Exp Appl Acarol
DOI 10.1007/s10493-015-9886-3

Ticks (Acari: Ixodidae) identified from prey–predator interactions via feacal analysis of Brazilian wild carnivores

Thiago F. Martins · Thaís R. Diniz-Reis · Gustavo S. Libardi · Alexandre R. Percequillo · Luciano M. Verdade · Eliana R. Matushima · Marcelo B. Labruna

Received: 1 September 2014 / Accepted: 8 February 2015

Abstract Between July 2008 and May 2010, we conducted a trophic study on 12 Brazilian wild carnivore species through their faecal analysis in a silvicultural landscape at Angatuba municipality, southern São Paulo state. Predator faeces was identified by morphology, predator hair, and surrounding tracks; prey remnants within faeces were used for morphological identification of the prey. Among the recovered ectoparasites, there were 89 specimens of six tick species in 21 (4.0 %) out of 523 analysed samples. Ticks were identified to species level, based on external morphological characters, as following: adults of *Amblyomma ovale* and *Amblyomma sculptum*; nymphs of *Amblyomma brasiliense, Amblyomma calcaratum, Amblyomma dubitatum, A. ovale,* and *Ixodes schulzei*; and larvae of *Amblyomma* sp. and *Ixodes* sp. Generally, the recovered immature ticks were associated

T. F. Martins (✉) · M. B. Labruna
Departamento de Medicina Veterinária Preventiva e Saúde Animal, Faculdade de Medicina Veterinária e Zootecnia, Universidade de São Paulo, São Paulo, SP 05508-270, Brazil
e-mail: thiagodogo@hotmail.com

M. B. Labruna
e-mail: labruna@usp.br

T. R. Diniz-Reis · L. M. Verdade
Centro de Energia Nuclear na Agricultura, Universidade de São Paulo, Piracicaba, SP, Brazil
e-mail: thaisdinizreis@gmail.com

L. M. Verdade
e-mail: lmverdade@usp.br

G. S. Libardi · A. R. Percequillo
Escola Superior de Agricultura "Luiz de Queiroz", Universidade de São Paulo, Piracicaba, SP, Brazil
e-mail: gslibardi@gmail.com

A. R. Percequillo
e-mail: percequillo@usp.br

E. R. Matushima
Departamento de Patologia, Faculdade de Medicina Veterinária e Zootecnia, Universidade de São Paulo, São Paulo, SP, Brazil
e-mail: ermatush@usp.br

Published online: 22 February 2015

with consumed prey (small birds or small mammals), whereas adults were associated with the predator itself, ingested during its self-grooming. Our data show that faeces is an additional information source on ticks in Brazil and which may provide information on ectoparasite-predator–prey interactions.

Keywords Ectoparasite · Ixodidae · Faeces · Carnivora · Brazil

Introduction

Ticks are obligate ectoparasites of amphibians, reptiles, birds, and mammals. They are important vectors of pathogenic virus, bacteria, protozoa, and nematodes to animals and humans; therefore ticks are of major medical and veterinary concern worldwide (Jongejan and Uilenberg 2004). The Brazilian tick fauna is currently composed of 66 species—45 Ixodidae and 21 Argasidae (Martins et al. 2014; Nava et al. 2014). At least 21 of those, mostly within the genus *Amblyomma* (15 species), have been reported on wild Carnivora hosts native to Brazil (Labruna et al. 2005). Brazilian native Carnivora are divided into five families: Felidae (eight species), Canidae (six species), Mustelidae (six species), Procyonidae (four species), and Mephitidae (two species) (Paglia et al. 2012). Although tick species that parasitize domestic animals have been well studied, knowledge on the natural history of ticks parasitizing wildlife is still incipient for most of the South American tick fauna.

Collecting ticks directly from hosts, is time and money consuming, and laborious for elusive and low density hosts, such as wild carnivores. Rosalino et al. (2007) reported an alternative approach based on the analysis of host faecal samples collected in the environment. Whereas such analysis is a common tool in studies on carnivores' diet, including identification of prey species (Reynolds and Aebischer 1991; Crawshaw Júnior 2006), the study of Rosalino et al. (2007) successfully applied the scat analysis of two European wild carnivores (*Vulpes vulpes* and *Genetta genetta*) for determination of host-tick interactions, with 276 ticks found inside 940 scat samples. In this context, the present study aimed at reporting the occurrence of different tick species that were identified at prey-predator interactions through faecal analysis of some free-ranging wild carnivores in Brazil.

Materials and methods

Between July 2008 and May 2010, we conducted a study on the diet of 12 Brazilian wild carnivores in a silvicultural landscape [Fazenda Três Lagoas (23°22′0″S; 48°28′0″W, 3242 ha) and Fazenda Arca (23°20′0″S; 48°27′30″W, 1123 ha)] in the municipality of Angatuba, state of São Paulo, southeastern Brazil. The landscape of this region is a mosaic of native vegetation remnants (Cerrado savannah and semideciduous forest) merged with an agro-forestry matrix, dominated by exotic pastures and *Eucalyptus* plantations (Athayde 2012). Its climate is subtropical (Cwa in Köppen climate classification) with mean temperatures ranging from 17 to 22 °C along the year (EECFI, 23°10′00″S, 48°40′00″O).

Carnivore faecal samples were collected through all landscape elements with the aid of a motorcycle and identified to the most precise taxonomic level by morphology (Kruuk 1978; Lloyd 1980; Chame 2003), predator hair structures (Teerink 1991; Quadros and Monteiro-Filho 2006) and surrounding footprints (Becker and Dalponte 1991). In the laboratory, faecal samples were washed through a 1 mm sieve, oven-dried, and non-digested prey remnants (e.g., feathers, hairs, bones, teeth and scales) and ticks were separated under a stereomicroscope. Prey remnants were identified to the possible lowest taxonomic level, with the help of experts and by comparison with reference collections and/or material in the following zoological museums: "Museu de Zoologia da Universidade de São Paulo" (MZUSP) and "Coleção de Mamíferos do Laboratório de Zoologia de Vertebrados da Escola Superior de Agricultura Luiz de Queiroz" (LZV), both of the University of São Paulo. The nomenclature used for the identification of prey and predators followed Wilson and Reeder (2005) and Trigo et al. (2013). Ticks were preserved in 70 % alcohol and identified to species (nymphs and adults) or to genus level (larvae) following Onofrio et al. (2006), Barros-Battesti et al. (2007), Martins et al. (2010) and Nava et al. (2014). Collected ticks were deposited in the tick collection "Coleção Nacional de Carrapatos" (CNC) of the University of São Paulo under accession numbers CNC- 2188-2207, 2867. Tick-predator–prey interactions were identified by the presence of each individual tick in predator faeces with consumed prey (bird, reptile and mammal).

Results

A total of 523 faecal samples of 12 species of free-ranging wild carnivores were collected, as follows: Canidae—*Chrysocyon brachyurus* (150 samples), *Cerdocyon thous* (62), *Lycalopex* sp. (20); Felidae—*Puma concolor* (21), *Puma yagouaroundi* (22), *Leopardus pardalis* (36), *Leopardus wiedii* (43), *Leopardus guttulus* (26), *Leopardus* sp. (74); Procyonidae—*Nasua nasua* (41), *Procyon cancrivorus* (13); Mustelidae—*Eira barbara* (10), *Galictis cuja* (5). A total of 89 ticks (seven adults, 14 nymphs and 68 larvae) were found in 21 faecal samples (4.0 %) of eight carnivore species, mainly from felids (Table 1), and were identified as follows: *Amblyomma ovale* (three males, three females, and five nymphs), *Amblyomma dubitatum* (four nymphs), *Amblyomma calcaratum* (two nymphs), *Ixodes schulzei* (two nymphs), *Amblyomma sculptum* (one female), *Amblyomma brasiliense* (one nymph), *Amblyomma* sp. (67 larvae), and *Ixodes* sp. (one larva). Prey remnants were identified to each of three vertebrate groups: birds, reptilian, or mammals. Whereas birds could not be assigned to any lower taxonomic level, reptilia could be assigned to the Squamata order, and most of the mammals were assigned to family, tribe, genus or species level. The description of tick-predator–prey species interactions is presented in Table 1.

Discussion

Among the six tick species found in wild carnivore faecal samples in the present study, *A. ovale* was the most abundant, with a total of six adults and five nymphs. This species was reported as the most common tick species on wild carnivores in most regions of Brazil (Labruna et al. 2005). With very few exceptions (Guglielmone et al. 2003), only the adult stage of *A. ovale* is found feeding on carnivores (Labruna et al. 2005). On the other hand, small rodents are preffered hosts for *A. ovale* larva and nymphs (Jones et al. 1972; Martins et al. 2012; Saraiva et al. 2012; Szabó et al. 2012). Thus, it is reasonable to speculate that the six *A. ovale* adults of the present study are associated with ingestion during self-cleaning behaviour (grooming) of carnivore hosts (Felidae, Canidae and Mustelidae), whereas the five nymphs are associated with prey, since these nymphs were found together with a variety of small rodent remnants in the faecal samples (Table 1). The two nymphs of

Table 1 Ticks and prey remnants found in faecal samples of free-ranging wild carnivores collected in a silvicultural landscape in Angatuba, southeastern Brazil

Predators	Preys identified in predators' faecal samples	No. Ticks (L: larvae; N: nymphs; M: males; F: females)
Felidae		
Puma concolor	Squamata; small mammal	2L *Amblyomma* sp.; 1N *Amblyomma brasiliense*; 1M, 1F *A. ovale*
Puma yagouaroundi	Squamata; small mammal	1L *Amblyomma* sp.
Leopardus pardalis	*Calomys* sp.; *Oligoryzomys* sp.	1N *Amblyomma ovale*
L. pardalis	Small bird; *Akodon* sp.; *Nectomys* sp.; *Oligoryzomys* sp.	1N *Ixodes schulzei*
L. pardalis	*Akodon* sp.; *Calomys* sp.; *Oligoryzomys* sp.; small rodent	3L *Amblyomma* sp.; 1N *A. ovale*
L. pardalis	Reptilia; Didelphidae; *Akodon* sp.; *Calomys* sp.; *Oligoryzomys* sp.; *Necromys lasiurus*	1L *Ixodes* sp.
L. pardalis	Small bird; *Akodon* sp.; *Oligoryzomys* sp.	1N *Amblyomma calcaratum*
L. pardalis	Small bird; *Necromys lasiurus*	1L *Amblyomma* sp.
L. pardalis	Small mammal	2L *Amblyomma* sp.
Leopardus wiedii	Didelphidae; *Calomys* sp.; *Oligoryzomys* sp.	1F *Amblyomma sculptum*
Leopardus guttulus	Squamata; *Akodon* sp.	1M *A. ovale*
L. guttulus	Squamata; small bird; Didelphidae; small rodent	5L *Amblyomma* sp.
L. guttulus	Small bird; *Akodon* sp.; *Oligoryzomys* sp.	35L *Amblyomma* sp.
Leopardus sp.	Small bird; Didelphidae; *Akodon* sp.; *Calomys* sp.; *N. lasiurus*; *Oligoryzomys* sp.	16L *Amblyomma* sp.
Leopardus sp.	Squamata; *Akodon* sp.; small rodent	1N *A. ovale*
Leopardus sp.	Small bird; Didelphidae; *Akodon* sp.; *N. lasiurus*; *Oligoryzomys* sp.; small rodent	1L *Amblyomma* sp.; 1N *A. calcaratum*; 1N *I. schulzei*
Leopardus sp.	Squamata; small bird; *Akodon* sp.; *Calomys* sp.; *N. lasiurus*; small rodent	1L *Amblyomma* sp.
Canidae		
Cerdocyon thous	Small bird; Didelphidae; *N. lasiurus*; *Nectomys* sp.; Akodontini	1M, 1F *A. ovale*
C. thous	Small bird; *Oligoryzomys* sp.	1N *A. ovale*
Chrysocyon brachyurus	Squamata; small bird; *Calomys* sp.; *Oligoryzomys* sp.; *Hydrochoerus hydrochaeris*	1N *A. ovale*; 4N *Amblyomma dubitatum*
Mustelidae		
Eira barbara	Small mammal	1F *A. ovale*

A. calcaratum found in the faeces of two felids of the genus *Leopardus* are also likely to be associated with a prey item (in these cases, small birds; Table 1), because immature stages of *A. calcaratum* feed primarily on passerine birds (Jones et al. 1972; Labruna et al. 2007; Ogrzewalska et al. 2010, 2014; Sanches et al. 2013). Similarly, the findings of two nymphs of *I. schulzei* along with remnants of small rodents (including a *Nectomys* sp.; Table 1) also indicate that these ticks were attached to ingested prey, because nymphs of *I. schulzei* are known to feed exclusively on small rodents, especially of the genus *Nectomys* (Labruna et al. 2003; Guglielmone et al. 2011; Saraiva et al. 2012; Onofrio et al. 2013). The four nymphs of *A. dubitatum* found in a *C. brachyurus* faecal sample were probably associated with the consumed capybara (*Hydrochoerus hydrochaeris*), the primarily host of all parasitic stages of *A. dubitatum* or, to a much lesser extent, with the consumed small rodents (Table 1), which have been found infested by immature stages of *A. dubitatum* (Nava et al. 2010; Débarbora et al. 2014). Finally, the *A. sculptum* female and the *A. brasiliense* nymph could be related either with predator or prey, since these ticks are known to have a broad host range, including small to large mammals (Aragão 1936; Szabó et al. 2013; Nava et al. 2014).

The present study corroborates a previous report from Portugal (Rosalino et al. 2007), by adding faecal samples as suitable source of valuable information for the study of ticks, being a complementary method for the traditional ones that require capture of live wild animals, especially elusive carnivores. On the other hand, this approach needs to be carefully carried on because faecal samples could be misidentified among close-related species, and in some cases, it could be impossible to determine the host of the ingested tick, namely the predator or the plurality of consumed preys.

Our results also provide epidemiological support for the life cycle of the protozoan *Hepatozoon canis* in Brazil, which is thought to be transmitted to carnivores through the ingestion of *H. canis*-infected *A. ovale* ticks (Forlano et al. 2005; Rubini et al. 2009). Many other tick-borne pathogens, such as *Rickettsia rickettsii* (the agent of Rocky Mountain spotted fever), are transmitted to vertebrate hosts during the parasitism of infected ticks (Parola et al. 2013). Because it was shown in the laboratory that domestic dogs can acquire *R. rickettsii* infection through the ingestion of infected rodents (Moreira and Magalhães 1935), our results support the assumption that predator carnivores are exposed to a broad array of tick-borne agents, which include not only those agents transmitted by carnivore ticks, but also to a variety of agents primarily associated with prey and their ticks (Widmer et al. 2011). As demonstrated here, faecal analysis might be a cheap and unique tool for tick investigations, especially because it provides simultaneous information on ectoparasite-predator–prey interaction, what cannot be obtained by traditional direct-host collection. For this reason, this methodology should be further applied and refined on future sanitary and ecological studies.

Acknowledgments This study was supported by Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP) and Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq). Luciano M. Verdade holds a CNPq Productivity Scholarship (309468/2011-6).

References

Aragão HB (1936) Ixodidas brasileiros e de alguns países limítrofes. Mem Inst Oswaldo Cruz 31:759–843

Athayde EA (2012) Importância da Heterogeneidade Natural na Conservação da Biversidade de Árvores em Paisagem agrosilvicultural. Tese de doutorado. Universidade Estadual Paulista, Rio Claro, p 196

Barros-Battesti DM, Onofrio VC, Faccini JLH, Labruna MB, Arruda-Santos AD, Giacomin FG (2007) Description of the immature stages and redescription of the female of *Ixodes schulzei* Aragão and Fonseca, 1951 (Acari: Ixodidae), an endemic tick species of Brazil. Syst Parasitol 68:157–166

Becker M, Dalponte CJ (1991) Rastros de mamíferos silvestres brasileiros: um guia de campo. Universidade de Brasília, Brasília, p 181

Chame M (2003) Terrestrial mammal feces: a morphometric summary and description. Mem Inst Oswaldo Cruz 98:71–94

Crawshaw Júnior PG (2006) The history of carnivore research in Brazil. In: Morato RG, Rodrigues FHG, Eizirik E, Mangini PC, Azevedo FCC, Marinho-Filho J (eds) Manejo e conservação de carnívoros neotropicais. Ibama, São Paulo, p 396

Débarbora VN, Mangold AJ, Oscherov EB, Guglielmone AA, Nava S (2014) Study of the life cycle of *Amblyomma dubitatum* (Acari: Ixodidae) based on field and laboratory data. Exp Appl Acarol 63:93–105

Forlano M, Scofield A, Elisei C, Fernandes KR, Ewing SA, Massard CL (2005) Diagnosis of *Hepatozoon* spp. In *Amblyomma ovale* and its experimental transmission in domestic dogs in Brazil. Vet Parasitol 134:1–7

Guglielmone AA, Estrada-Peña A, Mangold AJ, Barros-Battesti DM, Labruna MB, Martins JR, Venzal JM, Arzua M, Keirans JE (2003) *Amblyomma aureolatum* (Pallas, 1772) and *Amblyomma ovale* Kock, 1844: hosts, distribution and 16S rDNA sequences. Vet Parasitol 113:273–288

Guglielmone AA, Nava S, Díaz MM (2011) Relationships of South American marsupials (Didelphimorphia, Microbiotheria and Paucituberculata) and hard ticks (Acari: Ixodidae) with distribution of four species of Ixodes. Zootaxa 3086:1–30

Jones EK, Clifford CM, Keirans JE, Kohls GM (1972) The ticks of Venezuela (Acarina: Ixodoidea) with a key to the species of *Amblyomma* in the Western Hemisphere. Brigham Young Univ Biol Sci Bull Biol Ser 17:1–40

Jongejan F, Uilenberg G (2004) The global importance of ticks. Parasitol 129(Suppl.):S3–S14

Kruuk H (1978) Spatial organisation and territorial behaviour of the European badger *Meles meles*. J Zool 184:1–19

Labruna MB, da Silva MJ, de Oliveira MDF, Barros-Battesti DM, Keirans JE (2003) New records and laboratory-rearing data for *Ixodes schulzei* (Acari: Ixodidae) in Brazil. J Med Entomol 40:116–118

Labruna MB, Jorge RSP, Sana DA, Jácomo ATA, Kashivakura CK, Furtado MM, Ferro C, Perez SA, Silveira L, Santos TS Jr, Marques SR, Morato RG, Nava A, Adania CH, Teixeira RHF, Gomes AAB, Conforti VA, Azevedo FCC, Prada CS, Silva JCR, Batista AF, Marvulo MFV, Morato RLG, Alho CJR, Pinter A, Ferreira PM, Ferreira F, Barros-Battesti DM (2005) Ticks (Acari: Ixodida) on wild carnivores in Brazil. Exp Appl Acarol 36:149–163

Labruna MB, Sanfilippo LF, Demetrio C, Menezes AC, Pinter A, Guglielmone AA, Silveira LF (2007) Ticks collected on birds in the state of São Paulo, Brazil. Exp Appl Acarol 43:147–160

Lloyd HG (1980) The red fox. Batsford, London, p 319

Martins TF, Onofrio VC, Barros-Battesti DM, Labruna MB (2010) Nymphs of the genus *Amblyomma* (Acari: Ixodidae) of Brazil: descriptions, redescriptions, and identification key. Ticks Tick Borne Dis 1:75–99

Martins TF, Moura MM, Labruna MB (2012) Life-cycle and host preference of *Amblyomma ovale* (Acari: Ixodidae) under laboratory conditions. Exp Appl Acarol 56:151–158

Martins TF, Venzal JM, Terassini FA, Costa FB, Marcili A, Camargo LMA, Barros-Battesti DM, Labruna MB (2014) New tick records from the state of Rondônia, western Amazon, Brazil. Exp Appl Acarol 62:121–128

Moreira JA, Magalhães O (1935) Typho exanthematico em Minas Gerais. Bras Med 49:465–470

Nava S, Venzal JM, Labruna MB, Mastropaolo M, González EM, Mangold AJ, Guglielmone AA (2010) Hosts, distribution and genetic divergence (16S rDNA) of *Amblyomma dubitatum* (Acari: Ixodidae). Exp Appl Acarol 51:335–351

Nava S, Beati L, Labruna MB, Cáceres AG, Mangold AJ, Guglielmone AA (2014) Reassessment of the taxonomic status of *Amblyomma cajennense* (Fabricius, 1787) with the description of three new species, *Amblyomma tonelliae* n. sp., *Amblyomma interandinum* n. sp. and *Amblyomma patinoi* n. sp., and reinstatement of *Amblyomma mixtum* Koch, 1844 and *Amblyomma sculptum* Berlese, 1888 (Ixodida: Ixodidae). Ticks Tick Borne Dis 5:252–276

Ogrzewalska M, Uezu A, Labruna MB (2010) Ticks (Acari: Ixodidae) infesting birds in the eastern Amazon, northern Brazil, with notes on rickettsial infection in ticks. Parasitol Res 106:809–816

Ogrzewalska M, Literak I, Martins TF, Labruna MB (2014) Rickettsial infections in ticks from wild birds in Paraguay. Ticks Tick Borne Dis 5:83–89

Onofrio VC, Labruna MB, Pinter A, Giacomin FG, Barros-Battesti DM (2006) Comentários e chaves para as espécies do gênero *Amblyomma*. In: Arzua M, Bechara GH, Barros-Battesti DM (eds) Carrapatos de importância médico-veterinária da Região Neotropical: um guia ilustrado para identificação de espécies. Vox/International consortium on ticks and tick-borne diseases (ICTTD-3)/Butantan, São Paulo, pp 53–113

Onofrio VC, Nieri-Bastos FA, Sampaio JS, Soares JF, Silva MJJ, Barros-Battesti DM (2013) Noteworthy records of *Ixodes schulzei* (Acari: Ixodidae) on rodents from the State of Paraná, southern Brazil. Rev Bras Parasitol Vet 22:159–161

Paglia AP, Fonseca GAB, Rylands AB, Herrmann G, Aguiar LMS, Chiarello AG, Leite YLR, Costa LP, Siciliano S, Kierulff MCM, Mendes SL, Tavares VC, Mittermeier RA, Patton JL (2012) Lista anotada dos mamíferos do Brasil. (2. ed.). Occas Pap Conserv Biol 6:1–76

Parola P, Paddock CD, Socolovschi C, Labruna MB, Mediannikov O, Kernif T, Abdad MY, Stenos J, Bitam I, Fournier PE, Raoult D (2013) Update on tick-borne rickettsioses around the world: a geographic approach. Clin Microbiol Rev 26:657–702

Quadros J, Monteiro-Filho ELA (2006) Coleta e preparação de pêlos de mamíferos para identificação em microscopia óptica. Rev Bras Zool 23:274–278

Reynolds JC, Aebischer NJ (1991) Comparison and quantification of carnivore diet by faecal analysis: a critique, with recommendations, based on a study of the fox *Vulpes vulpes*. Mamm Rev 21:97–122

Rosalino LM, Rodrigues M, Santos-Silva M, Santos-Reis M (2007) Unusual findings on host-tick interactions through carnivore scat analysis. Exp Appl Acarol 43:293–302

Rubini AS, dos Paduan KS, Martins TF, Labruna MB, O'Dwyer LH (2009) Acquisition and transmission of *Hepatozoon canis* (Apicomplexa: Hepatozoidae) by the tick *Amblyomma ovale* (Acari: Ixodidae). Vet Parasitol 164:324–327

Sanches GS, Martins TF, Lopes IT, Costa LFS, Nunes PH, Camargo-Mathias MI, Labruna MB (2013) Ticks infesting birds in Atlantic Forest fragments in Rio Claro, State of São Paulo, Brazil. Rev Bras Parasitol Vet 22:6–12

Saraiva DG, Fournier GF, Martins TF, Leal KP, Vieira FN, Câmara EM, Costa CG, Onofrio VC, Barros-Battesti DM, Guglielmone AA, Labruna MB (2012) Ticks (Acari: Ixodidae) associated with small terrestrial mammals in the state of Minas Gerais, southeastern Brazil. Exp Appl Acarol 58:159–166

Szabó MPJ, Martins TF, Nieri-Bastos FA, Spolidorio MG, Labruna MB (2012) A surrogate life cycle of *Amblyomma ovale* Koch, 1844. Ticks Tick Borne Dis 3:262–264

Szabó MPJ, Nieri-Bastos FA, Spolidorio MG, Martins TF, Barbieri AM, Labruna MB (2013) In vitro isolation from *Amblyomma ovale* (Acari: Ixodidae) and ecological aspects of the Atlantic rainforest *Rickettsia*, the causative agent of a novel spotted fever rickettsiosis in Brazil. Parasitol 140:719–728

Teerink BJ (1991) Hair of West-European mammals: atlas and identification key. Cambridge University Press, New York, p 224

Trigo TC, Schneider A, de Oliveira TG, Lehugeur LM, Silveira L, Freitas TRO, Eizirik E (2013) Molecular data reveal complex hybridization and a cryptic species of neotropical wild cat. Curr Biol 23:2528–2533

Widmer CE, Azevedo FC, Almeida AP, Ferreira F, Labruna MB (2011) Tick-borne bacteria in free-living jaguars (*Panthera onca*) in Pantanal, Brazil. Vector Borne Zoonotic Dis 11:1001–1005

Wilson DE, Reeder DM (2005) Mammal species of the world: a taxonomic and geographic reference, 3rd edn. Johns Hopkins University Press, Baltimore 142