



Of bats and livestock: The epidemiology of rabies in Trinidad, West Indies

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ABSTRACT

Vampire bat-transmitted human rabies was first recognized in Trinidad during a major outbreak during the first half of the 20th century. To date, Trinidad is the only Caribbean island with vampire bat-transmitted rabies. Herein, we summarized the epidemiological situation of rabies in Trinidad during the period 1971–2015 through the analysis of field and laboratory records. During the study period, 259 domestic and wild animal rabies cases were laboratory confirmed with an annual median of 2 animal rabies cases. Over the 45 years, five significant epizootic events occurred (in 1974, 1997–1998, 2000, 2010 and 2012–2013) over which there was a significant increasing trend for the occurrence of rabies cases. The highest number of cases (87 cases) occurred during the 1997–1998 event, and the rabies positive proportion, was highest (0.7, 95% CI 0.52–0.84) for the year 2000. Rabies risk was highest for cattle (negative binomial parameter estimate 4.84, 95% CI 3.45–6.76), although numerous rabies cases were seen in the caprine population during the study period. In light of this finding, consideration should be given to including the small ruminant population in the national rabies vaccination program. Outbreaks affected mainly the counties of St. Patrick and St. George East, with epidemic progression outwards, and these areas should be prioritized for prevention and control efforts.

1. Introduction

Rabies is a neglected viral zoonosis of major global public health and veterinary importance (Blanton and Rupprecht, 2008; Rupprecht et al., 2002; Schneider et al., 2009; World Health Organization, 2010). Although dogs are the major reservoir in Africa and Asia, in the Americas, bats are considered primary reservoirs of rabies viruses (Greenhall, 1985; Nadin-Davis et al., 2001; Rupprecht et al., 2002). Found only in the New World, vampires bats (subfamily Desmodontinae) are the most important bat species associated with rabies (Johnson et al., 2014) and vampire bat-transmitted rabies is increasingly considered a limiting factor for livestock development in this region (Greenhall, 1968a; World Health Organization, 1966, 2013).

Trinidad is the only Caribbean island with vampire bat-transmitted rabies. The island is part of the twin island republic of Trinidad and Tobago and is located approximately 12 km off the northeastern coast of Venezuela, South America (see Fig. 1) covering an area of 4768 km². In Trinidad, during 1931, the correlation between vampire bats and

human paralytic rabies was demonstrated, for the first time, during a multi-species encephalitis outbreak from 1925 to 1937 (Baer, 1991; Metivier, 1935; Pawan, 1936b; Waterman, 1959). Thereafter, national rabies vaccination and vector control programs, were implemented to prevent the disease in humans and animals (Waterman, 1959). Similar to the South American mainland, the main source of the rabies virus in Trinidad is the common vampire bat, *Desmodus rotundus* (Seetahal et al., 2018, 2013). However, a distinguishing epidemiological characteristic is that carnivore-mediated rabies does not occur on the island, which also has the interplay of insular viral dynamics which is less likely to independently sustain endemic transmission (Kucharski et al., 2016).

Rabies epidemiological surveillance in Trinidad comprises largely of passive surveillance (in the domestic animal population) for rabies suspect cases based on clinical signs and case history (including evidence of bat bites and animal vaccination status) (Seetahal et al., 2018). Active vampire bat trapping and testing is also conducted based on public reporting of bat biting cases in livestock and humans and the

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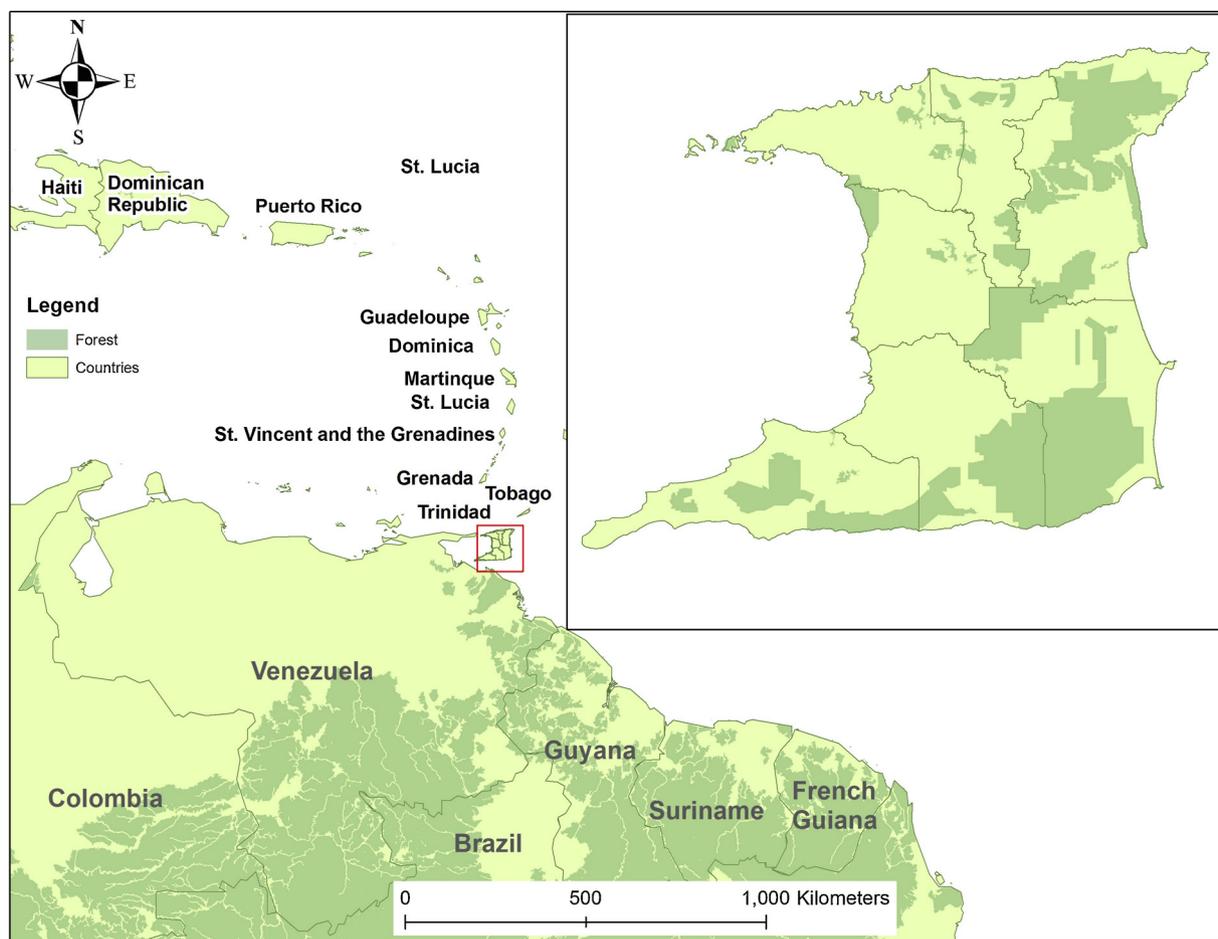


Fig. 1. Map showing the geographical location of the island of Trinidad in the Caribbean.

location of confirmed rabies cases (Seetahal et al., 2017). Understanding the spatio-temporal epidemiology of rabies is an essential step in analyzing transmission dynamics, which is critical to determine disease emergence and spread, to measure impact and ultimately improve prevention and control programs (Guo et al., 2013). Spatial analytical techniques have been utilized successfully in other countries, as a guide for improving surveillance and control strategies (Oviedo-Pastrana et al., 2015). Epidemiological analyses can also provide supporting data for phylogenetic studies on rabies viruses on the island (Seetahal et al., 2013).

Trinidad has the potential to act as a useful model for the detection and control of vampire bat-transmitted rabies as it is a small island and therefore provides a relatively closed study system with diverse and easily accessible habitats. It is in this context and given the importance of rabies throughout the Americas that we sought to describe the epidemiological situation and surveillance of rabies in Trinidad during the period of 1971–2015. Specifically, we focused upon the historical temporal, geographical and species distribution of rabies occurrence, along with the predominant species involved in outbreaks, to elucidate potential factors influencing occurrence of this zoonosis in Trinidad.

2. Material and methods

2.1. Data source, laboratory testing and study population

Laboratory records at the Veterinary Diagnostic Laboratory (VDL), related to the national animal rabies surveillance strategy for the period 1971 to 2015 were analyzed. The laboratory was relocated around 1971 and records prior to this date were not available for analysis. The

available records were derived from laboratory submissions of animal samples for rabies testing from Trinidad. These were mainly based on passive surveillance in livestock with submissions on the basis of clinical suspicion. They also included apparently healthy bats actively trapped and submitted for testing through the Anti-rabies Unit of the Ministry of Agriculture, Land and Fisheries, which conducts vector control activities on the *D. rotundus* bat population. Bat submissions which were primarily from active surveillance generally outnumbered that of livestock, but the rates were highly variable throughout the study period depending on trapping effort and available resources. The reference population in this study was all rabies-susceptible mammals present in Trinidad that were under epidemiological surveillance, based on clinical presentation and bat biting of livestock.

For samples from 1971 to 1975, laboratory testing was conducted by histopathological examination of brain tissue from rabies suspects for detection of Negri bodies, along with the mouse inoculation test (De Verteuil and Ulrich, 1936; Pawan, 1936a,b, 1948; Seetahal et al., 2017). In 1976, the Direct Fluorescent Antibody (DFA) Test was introduced at the VDL for the diagnosis of animal rabies and eventually replaced both histopathology and mouse inoculation (Bissessar, Personal communication). For the purpose of this study, the results of these two test methods were considered comparable, and all laboratory confirmed rabies cases either by histopathological examination and mouse inoculation or by DFA testing were combined in the same dataset. Additional information concerning the species and county location of rabies cases were also added to the dataset although the latter was only available from 1990. The reporting date and data on vector control and rabies vaccination efforts were not consistently recorded during the study period therefore could not be investigated in the statistical

analysis performed in this study.

2.2. Data description and statistical analyses

2.2.1. The strategy

Rabies epidemiology was described by the number of significant rabies outbreaks, cases and total number of rabies tests performed per year during the study period using descriptive statistics. ‘Significant epizootic events’, defined as rabies outbreaks in which more than 10 animal cases occurred with cases considered to be part of the same epizootic event if they fell within the same year or if there was less than one month between successive cases, were identified for the period under study. Additionally, the relationship between confirmed positive rabies cases and total number of samples submitted for rabies testing, i.e. the rabies positive proportion, was computed for specific time-periods. All bats, regardless of species, were treated as a single species group for this analysis. The rabies species prevalence (with the 95% Confidence Intervals) for an epizootic event was calculated as the number of cases confirmed positive for a particular species as a percentage of the estimated susceptible population for that species which were based on the closest available population census information. The rabies positive proportions (with the 95% CI) were calculated to highlight events of particular animal health relevance during the period under investigation. In addition to year, the month that each case was isolated was recorded where available (i.e. from 1997 to 2015), and this was used to differentiate between cases occurring in the dry (January – May) and wet (June – December) seasons.

The statistical analyses to investigate the time-trend, followed two different strategies according to the availability and completeness of the data: (i) for the period 1971–2015, the time-trend was investigated accounting for species and; (ii) for the period 1990–2015, the time-trend was investigated together with geographical distribution and accounting for species.

2.2.2. Analyses for the period 1971–2015

Rabies occurrence (laboratory confirmation of rabies) was modelled against time in yearly intervals. The effect of species was tested and added as a model covariate. Three models were attempted to approximate the occurrence of rabies as counts. In the first stage, a simple Poisson model was used, and this model was assessed for over-dispersion (due to the relative high number of zeros) (Cameron and Trivedi, 1990). In the second stage, a negative binomial model and a zero-inflated model were attempted to model over-dispersion. Time (year) was modelled as a polynomial function (quadratic and cubic) to allow for flexibility beyond a simple linear relationship. The Akaike’s Information Criterion (AIC), was used to compare the fit of different polynomial functions attempted and of the nested models (with or without species covariate) through a stepwise covariates selection process. The Wald test was used to examine the significance level (p value < 0.05) of the variables retained in the final model, particularly for those with multiple classes (i.e. species). Additionally, the Vuong non-nested test, together with the information from the assessment of the model fit (mean and standard error of the predicted values), was used to choose among the three different models attempted: Poisson, negative binomial, and zero-inflated. Residual diagnostic plots were used to detect features of concern in the model and to identify the presence of potential outliers. The fact that species was the only covariate available was a limiting factor to assess for confounding in this investigation.

2.2.3. Analyses for the period 1990 to 2015

Rabies occurrence (laboratory confirmation of rabies) was modelled against geographical location (county) and time in yearly intervals, with the effect of species also tested and added as a model covariate. These investigations followed the same strategy described for analyses for the period 1971–2015, and also attempted to use the three different distributions to model the occurrence of rabies as counts: a simple

Poisson model, the negative binomial model and the zero-inflated model. The fact that species and geographical location were the only covariates available was a limiting factor to assess for confounding in this investigation.

All analyses were performed using the R statistical software environment (R Development Core Team, 2015) using libraries ‘stats’, ‘pscl’ and ‘AER’.

3. Results

3.1. Overview

For the period 1971 to 2015, a total of 4960 specimens (annual range from 0 to 840 specimens per year) were submitted to the VDL for rabies diagnostic testing, of which 89% (4399 of 4960) were bat species (mainly *Desmodus* species). The remainder was from other wildlife and domestic animals, of which domestic ruminants predominated, 85% (478 of 561). The median annual number of confirmed rabies cases between 1971 and 2015 in Trinidad was 2 cases (range of 0 to 56 cases), with a total of 259 rabies cases (positive proportion = 0.052; 95% CI 0.046–0.059). During the 45 year period, there were 18 years during which cases exceeded the median number of cases (ranging from 3 to 56 cases) and there were also 13 years with no recorded cases.

3.2. Significant epizootics (1971–2015)

As illustrated in Fig. 2, five significant epizootics (see definition in Materials and Methods Section 2.2.1.) occurred between 1971 and 2015 (i.e. in 1974, 1997–1998, 2000, 2010 and 2012–2013). The largest was the 1997–1998 epizootic and the smallest was in 1974. For these five epizootic events, the highest annual number of cases occurred in 1997 (56 cases) and the least in 2013 (4 cases). Individual descriptions of each event are detailed below.

3.2.1. The 1974 epizootic

In 1974 there was a total of 12 cases (positive proportion = 0.41; 95% CI 0.26–0.59), most of which were accounted for by cattle (67%) with a disease prevalence of 0.02% (95% CI 0.01–0.04; 2 per 10,000 animals) for the bovine population (estimated at 37,000 animals) (Moe, 1997) and the remainder goats (33%) with a prevalence of 0.01% (95% CI 0.004–0.03; 1 per 10,000 animals) estimated for this population (estimated at 30,700 animals) (Moe, 1997). Thereafter, in the years to follow until 1997, cases remained at a low level (< 10 cases per year) on the island with a total of 63 cases (95% bovine, 3% equine and 2% ovine) over the 22 year period.

3.2.2. The 1997–1998 epizootic

The second epizootic event occurred from January 1997 to September 1998, with 87 livestock cases, the majority (90%) being cattle with a disease prevalence of 0.21% (95% CI 0.17–0.26; 21 per 10,000 animals) for the bovine population (estimated at 37,000 animals) (Moe, 1997). Caprine cases accounted for only 2% of livestock cases with a disease prevalence of 0.005% (95% CI 0.001–0.02; 1 per 10,000 animals) for the caprine population (estimated at 30,700 animals) (Moe, 1997). Overall, 32% (87 of 275) of animal specimens submitted for diagnostic testing during this outbreak were confirmed rabid, representing positive proportions of 0.38 (95% CI 0.31–0.46), for 1997 and 0.24 (95% CI 0.18–0.32) for 1998. On average, there were approximately 4 cases per month (range 0–44), with the majority (51%) of cases occurring during December 1997. Most (76%) of the cases occurred in Wallerfield of the St. George East County in the north-east of the island (Fig. 3).

3.2.3. The 2000 epizootic

The rabies outbreak of 2000 occurred from January to November with 19 cases, all of which were cattle with a disease prevalence of

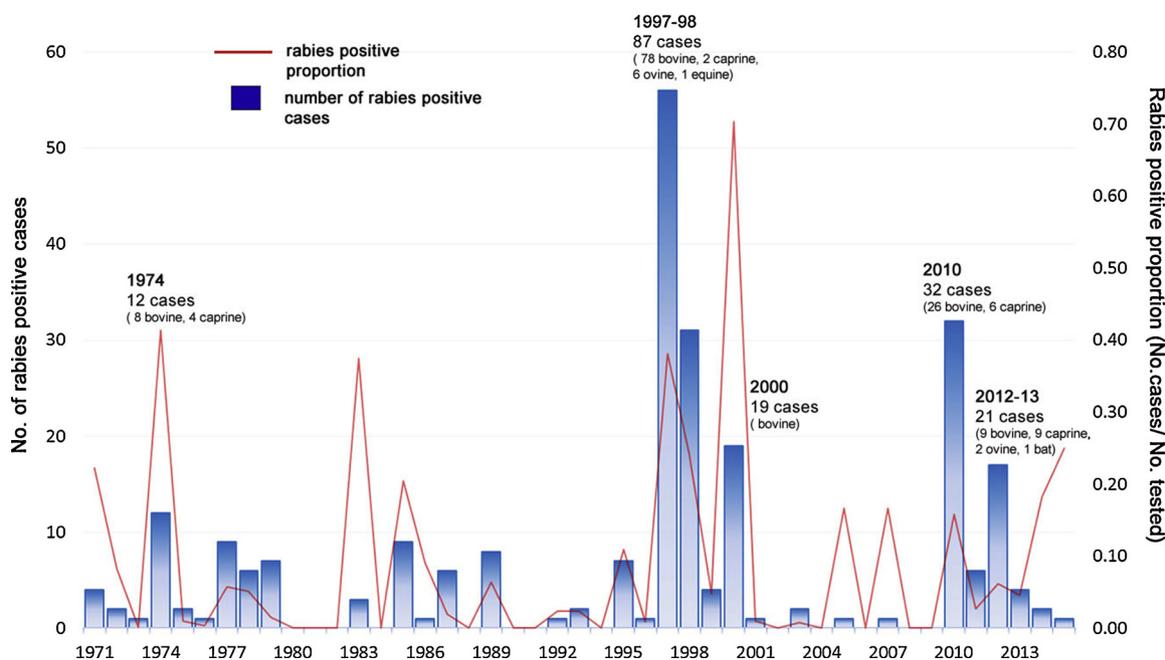


Fig. 2. Annual number of rabies cases and rabies positive proportion in the animal population of Trinidad during the period 1971–2015.

0.05% (95% CI 0.03–0.08; 5 per 10,000 animals) for the bovine population (estimated at 37,000 animals) (Moe, 1997). Seventy percent (19 of 27) of the suspect cases tested during this outbreak were positive, representing the highest positive proportion (positive proportion = 0.7; 95% CI 0.52–0.84) for the study period. On average, 2 cases (range 0–8) occurred per month, with the most (8 cases) occurring during October 2000. The majority (58%) of cases occurred in the eastern region of the island in counties of St. Andrew/St. David and Nariva/Mayaro (Figs. 2 and 3). Thereafter, for the next 9 years, sporadic bovine cases (5 in total) occurred in both the south and north, until the 2010 epizootic.

3.2.4. The 2010 epizootic

During 2010, 32 rabies cases were documented over the eight month period from May to December, with the majority (94%) demonstrated during the wet season (June to November). Overall, a positive proportion of 0.16 (95% CI 0.11–0.22), was observed (32 of 202) for submissions. A mean of 4 cases (range 2–10) occurred per month, with the most cases occurring during October 2010 (10 cases). The majority (81%) of rabies cases for this epizootic were in cattle, with a disease prevalence of 0.14% (95% CI 0.08–0.23; 14 per 10,000 animals) for the bovine population (estimated at 19,088 animals) (Trinidad and Tobago Central Statistical Office, 2004). The remainder of cases (19%) was in goats, with a prevalence of 0.05% (95% CI 0.02–0.12; 5 per 10,000 animals) estimated for this population (estimated at 12,500 animals) (Trinidad and Tobago Central Statistical Office, 2004). In general, cases were confined to the south-western region of the island (Fig. 3) in the counties of St. Patrick, 88% (28 of 32) and Victoria, 9% (3 of 32), with one isolated case in St. George East at the end of the outbreak.

3.2.5. The 2012–2013 epizootic

In January 2012, a vampire bat was confirmed rabid and thereafter 20 cases of rabies in livestock were confirmed from September 2012 to February 2013, with an average of 3 livestock cases per month (range 0–7 cases). Cases peaked during September–October 2012 with 7 cases occurring per month. In general, similar to the 2010 epizootic, the majority (95%) of rabies cases were demonstrated during the wet season (June to November). Of 361 tests conducted from all animal submissions for 2012–2013, 6% (21 of 361) were confirmed rabid (positive proportions = 0.06 (95% CI 0.04–0.1), and 0.05 (95% CI 0.02–0.11), for 2012 and 2013 respectively). Cases were generally confined

to the south-western region of the island in the counties of St. Patrick (20 of 21) and Victoria (1 of 21), as seen in Fig. 3. The majority (82%) of cases for 2012–2013 was within the bovine and caprine populations (9 cases each) with the remainder of cases accounted for by ovine (2) cases. The prevalence for the bovine population (estimated at 19,088 animals) (Trinidad and Tobago Central Statistical Office, 2004) was 0.05% or 5 per 10,000 animals, whereas the prevalence for the caprine population (estimated at 12,500 animals) (Trinidad and Tobago Central Statistical Office, 2004), was 0.07% or 7 per 10,000 animals.

3.3. Statistical analyses of rabies cases for the period 1971–2015

The negative binomial model was the chosen model since the Poisson model presented overdispersion, which invalidates the assumption of Poisson distribution and the results of the Vuong non-nested test indicated that the negative binomial model was superior to the zero-inflated model. The model with a simple linear relationship for trend (measured in yearly intervals) gave a better fit to the data than the models with a quadratic or cubic term. The results for the final negative binomial model that includes time-trend and species are presented in Table 1. The parameter estimate defining the linear relationship (0.03, 95% CI: 0.01–0.06) indicated a significant increasing trend for the occurrence of rabies over time (also see S1 Figure). Compared to the category ‘bat’ (the species with the lowest number of cases taken as baseline), ‘bovine’ had a significantly higher risk of rabies (estimate 4.84, 95% CI: 3.45–6.76).

3.4. Statistical analyses of rabies cases for the period 1990 to 2015

As for the period 1971–2015, the negative binomial model was the final model chosen for analysis of the period 1990–2015. Time (year) was not included in the final model as it was not significantly associated to it. The results for the final negative binomial model that included county location of the event and species are presented in Table 2. St. Patrick appears in the model as the county with the greatest occurrence of rabies events (estimate 4.52, 95% CI: 2.44–7.6) compared to the baseline of St. George West. As for the period 1971–2015, ‘bovine’ was the species with the greatest occurrence of rabies and had a significantly higher risk of rabies (estimate 4.27, 95% CI: 2.74–6.27) compared to the categorical variable ‘bat’ (the species with the lowest

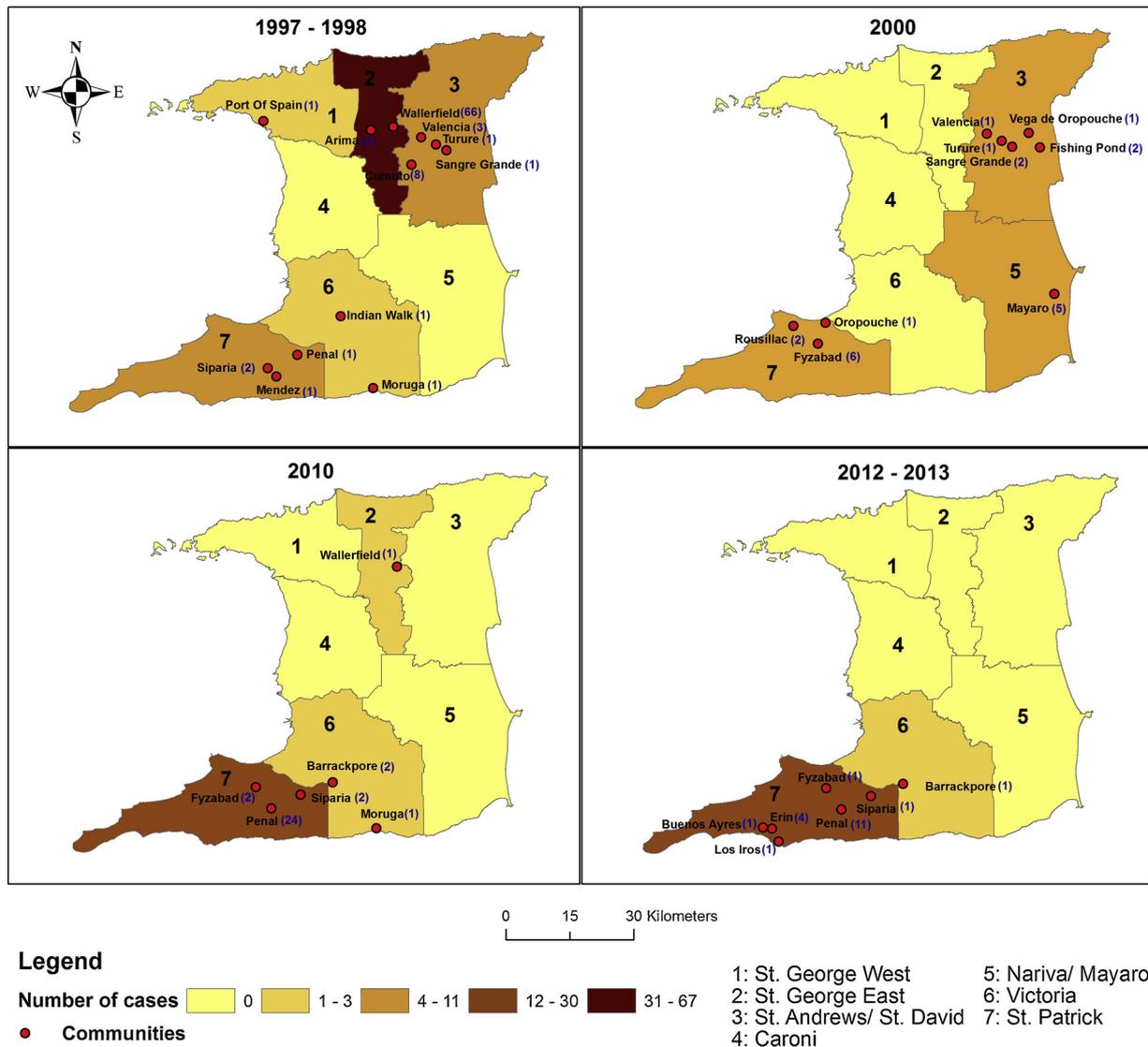


Fig. 3. Regional distribution of animal rabies cases by geographical location (county and community) in Trinidad (a) 1997–1998; (b) 2000; (c) 2010 and; (d) 2012–2013.

Table 1

Parameter estimates for linear term fitted to the temporal trend and covariates in the multivariable negative binomial model for the occurrence of animal rabies in Trinidad, 1971–2015.

Variables	Level	Estimates	95% CI
Trend	–	0.03	0.01-0.06
Species	Bat (baseline)	0	–
	Bovine	4.84	3.45-6.76
	Caprine	2.33	0.88-4.28
	Equine	0.77	–1.03-2.86
	Ovine	0.92	–0.79-2.98

number of cases acting as baseline).

4. Discussion

In this study we analyzed 45 years of laboratory records related to the rabies surveillance system in Trinidad - the first time that such a large national data set on rabies was compiled and analyzed for Trinidad. The period under study was after disease surveillance and prevention measures, (such as vampire bat population control and rabies vaccination of at risk species), were implemented in Trinidad

Table 2

Parameter estimates for the covariates in the multivariable negative binomial model for the occurrence of animal rabies in Trinidad, 1990–2015.

Variables	Level	Estimates	95% CI
County location	St. Georges West (baseline)	0	–
	St. Andrew/St. David	3.06	0.9-6.18
	St. George East	4.04	1.97-7.11
	Nariva/ Mayaro	2.13	–0.13-5.28
	St. Patrick	4.52	2.44-7.6
	Victoria	2.15	–0.13-5.32
Species	Bat (baseline)	0	–
	Bovine	4.27	2.74-6.27
	Caprine	1.96	0.33-4.02
	Equine	–0.67	–3.87-1.88
	Ovine	1.42	–0.28-3.52

(Director of Agriculture of Trinidad and Tobago, 1959; Greenhall, 1968b).

The increasing linear trend detected for the whole period (1971–2015) is reflecting the overall changes in the reported rabies cases, from low numbers of cases in the 1970s and 1980s to the peaks in the late 1990s and during the 2010 epizootic. This trend was not

identified in the model for the time subset investigated 1991–2015; which could be explained by the fact that during this shorter period there was not a clear linear trend but only two main peaks of cases. Moreover, as the 1991–2015 period model also includes county location as a determinant, it is possible that this later variable is absorbing part of the association related to the trend, subtracting statistical significance to this. The overall increase in the number of cases in the recent decades may be a result of more efficient reporting of cases, particularly after the 2010 epizootic which triggered the organization of several awareness events. Nevertheless, the prevention measures should be reviewed to ensure consistent and effective implementation.

In 2010 and 2012–2013, despite the practice of preventative animal rabies vaccination in Trinidad, 69% and 85% of confirmed rabies cases respectively were not vaccinated (Seetahal et al., 2017). Although this suggests that the remaining 15–31% are vaccine failures they are more likely to represent situations where vaccination was administered too late in the incubation of the disease or where there was improper vaccine administration, storage or handling (Seetahal et al., 2017). Vaccination has traditionally targeted large ruminants as they are the preferred feeding host of the vampire bats (Greenhall, 1968b; Johnson et al., 2014). As demonstrated by the aforementioned results, cattle had a significantly higher risk of rabies when compared to other mammals, consistent with them being the preferential blood source of *Desmodus rotundus* bats (Greenhall, 1985; Johnson et al., 2014; Woldehiwet, 2002). In light of this, the caprine population historically was not a target species for routine rabies vaccination in Trinidad (Greenhall, 1985). However, in this study in addition to the increasing trend in rabies cases over time there was an increase in the prevalence of cases in the caprine population and increased bat biting in this species across the island (Animal Production and Health Division, 2010, 2011, 2012, 2013). Therefore, although recent phylogenetic work confirmed *D. rotundus* as the primary rabies virus reservoir, the less common *Diaemus youngi* vampire bat may also be implicated in virus transmission in Trinidad, as it is known to preferentially feed on goats and birds (Goodwin and Greenhall, 1961; Seetahal et al., 2013). The increase in rabies cases within the small ruminant population during the last two epizootics suggest that the national rabies vaccination program should be extended to include small ruminants. Another factor to consider is that during the study period, while there was an increasing trend in cases, there were considerable decreases in production numbers for both cattle (from 37,000 in 1982 to 19,088 in 2004) and goats (from 30,700 in 1982 to 12,500 in 2004) (Moe, 1997; Trinidad and Tobago Central Statistical Office, 2004) effectively decreasing the at-risk populations (see S2 Figure for the current distribution of known ruminant farms in Trinidad).

Field vaccination coverage of livestock tends to be inconsistent from year to year in Trinidad and is dependent on the financial resources available for vaccine procurement and man-power for vaccine administration at the level of the government (Seetahal et al., 2017, 2015). Additionally, vaccine coverage may increase after epizootic events due to increased vaccination effort to contain the spread of the disease. In an effort to standardize the vaccine coverage for the at-risk animal populations, cost-sharing with livestock owners can be implemented to off-set some of the financial burden on the government which may facilitate more consistent vaccine procurement. Livestock vaccination cycle schedules can be informed by routine monitoring of the vampire bat population for viral activity, increases in population size and biting activity. Detection of high virus/viral antibody titer levels, increases in vampire populations or increases in vampire feeding activity should trigger a short cycling of the vaccine schedule (i.e. from biennial to annual) to ensure herd immunity.

During the study period (1971–2015) only two of 4399 (0.05%) bats sampled mainly by active surveillance were confirmed to be rabid and the risk for this species was considered the lowest amongst all species included in this study. However, these findings may be biased by the fact that healthy animals are more likely to be sampled with active

surveillance as compared to testing based on clinical suspicion of the disease (i.e. passive surveillance). Although multiple bat species are found on Trinidad, the common vampire bat was the only species found to be positive for rabies virus in this study. However, bias may exist as vampire bats, on account of their ubiquitous presence and haematophagous feeding habits (which favors viral transmission), are the primary focus of vector control efforts and are the bat species most often submitted for testing. After vector control operations, vampire bat populations in these areas are estimated to remain under control for at least three months, due to the slow rate of vampire bat population recovery given their uniparous nature and long gestation period (Acha, 1981; Greenhall, 1963), resulting in a decreased risk of viral spillover to livestock populations.

The 2010 epizootic was preceded by a notable increase in bat biting reports (Animal Production and Health Division, 2010), which may have in part been due to reduced vampire bat control measures (topical application of an anticoagulant to bats) within the last two decades (Seetahal et al., 2017), creating a favourable environment for population expansion. Although some studies have indicated that culling efforts in vampire bat populations may lead to a possible increase in circulating rabies virus due to the elimination of virus immune adults (Streicker et al., 2012), during this study period vampire control efforts which were inconsistent were conducted in response to increases in bat biting reports and confirmation of rabies cases.

Rabies diagnosis at the VDL prior to 1976 was made using histopathological examination for Negri bodies. However, the presence of these intra-cytoplasmic inclusions were proven to be inconsistently (50–80%) correlated with rabies, with one study suggesting that at least 25% of naturally occurring animal cases do not have demonstrable Negri bodies (Perl and Good, 1991; Trimarchi and Nadin-Davis, 2007). Therefore, although for the purposes of this epidemiological analysis, diagnostic methods were assumed equivalent, cases may have been missed prior to 1976 due to the lack of Negri body visualization. The DFA test, which is considered the ‘gold standard’ diagnostic method for rabies diagnosis (McElhinney et al., 2008), was implemented at the VDL in the 1970s and is the sole diagnostic method currently employed for the national animal rabies surveillance program (Bissessar, Personal communication).

During the period 1971–2015, animal rabies cases occurred primarily in the south-western area of Trinidad. However, during the 1997–1998 and 2000 epizootic events, many cases occurred in the north-eastern region of the island. A north-eastern pattern of intra-island progression was suggested for the 1929–1937 human paralytic rabies epidemic (Mungrue and Mahabir, 2011) which is consistent with the unidirectional concept of virus movement for vampire bat rabies epidemics (Acha, 1981; Benavides et al., 2016; Greenhall, 1985). Although this pattern of epizootic progression was seen thereafter in Trinidad for the majority of rabies epizootics, there have been specific instances in which north to south viral progression was postulated. For instance, in 1925, cattle deaths retrospectively attributed to paralytic rabies first occurred in the north-western area of the island with inward south-eastern spread (De Verteuil and Ulrich, 1936; Metivier, 1935; Waterman, 1959).

In the present study north to south viral progression was likely during the 1997–1998 and 2000 epizootics. A phylogenetic study on Trinidadian rabies viruses demonstrated two geographically distinct viral lineages, Trinidad I: isolated from north-east Trinidad and; Trinidad II: isolated from south-west Trinidad. (Seetahal et al., 2013). In 2000 these lineages were demonstrated to co-exist, each with separate estimated dates of introductions to the island (Seetahal et al., 2013). It is also plausible that viral importation may occur from both the south-west peninsular (with north-east progression) and north-west peninsular (with east to south-east progression) of the island, with the former being more obvious due to the higher concentration of ruminant livestock (i.e. vampire prey species) in the south-west (see S2 Figure). However, further work on vampire bat population dynamics is

necessary to ascertain bat movement and further analyze this phenomenon. Similarly, the statistical results and higher occurrence of cases in the south-western region of St. Patrick and north-eastern region of St. George East during epizootic events noted in this study may be correlated to the high densities of farmed livestock and locations of monitored active vampire bat roosts (see S2 Figure) in the vicinity of these areas. Therefore, in the event of limited programmatic resources, these areas should be prioritized for vaccination and vector control activities. Lastly, the concentration of case distribution between September to December during the 1997–98, 2000, 2010 and 2012–2013 epizootics was consistent with the previous hypothesis that rabies virus activity increases during the wet season (De Verteuil and Ulrich, 1936), which may be ascribed to increased bat contact with seasonal reproductive activities.

5. Conclusions

This study presents a description of the current epidemiological situation on rabies in Trinidad, where disease dynamics are driven by the occurrence of infected vampire bats and the distribution of susceptible hosts. Overall, although policies and legislation were in place for animal rabies control, there was a general increase in the trend of confirmed rabies cases over the 45 year study period suggesting gaps in control programs during the periods leading up to detected epizootic events. Cases were concentrated mainly in the south-west and north-east of the island, where high densities of livestock and active vampire roosts are considered to be major risk factors. The predominance of cattle cases justifies the bovine targeted national rabies vaccination program, while an increase in the prevalence of cases in the caprine population over the study period suggests that this species should also be included. The animal vaccination schedule, and range of species included in vaccination schemes should be holistically re-evaluated, in light of current scientific evidence. Follow up epidemiological studies including analyses such as those detailed herein should be implemented to monitor the effectiveness of the rabies surveillance programs as well as prevention and control measures over the long-term in Trinidad.

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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.vetmic.2018.11.020>.

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