Global Distribution, Host Range and Prevalence of Trypanosoma Vivax: A Systematic Review and Meta-Analysis

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Research

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Abstract

Background Trypanosomosis caused by Trypanosoma vivax is one of the diseases threatening the health and productivity of livestock in Africa and Latin America. T. vivax is mainly transmitted by tsetse flies; however, the parasite has acquired the ability to be also transmitted mechanically by hematophagous dipterans. Understanding its distribution, host range and prevalence is a key step in local and global efforts to control the disease.

Methods The study was conducted according to the methodological recommendations of the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) checklist. A systematic literature search was conducted on three search engines, namely Pubmed, Scopus and CAB Direct, to identify all publications reporting natural infection of T. vivax across the world. All the three search engines were screened using the search term Trypanosome vivax without time and language restrictions. Publications on T. vivax that met our inclusion criteria were considered for systematic review and meta-analysis.

Result The study provides a global database of T. vivax, consisting of 899 records from 245 peer reviewed articles in 41 countries. A total of 232,6277 tests were performed on 97 different mammalian hosts, including a wide range of wild animals. Natural infections of T. vivax were recorded in 39 different African and Latin American countries and 47 mammalian host species. All the 245 articles were included into the qualitative analysis, while information from 186 cross-sectional studies was used in the quantitative analysis mainly to estimate the pooled prevalence. Pooled prevalence estimates of T. vivax in buffalo, cattle, dog, dromedary camel, equine, pig, small ruminant and wild animals were 30.6%, 6.4%, 2.6%, 8.4%, 3.7%, 5.5%, 3.8% and 12.9%, respectively. Stratified according to the diagnostic method, the highest pooled prevalences were found with serological techniques in domesticated buffalo (57.6%) followed by equine (50.0%) and wild animals (49.3%).

Conclusion The study provides a comprehensive dataset on the geographical distribution and host range of T. vivax and demonstrates the potential of this parasite to invade other countries out of Africa and Latin America.

Introduction

Trypanosomes are protozoan parasites belonging to the family of Trypanosomatidae and the genus Trypanosoma (T.). The genus Trypanosoma comprises many species such as T. brucei, T. congolense, T. equiperdum, T. evansi, T. simiae, T. suis and T. vivax, that cause diseases called trypanosomoses in different mammalian hosts including humans [1]. Trypanosomoses are widely distributed in Africa, Latin America and Asia [2, 3]. T. vivax is one of the most important Trypanosoma species known to infect both domestic and wild ungulates [4, 5]. T. vivax is reported from cattle, dromedary camel, [6], goat, sheep, pig, dog [7], horse, donkey [8], buffalo, warthog, hippopotamus, reeduck, waterbuck [9], antelope [10], giraffe [11], rhinoceros [12], rodents, pangolin, primates, reptiles and different wild ungulates and carnivores [13]. In Sub-Saharan Africa, T. vivax is mainly transmitted by tsetse flies (Diptera: Glossinidae) in which the parasite can multiply and remain infective throughout the insect's life [14]. The parasite has acquired the ability to be also transmitted mechanically by hematophagous flies like Tabanus spp., Stomoxys calcitrans and Haematobia irritans, which are responsible for the spread of T. vivax in tsetse free areas of Africa and in Latin America [4, 15–18].

T. vivax infection can be suspected by clinical and/or serological evidence and can be confirmed by parasitological or molecular methods [19]. Reported prevalences of T. vivax show considerable variation with geography, abundance of tsetse or blood sucking flies, and host species. In tsetse infested areas of tropical Africa, the T. vivax prevalence is typically reported between 5–15% and often accounts for up to half of the total trypanosome prevalence. Outside of the tsetse belt, T. vivax prevalence is lower between 2–10% and it is related to local and seasonal variation in biting fly abundance [20].

Trypanosomosis caused by T. vivax is an important cause of economic losses related to morbidity, mortality, reproductive issues and decreased production [4]. For example, economic losses associated with bovine trypanosomosis have been estimated to be around US$5 billion a year in Africa and the continent spend at least $30 million every year to control bovine trypanosomosis in terms of curative and prophylactic treatments [21]. Estimates outside Africa indicate that more than 11 million head of cattle with a value of more than US$ 3 billion are at risk from T. vivax infection in the Brazilian Pantanal and Bolivian lowlands, with potential losses in excess of US$ 160 million [16].

Large numbers of studies have been conducted on T. vivax over the past 100 years. Studies before 1950's focused more on the morphology and taxonomy [22, 23], pathogenicity [24] and treatment [25, 26]. However, since the 1950’s, a considerable number of epidemiological studies have been conducted. Notwithstanding the excellent review on livestock trypanosomoses and their vectors in Latin America [18] and a recent general review on T. vivax [20], a systematic literature review on the global distribution, prevalence and host range of T. vivax is lacking. Moreover, no information on the global distribution of T. vivax is available at the World Animal Health Information System of the World Health Organisation (https://www.oie.int/wahis_2/public/wahid.php/Diseaseinformation/Diseasedistributionmap). Thus, this study was conducted to provide the global distribution of T. vivax and to estimate the pooled prevalence of trypanosomosis caused by T. vivax in naturally infected domestic and wild animals.

Methods

The systematic review and meta-analysis were conducted according to the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) checklist [27]. Screening and data extraction were performed by two authors (SL and EF) independently. All disagreements were discussed and resolved by consensus. A third author (PB) was also involved in the search for full text papers to ensure that all relevant publications were included.

Literature search
On 30th August 2019, a systematic literature search was conducted on three databases to identify all publications reporting natural infection of *T. vivax* across the world. PubMed, Scopus and CAB Direct were screened using the search term *Trypanosome vivax* without time and language restrictions. All references found were imported into Mendeley Desktop, reference manager software.

**Inclusion and exclusion criteria**

To be considered articles were required to meet the following inclusion criteria: (1) should be observational studies, published in indexed journals, reporting any natural infection of *T. vivax* using any diagnostic test or tests available; (2) the study design, sample size, sample type, diagnostic methods, and number of *T. vivax* infected individuals or prevalence, including 0%, must be provided; (3) species of animals with *T. vivax* infections must be provided. Experimental studies, publications which fail to describe diagnostic tools, study design and/or sample sources and reports solely based on clinical signs were removed despite reporting the prevalence of the disease. In addition, studies reporting *T. vivax* from multiple species without stratifying the report at species level were removed.

**Data extraction**

All relevant information such as author names, year of publication, study period, country, region, province, district, latitude, longitude (if provided or if they can be retrieved), host species, number of samples analyzed, type of samples collected, diagnostic method used, number of positives and prevalence or percentage were extracted to a pre-prepared Microsoft Excel spreadsheet (Microsoft Corp., Redmond, Washington, USA). When publications only reported the number of animals tested and the prevalence, the numbers of positives were calculated. When publications only reported the number of animals tested and the number of positives, prevalence values were calculated. Publications in other languages than English were translated using Google Translate.

**Data analysis**

Owing to heterogeneity within and between studies, random-effects meta-analysis was used to estimate the pooled prevalence and its 95% confidence interval (CI) in different hosts [28]. The estimation was carried out after categorization of the results according to the diagnostic tests used and the host species tested. Accordingly, diagnostic tests were categorized into three categories: (i) parasitological methods, including wet blood smear, stained blood smear, and microhematocrit concentration; (ii) serological methods, including enzyme-linked immunosorbent assay (ELISA) both antigen and antibody based, indirect fluorescence antibody test (IFAT) and antigen detection LATEX agglutination; (iii) molecular methods, including reverse line blot hybridization assay, real-time and conventional polymerase chain reaction (PCR). Species-wise, sheep and goat were categorized into “small ruminants”, horse, donkey and mule into “equine”, water buffalo and buffalo into “buffalo” and all studied wild animals including Cape buffalo into “wild animals”. For cattle, dromedary camel, pig and dog, pooled prevalence was estimated without categorization.

Heterogeneity between studies was evaluated through the Cochran’s Q test (reported as p value) and the inverse variance index ($\hat{I}^2$). $\hat{I}^2$ describes the percentage of observed total variation between studies that is due to heterogeneity rather than to random error (intra-study variation). $\hat{I}^2$ values less than 25% correspond with low heterogeneity, up to 50% with moderate and up to 75% with high heterogeneity [29]. Sub-group analysis using the variable test method was performed to determine the potential sources of heterogeneity among studies. The across study bias was examined by a funnel plot and Egger's regression asymmetry test. Funnel plot was used to visually examine the presence of publication bias and Egger's regression asymmetry test was used to test whether the bias is statistically significant or not [30]. The unbiased estimates were calculated using Duval and Tweedie non-parametric 'fill and trim' linear random method [31].

The meta-analysis was done using ‘meta’ package of R statistical software version 3.6.2 (R Foundation for Statistical Computing). The map representing the global distribution of *T. vivax* was created, using Quantum GIS software version 3.4.5 (Open Source Geospatial Foundation, Boston, USA).

**Results**

**Literature search selection and data extraction**

A total of 1691 publications were retrieved, 348 from PubMed, 1269 from Scopus and 74 from CAB Direct (Figure 1). After removal of 390 duplicates, the remaining 1301 publications were screened based on their titles and abstracts. Reviews and articles reporting on laboratory and field experiments (n=993) were excluded of further analysis. Articles without abstract or without sufficient information to take a decision were left for full text review. Of the remaining 308 articles, 11 the full text file remained inaccessible [32,33,42,34–41]. Finally, one additional reference, missed by the systematic literature search, was included. Full text papers of 298 articles were retrieved online or via the library of the Institute of Tropical Medicine Antwerp and eligibility assessed according to the pre-established inclusion/exclusion criteria. A further 53 articles were excluded thus leaving 245 articles fulfilling all inclusion criteria for the meta-analysis [4,5,43,133–142,44,143–152,45,153–162,46,163–172,47,173–182,48,183–192,49,193–202,50,203–212,51,213–222,52,223–232,53,233–242,54,243–252,55,253–262,56,263–272,57,273–277,58–62,7,63–72,8,73–82,9,83–92,10,93–102,12,103–112,13,113–122,14,123–132]. Among these 245 articles published between 1958 and 2019, 10 are case reports, 186 report on a cross sectional study, 35 on a longitudinal study and 14 on an outbreak investigation. All relevant data from these articles were recorded, according to diagnostic method and host species, in a Microsoft Excel file thus containing 899 records used in the meta-analysis (Supplementary file S1).

Of these 245 articles, 187 reported on studies conducted in 27 African countries, with Ethiopia taking the lead with 43 articles, followed by Nigeria with 29, Uganda with 21 and Kenya with 15 articles. Studies conducted in Latin America (including the French departments Martinique and French Guiana) were reported in 57 articles of which 32 from Brazil, 9 from Venezuela and 6 from Colombia.

**Geographic distribution**

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All the studies conducted in the 27 African countries reported the presence of *T. vivax* in at least one host species; natural *T. vivax* infections were found in 12 of the 13 studied Latin American countries (Figure 2 and Table 1). In Martinique, Alonso and co-workers didn’t find clinical nor serological evidence of *T. vivax* in cattle on this island [50]. One article mentions a cross-sectional study on 300 equines in Pakistan, but all animals were negative in molecular tests for *T. vivax* [231]. We couldn’t find any other reports on the presence of *T. vivax* in Asia, Antarctica, Australia, Europe and North America.

**Host range**

A total of 232,627 tests were performed and 24,420 of them were positive for natural infection of *T. vivax*. *Trypanosoma vivax* was reported from 9 domestic animal species: buffalo, cattle, dog, donkey, dromedary camel, goat, horse, pig and sheep. Among them, cattle were the most studied species with 198,593 tests performed on cattle in 36 countries and two territories (192 publications) and 20,964 were positive for *T. vivax*. Next to cattle, goat, sheep, pigs and donkey were the most frequently studied species. The protozoal parasite was also reported from wild animals including diverse species of antelopes, Cape buffalo, hippopotamus, black rhinoceros, pangolin and warthog. *Trypanosoma vivax* was reported from 39 wild fauna species, including many antelope species and Cape buffalo (Table 2 and 3).

**Pooled prevalence estimates according to host species and type of diagnostic test**

Pooled prevalence estimates by test methods for different hosts are presented in Table 4 and funnel plots of the meta-analysis and the subgroup analyses can be found in Supplementary files S2 and S3. Substantial heterogeneity was observed in the pooled estimate except for dog, which remained significant even after sub-group analysis.

*Cattle*: a total of 145 cross-sectional studies from 32 countries were included in estimation of natural infection of *T. vivax* in cattle. The random effect model indicates the pooled prevalence to be 6.4% (5.7-7.2, 95% CI). High in between studies heterogeneity was observed with 96.8% Higgins I^2^ test and P=0 Cochran's Q test. Small ruminants: pooled prevalence of *T. vivax* estimated from 33 studies in 16 countries was found to be 3.8% (2.5-5.6, 95% CI). The 93.2% I^2^ and P<0.0001 Cochran's Q test values indicate high in between studies heterogeneity. *Equines*: a total of 15 studies from ten different countries were used to estimate the pooled prevalence of *T. vivax* in equines. The random effect model estimates the pooled prevalence to be 3.7% (2.0-6.8, 95% CI). High in between studies heterogeneity was observed with 88.9% I^2^ test value and P=0.0001 Cochran's Q test. *Camel*: pooling the prevalence of *T. vivax* in camels was estimated from four studies in three different countries. The model estimates a pooled prevalence of 8.4% (3.4-19.3, 95% CI) with 94.8% I^2^ statistics and P=0.0001 Cochran's Q test which indicates high in between studies heterogeneity. *Pig*: a total of 12 studies from eight different countries were included in the estimation of pooled prevalence in pigs which was found to be 5.5% (3.0-10.1, 95% CI). High in between studies heterogeneity was observed by 90.1% I^2^ statistic test and P=0.0001 Cochran's Q test. *Dog*: five studies from five countries were used in the estimation pooled prevalence of *T. vivax* in dogs. The pooled prevalence was estimated to be 2.6% (1.0-6.3, 95% CI). Low in between studies heterogeneity is indicated with 5.9% I^2^ and P=0.3859 Cochran's Q test values. *Buffalo*: three studies reported natural infection of *T. vivax* in domestic buffaloes from Venezuela and the random effect model estimates a pooled prevalence of 30.6% (14.2-54.1, 95% CI) with high in between studies heterogeneity of 98.4% I^2^ and P<0.0001 Cochran's Q test values. *Wild animals*: a pooled prevalence of 12.9% (9.9-16.6, 95% CI) was estimated from six studies in five countries. High in between studies heterogeneity was indicated in 76.7% I^2^ Higg's test and P<0.0001 Cochran's Q test value.

Subgroup pooled prevalences estimated according to the type of diagnostic test, as represented in Table 4, were lowest with parasitological techniques (from 1.1% in pigs to 13.2% in wild animals) and highest with serological techniques (from 13.8% in small ruminants to 57.6% in buffalo).

**Publication bias**

The presence of publication bias was analyzed only in five species since there were not enough publications to discuss its possible influence in camel, buffalo and dogs. Possible publication bias was demonstrated by visualization of asymmetry in funnel plots for cattle (Figure 3A), small ruminants (Figure 3B), equines (Figure 3C), pigs (Figure 3D) and wild animals (Figure 3E). It was further confirmed by ‘metabias’ test (Egger's test) with p value less than 0.05. The ‘trimfill’ method imputed 170, 43, 30, 27 and 11 studies to obtain symmetry in funnel plots in cattle, wild animals, equines, small ruminants and pigs respectively. The new estimated prevalence equals to 14.8% for cattle, 26.8% for wild animals, 21.6% for equines, 9.5% for small ruminants and 24.5% for pigs.

**Discussion**

This study presents the first systematic review of published literature since the 1950s describing global distribution, host range and prevalence of trypanosomosis caused by *T. vivax*. Not surprisingly, most publications report on *T. vivax* infections in domestic mammalian species, in particular in cattle and small ruminants, while few publications describe natural infections in wildlife.

Looking at the *T. vivax* distribution map (Fig. 1), there is an evident data gap for some sub-Saharan African countries where tsetse flies are present and therefore *T. vivax* may be endemic. Although our formal search strategy couldn’t retrieve any publication on these “missing” countries, conventional Google search confirms the presence of *T. vivax* in South Sudan and Zimbabwe [285, 286] and Genevieve et al [287] reported on the presence of potential vectors in Central African Republic. Since Angola, the Central African Republic and the Republic of Congo are endemic for human African trypanosomosis, the presence of *T. vivax* in these countries is likely [288]. Due to its adaptation to mechanical transmission, *T. vivax* is also present outside the tsetse belt in Africa, e.g. in Ethiopia and Sudan [114, 289]. As a consequence, the trypanosomosis control efforts with focus on tsetse eradication might have little effect on *T. vivax*. Also, economic impact assessments that are solely based on tsetse distribution alone could seriously underestimate the problem of trypanosomosis due to *T. vivax*.

Out of Africa, *T. vivax* is present in Latin America but not in North America, Australia, Asia and the Pacific regions. *T. vivax* is believed to be introduced into Latin America in cattle and horse imported from Africa, possibly in the 16th century and spread to different Latin American countries including Brazil,
Colombia, French Guiana, Guadeloupe, Guyana, Martinique, Panama, Suriname and Venezuela. Stephen reviewed the presence of the parasite in Costa Rica, Ecuador, El Salvador, Paraguay, and Peru and according to Gardiner et al (15), T. vivax was present in the Caribbean thus posing a threat to the livestock industries. From our literature search we can only confirm T. vivax to be endemic in 12 Latin American countries of which 7 (Argentina, Bolivia, Brazil, Colombia, Guyana, Peru, Venezuela) are also endemic for T. evansi (291). Apparently, T. vivax has never spread into Asia, unlike T. evansi although similar to the latter; it can be mechanically transmitted by bloodsucking flies. Unless there is a particular biological or environmental factor preventing T. vivax to invade the Middle East and Asia, as well Northern Africa, North America and Europe, we must remain alert about the risk of importing T. vivax into non-endemic countries as it happened with Latin America.

This review suggests that T. vivax has a very diverse host range, including 9 domestic mammals and almost 40 wild fauna species. Regarding the latter however, data should be interpreted with caution. Diagnostic tests, whether parasitological, serological or even molecular, have their limitations. For examples, by sequencing of PCR amplicons, Auty and co-workers (11) clearly demonstrate that wildlife may harbor a diversity of trypanosomes, including taxonomically undefined species. Therefore, it is likely that many reports on T. vivax infection in wildlife and tsetse in fact deal with other trypanosome species that are not necessarily pathogenic for domestic animals.

The pooled prevalence of trypanosomosis in different hosts varies significantly depending on the detection methods; significantly higher estimates were reported in publications using serological techniques. Higher estimates using serological technique could be due to the persistence of antibody over several months after curative treatment and the possibility of low undetectable parasitemia in parasitological techniques (20, 93, 292, 293). Moti et al (187) compared the percentage positivity obtained with different diagnostic techniques and showed that relative to the microhaematocrit centrifugation technique, the percent positivity increased by 50 and 250% when using PCR-RFLP. Also Garcia et al (118) reported that the detection of trypanosomes, PCR-based assays are twice as sensitive as parasitological techniques such as the microhaematocrit centrifugation.

The study has the following limitations. The literature search was almost exclusively based on electronic databases whereby some older literature must have been missed. The data showed a large degree of heterogeneity among studies, which remain significant after sub-group analysis. There is a significant publication bias which could be due to incomplete or inaccurate information provided in the publications. In addition, studies were conducted between 1956 and 2017 and the result may not accurately reflect the current epidemiological situation and therefore could limit interpretation of the result to some degree. Furthermore, we suspect numerous data gaps mainly because of two reasons. Firstly, due to lack of a country level monitoring and reporting system for trypanosomosis, most of the data included in this analysis is from research activities. Secondly, trypanosomosis diagnosis in most endemic countries relied to a great extent on low-sensitivity parasitological methods, while more sensitive molecular tools are rarely used. Thus, prevalences presented here may significantly underestimate the real situation and the economic impact of T. vivax trypanosomosis in Africa and Latin America.

Conclusion

With this study, we intended to provide comprehensive information on the geographical distribution, host range and prevalence of trypanosomosis caused by T. vivax worldwide. The results confirm the wide geographical distribution and a diverse host range of T. vivax. The parasite parasitizes almost all domestic mammals and many wild animal species thus suggesting the potential to get established in other countries with favorable environmental conditions, e.g. in the Middle East, Asia and Australia. The meta-analysis showed a high degree of variability in estimated prevalence values. The variability can be attributed to diagnostic tests used and the species of the animal infected.

Declarations

Funding

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Availability of data and materials

All data analyzed in this paper are provided as supplementary file.

Authors’ contributions

PB. and F.R. conceived the research and S.L. designed the research, and E.F. and S.L. drafted the manuscript. E.F., S.L. and PB. extracted and compiled the data. All authors read and approved the final version.

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.
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**Tables**

**Table 1**: Countries with reported *T. vivax* infection in diverse host species tested with diverse methods
| Country                        | Host species studied                                                                 | Test method                                                                 | Number of tests (total = 232,627) | Number of positives (total = 24,420) | References                                                                 |
|-------------------------------|--------------------------------------------------------------------------------------|------------------------------------------------------------------------------|------------------------------------|-------------------------------------|---------------------------------------------------------------------------|
| Argentina                     | Cattle                                                                               | Reverse line blot                                                           | 186                                | 16                                  | [217]                                                                     |
| Benin                         | Buffoon kob, cattle, hartebeest, roan antelope, warthog, waterbuck                  | Thin and thick blood smears                                                  | 312                                | 205                                 | [10, 99]                                                                  |
| Bolivia                       | Cattle                                                                               | Thin blood smear, Giemsa stained blood smear, PCR                           | 1520                               | 311                                 | [123, 177, 243]                                                           |
| Botswana                      | Cape buffalo, cattle, donkey, goat, greater kudu, impala, lechwe, reedbuck, sable antelope, tsesebe | MHCT/Woo test, Giemsa stained thick and thin blood smear, PCR                 | 3040                               | 399                                 | [100, 239]                                                                |
| Brazil                        | Cattle, donkey, goat, horse, pampas deer, sheep, water buffalo                      | MHCT/Woo test, PCR, IFAT, thin and thick blood smear,uffy coat smear, Ab-ELISA, PCR | 11468                              | 4079                                | [4, 51, 83–85, 91, 94, 112, 116, 125–127, 58, 154, 156, 212, 219, 220, 226, 228, 242, 244, 250, 59, 274, 277, 60–62, 71, 72, 81] |
| Burkina Faso                  | Cattle                                                                               | Buffy coat smear, Ag-ELISA, Ab-ELISA, PCR                                   | 11095                              | 1095                                | [65, 90, 151, 216, 241, 251–253]                                          |
| Cameroon                      | African civet, black legged mongoose, black striped duiker, blue duiker, bosman potto, brush tailed porcupine, cattle, cloaked mangabey, crested mangabey, crocodile, dark mangoose, de Brazza's monkey, dog, dwarf guennon, giant forest squirrel, giant rat, goat, golden cat, golden potto, greater cane rat, greater white-nosed monkey, guereza white colobus, long-tailed pangolin, mandrill, mona monkey, monitor lizard, moustached monkey, ogilby's duiker, Peter's duiker, pig, red-legged sun squirrel, royal antelope, sheep, sitatunga, small-spotted genet, tree dassie, tree pangolin, two-spotted palm civet, water chevrotain, white-eyelid mangabey, yellow-backed duiker | Buffy coat smear, PCR                                                        | 4176                               | 406                                 | [7, 13, 14, 170, 202, 245][7, 13, 14, 170, 202, 245]                      |
| Chad                          | Cattle                                                                               | Buffy coat smear, Ab-ELISA                                                  | 1866                               | 435                                 | [93]                                                                      |
| Colombia                      | Cattle, goat, sheep                                                                    | Blood smear, PCR, IFAT                                                        | 6712                               | 1699                                | [135, 136, 215, 221, 232, 274]                                            |
| Costa Rica                    | Cattle                                                                               | Blood smear, IFAT                                                            | 642                                | 53                                  | [210, 274]                                                                |
| Côte d'Ivoire                 | Cattle, goat, pig, sheep                                                               | MHCT/Woo test, PCR                                                           | 2185                               | 195                                 | [45, 148, 197]                                                            |
| Democratic Republic of the Congo | Cattle, dog, goat, pig, sheep                                                          | MHCT/Woo test, ELISA                                                         | 685                                | 41                                  | [167, 168]                                                                |
| Ecuador                       | Cattle                                                                               | IFAT                                                                         | 310                                | 70                                  | [274]                                                                     |
| Country          | Species                | Method                          | Positive | Negative | Reference Numbers               |
|------------------|------------------------|---------------------------------|----------|----------|---------------------------------|
| El Salvador      | Cattle                 | IFAT                            | 100      | 15       | [274]                           |
| Equatorial Guinea| Goat, sheep            | PCR                             | 559      | 10       | [79]                            |
| Ethiopia         | Cattle, donkey, dromedary camel, goat, horse, mule, sheep | Giemsa stained blood smear, blood smear, buffy coat smear, MHCT/Woo test, thin and thick blood smear, Ab-ELISA, PCR | 55196    | 2600     | [6,43,86,79,92,98,101,103,107,113–115,44,122,142,144,145,152,178–182,48,184,187,191,229,230,240,248,257,258,262,64,264–266,69,70,74–76] |
| French Guiana    | Cattle                 | Ag-ELISA                        | 3000     | 870      | [95]                            |
| Gabon            | Cattle                 | Buffy coat smear, Ag-ELISA, PCR  | 442      | 26       | [80,157,268]                    |
| Gambia           | Cattle, donkey, goat, horse, sheep | Buffy coat smear, Giemsa stained blood smear, Ab-ELISA, PCR | 5745     | 1329     | [8,96,102,173,213,218]          |
| Ghana            | Cattle, goat, pig, sheep | Buffy coat smear, PCR, Ag-latex agglutination test | 1786     | 231      | [46,117,143,198]               |
| Guyana           | Goat, sheep            | MHCT/Woo test, IFAT              | 467      | 15       | [55,272]                       |
| Kenya            | Black rhinoceros, cattle, dromedary camel, goat, horse, pig, sheep | Thin and thick blood smear, Giemsa stained blood smear, buffy coat smear, MHCT/Woo test, Ag-ELISA, PCR | 5156     | 845      | [66,146,209,227,261,267,275,172,174,183,185,196,200,201,208] |
| Liberia          | Cattle                 | Giemsa stained blood smear, IFAT, Ab-ELISA | 700      | 327      | [155,176]                      |
| Malawi           | Cattle                 | Giemsa stained blood smear       | 9309     | 9        | [271]                          |
| Mali             | Cattle                 | Buffy coat smear                 | 796      | 34       | [192]                          |
| Martinique       | Cattle                 | IFAT                            | 227      | 0        | [50]                           |
| Mozambique       | Cattle                 | Blood smear                      | 16895    | 1245     | [254]                          |
| Namibia          | Cattle                 | Giemsa stained thick and thin blood smear, MHCT | 1481     | 15       | [270]                          |
| Nigeria          | Cattle, dog, goat, horse, sheep | Blood smear, Giemsa stained blood smear, MHCT/buffy coat smear, MHCT/Woo test, Ag-ELISA, PCR | 20080    | 2926     | [52,53,110,134,137–140,153,166,206,207,63,211,214,234–237,259,269,276,88,89,104–106,108,109] |
| Pakistan         | Donkey, horse, mule    | PCR                             | 300      | 0        | [231]                          |
| Paraguay         | Cattle                 | IFAT                            | 15       | 6        | [274]                          |
| Country        | Species                  | Tests and Methods                                                                 | Numbers | References |
|---------------|--------------------------|------------------------------------------------------------------------------------|---------|------------|
| Peru          | Cattle                   | Blood smear, MHCT/Woo test, Giemsa stained blood smear, IFAT, PCR                   | 985     | [171,177,222,274] |
| Rwanda        | Cattle                   | Blood smear                                                                        | 3630    | [12]       |
| Senegal       | Cattle, dog, donkey, goat, horse, sheep | Buffy coat smear, blood smears, Ab-ELISA, PCR                                    | 4890    | [111,128,129,225,238] |
| South Africa  | Cattle                   | PCR                                                                                | 143     | [169]      |
| Sudan         | Cattle, donkey, dromedary camel, horse | Blood smear                                                                        | 4426    | [132,186,223,233] |
| Tanzania      | African civet, bohor reedbuck, cattle, Coke's hartebeest, giraffe, Grant's gazelle, hunting dog, impala, Kirk's dikkid, klipspringer, Lichtenstein's hartebeest, oribi, oryx, ostrich, pig, roan antelope, southern reedbuck, steinbuck, Thomson's gazelle, tsessebe, warthog, wildebeest, zebra | Blood smear, thin and thick blood smear, Giemsa stained blood smear, buffy coat smear, PCR, PCR-LAMP | 9974    | [5,56,194,203,247,256,78,130,131,133,141,147,149,188] |
| Togo          | Cattle                   | PCR-RFLP                                                                           | 354     | [263]      |
| Uganda        | Cattle, dog, donkey, goat, pig, sheep | Giemsa stained blood smear, MHCT/Woo test, thick and thin blood smear, buffy coat smear, Ab-ELISA, PCR | 28510   | [47,49,160–165,189,190,195,205,54,273,57,67,68,77,82,158,159] |
| Venezuela     | Cattle, horse, sheep, water buffalo | MHCT/Woo test, stained blood smear, IFAT, Ab-ELISA, PCR                        | 6328    | [73,118–121,124,224,255,260] |
| Zambia        | African civet, baboon, bat, black rhinoceros, bushbuck, cane rat, Cape buffalo, cattle, crocodile, eland, elephant, genet, giraffe, goat, greater kudu, grey duiker, grysbok, hare, hartebeest, hippopotamus, hunting dog, hyena, impala, jackal, leopard, lion, mongoose, pig, porcupine, puku, reedbuck, roan antelope, serval, vervet monkey, warthog, waterbuck, wild cat, wildebeest, zebra | PCR, buffy coat smear | 6936    | [9,97,150,175,193,199,204,246] |

Footnote: Ab-ELISA = Antibody enzyme-linked immunosorbot assay, Ag-ELISA= antigen enzyme-linked immunosorbot assay, MHCT = micro hematocrit centrifugation technique, IFAT = immunofluorescence antibody test, PCR = Polymerase chain reaction, PCR-LAMP = Polymerase chain reaction - Loop mediated isothermal amplification, PCR-RFLP= Polymerase chain reaction-restriction fragment length polymorphism

Table 2: Domestic animal species tested for infection with *T. vivax*; *T. vivax* was not observed in Martinique and Pakistan
| Species      | List of countries                                                                 | Number of tests | Positive animals | References                                                                 |
|-------------|-----------------------------------------------------------------------------------|-----------------|------------------|---------------------------------------------------------------------------|
| Cattle      | Argentina, Benin, Bolivia, Botswana, Brazil, Burkina Faso, Cameroon, Chad, Colombia, Costa Rica, Côte d'Ivoire, Democratic Republic of the Congo, Ecuador, El Salvador, Ethiopia, French Guiana, Gabon, Gambia, Ghana, Kenya, Liberia, Malawi, Mali, Martinique*, Mozambique, Namibia, Nigeria, Paraguay, Peru, Rwanda, Senegal, South Africa, Sudan, Tanzania, Togo, Uganda, Venezuela, Zambia | 198593          | 20964            | [4, 5, 48, 171, 173–177, 180, 182, 184, 185, 49, 187–196, 50, 197–200, 202, 203, 205–208, 51, 209–212, 214–21 227, 229, 230, 232, 233, 53, 236, 238–243, 246–248, 54, 249–258, 57, 259, 261–269, 58, 270, 271, 273, 274, 276– 281, 282, 283, 61, 62, 64–66, 68–71, 73, 12, 74–78, 80–83, 85, 14, 86–88, 90–95, 99, 40, 101– 103, 105, 106, 108, 109, 111, 113, 114, 44, 116, 118, 122, 123, 125–127, 129–131, 45, 132, 134–136, 138, 139, 14* 149, 151–153, 155–158, 47, 159, 161–167, 169, 170] |
| Dromedary camel | Ethiopia, Kenya, Sudan                                                             | 1611            | 133              | [6, 115, 172, 186]                                                         |
| Dog         | Cameroon, Democratic Republic the Congo, Nigeria, Senegal, Uganda                 | 574             | 1                | [7, 137, 158, 168, 214, 225]                                               |
| Donkey      | Botswana, Brazil, Ethiopia, Pakistan*, Sudan, Uganda                               | 2713            | 152              | [6, 8, 233, 239, 248, 43, 96, 107, 178, 189, 225, 228, 231]                |
| Goat        | Botswana, Brazil, Cameroon, Colombia, Côte d'Ivoire, Democratic Republic of the Congo, Equatorial Guinea, Ethiopia, Gambia, Ghana, Guyana, Kenya, Nigeria, Senegal, Uganda, Zambia | 9715            | 526              | [6, 7, 128, 137, 140, 143, 144, 150, 158, 168, 179, 193, 55, 197, 201, 204, 211, 213, 218, 221, 225, 234, 237, 57, 239, 24] |
| Horse       | Brazil, Ethiopia, Gambia, Kenya, Nigeria, Pakistan*                                | 3305            | 857              | [8, 84, 233, 96, 104, 118, 146, 181, 214, 225, 231]                         |
| Species            | Countries                                      | Positive | Positive/Total | References          |
|--------------------|------------------------------------------------|----------|----------------|---------------------|
| Mule               | Ethiopia, Pakistan*                            | 353      | 0              | [43,181,231,248]    |
| Pig                | Cameroon, Côte d’Ivoire, Democratic Republic of the Congo, Ghana, Kenya, Tanzania, Uganda, Zambia | 2650     | 233            | [7,57,245,246,67,68,133,158,168,197,198,201] |
| Sheep              | Brazil, Cameroon, Colombia, Côte d’Ivoire, Democratic Republic of the Congo, Equatorial Guinea, Ethiopia, Gambia, Ghana, Guyana, Kenya, Nigeria, Senegal, Uganda, Zambia | 6447     | 455            | [6,7,128,134,137,140,143,144,168,197,201,213,55,221,225,234,248,272,57,60,79,98,116,118,120] |
| Small ruminants    | Kenya, Nigeria                                 | 988      | 69             | [89,110,227]        |
| Water buffalo      | Brazil, Venezuela                              | 2144     | 509            | [116,118,119,121,260] |

**Table 3:** Wild animal species tested positive for *T. vivax* infection
| Host species             | Scientific name     | Country          | Number of tests | Positive tests | Positivity rate | References |
|-------------------------|---------------------|------------------|-----------------|----------------|----------------|------------|
| Black rhinoceros        | Diceros bicornis    | Kenya            | 1               | 1              | 100            | [284]      |
| Black striped duiker    | Cephalophus dorsalis| Cameroon         | 37              | 3              | 8.1            | [13]       |
| Blue duiker             | Cephalophus monticola| Cameroon         | 290             | 24             | 8.3            | [13]       |
| Bosman potto            | Perodicticus potto | Cameroon         | 8               | 3              | 37.5           | [13]       |
| Brush tailed porcupine  | Atherurus africanus | Cameroon         | 106             | 7              | 6.6            | [13]       |
| Buffoon kob             | Kobus kob          | Benin            | 50              | 1              | 2              | [10]       |
| Bushbuck                | Tragolaphus scriptus| Zambia           | 51              | 4              | 7.8            | [97]       |
| Cape buffalo            | Syncerus caffer    | Botswana, Zambia | 1105            | 285            | 25.8           | [9,97,100] |
| Cloaked mangabey        | Cercopithecus albigena | Cameroon         | 12              | 2              | 16.7           | [13]       |
| Crocodile               | Crocodylus niloticus| Cameroon         | 3               | 1              | 33.3           | [13]       |
| De Brazza's Monkey      | Cercopithecus neglectus | Cameroon       | 1               | 1              | 100            | [13]       |
| Dwarf guenon            | Miopithecus tlapoin| Cameroon         | 55              | 5              | 9.1            | [13]       |
| Eland                   | Taurotragus oryx   | Zambia           | 3               | 1              | 33.3           | [97]       |
| Giant rat               | Cricetomys gambianus| Cameroon         | 135             | 4              | 2.9            | [13]       |
| Greater kudu            | Tragelaphus strepsicus | Botswana, Zambia | 36              | 26             | 72.2           | [97,100]  |
| Greater white-nosed monkey | Cercopithecus nictitans | Cameroon      | 155             | 22             | 14.2           | [13]       |
| Grey duiker             | Sylvicapra grimmia | Zambia           | 7               | 1              | 14.3           | [97]       |
| Guereza white colobus   | Colobus guereza    | Cameroon         | 14              | 2              | 14.3           | [13]       |
| Hartebeest              | Alcelaphus bubalis | Benin            | 20              | 1              | 5              | [10]       |
| Hippopotamus            | Hippopotamus amphibius | Zambia        | 29              | 1              | 3.4            | [9]        |
| Impala                  | Aepyceros melampus | Botswana         | 23              | 14             | 60.9           | [100]      |
| Lechwe                  | Kobus leche        | Botswana         | 110             | 39             | 35.5           | [100]      |
| Long tailed pangolin    | Manis tetradactyla | Cameroon         | 34              | 2              | 5.9            | [13]       |
| Mona monkey             | Cercopithecus mona | Cameroon         | 46              | 8              | 17.4           | [13]       |
| Monitor lizard          | Varanus omatus     | Cameroon         | 8               | 1              | 12.5           | [13]       |
| Moustached monkey       | Cercopithecus cephus| Cameroon        | 101             | 11             | 10.9           | [13]       |
| Oryx                    | Oryx beisa         | Tanzania         | 1               | 1              | 100            | [56]       |
| Puku                    | Kobus vardonii     | Zambia           | 24              | 1              | 4.2            | [97]       |
| Reedbuck                | Redunca sp.        | Botswana, Zambia | 3               | 3              | 100            | [9,100]   |
| Sable antelope          | Hippotragus niger  | Botswana         | 22              | 7              | 31.8           | [100]      |
| Sitatunga               | Tragelaphus spekei | Cameroon         | 5               | 1              | 20             | [13]       |
| Small-spotted genet     | Genetta servalina  | Cameroon         | 8               | 1              | 12.5           | [13]       |
| Southern reedbuck       | Redunca arundinum  | Tanzania         | 4               | 1              | 25             | [56]       |
| Tree pangolin           | Manis tricuspis    | Cameroon         | 20              | 5              | 25             | [13]       |
| Tsessebe                | Damaliscus lunatus | Botswana         | 15              | 6              | 40             | [100]      |
| Two-spotted palm civet  | Nandinia binotata  | Cameroon         | 32              | 3              | 9.4            | [13]       |
| Warthog                 | Phacochoerus aethiopicus | Zambia      | 56              | 1              | 1.8            | [9]        |
| Waterbuck               | Kobus ellipsiprymnus| Zambia          | 30              | 19             | 63.3           | [9,97]     |
| White-eyed mangabey     | Cercopithecus torquatus | Cameroon    | 5               | 2              | 40             | [13]       |

Table 4: Sub group Meta-analysis for different species using different diagnostic methods
| Host species  | Diagnostic method | Number of publications | Number of tests | Number of positives | Pooled prevalence in % | 95% CI |
|--------------|-------------------|------------------------|----------------|---------------------|------------------------|--------|
| Water buffalo| Parasitological   | 1                      | 316            | 36                  | 11.4                   | 8.3-15.4 |
|              | Molecular         | 2                      | 609            | 127                 | 20.9                   | 17.4-25.0 |
|              | Serological       | 2                      | 556            | 301                 | 57.6                   | 22.5-86.4 |
| Camel        | Molecular         | 4                      | 1611           | 133                 | 8.4                    | 3.4-19.3 |
| Cattle       | Parasitological   | 92                     | 102910         | 5414                | 4.6                    | 4.0-5.3  |
|              | Molecular         | 51                     | 31549          | 3140                | 7.4                    | 6.2-8.7  |
|              | Serological       | 23                     | 16469          | 4495                | 34.6                   | 28.0-41.9 |
| Dog          | Parasitological   | 3                      | 257            | 0                   | 3.4                    | 1.1-9.6  |
|              | Molecular         | 2                      | 189            | 1                   | 1.2                    | 0.2-8.5  |
| Equine       | Parasitological   | 8                      | 2471           | 20                  | 1.5                    | 0.9-2.6  |
|              | Molecular         | 7                      | 1425           | 251                 | 5.6                    | 2.7-11.3 |
|              | Serological       | 1                      | 6              | 3                   | 50.0                   | 16.8-83.2 |
| Pig          | Parasitological   | 4                      | 799            | 3                   | 1.1                    | 0.4-2.9  |
|              | Molecular         | 10                     | 1851           | 230                 | 9.0                    | 4.9-15.9 |
| Small ruminant| Parasitological | 19                     | 8990           | 220                 | 2.3                    | 1.5-3.6  |
|              | Molecular         | 15                     | 4045           | 327                 | 5.0                    | 2.7-9.3  |
|              | Serological       | 3                      | 408            | 43                  | 13.8                   | 6.1-28.4 |
| Wild animal  | Parasitological   | 3                      | 1093           | 75                  | 11.8                   | 7.1-16.9 |
|              | Molecular         | 3                      | 1618           | 121                 | 10.7                   | 8.6-13.3 |
|              | Serological       | 1                      | 748            | 318                 | 49.3                   | 37.5-61.2 |