(mgcv)) install.packages("mgcv", dep=T); library(mgcv)
if(!require(date)) install.packages("date", dep=T); library(date)
if(!require(bbmle)) install.packages("bbmle", dep=T); library(bbmle)
if(!require(png)) install.packages("png", dep = T); library(png)
if(!require(xlsx)) install.packages("xlsx", dep=T); library(xlsx)

#Carregando dados
lobos_total<-read.table("MW_original.csv", header=T, sep=";")
head (lobos_total)

#convertendo lat long em utm
#Make a two-column matrix, col1 = long, col2 = lat
xy<- cbind(lobos_total$location.long, lobos_total$location.lat)
# Convert it to UTM coordinates (in units of meters)
xy2 <- project(xy, "+proj=utm +datum=WGS84 +zone=23 +south +ellps=WGS84
+towgs84=0,0,0")
colnames(xy2)<-c("x", "y")
head(xy2)

lobos<-data.frame(xy2, lobos_total$timestamp, lobos_total$individual.local.identifier)
colnames(lobos)<-c("x", "y", "timestamp", "id")
lobos<-lobos[complete.cases(lobos),]

# Removing duplicated data
duplicated(paste(da, lobos$id))
duplicate_indexes <- which(duplicated(paste(da, lobos$id)),)
duplicate_indexes
#dataset without the duplicates:
lobos<- lobos[!duplicated(paste(da, lobos$id)),]
nrow(lobos)

# Converting date e time
da<- paste(lobos$timestamp)
da1<- as.POSIXct(strptime(da, format="%d/%m/%Y %H:%M", tz="America/Bahia"))

# Bursts
id<- lobos$id
```

```
bursts<- lobos$id

# Data
path<- as.ltraj(xy = lobos[,c("x", "y")], date = da1, id = id,
burst=bursts, typell=T)

path
path.df <- ld(path)
plot(path)

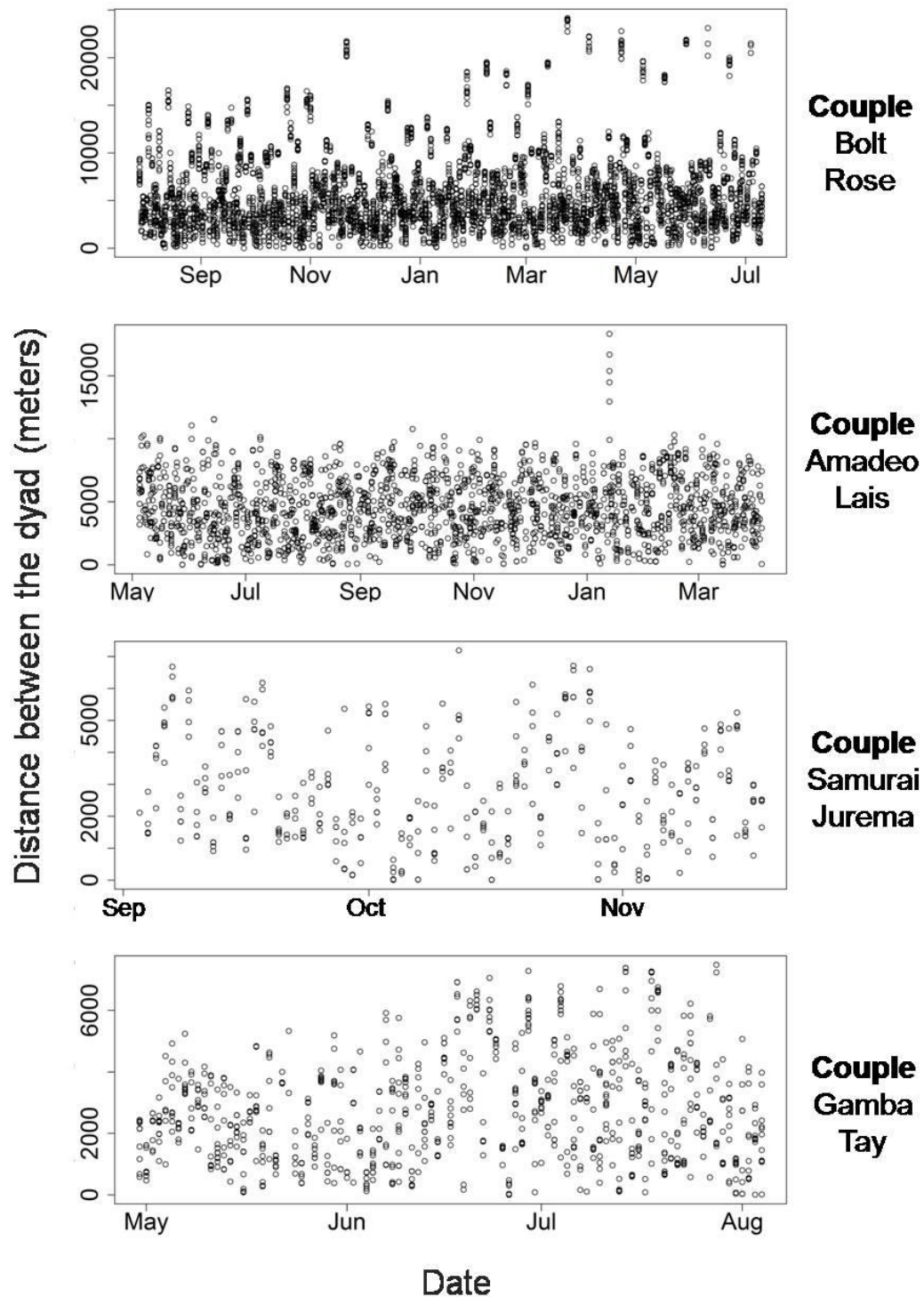
ind_Y<-path[1,]
ind_X<-path[2,]
#do it t all the individuals

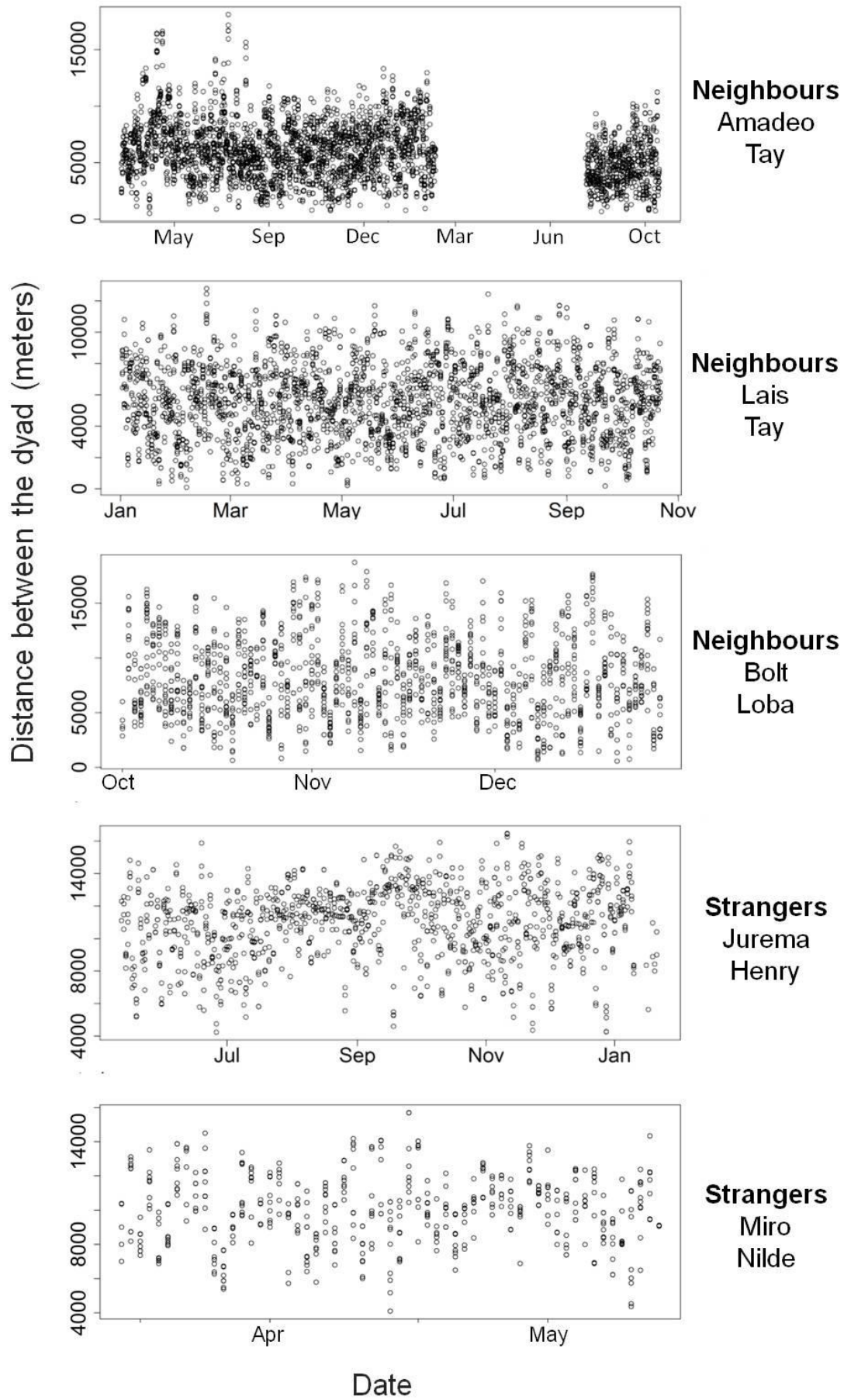
### DI - INDEX
GetSimultaneous(ind_Y, ind_X, tc = 240*60)
di.global.ind_Y.ind_X <- DI(ind_Y, ind_X, tc = 240*60, alpha = 3, local = FALSE,
TimeWeight = TRUE, DistWeight = FALSE)
di.ind_Y.ind_X <- DI (ind_Y, ind_X, tc = 240*60, alpha = 3, local = TRUE,
TimeWeight = TRUE, DistWeight = FALSE)
plot(di.ind_Y.ind_X$date,di.ind_Y.ind_X$di, type="l")
plot(di.ind_Y.ind_X$date,di.ind_Y.ind_X$di.theta, type="l")
plot(di.ind_Y.ind_X$date,di.ind_Y.ind_X$di.d, type="l")
```

Supplementary Material 2. Pairwise distances to all the dyads studied.

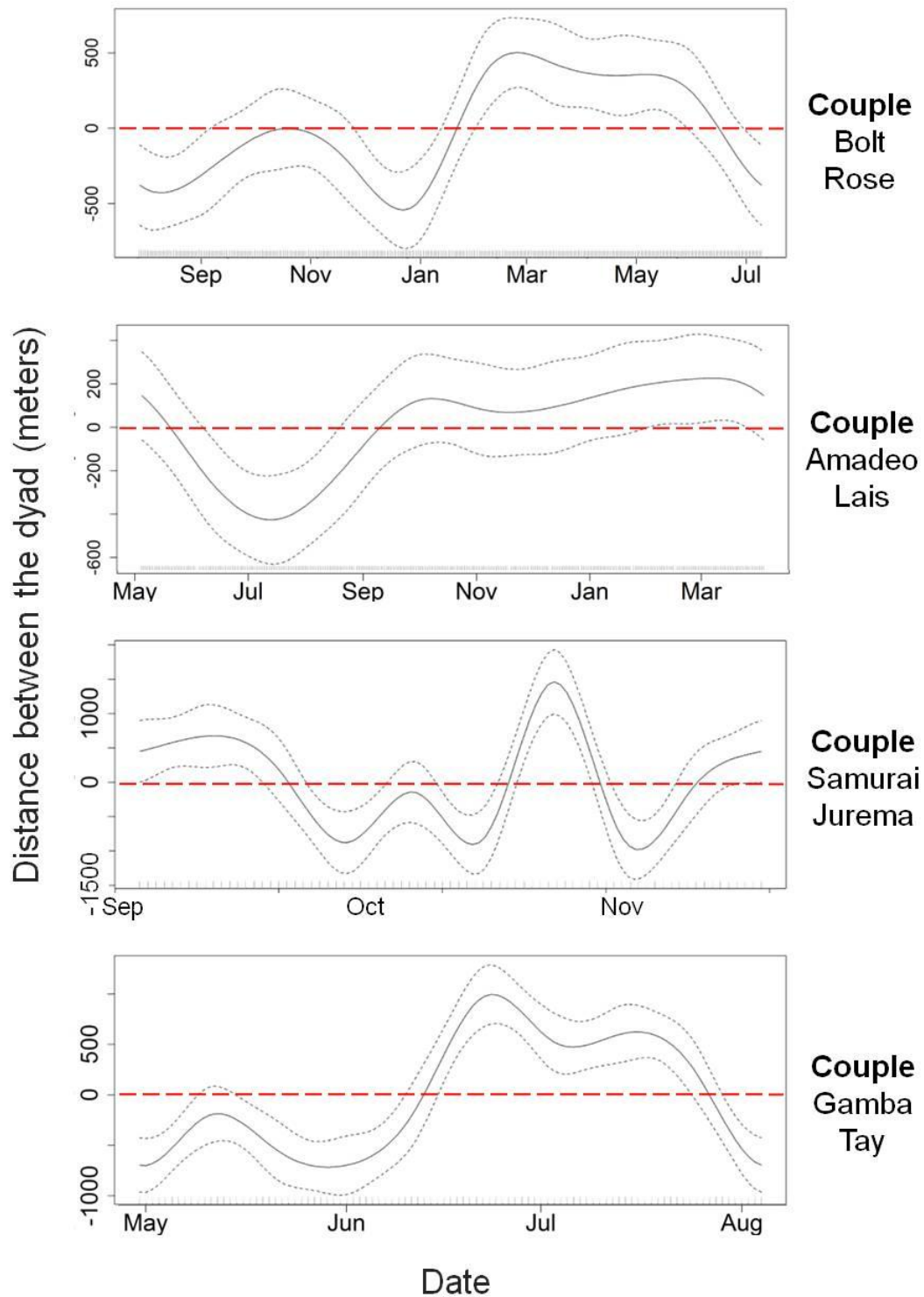
		Min	Median	Max	Mean	Sd
Couple	Bolt/Rose	12.28	4938	24160	6048	4417
	Amadeo/Lais	2.99	4376	18320	4523	2461
	Samurai/Jurema	3.37	2529	8200	2824	1693
	Gamba/Tay	4.83	2442	7474	2704	1710
Neighbors	Amadeo/Tay	87.12	5740	19130	5932	2523
	Lais/Tay	97.95	5708	12780	5726	2324
	Loba/Bolt	565.5	7881	19060	8280	3616
Strangers	Jurema/Henry	4243	11170	16720	10900	2229
	Miro/Nilde	4100	10120	16250	10030	2028

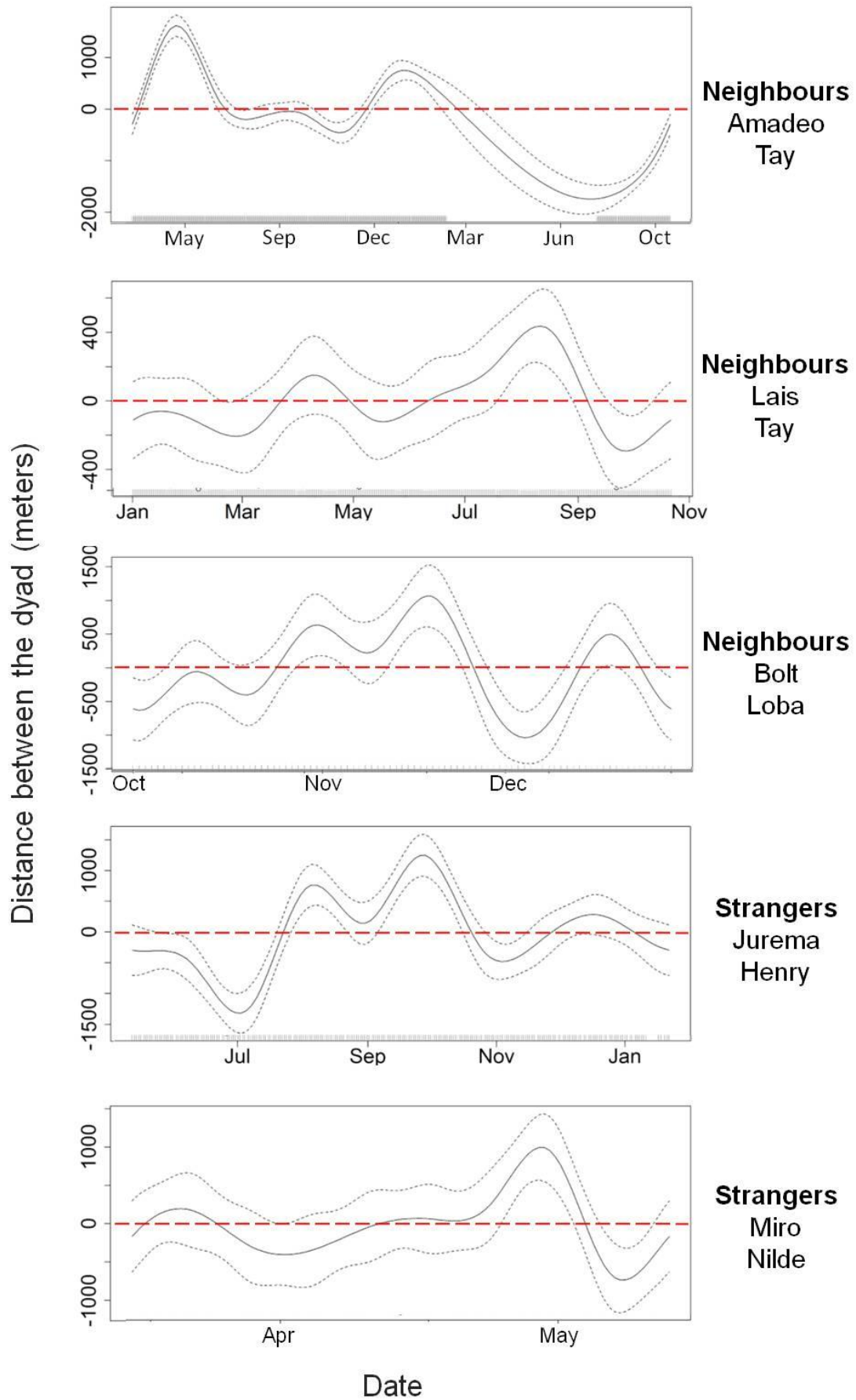
Supplementary Material 3. Pairwise distance plots over the period of study to all the studied dyads. The y axes indicates the distance between each dyad (in meters) and the x axes indicate the period (months) with a overlap of data collection to the individuals of a dyad. The axes are different to each dyad.





Supplementary Material 4. GAM plots of pairwise distances over the period of study to all the studied dyads. The red line on y axes indicates the mean of the distance between the dyads and the values above and under the red line indicates how much the values are different of the mean. The x axes indicate the period (months) with a overlap of data collection to the individuals of a dyad. The axes are different to each dyad.





Chapter 3

Effects of frugivores canids on the seed dispersal and spatial distribution of *Solanum lycocarpum* in a Brazilian savanna

To be submitted to PlosOne

Milene Alves-Eigenheer, Carly Vynne, Mariana Madeira, Leandro Silveira, Thomas Arkwright, Mauro Galetti and Milton Cezar Ribeiro

Keywords: Mutualism, Landscape Ecology, *Chrysocyon brachyurus*, *Cerdocyon thous*, Cerrado.

Abstract

Frugivore canids are an important group of seed dispersers, once they often consume large amounts of fruit and may be responsible for the seed shadow of many animal-dispersed plant species. However, their role as seed-dispersers remains relatively unexplored. We tested the role of two canid frugivore species – maned wolf (*Chrysocyon brachyurus*) and crab-eating fox (*Cerdocyon thous*) – on the seed dispersal and spatial distribution of *Solanum lycocarpum*, a large fruit dispersed by few species. We also assessed the importance of this fruit to these canid species in habitats where less plant resource is available. Samples of maned wolves' and crab-eating foxes' feces, besides spatial location of *Solanum* trees, were collected in the period 2004-2008 in Ema's National Park and its surroundings (central Brazil), a mosaic-like landscape with different microhabitats for such species. Part of the feces samples was used to organize a data bank of presence/absence of *Solanum* and other seeds, while the other part was used on a data bank integrating the counting of seeds and spatial location of feces samples and lobeira trees. All the samples had the species identified by DNA analysis. Our results shown that maned wolves disperse more seeds than crab-eating foxes and both animals consume *S. lycocarpum* mainly in human-altered areas, where less other fruit resources are available. We also found that the distribution of *Solanum* trees is explained by maned wolf scats, that disperse *S. lycocarpum* seeds throughout the study area, while crab-eating foxes select areas close to the border of the park. Within this study, we showed the differences in the role of these two carnivores on seed dispersal and spatial distribution of a plant species.

Introduction

The role of frugivores on seed dispersal

Several facets played by frugivores have been highlighted to favor plant fitness. Removing seeds from the high mortality zone near the maternal plant, increasing germination rate, moving the seeds to favorable sites, and promoting gene flow via seed dispersal are some of the few direct examples of how frugivores increase the chances of plant's survival (Herrera, 1985; Jordano *et al.*, 2007). This is particularly important in tropical regions, where most of the plant species are dispersed by animals (Almeida-Neto *et al.*, 2008).

Frugivores may determine the spatial distribution of the plants they feed on (Jordano *et al.*, 2007). However, it is hard to tease apart the role of each species on the spatial distribution these plants. Fleshy fruit species are eaten by several species with distinct feeding behaviors and mobility ability, which can result in seed deposition in different microhabitats spread within species home ranges. For instance, 78% of Neotropical fruits are eaten by birds and mammals, and the species that compose these groups provided distinct spatial distribution of seeds (Almeida-Neto *et al.* 2008).

Frugivore canids often consume large amounts of fruit and may be responsible for the seed shadow of many animal-dispersed plant species, however their role as seed-dispersers remains relatively unexplored. These species generate seed rain patterns that capture their foraging and post-feeding movements, therefore, sites chosen for patrolling or territorial marking receives a disproportionate number of seeds (Jordano *et al.*, 2007; González-Varo *et al.*, 2013). In addition, movement in heterogeneous landscapes imposes markedly non-random patterns of seed rain among distinct microhabitat types (García *et al.*, 2009). Canids are important seed dispersers for fruits of the Cerrado vegetation—a Brazilian like savanna— as they do not possess physiological adaptations for digesting cellulose. As seeds pass through the canids gut largely intact —they exhibit limited mastication during consumption—seed damage rate are low (Juarez & Marinho-Filho, 2002).

The expectation of non-random seed dispersal is particularly likely in a tightly-coupled system where a plant species may have limited dispersers and when movement of dispersers may be limited by natural (territoriality) or human-induced causes (habitat fragmentation) (Mack, 1995; Lehouck *et al.*, 2009). Whereas fleshy fruits may be dispersed by a myriad of frugivores, making it hard to tease apart a given disperser's

role on plant spatial distribution, large fruits have a smaller assemblage of potential dispersers (Wheelwright, 1985).

The wolf-fruit and its relation with frugivore canids

One of these large fruit species is *Solanum lycocarpum* (Solanaceae), which is common throughout the Brazilian savanna region known as the Cerrado. Also known as “lobeira” or “wolf-fruit”, *S. lycocarpum* is a conspicuous plant in the Cerrado, where it occurs in natural areas, pastures, and at in natural remnants immerses within agricultural landscapes. This species in central Brazil display both arborous and shrub shapes, attaining 4 meters in height. Their green, hairy, spheroidal fruits are produced year round, weigh up to 750 g and produce an average of more than 500 suboval, black seeds per fruit (Lombardi & Motta-Junior, 1993). The fruits lose their pilosity becoming distinctly aromatic while also changing to dark green and yellow color, dropping to the ground upon ripening (Lombardi & Motta-Junior, 1993; Pinto *et al.*, 2007).

Three canids and a ungulate frugivores are the main consumers of *S. lycocarpum*: maned wolf (*Chrysocyon brachyurus*) (Silva & Talomoni, 2003; Santos *et al.*, 2003; Bueno & Motta-Junior, 2009), crab-eating fox (*Cerdocyon thous*) (Juarez & Marinho-Filho, 2002, Bueno & Motta-Junior, 2004), hoary fox (*Lycalopex vetulus*) (Dalponte & Lima, 1999; Bueno & Motta-Junior, 2004; Jácomo *et al.* 2004) and tapir (*Tapirus terrestris*) (Pinto, 1998). While single fruit-disperser systems in nature are rare (Bascompte & Jordano, 2007), the maned wolf – *S. lycocarpum* relationship is more closely associated.

Fruits of *S. lycocarpum* are an important food source for maned wolves, the largest canid in South America (Dietz, 1984; Motta-Junior & Martins, 2002). *S. lycocarpum* fruits year round and is reported to make up between 3.4% and 53.5% of total occurrence in maned wolf scat samples (Bueno & Motta-Junior, 2004, 2009; Juarez & Marinho-Filho, 2002; Motta-Junior & Martins, 2002; Santos *et al.*, 2003; Silva & Talomoni, 2003), with highest occurrence in dry seasons when other fruits are less available. Since *S. lycocarpum* presents successful growth and development in unfavorable ambient conditions, such as water stress, acidic soils, and nutrient-poor soils (Vida, 1999) and occurs in degraded areas, *S. lycocarpum* provide a potential alternative food source that may enable the maned wolf to persist where food otherwise scarce.

The effective seed dispersal of wolf-fruit by maned wolf is balanced by benefits to the animal, beside the feeding of *C. brachyurus*, this fruit might help to inhibit the effect of parasites, like *Dyoctophyma renale* (giant kidney worm), a nematode that frequently kill the maned wolf and other carnivores (Silveira, 1969). Fruit species consumed by the wolves have most seeds unharmed after passing through the wolf's gut and also enhance germination (Motta-Junior and Martins 2002; Santos *et al.*, 2003). Therefore, the wolves' treatment of *S. lycocarpum* seeds may be necessary to remove compounds in the fruit pulp that inhibit germination (Santos *et al.*, 2014).

The crab-eating fox is also an important seed disperser of *S. lycocarpum* (Bueno & Motta-Junior, 2004; Jácomo *et al.*, 2004; Emmons, 2012). This frugivore canid has both a large home range and geographical range and high relative abundance in fragmented and disturbed landscapes, where the plant is also observed to inhabit (Lorenzi, 1998; Juarez & Marinho-Filho, 2002; Courtenay & Maffei, 2004; Oliveira *et al.*, 2004; Lessa *et al.*, 2012). The niche overlap between the maned wolf and crab-eating fox has been recognized within the literature, which poses these species as having sympatric complementary importance on seed dispersal of *S. lycocarpum* (Juarez & Marinho-Filho, 2002).

Ants are likely only moving seeds by a few meters – 3.4 meters dispersal distance was recorded by Pinto (1998) – although they tend to associate with the seeds primarily as seed predators and in transporting seeds to the nest for use in fungal cultivation, leaving few of the collected seeds to achieve germination (Tavares *et al.*, 2016). Equally so, rodents are seed removers of *S. lycocarpum*, despite the interactions being primarily for the purpose of predation, seed caching behavior can create secondary seed dispersal opportunities for large fruit species (Briani & Guimarães, 2007; Jansen *et al.*, 2012; Rocha-Ortega *et al.*, 2017).

Considering the consumers of *S. lycocarpum* fruits and its potential to test the role of canid frugivores species on the distribution of fruiting plants, we investigated the effects of maned wolves and crab-eating foxes on the seed dispersal and spatial distribution of adult *Solanum lycocarpum*. In particular, we tested the following hypotheses:

- (1) Maned wolves disperse more seeds of *S. lycocarpum* than do crab-eating foxes;
- (2) Maned wolves and crab-eating foxes consume *S. lycocarpum* mainly in habitats where less other fruit resources are available;
- (3) The distribution of adult *S. lycocarpum* plants is explained by maned wolf scats.

Understanding the relationships among diet, seed dispersal, and spatial heterogeneity is an important contribution to the general goal of linking the aspects of organisms to population and community dynamics and an improved ecological understanding.

Methods

Study region and field survey

Our study site was located in a mosaic-like landscape with physiognomically distinct vegetation patches and soil types (hereafter microhabitats) in and around Emas National Park, located in the center-west region of Brazil (18°6'S, 52°55'W). The Park covers 1320 km² and is surrounded by soya and corn plantations, therefore the total study area is 4000 km². The Park is considered one of the most important protected areas of the Cerrado biome. Cerrado comprises 21% of Brazil and is the world's largest, richest, and possibly most threatened tropical savanna (Silva & Bates 2002). Our study region protects large tracts of grassland plains (97%), small patches of shrublands (1%), and marshes and riparian forest (2%) (Figure 1). See below more information regarding the search quadrats that appears on the figure.

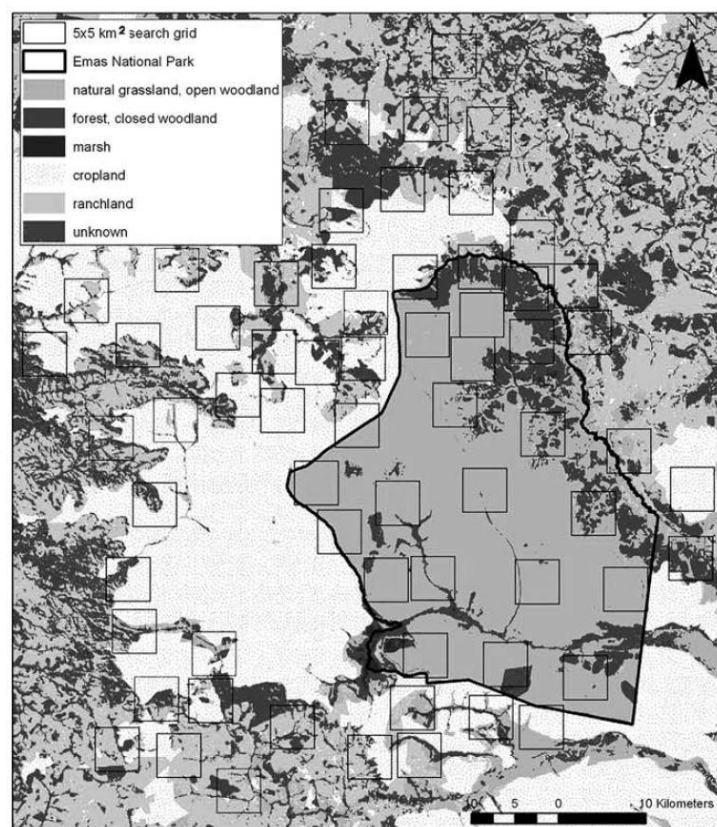


Figure 1. Land cover and land use at Emas National Park and surrounds – Brazil. The squares refer to the 57 search quadrats sites visited between 2004 and 2008 for collection of maned wolves and crab-eating foxes scats, and to register the spatial location of *Solanum* trees (Vynne *et al.*, 2014).

Organization of datasets

The current study integrates data of four different groups of data collected between 2004 and 2008 within the study area that incorporated similar methods:

Dataset 1: records of presence/absence of primary and secondary contents (*Solanum* or other fruits seeds, bones, fur, feathers, etc) within feces collected from 2004 to 2008 and with spatial precision at search quadrats;

Dataset 2: detailed identification of food items in feces collected from 2004 to 2006 and with spatial precision at search quadrats;

Dataset 3: seed counting, where all the samples collected from 2006 to 2008 were georeferenced using GPS;

Dataset 4: spatial location information of all the adult individuals of *S. lycocarpum* that were found on sampling sites.

To test the occurrence of *S. lycocarpum* in the feces of maned wolves and crab eating foxes, we constructed a unique table of food items using presence/absence data from the three original groups of data (dataset 1, 2 and 3, n=1055, 267 and 787 samples to foxes and wolves, respectively). To test whether the number of seeds dispersed differs between the canid species, as well to test the habitats where the *Solanum* seeds are dispersed, we only used the datasets 3 and 4, which comprises seed counts (n=361, 56 and 305 samples to foxes and wolves, respectively) and spatial location of scat samples and *Solanum* trees.

The Figure 2 presents a schematic representation of the data organization.

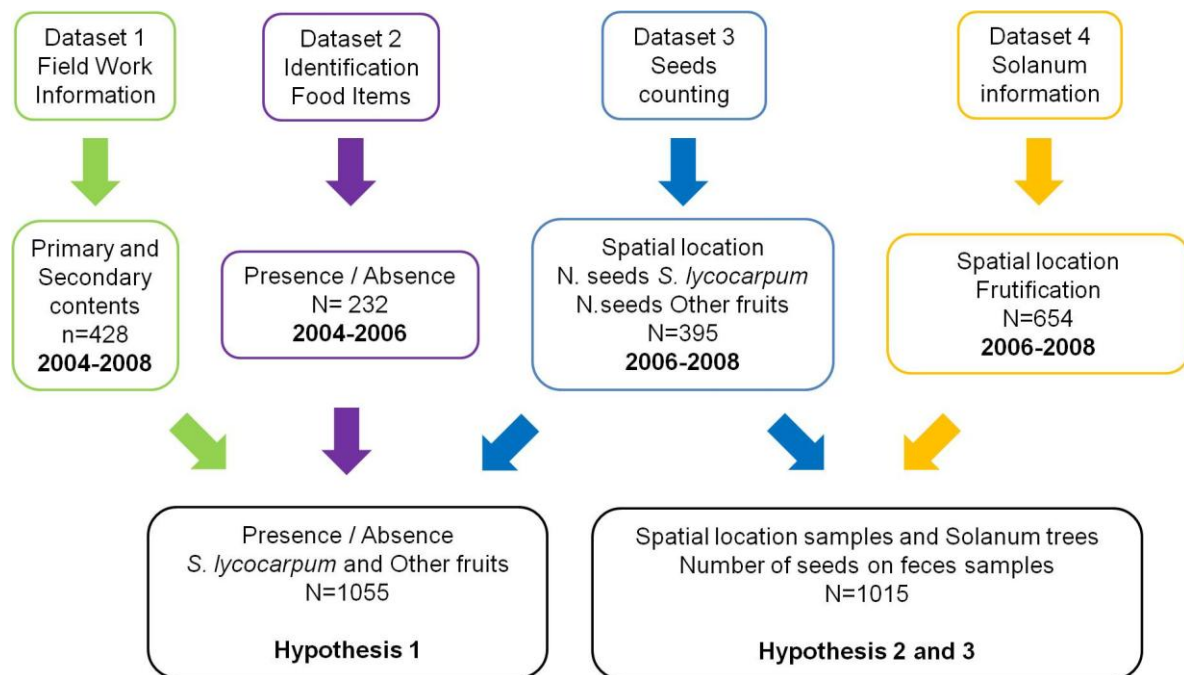


Figure 2. Diagram explaining the organization of the databank used on this study. Three different kinds of information were used to build a unique presence/absence measure of fruits identified in maned wolf and crab-eating fox scats. Two datasets were merged into a unique databank, integrating information on identification/counting of seeds per sample and spatial location of feces samples and Solanum trees. The first line of boxes indicates the origin of the data, the second line present details on information of each dataset, the number of samples collected and the period of collection and the third line indicates the information present on each final databank, as well as the hypothesis that were tested to it.

Collection of samples and marking of plants

The sample sites includes 57 search quadrats of 5X5km (Figure 1), which were visited by one to three scat detection teams (a trained dog according to the method of Wasser *et al.* (2004), a dog-handler and a field assistant), totalizing 415 transects. The quadrats were predetermined arbitrarily to maximize collection efforts in areas consisting of different types of vegetation and land use. Each square was visited by the teams who collecting canid scats, subsequently registering the primary and secondary contents of each sample (dataset 1). Scats that were less than 5 meters apart of the same content and age were recorded as the same sample.

Primary and secondary contents (seeds of Solanum and other fruits, bones, fur, feathers, etc) were registered for all the samples, but 428 were classified based only on field observations, without any other detailed analyses (dataset1). Alternatively, part of the samples were collected, washed under running water through a sieve, and air-dried

prior to content analysis. A total of 232 samples were separated by item and had all contents recorded (to taxa for animal material and species level for seeds and plant material – dataset 2). Additionally, 361 samples were used were used to measure seed numbers for *S. lycocarpum* and other fruits (dataset 3).

DNA analysis to assign scats to correct species of origin

We screened all samples via DNA analysis to determine the species of origin. Thereafter, we processed samples at the Center for Conservation Biology, University of Washington (Seattle, USA) using the Qiagen QiaAmp Stool and Blood/Tissue kits (Qiagen, Valencia, CA) with modified protocols. The species test consisted of fragment analysis from PCR amplification of the mitochondrial control region (D-loop) (Wasser *et al.*, 1997). Results were compared to a library of known-species reference samples. We excluded samples that did not yield DNA for species identification, or yielded an ambiguous result, from further analysis.

Spatial and statistical analyses

Hypothesis 1 – Maned wolves disperse more seeds than do crab-eating foxes

To measure the role of maned wolves and crab-eating foxes as seed dispersers of *S. lycocarpum*, we calculated the occurrence of this plant based on the presence of their seeds on animal scats. In addition to this, we assessed the presence of any other fruits and tested the occurrence of *Solanum* exclusively as a unique food item. We also measured the number of seeds dispersed per each species, and compare then using ANOVA test.

*Hypothesis 2 – Maned wolves and crab-eating foxes consume *S. lycocarpum* mainly in habitats where less other fruit resources are available*

To comprehend where *S. lycocarpum* is being more consumed, we assessed the presence of *Solanum* trees, as well as scats with any number of *Solanum* seeds in each microhabitat. This was achieved by correlating the landscape use map developed by Vynne *et al.* (2014; Figure 1) with both the *Solanum* trees, and samples of the animal species feces containing *Solanum* seeds. To avoid mistakes related with the differences on sample size between the datasets of maned wolves, crab-eating foxes and *Solanum* trees, we calculated the relative frequency of each species in each microhabitat, that were compared using chi-square statistics. We also related the frequency of maned

wolves' and crab-eating foxes' feces with *Solanum* trees per microhabitat using Pearson's correlation.

*Hypothesis 3 – The distribution of adult *S. lycocarpum* plants is explained by maned wolf scats*

To analyze the distribution of *Solanum* trees on the study area, we measured the Euclidean distances between each sample of georeferenced feces with *S. lycocarpum* seeds and the nearest *Solanum* tree. We calculated the frequency of these distances, and compare it to a random distribution of 6250 points distributed on the study area. To analyze these frequencies we used Kolmogorov-Smirnov statistics, that allowed us a comparison between the random distribution and the distances of *Solanum* seed dispersal, assessed by the presence of *S. lycocarpum* seeds on maned wolf' and crab-eating fox' feces. We also overlap the spatial locations of our three species of study and calculated a buffer based on distance of *S. lycocarpum* seed dispersal, what allow us to identify who and where is dispersing *Solanum* seeds. To comprehend if maned wolves and crab eating foxes disperse seeds differentially on each microhabitat we used ANOVA statistics.

All the statistical analysis was conducted on Software R 3.4.2 (R Development Team, 2017), whereas all the spatial analysis was conducted at QGis 2.18.13 (QGis Development Team, 2017).

Results

Hypothesis 1 – Maned wolves disperse more seeds than do crab-eating foxes

S. lycocarpum was found in 612 of 787 (78%) DNA-confirmed maned wolf scats, while it was found in only 46% (n=123/268) crab-eating fox scats. Of scats containing any fruit (85% for maned wolves, 68% for the foxes), *Solanum* was the only fruit in 56% of fecal samples for maned wolf, and 27% for the fox. The number of seeds of *Solanum* dispersed per scat is also higher for maned wolves than for foxes, with wolves dispersing twice as many seeds per scat than crab-eating foxes (34.5 ± 48 and 17 ± 34 respectively; ANOVA, $p=0.01$, $f=6.65$; Figure 3).

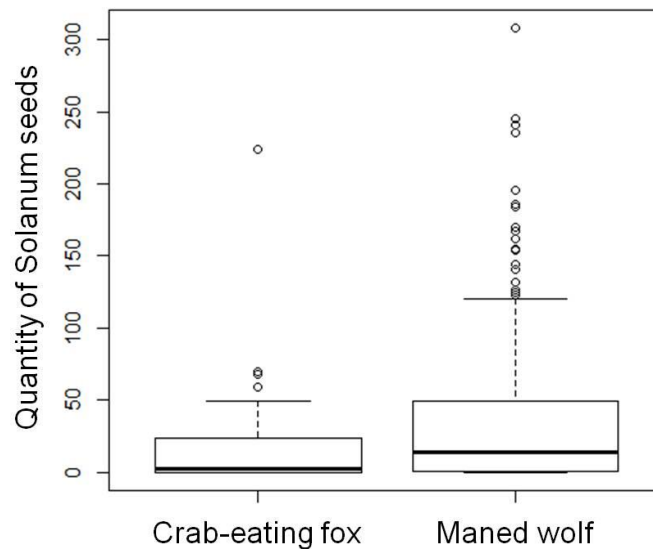


Figure 3. Quantity of *Solanum* seeds dispersed in crab-eating fox and maned wolf feces collected in Emas National Park (Brazil) from 2006 to 2008. Each box indicate one species – the thicker line indicates the median and the inferior and superior edges of the box indicates the quartiles. The outliers are indicated by the isolated dots.

Hypothesis 2 – Maned wolves and crab-eating foxes consume S. lycocarpum mainly in habitats where less other fruit resources are available

We recorded 654 adult plants, 229 of which (35%) were noted to have fruits present. The individuals were present mainly in natural grasslands (n=305, 48%), but also exhibited a strong presence in human-altered areas (croplands and ranchlands, n=267, 42%) (Figure 3). Using the dataset 3 (seed counting), we observed that maned wolf feed on *S. lycocarpum* in all the microhabitats, but with a high affinity for human altered areas (40.3% in total, with 23.3% in croplands and 17% in ranchlands) and natural grasslands (26.2%). Crab-eating foxes feed on *S. lycocarpum* mainly in human altered areas (37.5% in total, with 21.4% in croplands and 16.1% in ranchlands) and forests (14.3%; Figure 4). We found a significant covariance between the frequency of scats with *Solanum* seeds dispersed by both species in each habitat and the frequency of adult *Solanum* plants ($\chi^2=20.4$, $df=8$, $p < 0.01$). However, when we correlate the frequency of adult *S. lycocarpum* with frequency of scats containing *Solanum* seeds per species, we found a significative correlation to maned wolf ($r=0.8$, $p=0.05$), but not to crab eating foxes ($r=0.3$, $p=0.62$).

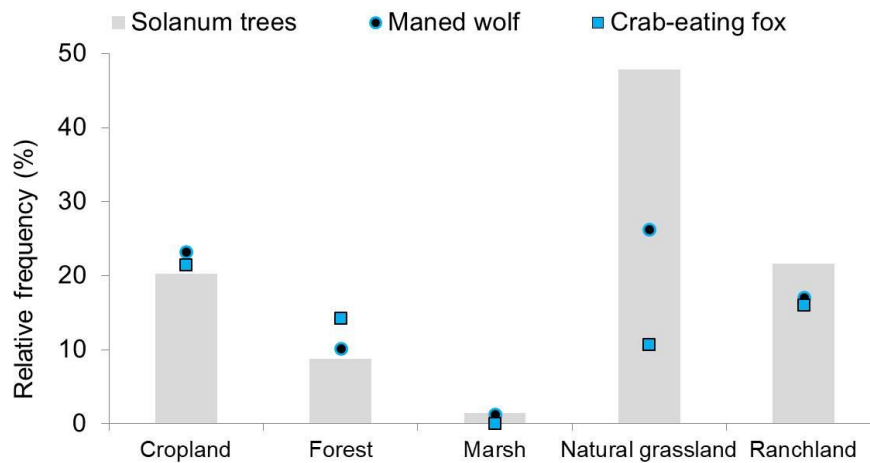


Figure 4. Frequency (%) of *Solanum* trees (grey bars) and maned wolf (black dots) and crab-eating fox (blue squares) scats containing *S. lycocarpum* seeds in different microhabitats from Emas National Park and surrounding area.

*Hypothesis 3 – The distribution of adult *S. lycocarpum* plants is explained by maned wolf scats*

The distances of the scats from *Solanum* trees were similar for both species. No scat was registered less than 141 meters from a plant, and maned wolves and foxes defecate 1180 ± 1578 and 1167 ± 1552 meters away from the closest *Solanum* tree. The maximum distance of scats from the adult individuals was 9663 meters for maned wolves and 8900 meters for the crab-eating foxes (Figure 5). The frequencies for both animal species are not different to each other (Kolmogorov-Smirnov, $p=0.18$), however are significantly different from random distribution (Kolmogorov-Smirnov, $p<0.001$).

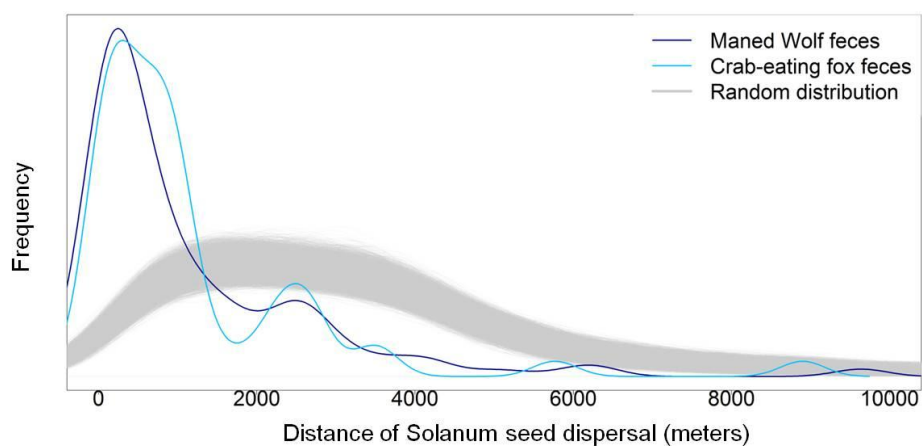


Figure 5. Frequency of distances (meters) of maned wolf (dark blue) and crab-eating fox (light blue) feces from adult *Solanum lycocarpum* individuals collected in the period

2006-2008 in Emas National Park (Brazil). The grey line indicates a random distribution.

Maned wolves dispersed seeds in all of the study areas tested, while the occurrence of crab-eating fox scats containing *Solanum* seeds were mainly located on the border of the park (Figure 6). The distances of *Solanum* seed dispersal were significantly different to each microhabitat on maned wolf scats (ANOVA, $p < 0.01$, $f = 3.56$), but do not to crab-eating foxes (ANOVA, $p < 0.9$, $f = 0.27$).

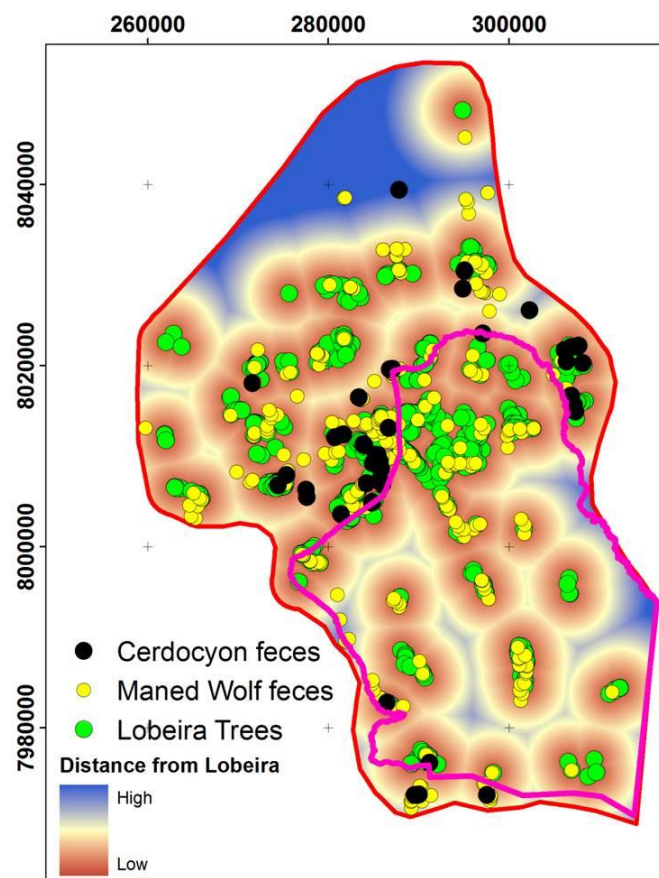


Figure 6. Overlap of adult *S. lycocarpum* (green dots) over maned wolf (yellow dots) and crab-eating fox (black dots) feces within the study area. The colors on the background indicate the distances of the feces from the *Solanum* tree. The pink line indicates the boundary of Emas National Park, Brazil.

Discussion

Canids frugivores are considered long-distance seed dispersers (Jordano *et al.*, 2007; González-Varo *et al.*, 2013), however, few studies have been conducted to comprehend this relationship. Within the current study we showed the importance of

two species of canids – the maned wolf and the crab eating fox – as seed dispersers of *Solanum lycocarpum* seeds in South America.

Maned wolves as main seed dispersers of S. lycocarpum

Our results indicate that maned wolves eat and disperse more fruits of any kind than crab-eating foxes. Focusing just on *Solanum*, the number of seeds per scat was twice as high for maned wolves, which also presented almost 8 times more samples containing exclusively *Solanum* seeds. *S. lycocarpum* was also the most abundant fruit in both species' feces, confirming our first hypothesis. Wolves exhibited a strong and consistent preference for these fruits, which has been previously noted in several studies (Dietz, 1984; Motta-Junior *et al.*, 1996; Juarez & Marinho-Filho, 2002; Rodrigues *et al.*, 2007).

The larger size of the maned wolf better supports its role as a seed disperser than the crab-eating fox, primarily as its larger body mass allows for a higher biomass of fruit consumption before satiation, and thus higher numbers of seed occurrence within scats, but also on account of its height (Dietz, 1984). The maned wolf is the tallest extant canid with a shoulder height of 90cm (scapula to manus; Dietz, 1984), the height of the maned wolf allows it to reach the hanging fruit of tall shrubs that may not be accessible to other frugivores (Emmons, 2012). This gives a competitive advantage to the wolf which may access ripe fruits before they have fallen, while also retaining the unique ability to consume unripe fruits off the branches unlike the other consumers of *S. lycocarpum*, thus potentially increasing the quantity of fruit eaten (Dietz, 1984; Motta-Junior *et al.*, 1996).

The correlation between frequency of *Solanum* trees and crab-eating fox scats containing seeds was not significant, indicating that crab-eating foxes likely only feed opportunistically on *Solanum lycocarpum*. This outcome was expected as several studies have found a highly opportunistic diet for the species (Juarez & Marinho-Filho, 2002; Pedó *et al.*, 2006; Rocha *et al.*, 2008). Different results were found for maned wolves, which present preference for areas with *S. lycocarpum* present, as supported by the significant correlation between frequency of *Solanum* trees and maned wolves' scats with its seeds observed within the current study. It also indicates a strong relationship between maned wolves and *Solanum*, which is fundamental to the reproductive success of the plant, particularly as plant populations are often shaped

based on the decisions and space use of frugivores (Hampe *et al.*, 2008; Carlo & Morales, 2008).

Solanum lycocarpum as an important fruit source to canids on human-altered areas

Solanum trees were present in both natural and human-altered areas, however in higher abundance on natural grasslands, croplands and ranchlands, while being at lower abundance in marshes and forests. We found a covariance between the frequency of plants and frequency of scats containing *Solanum* seeds per microhabitat for both animal species, indicating a general correlation between both variables. Maned wolves and crab-eating foxes presented a high frequency of feces containing *Solanum* seeds in the human-altered areas, confirming our second hypothesis. The tolerance of *S. lycocarpum* for unfavorable ambient conditions (Vida, 1999) allows the colonization of degraded areas when other sources are more limited.

The distribution of Solanum trees is explained by maned wolf scats

Large bodied animals often disperse seeds the largest distances (Jordano, 2017). The patterns of dispersal distance of scats containing seeds and *Solanum* trees, displayed by the maned wolf and crab-eating fox was significantly similar and not random for both species, which can disperse seeds more than 8 kilometers. This dispersal is a big advantage to *Solanum lycocarpum*, as long distance seed dispersal is essential to connect populations and to colonize new areas (Jordano, 2017; Howe, 2014). Long distance seed dispersal is important to avoid spatial aggregation of seedlings that can cause competition and mortality (Harrison *et al.*, 2013; Caughlin *et al.*, 2015).

Maned wolves disperse seeds across the entire study area, making them the primary disperser responsible for the *Solanum* seed shadow inside the park area. Crab-eating foxes feed on *Solanum* fruits mainly at the border of the park, with few registered inside the protected area. The distances of *Solanum* seed dispersal by maned wolves were different in each microhabitat, showing the importance of this species to *S. lycocarpum*. Crab-eating foxes don't present the same pattern, showing that they feed opportunistically on *Solanum* trees. It can also be explained by their landscape use – Jácomo *et al.*, (2004) and Vynne *et al.*, (2011) found in the same study area that both animal species present differences on their spatial use, with crab-eating foxes being

more generalist on the space use and maned wolves being more selective to open areas and avoiding closed canopy areas, as forests.

Carnivores in general have simple guts, allowing most seeds to pass though undamaged. They also frequently have large home ranges and a long gut passage time, allowing a longer seed dispersal distance for plant species (Corlett, 2017; Schupp *et al.*, 2017). Within this study, we showed the role of two species of canids on seed dispersal and spatial distribution of a plant species. We recommend more studies on *Solanum* seed dispersal, as the low number of seed disperser species related to this plant allows for a deeper comprehension of this important ecological process.

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Final considerations

This study provides information on movement ecology and their consequences on social interactions and seed dispersal. We could identify the main challenges on movement ecology in Brazil and suggest possible solutions, such as access to technology without bureaucracy, incentives to Brazilian companies that develop tracking equipment and collaborations among science fields and interdisciplinary research centers and institutes related to movement ecology. We also highlight the need to link the mechanisms, processes and causes that influence movement in nature, to shape better ecological questions and to understand the consequences of movement for conservation.

The main suggestion for the future directions in movement ecology research in Brazil is to explore organism movement data without forgetting the guiding principles, i.e. the underlying ecological questions. Now it is time to move beyond researching animal movement for its own sake and integrate patterns and specific questions with ecological processes involved in movement itself, such as predation, pollination and seed dispersal. Further exploration on how movement facilitates natural forest restoration, ecosystem services and other phenomena could advance conservation policy planning and implementation.

We also explored the consequences of movement on social behavior and interactions of maned wolves (*Chrysocyon brachyurus*), once the contact between conspecifics is one of the most important occurrences within an animal life. We found that although maned wolves are solitary, they present some interactions between couples and a high tolerance between spatially contiguous neighbors and thus providing evidence for a degree of sociality. The interactions between couples are more related to space than time, and are stronger on reproductive seasons.

The landscape use within the home range of maned wolves can influence the length of the pairwise distances, which therefore reflects the impact of human-dominated areas on behavior and movement of this important species. However, we did not find evidences that the movement of an individual maned wolf can affect the direction of movement of another individual, independent of the landscape in which they live.

We also found that maned wolves are the main responsible by the distribution of *Solanum* trees on Emas National Park. Besides being a more efficient seed disperser than crab-eating foxes, they also present preference on habitats where they can feed on

Solanum trees. Maned wolves also moved throughout the studied area, dispersing seeds in all available microhabitats, while crab-eating foxes distributed seeds mainly on the border of the park. On this thesis we showed the importance of movement ecology, as well as its consequences on social behavior and seed dispersal. Using spatial data we could discover more about the ecology of important species present on South America, as well as their interactions animal-animal and animal-plant. We recommend the development of more studies that integrates aspects and consequences of movement, especially on tropical ecosystems.