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Original article

Survey of ticks in French Guiana

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ABSTRACT

In this study, we examine the current pattern of tick diversity and host use in French Guiana, South America, from 97 sampling localities encompassing peri-urban, rural and natural habitats. We collected 3395 ticks, including 1485 specimens from 45 vertebrate species (humans, domestic and wild animals) and 1910 questing specimens from vegetation. Morphological examinations identified 22 species belonging to six genera: *Amblyomma* (16 species), *Rhipicephalus* (two species), *Ixodes* (one species), *Dermacentor* (one species), *Haemaphysalis* (one species), *Ornithodoros* (one species). To facilitate future identification, we produced a bank of pictures of different stages for all these species. Taxonomic identification was then confirmed by molecular characterization of two mitochondrial genes, cytochrome c oxidase *CO1* and 16S rDNA. Eleven of the 22 reported species were collected on humans, six on domestic animals and 12 on wild animals. The most widespread tick species collected were *A. cajennense* sensu stricto and, to a lesser extent, *A. oblongoguttatum*; both of these species were frequently found on humans. We used these results to discuss the tick-associated risks for human and animal health in French Guiana.

1. Introduction

Considerable research efforts are focusing on the impacts of ticks and tick-borne pathogens (TBPs) on humans and livestock. The specific diversity of ticks, their distribution and host-use patterns have been extensively described in very diverse geographic zones with the aim to understand the circulation and infection dynamics of TBPs (e.g., Labruna et al., 2005a; Szabó et al., 2013). However, knowledge on tick fauna remains scarce in some regions such as French Guiana, a vast equatorial land covering ca. 83,000 km^2 located on the north-east coast of South America and mostly covered by dense rainforests. French Guiana's human population (ca. 245,000 inhabitants) is concentrated principally in a handful of towns spread along the coastline and two main rivers, while the interior is largely uninhabited. No extensive survey of ticks has been conducted in this territory over the past 60 years, since the publication of Floch and Fauran's (1958) review. This last inventory to date was mainly based on early studies from Floch and Abonnenc (1940, 1941, 1942) and counted 28 indigenous tick species which were mostly associated with wildlife (Table 1). Since this early work, only two other tick species were reported (Davoust et al., 2016; Labruna et al., 2005b; Tahir et al., 2016), raising to 30 the tick species reported in French Guiana (Table 1). Nonetheless, during the past 60 years, urbanisation has modified the ecological conditions in some zones of French Guiana (principally along the coastline) and has thus probably impacted the tick fauna. Therefore, an updated inventory based on recent tick collections from French Guiana is needed to respond to these changes.

The present study aimed at documenting the current pattern of tick diversity and host use in French Guiana. We conducted a wide survey across sites with distinct ecological conditions (including anthropogenic, agricultural and natural ecological conditions), sampling ticks either in seabird nests, on different hosts (including humans, domestic animals and wildlife) or as questing ticks found on vegetation. We further identified, both morphologically and genetically, the specimens collected. Since the morphological similarities between some species (especially at the larval stage) make their identification a difficult task, we produced a series of photos as well as a bank of molecular data to facilitate future identifications of ticks collected in French Guiana. We also discuss the potential health risk associated with the tick species currently present in French Guiana.

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Table 1
List of tick species collected in this study or reported in early studies conducted in French Guiana.

Ticks Species	Floch and Fauran, 1958	Labruna et al., 2005b	Davoust et al., 2016; Tahir et al., 2016	This study
Ixodidae (hard ticks):				
Amblyomma aureolatum (Pallas, 1772)	+	–	–	–
A. auricularium (Conil, 1878)	+	–	–	–
A. cajennense sensu stricto (Fabricius, 1787)	+	–	–	+
A. calcaratum Neumann, 1899	+	–	–	–
A. coelebs Neumann, 1899	+	–	–	+
A. dissimile Koch, 1884	+	–	–	+
A. geayi Neumann, 1899	+	–	–	+
A. goeldii Neumann, 1899	+	–	–	+
A. humerale Koch, 1844	+	–	–	+
A. incisum Neumann, 1906	+	–	–	–
A. latepunctatum Tonelli-Rondelli, 1939	–	+	–	+
A. longirostre (Koch, 1844)	+	–	–	+
A. naponense (Packard, 1869)	+	–	–	+
A. oblongoguttatum Koch, 1844	+	–	–	+
A. ovale Koch, 1844	+	–	–	+
A. pacae Aragão, 1911	–	–	–	+
A. parvum Aragão, 1908	+	–	–	–
A. pictum Neumann, 1906	+	–	–	–
A. pseudoconcolor Aragão, 1908	+	–	–	–
A. romitii Tonelli-Rondelli, 1939	+	–	–	+
A. rotundatum Koch, 1844	+	–	–	+
A. scalpturatum Neumann, 1906	+	–	–	+
A. tigrinum Koch, 1844	+	–	–	–
A. varium Koch, 1844	+	–	–	+
Dermacentor nitens Neumann, 1897	–	–	–	+
Haemaphysalis juxtakochi Cooley, 1946	+	–	–	+
Ixodes luciae Senevet, 1940	+	–	–	+
Rhipicephalus microplus (Canestrini, 1888)	+	–	–	+
R. sanguineus sensu lato (Latreille, 1806)	+	–	–	+
Argasidae (soft ticks):				
Argas persicus (Oken, 1818)	+	–	–	–
*Ornithodoros capensis*sensu stricto Neumann, 1901	–	–	–	+
O. hasei (Schulze, 1935)	–	–	+	–
O. talaje (Guérin-Méneville, 1849)	+	–	–	–

2. Material and methods

2.1. Tick collection

Most ticks (n = 3129 or 92% total) were collected in French Guiana in 2016 and 2017 while a few others were sporadically collected between 1994 and 2014 (n = 266; Table S1 and Fig. 1). Questing ticks were collected on vegetation by a drag-flag method over 17 sites distributed on an East-West transect and covering three types of ecological conditions (peri-urban, agricultural and natural). Ticks were also directly collected in seabird nests of Grand Connétable Island or on hosts (including humans, four domestic animal species and 40 wild animal species). Some of these ticks were also obtained through a broadcast advertisement to scientists from various fields (e.g. botanists, ecologists, microbiologists, epidemiologists, etc.) as well as wildlife managers working in French Guiana. This advertisement allowed us to obtain ticks collected in remote areas which otherwise remain difficult to visit. All ticks were stored in 75% ethanol until examination.

2.2. Morphological identification and photography collection

All tick specimens were examined under a Leica Z16 APO-A macroscope and categorised by stage and sex. Adults were morphologically identified to species using the study of Labruna et al. (2005b) and the dichotomous keys from Floch and Fauran (1958) and Jones et al. (1972). Nymphs were morphologically determined using the identification key by Martins et al. (2010). To the best of our knowledge, there is no identification key for South American tick larvae. Larvae were identified to genus based on morphological comparisons with adults and identification keys (at the genus level; Clifford et al.,1961), before being partitioned into distinct morphological groups: larvae sharing the same morphological characteristics (e.g. average body size, gnathosoma and scutum shape and size, presence of cornua or number of spurs on each coxa, etc.) were assigned to same group before to be investigated for a further molecular confirmation (see below). One representative per species, sex and stage or per morphological group was photographed. Ventral and dorsal views of these specimens were photographed using a Leica DFC425 camera coupled with a Leica Z16 APO-A zoom system.

2.3. Molecular typing

A subset of tick specimens (for each sex, stage and species or for each larval morphological group) was used for molecular typing in order to confirm morphological identification. Total DNA from nymphs and larvae or DNA from one adult leg were extracted using the DNeasy Blood and Tissue Kit (QIAGEN) following the manufacturer's instructions. For each tick DNA sample, mitochondrial gene fragments of the 16S rDNA (ca. 450 bp) and the cytochrome c oxidase *C01* (655–680 bp) were amplified by polymerase chain reaction (PCR) using specific primers (listed in Table 2). PCRs were performed in a 25 μL reaction volume containing 12.85 μL of H_2O, 2.5 μL of 10x PCR buffer (Roche), 5 μL of 2.5 mM of dNTP mix (Thermo Scientific), 2 μL of 25 mM $MgCl_2$ (Roche), 0.7 μL of each primer (10 μM), 0.25 μL of Taq Roche polymerase (5U/μL) and 1 μL of DNA. The amplification cycle involved a denaturation step at 94 °C for 3 min followed by 35 cycles of 30 s at 94 °C, 30 s at 50 °C, 1 min at 72 °C and a final 5 min elongation step of at 72 °C. The amplified products were detected by electrophoresis on 1.5% agarose gel in TAE 0.5X buffer and stained with EZ-Vision (Amaresco). Positive amplifications were sequenced by Eurofins (Ebersberg, Germany). Sequence chromatograms were manually cleaned with Chromas Lite (http://www.technelysium.com.au/chromas_lite.html) and aligned

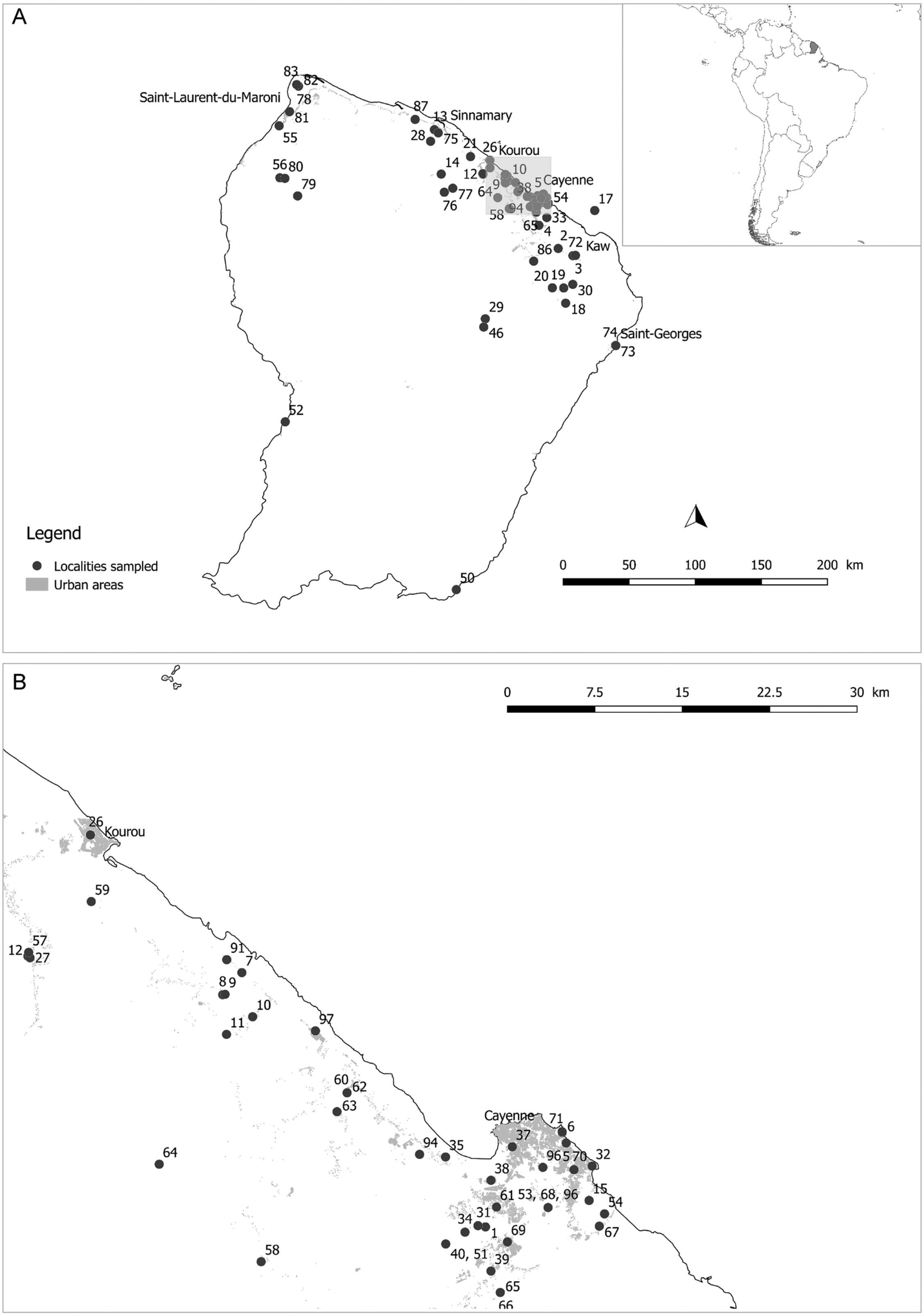

Fig. 1. Localization of sampling sites. Localities are represented by dark dots and urban areas by grey areas. Numbers correspond to the population number given in Table S1. Figure B is the magnification of the area bounded by the translucid grey rectangle in Figure A. Localities with no GPS coordinates are not indicated in this map (see #22-25, 36, 41–50, 75, 84, 85, 88–90, 92 and 93 in Table S1).

Table 2
Primers used for characterising tick species.

Genes	Primers (5'-3')	Amplified species	References
16S RNA	Tm16S + 1 (CTGCTCAATGATTTTTTAAATTGC) Tm16S-1 (CCGGTCTGAACTCAGATCATGTA)	All species (Tm16 + 1-Tm16S-1: 450bp)	Fukunaga et al., 2001
C01	TickC01 F (ATTTTACCGCGATGAHTWTTYT) TickC01R (CWGGRTGRCCAAARAATCAAAATA)	*A. cajennense* ss, *A. coelebs*, *A. dissimile*, *A. geayi*, *A. latepunctatum*, *A. longirostre*, *A. oblongoguttatum*, *A. scalpturatum*, *A. varium*, *D. nitens*, *H. juxtakochi*, *O. capensis* ss, *R. microplus* (TickC01 F-TickCO1R: 676bp)	This study
	AmbC01 F (TACCGCGATGAATATACTC)	*A. humerale*, *A. naponense*, *A. ovale*, *A. pacae*, *R. sanguineus* sl (AmbC01 F-TickC01R: 675bp)	This study
	Lco1490 (GGTCAACAAATCATAAAGATATTGG) Hco2198 (TAAACTTCAGGGTGACCAAAAAATCA)	*A. goeldii*, *A. rotundatum* (Lco1490-Hco2198: 660bp); *A. romitii*, *I. luciae* (Lco1490-TickCO1R: 654bp)	Folmer et al., 1994

with MEGA 7 (http://www.megasoftware.net). The DNA sequences obtained were compared with sequences referenced in Genbank nucleotide database using the BLAST algorithm (megablast) (Table S2). All 16S rDNA and *CO1* gene sequences obtained in this study were deposited on Genbank (accessions numbers are listed in Table S2).

2.4. Ethics statement

All animals were handled in strict accordance with good animal practice as defined by the French code of practice for the care and use of animals for scientific purposes, established by articles R214-87 to R214-137 of the French rural code. The capture of ticks in the Grand Connétable protected area was authorized by the Prefecture of French Guiana by the prefectoral decree R03-2016-09-23-003. The use of the genetic resources was declared to the French Ministry of Environment under the reference #150401230100, in compliance with the Access and Benefit Sharing procedure implemented by the Loi pour la Reconquête de la Biodiversité.

3. Results

A total of 3395 tick specimens (2,026 Larvae, 687 nymphs and 682 adults) were collected from 97 localities in French Guiana, mostly located along the coast line, including 16 peri-urban sites, four agricultural sites and 76 natural sites (Table S1, Fig. 1). Of the 3395 ticks, 1910 (56%) were collected on vegetation (1,588 Larvae, 248 nymphs and 74 adults) while 1485 (44%) were collected on vertebrate hosts (437 larvae, 435 nymphs and 613 adults). The sampling origin is further detailed in the Table S1.

The 3395 tick specimens were morphologically identified to 22 species (Table 3). Pictures of representative specimens (including larvae, nymphs and adults; Table 3) are shown in Supplementary File 1. Molecular typing based on 16S rDNA and *CO1* gene sequences corroborated most of these morphological identifications: sequences from 21 of the 22 species showed a satisfactory percentage of identities (96–100%) with referenced sequences of the same tick species already available in GenBank (Table S2). It is worth to noting that 16S rDNA appears as a better molecular tool for *Amblyomma* identification since only a few *Amblyomma C01* sequences are currently available in GenBank. Nonetheless one species, *A. latepunctatum,* could not reach proper molecular identification since no 16S rDNA and *CO1* gene sequences were available in GenBank for this species.

Among the 22 species identified, 17 belong to the *Amblyomma* genus, two to the *Rhipicephalus* genus and four others to *Dermacentor*, *Haemaphysalis*, *Ixodes* and *Ornithodoros* genera. Among the 3395 tick specimens, the most abundant species collected were *A. dissimile* ($n = 735$; 22%), *A. cajennense* s.s. ($n = 557$; 16%) and *D. nitens* ($n = 493$; 15%) whereas the least abundant species were *A. ovale* ($n = 4$; 0.1%), *A. romitii* ($n = 4$; 0.1%) and *O. capensis* s.s. ($n = 11$; 0.3%) (Table 3). Across the 97 Localities sampled, *A. cajennense* and *A. oblongoguttatum* were the most widespread tick-species, being observed in 48 and 19 Localities, respectively. By contrast, *A. ovale*, *A. pacae*, *A. romitii*, *D. nitens* and *O. capensis* s.s. were only collected in one locality each (Table 3).

Ticks were collected on 45 different vertebrate species (24 mammals including humans, 14 birds, six reptiles and one amphibian) (Table 3). The host range varied greatly depending on tick species and stages. Indeed, all stages of *D. nitens* and *R. sanguineus* s.l. were found on only one host species (horses and dogs) whereas *A. longirostre*, *A. cajennense* s.s. and *A. dissimile* were generalist species that were respectively collected on 14 passerines, 11 mammals and 10 vertebrate species (six mammals, three reptiles and one amphibian). The greatest tick diversity was found on humans with 11 tick species collected: *A. cajennense* s.s. ($n = 259$ collected on humans), *A. coelebs* (53), *A. dissimile* (1), *A. humerale* (3), *A. latepunctatum* (3), *A. naponense* (9), *A. oblongoguttatum* (89), *A. pacae* (13), *A. scalpturatum* (45), *A. varium* (6) and *Haemaphysalis juxtakochi* (4).

4. Discussion

With the report of 22 tick species (21 Ixodidae and one Argasidae; Table 1, Table 3), the present survey represents is the largest update of the tick fauna in this Amazonian region that has been conducted over the past 60 years. To facilitate future identification for all potential users, including taxonomists, medical and veterinary practitioners, we also produced a bank of pictures of different tick stages and species combined with *CO1* and the 16S rDNA molecular barcoding.

Compared with the previous inventory (Floch and Fauran, 1958), three additional tick species are reported here (*A. pacae*, *Dermacentor nitens* and *Ornithodoros capensis* s.s), bringing the total number of tick species recorded in French Guiana to 33 (Table 1). It is noteworthy that the presence of *A. pacae* and *D. nitens* in French Guiana was strongly presumed because both species are widely distributed in the Neotropical region and because their main hosts (respectively paca and horses) are present in French Guiana (Guglielmone et al., 2003; Jones et al., 1972; Nava et al., 2017).We confirm the previously reported presence of *A. latepunctatum* in French Guiana (Labruna et al., 2005b). This is likely to indicate that, as suggested by Labruna et al. (2005b), *A. latepunctatum* could have been misidentified with *A. incisum* and/or *A. scalpturatum* in the early surveys reviewed by Floch and Fauran (1958). The lack of 16S rRNA and *CO1* referenced sequences of *A. latepunctatum* in GenBank complicated the taxonomic identification. However, we are confident in our identification to *A. latepunctatum* since (i) the morphological diagnostic characteristics described by Labruna et al. (2005b) were unambiguously observed in our specimens, and that (ii) the 16S rDNA and *CO1* sequences obtained from these specimens show a low level of identity with those retrieved from any other *Amblyomma* species (< 91%). By contrast to these Ixodidae species, the presence of *O. capensis* s.s. in South America had long remained controversial or speculative (Dupraz et al., 2016; Nava et al., 2017). In that context, our sampling of several specimens in the seabird colony of Grand Connétable Island (Table S1) along with that of Muñoz-Leal et al (2017) in Queimada Grande Island, Brazil, both confirm the presence of *O. capensis* s.s. on the Atlantic coast of South America.

Table 3
List of tick species collected in this study with their abundance (number of populations where each tick species was found), sampling sizes and specific identity of the hosts on which they were collected. Relevant (non-exhaustive) references for the main host usages of the ticks collected are also indicated.

Ticks Species	Number of collections	*n* total	*n* adult	*n* nymph	*n* larvae	*n* questing ticks on vegetation	*n* on hosts	Hosts (this study)	Main hosts (litterature)
A. cajennense sensu stricto (Fabricius, 1787)	41	557	313	230	14	259	298	Humans [138 F; 92 M; 19 N; 9 L], horse (*Equus caballus*) [3 M; 1 N], jaguar (*Panthera onca*) [2 N], white-lipped peccary (*Tayassu pecari*) [4 F; 4 M], nine-banded armadillo (*Dasypus novemcinctus*) [11 M; 1 N], southern tamandua (*Tamandua tetradactyla*) [1 F], southern naked-tailed armadillo (*Cabassous unicinctus*) [1 M], South American tapir (*Tapirus terrestris*) [1 F; 2 N], pale-throated sloth (*Bradypus tridactylus*) [4 M; 1 N], Guianan white-eared opossum (*Didelphis imperfecta*) [1 N], common opossum (*Didelphis marsupialis*) [3 N]	Mammals (Estrada-Peña et al., 2004; Floch and Fauran, 1958; Guglielmone et al., 2006; Lopes et al., 1998; Martins et al., 2011)
A. coelebs Neumann, 1899	16	163	2	45	116	106	57	Humans [1 M; 25 N; 28 L], South American tapir (*Tapirus terrestris*) [1 F], common opossum (*Didelphis marsupialis*) [2 N]	Mammals (Floch and Fauran, 1958; Garcia et al., 2015; Guglielmone et al., 2006; Martins et al., 2014, 2011)
A. dissimile Koch, 1884	16	735	30	18	687	674	61	Human [1 F], horse (*Equus caballus*) [2 L], common opossum (*Didelphis marsupialis*) [1 N], woolly mouse opossum (*Micoureus demerarae*) [1 N; 1 L], linnaeus's mouse opossum (*Marmosa murina*) [1 L], gray four-eyed opossum (*Philander opossum*) [2 N], smooth machete savane (*Chironius scurrulus*) [2 F; 2 M], pseudoboa (*Pseudoboa sp*) [1 N], green iguana (*Iguana iguana*) [3 F; 4 M; 7 N; 1 L], cane toad (*Rhinella marina*) [3 F; 12 M; 6 N; 11 L]	Reptiles and amphibians (Floch and Fauran, 1958; Guglielmone and Nava, 2010)
A. geayi Neumann, 1899	6	13	5	0	8	8	5	Pale-throated sloths (*Bradypus tridactylus*) [5 M]	Sloths (Floch and Fauran, 1958; Labruna et al., 2009b)
A. goeldii Neumann, 1899	3	35	35	0	0	0	35	Southern tamanduas (*Tamandua tetradactyla*) [5 F; 30 M]	Anteaters (Floch and Fauran, 1958; Martins et al., 2015)
A. humerale Koch, 1844	17	116	7	24	85	61	55	Human [3 L], southern tamandua (*Tamandua tetradactyla*) [1 N], red acouchi (*Myoprocta acouchy*) [1 N], rodents (*Euryoryzomys sp*) [1 N], gray four-eyed opossum (*Philander opossum*) [12 N; 12 L], common opossum (*Didelphis marsupialis*) [3 N; 11 L], opossum (*Marmosops sp*) [2 L], white-flanked antwren (*Myrmotherula axillaris*) [1 N], Werner's false lancehead (*Xenodon werneri*) [1 N], tortoise (*Chelonoidis sp*) [7 M]	Tortoises (Floch and Fauran, 1958; Labruna et al., 2002b)
A. latepunctatum Tonelli-Rondelli, 1939	5	12	4	7	1	5	7	Human [2 N; 1 L], South American tapir (*Tapirus terrestris*) [3 F; 1 M]	Tapirs and peccaries (Labruna et al., 2010, 2005b; Martins et al., 2014)
A. longirostre (Koch, 1844)	18	142	0	7	135	2	140	White-bearded manakin (*Manacus manacus*) [1 N; 6 L], buff-throated saltator (*Saltator maximus*) [1 L], crimson-hooded manakin (*Pipra aureola*) [2 N; 28 L], barred antshrike (*Thamnophilus doliatus*) [6 L], silver-beaked tanager (*Ramphocelus carbo*) [2 L], yellow-olive flatbill (*Tolmomyias sulphurescens*) [1 L], straight-billed woodcreeper (*Dendroplex picus*) [1 L], golden-spangled piculet (*Picumnus exilis*) [1 L], blue-backed manakin (*Chiroxiphia pareola*) [1 N; 48 L], wedge-billed woodcreeper (*Glyphorynchus spirurus*) [34 L], McConnell's flycatcher (*Mionectes macconnelli*) [4 L], white-necked thrush (*Turdus albicollis*) [1 N; 1 L], white-flanked antwren (*Myrmotherula axillaris*) [1 N] and golden-headed manakin (*Pipra erythrocephala*) [1 L]	Porcupines, passerines (immatures) (Floch and Fauran, 1958; Jones et al., 1972; Nava et al., 2010; Ogrzewalska et al., 2010, 2009)
A. naponense (Packard, 1869)	10	202	1	18	183	193	9	Human [1 M; 8 N]	Suina (Floch and Fauran, 1958; Labruna et al., 2002a)

(*continued on next page*)

Table 3 (*continued*)

Ticks Species	Number of collections	*n* total	*n* adult	*n* nymph	*n* larvae	*n* questing ticks on vegetation	*n* on hosts	Hosts (this study)	Main hosts (litterature)
A. oblongoguttatum Koch, 1844	19	118	100	18	0	18	100	Humans [36 F; 38 M; 15 N], cat (*Felis silvestris catus*) [1 F], jaguar (*Panthera onca*) [3 F], cougar (*Puma concolor*) [4 F], white-lipped peccary (*Tayassu pecari*) [1 F], South American tapir (*Tapirus terrestris*) [1 F], gray four-eyed opossum (*Philander opossum*) [1 N]	Mammals (Fairchild et al., 1966; Floch and Fauran, 1958; Guglielmone et al., 2006; Martins et al., 2017; Nuttall, 1912)
A. ovale Koch, 1844	1	4	4	0	0	0	4	South American tapir (*Tapirus terrestris*) [3 F; 1 M]	Mammals (Aragão, 1936; Floch and Fauran, 1958; Guglielmone et al., 2006; Martins et al., 2012)
A. pacae Aragão, 1911	1	13	0	0	13	0	13	Human [13 L]	Paca (Jones et al., 1972; Guglielmone et al., 2003)
A. romitii Tonelli-Rondelli, 1939	1	4	4	0	0	0	4	Capybara (*Hydrochoerus hydrochaeris*) [4 F]	Capybaras (Barros-Battesti et al., 2007; Floch and Fauran, 1958; Jones et al., 1972; Landulfo et al., 2016)
A. rotundatum Koch, 1844	2	127	1	0	126	126	1	Red-footed tortoise (*Chelonoidis carbonaria*) [1 F]	Amphibians and reptiles (Floch and Fauran, 1958; Guglielmone and Nava, 2010; Jones et al., 1972; Labruna et al., 2005c; Rodrigues et al., 2010)
A. scalpturatum Neumann, 1906	7	49	3	7	39	3	46	Human [1 M; 5 N; 39 L], jaguar (*Panthera onca*) [1 N]	Tapirs (Floch and Fauran, 1958; Jones et al., 1972; Labruna et al., 2005b, 2010)
A. varium Koch, 1844	11	95	6	4	85	81	14	Humans [1 N; 5 L], pale-throated sloth (*Bradypus tridactylus*) [2 F; 4 M; 1 N], wedge-billed woodcreeper (*Glyphorynchus spirurus*) [1 N]	Sloths (Floch and Fauran, 1958; Jones et al., 1972; Marques et al., 2002)
Dermacentor nitens Neumann, 1897	1	493	72	259	162	0	493	Horses (*Equus caballus*) [37 F; 40 M; 254 N; 162 L]	Equines (Labruna et al., 2001; Rodrigues et al., 2017)
Haemaphysalis juxtakochi Cooley, 1946	5	13	0	9	4	9	4	Human [4 L]	Deer (Floch and Fauran, 1958; Guglielmone et al., 1992; Jones et al., 1972)
Ixodes luciae Senevet, 1940	8	50	12	38	0	0	50	Large-headed rice rat (*Hylaeamys megacephalus*) [3 N], Guianan oecomys (*Oecomys auyantepui*) [2 N], common opossum (*Didelphis marsupialis*) [1 M], woolly mouse opossum (*Micoureus demerarae*) [3 F; 27 N], linnaeus's mouse opossum (*Marmosa murina*) [2 F; 6 N], gray four-eyed opossum (*Philander opossum*) [5 F; 1 M]	Metatherians and small rodents (Díaz et al., 2009; Floch and Fauran, 1958; Hoogstraal and Aeschlimann, 1982; Labruna et al., 2009a; Luz et al., 2013)
*Ornithodoros capensis*sensu stricto Neumann, 1901	1	11	8	3	0	11	0	In laughing gull nest (*Leucophaeus atricilla*)	Seabirds (Dietrich et al., 2011; Hoogstraal, 1985)
Rhipicephalus microplus (Canestrini, 1888)	3	392	24	1	367	367	25	Brahmans (*Bos taurus indicus*) [18 F; 6 M; 1 N]	Cattle (Floch and Fauran, 1958; Jones et al., 1972)
R. sanguineus sensu lato (Latreille, 1806)	2	51	51	0	0	0	51	Dogs (*Canis lupus familiaris*) [28 F; 23 M]	Dogs (Dantas-Torres, 2010; Dantas-Torres et al., 2010; Estrada-Peña and Jongejan, 1999; Floch and Fauran, 1958)

Despite an intensive sampling effort, the present study has failed to detect 11 tick species reported in Floch and Fauran's (1958) inventory (Table 1; Table 3). This could be explained by sampling differences: the present survey gave some preference to coastal habitats and used sampling strategies that were not perfectly suited to collecting nidicolous soft tick species (e.g. *Argas persicus* and *O. talaje* reported by Floch and Fauran, 1958, but not detected in the present study). Nevertheless, the wide geographical coverage of the present survey allows us to report *A. cajennense* s.s. as the most prevalent tick species from French Guiana. Interestingly, this conclusion is consistent with that of Floch and Fauran (1958). Moreover, other tick species which were described as widely distributed by Floch and Fauran (1958) such as *A. oblongoguttatum*, *A. humerale* and *A. dissimile* also remain very common in the present survey (Table 3). *A. cajennense* s.s. appears to be far more prevalent in human-disturbed environments or at the edge of primary forest than in deep rainforest (Table 3; Table S1), a result congruent with the literature regarding *A. cajennense* s.l. in South-America (Martins et al., 2016; Szabó et al., 2013). It is worth noting that half of the tick species collected (11/22) were found at least once on humans in the present survey (Table 3). In addition, *A. oblongoguttatum*, *A. coelebs* and *A. scalpturatum* are the most common species found on humans after *A. cajennense* (Table 3). These species were commonly sampled on large mammals (e.g. tapirs) and have also been frequently found on humans in other South American countries (Guglielmone et al., 2006).

In French Guiana, TBPs circulating in tick populations are largely overlooked. A few cases have nevertheless been reported, including an outbreak of Q fever due to a very virulent strain of the intracellular bacterium *Coxiella burnetii* (Mahamat et al., 2013). Remarkably, this *C. burnetii* strain was recently detected in *A. geayi* specimens engorged on a dead sloth found in the Cayenne peri-urban area after a Q fever outbreak (Davoust et al., 2014; Eldin et al., 2014; Epelboin et al., 2016). These findings suggest that sloths play a role as a reservoir for *Coxiella burnetii* and a putative role for the ticks feeding on sloths in the transmission of this TBP. While *A. geayi* is not known to feed on humans (Guglielmone et al., 2006), other species feeding on sloth such as *A. cajennnense* s.s. and *A. varium* (the sloth tick) could play a role in the transmission of Q fever to human and others vertebrates. This hypothesis has also been considered in Argentina where *Amblyomma* spp. specimens were found to be infected by *C. burnetii* (Pacheco et al., 2013). In this context, it was suggested that ticks may play a pivotal role in the spread of Q fever in South America, while it is instead an airborne disease in the Northern hemisphere (Duron et al., 2015). Further surveys in French Guiana are needed to elucidate the role of ticks in the transmission of this particular virulent strain of Q fever agent.

Complementarily, the TBP infection risks involving *A. cajennnense* s.s. deserveattention since this tick species was found to display the widest distribution in French Guiana as well as the highest abundance across local anthropogenic landscapes. It is noteworthy indeed that, in South-America, *A. cajennense* s.l. is considered as an important vector of tick-borne rickettsiosis to human and domestic animals (da Silva et al., 2015; Labruna, 2009; Szabó et al., 2013) and may potentially transmit the Brazilian borreliosis agent (Basile et al., 2017). The present survey also reports three other Ixodidae species which, although less widely distributed than *A. cajennnense,* may account for certain infection risks in French Guiana: *A. oblongoguttatum*, *A. coelebs*, and *R. sanguineus* s.l. have been associated with TBPs (mainly *Rickettsia* spp.) in South-America (da Silva et al., 2015; Labruna, 2009; Parola et al., 2013; Szabó et al., 2013). Finally, some soft ticks may also be a threat to human or animal health in French Guiana. Recently, *O. hasei* collected from bats in unoccupied buildings in Saint-Jean-du-Maroni were found infected by a new *Rickettsia* species and two potential new *Bartonella* species but risks to human health remain currently unknown (Davoust et al., 2016; Tahir et al., 2016). Other soft tick species described in French Guiana (i.e *A. persicus*, *O. capensis* s.s and *O. talaje*) are also thought as potential vector of TBPs (Dietrich et al., 2011; Manzano-Román et al., 2012).

In conclusion, the present survey showed that French Guiana currently harbours substantial diversity in tick species including some known as TBP vectors in South America. However, we have likely underestimated this diversity since our sampling regime suffered from an important geographical bias: most of the samples came from the coastline where French Guiana's population is concentrated while the inner territory remains largely underexplored. Future surveys will be necessary to fully describe the tick fauna in French Guiana in these remote areas. Overall, the results reported herein also highlight the potential acarological risk in French Guiana for both human and animal health, highlighting the need to document the local prevalence and diversity of TBP there.

Competing interests

The authors declare that they have no competing interests.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.ttbdis.2018.09.002.

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