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REVIEW ARTICLE
Animal leptospirosis in small tropical areas

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SUMMARY

Leptospirosis is the most widespread zoonosis in the world. Humans become infected through contact with the urine of carrier animals, directly or via contaminated environments. This review reports available data on animal leptospirosis in ten tropical islands: Barbados, Martinique, Guadeloupe, Grenada, Trinidad, New Caledonia, Hawaii, French Polynesia, La Réunion and Mayotte. Leptospirosis is endemic in these insular wild and domestic fauna. Each island presents a specific panel of circulating serovars, closely linked with animal and environmental biodiversity, making it epidemiologically different from the mainland. Rats, mongooses and mice are proven major renal carriers of leptospires in these areas but dogs also constitute a significant potential reservoir. In some islands seroprevalence of leptospirosis in animals evolves with time, inducing changes in the epidemiology of the human disease. Consequently more investigations on animal leptospirosis in these ecosystems and use of molecular tools are essential for prevention and control of the human disease.

Key words: Animal, epidemiology, island, leptospirosis, serovar, tropical.

INTRODUCTION

Leptospirosis is the most widespread zoonosis in the world but incidence of this disease is higher in tropical areas than in temperate countries [1]. Leptospires are bacteria belonging to the family Leptospiraceae, order Spirochaetales. These spirochetes are about 0·1 μm in diameter and 6–20 μm in length [2]. The genus *Leptospira* includes saprophytic (*L. biflexa sensu lato*) and pathogenic (*L. interrogans sensu lato*) bacteria [3] and the serological classification allows discrimination between more than 260 serovars of *L. interrogans*. Serovars that are antigenically related are grouped into serogroups but this classification is now challenged by a taxonomically more relevant genomic classification which distinguishes 13 pathogenic genomospecies [4]. Human infection most often occurs when mucous membranes or abraded skin are exposed to infected animal urine, contaminated water or soil, or infected animal tissue [2]. Many wild and domestic animals species have been identified as hosts of infecting leptospiral organisms and are able to maintain the leptospires in their kidneys and become chronic carriers, shedding the organisms in their urine [5]. Therefore, although the organism has been recovered from rats, swine, dogs, cattle, and numerous wild animals [6], micromammals (particularly rats)

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remain the main chronic renal carriers of leptospires [7–9].

We choose to present a limited number of tropical insular areas, selected according to three criteria: (i) island located in the tropics, (ii) land surface of $<20\,000$ km^2 and (iii) availability of published data on animal leptospirosis. Thus, this review deals with the following islands: Barbados, Martinique, Guadeloupe, Grenada and Trinidad in the Caribbean Sea; New Caledonia, Hawaii and French Polynesia in the Pacific Ocean; and La Réunion and Mayotte in the Indian Ocean (Table 1) [10–13]. This review presents data on leptospirosis by island and by animal species chronologically (Tables 2 and 3) [14–24]. This data-gathering can be considered as a tool for those who work on leptospirosis in tropical islands. Knowledge on the animal reservoirs of *Leptospira* allows a better understanding of the epidemiology of the disease in these areas and also facilitates finding practical applications for control of the disease in humans.

All the areas described are tropical islands with a land surface area $<20\,000$ km^2. In these regions the climate has two contrasting seasons: a cool and dry season and a hot rainy season. Rainfall on the islands is principally orographic (mountain caused), with the resulting annual rainfall distribution closely following the topographic contours: amounts are greatest over the upper slopes and least on the leeward coast. Geologically, except for Barbados, all these islands are totally or partially of volcanic origin. Because of their small surface area and their isolation, for a given biogeographical area, islands have less species richness per surface unit than the mainland [25]. Moreover, animal populations are often small because of the limited surface area which reduces the capacity of housing. Each tropical island has its own fauna, but all are characterized by a high density of invasive rodents of the family Muridae [26, 27], rats (*Rattus* sp.) or mice (*Mus musculus*) [22, 23, 28]. Several hunting or wild species have also been introduced by humans [20, 22, 29] and domestic animals (dogs, cats) and livestock (cattle, goats, pigs, sheep, horses) are present in all the islands [22]. Except for Trinidad, which has a huge animal biodiversity, bats (order Chiroptera) represent generally the only endemic or indigenous terrestrial mammalian species of these ecosystems. On each island only a small part of the fauna has been studied for leptospirosis (Table 2) [15, 16, 18–23, 30–32]. In this review, we use the species taxonomic level in its Linnean designation. In consequence, domestic animals or wild animals born of domestic forms, have the same Latin name as the wild ancestral species [33].

Two methods are commonly used to investigate leptospirosis in animals: the microscopic agglutination test (MAT) and the culture in a specific medium. The MAT is the gold standard test and is the one most utilized for the serological diagnosis of leptospirosis [34]. It is based on the use of agglutinating specific antisera and cross-absorption with homologous antigens. Authors can give the results of the MAT at the serogroup or at the serovar level. Serogroups corresponding to the serovars cited in this paper are given in Table 4 [2]. One limitation is that serological results depend on the number of serovars included in the panel [34], but another limitation of the MAT is the difficulty in setting a threshold of positivity which can range from 1:10 to 1:800, according to the authors and the location of the study [35–39]. In contrast, *in vitro* culture of *Leptospira* from kidney, blood or urine allows the serotyping of the isolated strains with certainty [40] but this method is lengthy, of low sensitivity and notably limited by contaminants outgrowth.

BARBADOS

Micromammals and mongooses

A study conducted during 1964–1965 [41] on *Rattus* sp. in Barbados showed that 33% (32/98) of *R. rattus* and 35% (48/138) of *R. norvegicus* were seropositive for leptospirosis by MAT. In 1986–1987 and 1994–1995, Levett *et al.* [42] isolated leptospires by culture of kidneys, urine or blood from 19% (12/63) and 16% (16/100) of rats, respectively. In these studies, the prevalence of renal infection was higher in *R. norvegicus* than in *R. rattus* [41, 42], with 27% (37/138) and 15% (15/98) testing positive, respectively [41]. Isolates identified in *Rattus* were serovars copenhageni (serogroup Icterohaemorrhagiae), arborea (Ballum) and bim (Autumnalis). *R. norvegicus* carried mostly leptospires from serogroup Icterohaemorrhagiae, whereas serogroup Autumnalis was mainly found in *R. rattus* [41].

In 2002, Matthias & Levett [21] showed that 28·2% (24/85) of mice (*Mus musculus*) and 40·7% (48/118) of mongooses (*Herpestes auropunctatus*) in Barbados had antibodies against *Leptospira* sp. In mice, the prevailing serovars assessed by serology (MAT) were arborea (Ballum) and bim (Autumnalis), whereas in mongooses the dominant serogroup was Autumnalis.

Table 1. *Presentation of the islands*

Island (country)	Location	Number of islands of the archipelago (number inhabited)	Main town, latitude, longitude (highest point)	Total terrestrial surface	Number of inhabitants (year of the census)	Density (inhab./km²)	Incidence of human leptospirosis (number of cases per year per 100 000 inhabitants)*
Barbados (Barbados)	Caribbean Sea	1 (1)	Bridgetown, 13°5′N, 59°37′W (336 m)	430 km²	281 968 (2008)	642	13·3 [11]
New Caledonia (France)	Southern Pacific Ocean	21 (7)	Nouméa, 22°16′S, 166°27′E (1629 m)	18 575 km²	244 410 (2008)	13·16	22·85 [10]
Hawaii (USA)	Northern Pacific Ocean	122 (8 main islands)	Honolulu, 21°19′N, 157°50′W (4205 m)	16 760 km²	1 211 537 (2000)	42·75	7·9 in Kauai [12] 5·9 in Hawaii [12] 0·3 in Oahu [12] 0·2 in Maui [12]
French Polynesia (France)	Southern Pacific Ocean	118 (shared out in 5 atolls)	Papeete, 17°32′S, 149°34′W (2241 m)	4167 km²	259 706 (2007)	65	22·69 [10]
La Réunion (France)	Indian Ocean	1 (1)	Saint-Denis, 20°52′S, 55°26′E (3071 m)	2512 km²	810 000 (2009)	313	5·48 [10]
Mayotte (France)	Indian Ocean (Mozambique Channel)	4 (2)	Mamoudzou, 12°46′S, 45°13′E (660 m)	376 km²	186 452 (2006)	499	11·44 [10]
Martinique (France)	Caribbean Sea	1 (1)	Fort-de-France, 14°36′N, 61°05′W (1397 m)	1128 km²	397 732 (2006)	352·59	13·5 (Martinique + Guadeloupe) [10]
Guadeloupe (France)	Caribbean Sea	5 (5)	Basse-Terre, 16°00′N, 61°44′W (1467 m)	1434 km²	400 736 (2006)	246	
Grenada (Grenada)	Caribbean Sea	10 (3)	St-George's, 12°03′N, 61°45′W (840 m)	344 km²	110 000 (2005)	319·8	Not found
Trinidad (Trinidad and Tobago)	Caribbean Sea	20 (2)	San Fernando, 10°17′N, 61°28′W (940 m)	6768 km²	1 262 366 (2000)	246	0·08 [13]

* Registered cases only.

Table 2. *Insular repartition of the animal cited* (*class, order, family, Latin name and common name*) *and existence of studies on leptospirosis by species and island*

	Barbados	Martinique	Guadeloupe	Grenada	Trinidad	New Caledonia	Hawaii	French Polynesia	La Réunion	Mayotte
CLASS MAMMALIA										
ORDER RODENTIA										
Family Muridae										
Rattus rattus (ship rat)	● *	● [20, 22]	● [20, 22] *	● [19] *	● [18] *	● [21, 22] *	● [23] *	● [22]	● [22]	● [22] *
R. norvegicus (Norway rat)	● *	● [20, 22]	● [20, 22] *	● [19] *	● [18] *	● [21, 22] *	● [23] *	● [22]	● [22]	
R. exulans (Pacific rat)						● [21, 22] *	● [23] *	● [22]	● [22]	
Mus musculus (domestic mouse)	● *	● [20, 22]	● [20, 22] *	● [19]	● [18]	● [21, 22]	● [23] *	● [22]	● [22]	● [22]
Family Cricetidae										
Oryzomis capito (rice rat)					● *					
Rhipidomys couesi (Coues's climbing mouse)					● *					
Nectomys squamipes (South American water rat)					● *					
Necromys urichi (northern akodont)					● *					
Zygodontomys brevicauda (short-tailed cane mouse)					● *					
Family Heteromyidae										
Heteromys anomalus (Trinidad spiny pocket mouse)					● *					
ORDER LIPOTYPHLA										
Family Tenrecidae										
Tenrec ecaudatus (tailless tenrec)									● [22] *	● [22] *
ORDER DIDELPHIMORPHIA										
Family Didelphidae										
Marmosa mitis (=*robinsoni*) (mouse opossum)				● [30]	● [30]*					
Marmosa fuscata (dusky mouse opossum)				● [31]	● *					
Didelphis marsupialis (common opossum)		● [20, 22]		● [31]	● [18] *					
Family Caluromyidae										
Caluromys philander (bare-tailed woolly opossum)					● *					
ORDER CARNIVORA										
Family Canidae										
Canis lupus (dog)	● *	● *	● [22] *	●	● *	● [21, 22] *	● [23]	● [22]	● [22] *	● [22] *
Family Felidae										
Felis sylvestris (cat)	●	●	● [22]	●	● *	● [21, 22]	● [23]	● [22]	● [22]	● [22]
Family Herpestidae										
Herpestes auropunctatus (small Indian mongoose)	● *	● [20, 22]	● [20, 22] *	● [16] *	● [18] *		● [23] *			
Family Viverridae										
Viverricula indica (small Indian civet)										● [22] *

Table 2 (*cont.*)

	Barbados	Martinique	Guadeloupe	Grenada	Trinidad	New Caledonia	Hawaii	French Polynesia	La Réunion	Mayotte
Family Phocidae										
Monachus schauinslandi (Hawaiian monk seal)							● *			
ORDER ARTIODACTYLA										
Family Bovidae										
Bos primigenius (cattle)	●	● [22] *	● [22] *	● *	● *	● [21, 22] *	● [23] *	● [22] *	● [22] *	● [22] *
Bubalus bubalis (water buffalo)					● *					
Capra aegagrus (goat)	● *	● [22]	● [22] *	● *	●	● [21, 22]	● [23]	● [22]	● [22]	● [22] *
Ovis orientalis (sheep)	● *	● [22]	● [22]	●	●	● [21, 22]	● [23]	● [22]	● [22]	● [22]
Family Suidae										
Sus scrofa (pig)	●	● [22] *	● [22] *	● *	● *	● [21, 22] *	● [23]	● [22] *	● [22] *	● [22]
Family Cervidae										
Cervus timorensis (rusa deer)						● [21, 22] *			● [22]	
ORDER PERISSODACTYLA										
Family Equidae										
Equus ferus (horse)	●	● [22]	● [22] *	●	● *	● [21, 22] *	● [23]	● [22] *	● [22] *	● [22]
Equus asinus (ass)	●				● *	● *	●		● [22]	
ORDER CHIROPTERA										
Family Phyllostomidae										
Anoura geoffroyi (Geoffroy's tailless bat)				● *						
Glossophaga longirostris (Miller's long-tongued bat)				● *						
Carollia perspicillata (Seba's short-tailed bat)				●	● *					
Phyllostomus hastanus (greater spear-nosed bat)					● *					
Family Molossidae										
Molossus major					● *					
Family Mormoopidae										
Pteronotus davyi (Davy's naked-backed bat)		●	● [15]		● *					
Family Pteropodidae										
Pteropus seychellensis (Seychelles flying fox)										● *
ORDER PRIMATES										
Family Cercopithecidae										
Cercopithecus aethiops (vervet monkey)	● *									
Family Cebidae										
Cebus albifrons (Trinidad white-fronted capuchin)					● [18] *					

Table 2 (*cont.*)

	Barbados	Martinique	Guadeloupe	Grenada	Trinidad	New Caledonia	Hawaii	French Polynesia	La Réunion	Mayotte
ORDER CINGULATA										
Family Dasipodidae										
Dasypus novemcinctus (nine-banded armadillo)				● [19]						
CLASS AMPHIBIA										
ORDER ANURA										
Family Bufonidae										
Bufo marinus	● [16] *	● [16]	● [16]	● [16] *	● [16] *		● [16]			
Family Leptodactylidae										
Eleutherodactylus sp.	● *	● [16]	● [16]	● [16]			● [16]			
Family Hylidae										
Hyla minuta (lesser tree frog)					● *					
CLASS REPTILIA										
ORDER SQUAMATA										
Family Teiidae										
Tupinambis nigropunctatus (gold tegu)					● *					
Ameiva ameiva (giant ameiva)				● [32]	● *					
Family Iguanidae										
Iguana iguana (common green iguana)			● [31]	● [31]	● *					
CLASS AVES										
ORDER GALLIFORMES										
Family Phasianidae										
Gallus gallus (fowl)	●	●	●	● *	● *	●	●	●	●	●
ORDER FALCONIFORMES										
Family Cathartidae										
Coragyps astratus (black vulture)					● *					

● Presence of the species on the island.
* Presence of data on leptospirosis for this species in the island concerned.

Primates

A survey conducted on a wild population of vervet monkeys *Chlorocebus* (*Cercopithecus*) *aethiops* revealed a seroprevalence to *Leptospira* of 29·9% (150/501). Serogroups identified were Ballum (61%), Icterohaemorrhagiae (16%), Autumnalis (15%), Pyrogenes, Panama, Pomona and Canicola (8% combined) [43].

Amphibians

Everard & Gravekamp [44–46] showed that amphibians were carriers of leptospires and two pathogenic strains were grown from kidneys of toads *Bufo marinus* (family Bufonidae) and frogs *Eleutherodactylus johnstonei* (family Leptodactylidae). The most prevalent strain in amphibians was *L. noguchii* serovar bajan (Australis) [45, 46], followed by serovar bim (Autumnalis) [44–46].

Domestic carnivores

A serological survey showed that 62% (48/78) of asymptomatic (stray or domestic) dogs had a positive MAT titre, with the dominant serogroup being Autumnalis (45%), followed by serogroups Icterohaemorrhagiae and Australis (16% each), then Pomona (13%). However, in dogs presenting clinical signs of leptospirosis, the prevailing serogroup was Icterohaemorrhagiae [47]. In this study, *Leptospira* grown from dogs' kidneys were principally serovars copenhageni (Icterohaemorrhagiae) and bim (Autumnalis) [47, 48].

Livestock

Levett *et al.* [49] showed that 4·3% of sheep (1/23) and 9·3% of goats (4/43) were seropositive for leptospirosis and antibodies against serogroup Cynopteri were identified in both species [49].

MARTINIQUE

Domestic carnivores

A serosurvey conducted in Martinique on dogs showed that the seroprevalence against leptospires was 76% (219/288) [50].

Livestock

Levett *et al.* [49] showed that 25·7% (45/175) of cattle were seropositive for leptospirosis and that Sejroe was the most prevalent serogroup (44·4% of the positives), followed by Icterohaemorrhagiae (24·4%) and Autumnalis (17·7%) [49]. In pigs, the seroprevalence was 39% (110/282), with a predominance of serogroups Icterohaemorrhagiae and Sejroe, followed by Australis and Cynopteri [50].

GUADELOUPE

Micromammals and wild carnivores (mongooses and racoons)

Michel [51] observed the renal carriage of the bacteria *Leptospira* in 16·6% (2/12), 36·8% (14/38) and 57·1% (8/14) of *R. norvegicus*, *R. rattus* and mice, respectively. MAT tests showed that seroprevalences in the racoon and the mongoose were similar with 48% (354/737) and 47% (8/17) positive, respectively [51, 52]. The serovar arborea (Ballum) was predominantly found in kidneys of mice [51], while serogroup Icterohaemorrhagiae was isolated from *R. rattus*, and serogroups Icterohaemorrhagiae, Sejroe and Australis were isolated from mongooses [51, 52].

Domestic carnivores

A recent MAT survey showed that 78·3% (83/106) of the Guadelupian dogs were seropositive against *Leptospira* [50].

Livestock

In 1973–1974, the dominant serogroup in cattle in Guadeloupe was Ballum (prevalence not shown) and the other serogroups found in cattle were Icterohaemorrhagiae, Bataviae, Australis, Pomona, and Sejroe [53]. A serosurvey in 2002–2003 showed that 14% (29/205) of cattle were serologically positive against *Leptospira* [50].

Levett *et al.* [49] showed that 6·4% (13/203) of goats were seropositive for leptospirosis and Autumnalis, Cynopteri and Sejroe were identified as the infecting serogroups [49].

A serological study in 27 pig farms in the 1990s in Guadeloupe showed that 93% of swine were positive [54] but this seroprevalence fell to 35% (141/403) in 2002–2003 [50].

Equines

In 2002–2003, 61% (74/121) of horses were serologically positive against *Leptospira* [50].

Table 3. *Main animal species studied for leptospirosis in the considered islands and results*

	Barbados	Martinique	Guadeloupe	Grenada	Trinidad	New Caledonia	Hawaii	French Polynesia	La Réunion	Mayotte
Rattus rattus										
Seropositive	33% (32/98)	ND	36·8% (14/38)	ND	16% (5/32)	ND	19.7% (72/366)	ND	ND	0% (0/19)
Main serogroups found by MAT	ND		ND	ND	Ictero. Autumnalis Hebdomadi Javanica	ND				/
Renal carriers	15% (15/98)		ND	ND	ND	61·1% (11/18) (*R. rattus*, *R. norvegicus*, *R. exulans*)	43·7% (160/366)			ND
Serogroups isolated from kidney	Ictero. Ballum Autumnalis		Ictero.	Ictero. Ballum	Ictero. Ballum Louisiana	Ictero. Canicola	Ictero. Ballum			ND
Rattus norvegicus										
Seropositive	35% (48/138)	ND	16·6% (2/12)	ND	43% (3/7)	See *R. rattus*	32·4% (165/510)	ND	ND	Absent
Main serogroups found by MAT	ND		ND	ND	Ictero. Autumnalis Hebdomadi Javanica					
Renal carriers	27% (37/138)		ND	ND	ND		60·2% (307/510)			
Serogroups isolated from kidney	Ictero. Ballum Autumnalis		ND	Ictero.	Ictero.		Ictero. Ballum Australis			
Mus musculus										
Seropositive	28·2% (24/85)	ND	57·1% (8/14)	ND	29% (2/7)	ND	66·7% (26/39)	ND	ND	ND
Main serogroups found by MAT	Ballum Autumnalis		ND		Ictero.					
Renal carriers	ND		ND		ND		79·5% (31/39)			
Serogroups isolated from kidney	ND		Ballum		ND		Ictero. Ballum			

Table 3 (*cont*.)

	Barbados	Martinique	Guadeloupe	Grenada	Trinidad	New Caledonia	Hawaii	French Polynesia	La Réunion	Mayotte
Herpestes auropunctatus										
Seropositive	40·7 % (48/118)	ND	47 % (8/17)	35–36 % (152/432–71/200)	48 % (17/37)	Absent	28·6 % (36/126)	Absent	Absent	Absent
Main serogroups found by MAT	Autumnalis		ND	Ictero. (37·5 %) Pomona (21·1 %) Canicola (6·6 %)	Canicola Ictero. Pomona					
Renal carriers	ND		ND	5·3 % (10/190)	4·7 % (5/106)		14·3 % (18/126)			
Serogroups isolated from kidney	ND		Ictero. Sejroe Australis	Ictero. Bataviae Tarassovi	Canicola		Ictero. Canicola Sejroe			
Bos primigenius										
Seropositive	ND	25·7 % (45/175)	14 % (29/205)	25 % (80/324)	92 % (24/26)	58·3 % (204/350)	ND	15·5 % (23/148) (dairy cattle)	29–32 % (452/1582–337/1063)	85 % (34/40)
Main serogroups found by MAT		Sejroe (44·4 %) Ictero. (24·4 %) Autumnalis (17·7 %)	Ballum Ictero. Bataviae Australis Pomona Sejroe	Ictero. (28 %) Autumnalis (24 %) Hebdomadis/Sejroe/Mini (12 %)	Hebdomadis	Sejroe (59·3 %) Tarassovi (19·6 %) Pomona (7·8 %)	Sejroe Bataviae	Sejroe (43 %) Tarassovi (14 %) Sejroe (10 %)	Hebdomadis (25 %) Sejroe (25 %) Ictero. (12–13 %) Pomona (12 %) Autumnalis (10–12 %) Ballum (5 %) Australis (4·5 %) Bataviae (4·5 %) Grippotyphosa (4·5 %) Canicola (0·5 %)	Sejroe (29·3 %) Canicola (23·5 %) Grippotyphosa (23·5 %) Ballum (11·7 %), Pyrogenes (8·8 %) Australis (2·9 %)
Renal carriers		ND	ND	ND	ND	ND	ND	ND	ND	ND
Serogroups isolated from kidney		ND	ND	ND	ND	ND	ND	ND	ND	ND

Table 3 (*cont*.)

	Barbados	Martinique	Guadeloupe	Grenada	Trinidad	New Caledonia	Hawaii	French Polynesia	La Réunion	Mayotte
Capra aegagrus										
Seropositive	9·3% (4/43)	ND	6·4% (13/203)	25% (11/44)	ND	ND	ND	ND	ND	70% (7/10)
Main serogroups found by MAT	Cynopteri		Autumnalis Cynopteri Sejroe	Pyrogenes						Ictero. (28·6%) Sejroe (28·6%) Canicola (14·3%) Ballum (14·3%) Grippotyphosa (14·3%)
Renal carriers	ND		ND	ND						ND
Serogroups isolated from kidney	ND		ND	ND						ND
Sus scrofa										
Seropositive	ND	39% (110/282)	35% (141/403)	35% (45/130)	52% (64/122)	58·3% (21/36)	ND	32–39% (37/115–140/360)	5% (3/57)	ND
Main serogroups found by MAT		Ictero. Sejroe Australis Cynopteri	ND	Autumnalis (35%) Ictero. (32%)	Ictero. (56%) Autumnalis (29%)	Pomona Ictero.		Ictero. (22·6%) Pomona (18%) Australis (16·7%) Canicola (10·8%) Cynopteri (9·9%) Autumnalis (7·1%)	Hebdomadis Autumnalis	
Renal carriers		ND	ND	ND	ND	ND		ND	ND	
Serogroups isolated from kidney		ND	ND	ND	ND	ND		ND	ND	

Table 3 (*cont.*)

	Barbados	Martinique	Guadeloupe	Grenada	Trinidad	New Caledonia	Hawaii	French Polynesia	La Réunion	Mayotte
Equus ferus										
Seropositive	ND	ND	61% (74/121)	ND	76% (66/87) (horses and donkeys)	94·4% (17/18)	ND	100% (5/5)	69–71% (100/145–121/171)	ND
Main serogroups found by MAT			ND		Panama (23%) Ictero. (15%) Canicola (9%) Hebdomadis (9%)	Ictero. Pyrogenes Hurtsbridge		Pomona Australis Ictero.	Autumnalis (30–34%) Ictero. (14–18%) Australis Ballum	
Renal carriers			ND		ND	ND		ND	ND	
Serogroups isolated from kidney			ND		ND	ND		ND	ND	
Canis lupus										
Seropositive	62% (48/78)	76% (219/288)	78·3% (83/106)	ND	55% (stray dogs)	59·25% (48/81)	ND	ND	40% (58/142–60/150) (stray dogs)	ND
Main serogroups found by MAT	Autumnalis (45%) Ictero. (16%) Australis (16%) Pomona (13%)	ND	ND		Canicola Ictero. Hebdomadis	Ictero. Canicola			Canicola (69%) Ictero. (16–26%)	Ictero.
Renal carriers		ND	ND		20% (10/50)	ND			ND	ND
Serogroups isolated from kidney	Copenhageni Bim	ND	ND		Canicola Ictero. Hebdomadis Autumnalis Ballum Sejroe	ND			ND	ND

ND, No data.
Absent, Species not present on this island.

Table 4. *Relation between serovars cited in the text and serogroups* (*from* [2])

Serovars	Serogroups
arborea, ballum	Ballum
autumnalis, bim, bragg	Autumnalis
icterohaemorrhagiae, copenhageni, mankarso, RGA	Icterohaemorrhagiae
australis, bajan, bangkok, bratislava, peruviana	Australis
sejroe, hardjo, wolffi	Sejroe
bataviae	Bataviae
pomona	Pomona
tarassovi, atchafalaya, navet	Tarassovi
canicola, portlandvere	Canicola
cynopteri	Cynopteri
georgia	Hebdomadis
lanka	Louisiana
brasiliensis	Bataviae
grippotyphosa	Grippotyphosa

GRENADA

Micromammals and mongooses

Utilizing kidney culture, Everard *et al*. [19] showed the renal carriage of serovar copenhageni (Icterohaemorrhagiae) in *R. norvegicus*, while serovars copenhageni (Icterohaemorrhagiae) and ballum (Ballum) were cultured from kidneys of *R. rattus*.

In 1971–1972 and in 1983, two serosurveys showed that 35% (152/432) [13] to 36% (71/200) [19] of the Grenadian mongooses were seropositive by MAT and three serogroups were identified: Icterohaemorrhagiae was the dominant serogroup [13, 19] representing 37·5% (57/152) of the positives, then Pomona in 21·1% (32/152) of the positives and Canicola in 6·6% (10/152) of the positives [13]. Leptospires were isolated from kidneys in 5·3% (10/190) of the mongooses and serovars copenhageni (Icterohaemorrhagiae), brasiliensis (Bataviae) and atchafalaya (Tarassovi) were identified [19].

Bats

In bats of the family Phyllostomidae, 8% (4/52) of *Glossophaga* sp. were found positive for leptospirosis, while 21% (13/61) of positives were found in *Anoura* sp. (13/61) [19]. Of the 121 cultures of bat kidneys none gave a positive result [19].

Amphibians

Everard *et al*. [19] reported 15% (10/66) seropositive in the toad *B. marinus*. Serovars navet (Tarassovi) and peruviana (Australis) were cultured from kidneys in two of these animals.

Livestock

Everard *et al*. [55] found 25% (80/324) of cattle to be seropositive for leptospirosis and Icterohaemorrhagiae was the dominant serogroup (28%), followed by Autumnalis (24%) and Hebdomadis and related serogroups Sejroe and Mini (12%) [55]. They also reported that 35% (45/130) of Grenadian pigs tested were seropositive, of which 35% were against serogroup Autumnalis and 32% against Icterohaemorrhagiae [55]. In sheep, 17% (18/108) were seropositive and Autumnalis was the predominant serogroup (33% of the positive sera). In goats, seroprevalence of leptospirosis was of 25% (11/44) and the dominating serogroup was Pyrogenes [55].

Chickens

Everard *et al*. [55] reported that 11% (19/175) of chickens were seropositive by MAT and antibodies found were mainly against serogroups Hebdomadis (42% of the positives) and Shermani (32%).

TRINIDAD

Micromammals and mongooses

Everard *et al*. [19] showed that 16% (5/32) of *R. rattus* were seropositive by MAT, while 43% (3/7) of *R. norvegicus* and 29% (2/7) of mice were seropositive. In *Rattus* sp. antibodies detected were directed against serogroups Icterohaemorrhagiae, Autumnalis, Hebdomadis and Javanica, while in mice, these authors found antibodies against Icterohaemorrhagiae only. Serovar copenhageni (Icterohaemorrhagiae) was isolated from the kidney of *R. norvegicus* and *R. rattus*, whereas serovars ballum (Ballum) and lanka (Louisiana) were isolated from kidneys of *R. rattus* only [19]. Everard *et al*. also showed that in the family Muridae, 24% (4/17) of the scaly-footed water rat *Nectomys squamipes* and 29% (2/7) of the rice rat *Oryzomys capito* were serologically positive. Twenty-five per cent (1/4) of the Trinidad spiny pocket mice *Heteromys anomalus* (family Heteromyidae) tested were positive. No antibodies against leptospires were found in Coues's climbing mouse *Rhipidomys couesi* (family Cricetidae) (0/2), nor the northern grass mouse *Necromys urichi* (family Cricetidae) (0/1) or the cane mouse *Zygodontomys brevicauda* (family Muridae) (0/1) [19].

In 1976, the proportion of seropositive Trinidadian mongooses ranged between 33·3% and 51·1% [13], whereas in 1983, 48% (17/37) of the mongooses sampled were seropositive [19]. In both studies, MAT results showed that serogroup Canicola predominated in this species [13, 19], but Icterohaemorrhagiae and Pomona were also encountered [13]. Canicola strains were isolated from the kidneys of mongooses [13, 19], with an infectivity rate of 4·7% (5/106) [13].

Bats

On the eight species of bats caught by Everard *et al.* [19], four presented a seropositive result with the MAT method: *Carollia perspicillata* (family Phyllostomidae), with 11% (2/19) seropositive; *Phyllostomus hastatus* (family Phillostomidae), with 27% (13/48) seropositive; *Pteronotus davyi* (family Mormoopidae), with 13% (2/15) seropositive and *Molossus major* (family Molossidae) with 25% (5/20) seropositive. Serogroups identified in bats were: Autumnalis, Hebdomadis, Javanica, Panama, Pyrogenes, Tarassovi, and Cynopteri [19].

Didelphimorphia

Everard *et al.* [19] showed that in the order Didelphimorphia, 5% (1/22) of the black-eared opossums *Didelphis marsupialis* (family Didelphidae) and 4% (5/73) of the the murine opossums *Marmosa mitis* (=*M. robinsoni*, family Didelphidae) were found seropositive. Seven per cent (1/14) of the white-eared opossums *Caluromys philander* (family Caluromyidae) were seropositive. Serovars lanka (Louisiana) and ballum (Ballum) were cultured from kidneys of *M. mitis* and serovar ballum (Ballum) was isolated from *C. philander*. Serological research of leptospiral antibodies was negative in *Marmosa fuscata* (*fuscatus*) but renal cultures revealed the presence of serovar lanka (Louisiana) in this species [19].

Primates

Leptospiral antibodies were researched in *Cebus* sp. (family Cebidae) but revealed as negative [19].

Squamates and amphibians

Forty-two per cent (5/12) of the gold tegus *Tupinambis nigropunctatus* (order Squamata, family Teiidae) sampled were found positive by MAT, while all the lizards *Ameiva ameiva* (family Teiidae) (4/4) and all the iguanas *Iguana iguana* (family Iguanidae) (1/1) caught were seropositive [19]. Everard *et al.* [19] showed that 25% (20/80) of the marine toads *B. marinus* were seropositive but none (0/2) of the lesser tree frogs *Hyla minuta* (order Anura, family Hylidae) tested positive. Serovar autumnalis (Autumnalis) was isolated from the marine toad [19].

Domestic carnivores

In 1979, serological data reported that at least 55% of the stray dogs had been exposed to leptospires as opposed to only 12·5% of the cats. Agglutinins against serogroups Canicola, Icterohaemorrhagiae and Hebdomadis were found most frequently in these species [56]. Twenty per cent (10/50) of the sampled dogs carried leptospires in their kidneys [56]. Serovars isolated in dogs were portlandvere (Canicola), canicola (Canicola), copenhageni (Icterohaemorrhagiae) and georgia (Hebdomadis), whereas serovar canicola was isolated from one cat. A seroepidemiological survey was conducted in 2005 in different populations of Trinidadian dogs [57]: among house dogs 7·7% (5/65) of the non-vaccinated animals were seropositive. The prevalence was the highest among hunting dogs with 25·5% (12/47) positive, while 20·4% (10/49) and 4·4% (5/113) of the farm and stray dogs, respectively, were seropositive. In the population of dogs suspected of leptospirosis, 48% (24/50) were seropositive. Nine serovars of *L. interrogans* were identified in this species. The most prevalent serovar was mankarso (Icterohaemorrhagiae), in 47·5% of the seropositive dogs (29/61). The other serovars were icterohaemorrhagiae RGA (Icterohaemorrhagiae 32·8%, 20/61), autumnalis (Autumnalis 41%, 25/61), copenhageni (Icterohaemorrhagiae 16·4%, 10/61), bratislava (Australis 13·1%, 8/61), georgia (Hebdomadis), ballum (Ballum) and wolffi (Sejroe) (1·6% each, 1/61) [57].

Livestock

In 1985, MAT results reported that 92% (24/26) of cattle were seropositive with serogroup Hebdomadis predominating [55]. All of the ten 'bufflypso' (water buffaloes, *Bubalus bubalis*) tested were positive and the prevailing serogroup in these animals was Grippotyphosa [55]. In 2009, a larger study reported that 14·6% (33/226) of the water buffaloes were seropositive [58].

Among swine, it was shown that 52% (64/122) of the sampled animals were serologically positive with 56% and 29% of those seropositive having antibodies against serogroups Icterohaemorrhagiae and Autumnalis, respectively [55].

Equines

MAT results showed that 76% (66/87) of horses and donkeys were seropositive [55]. Panama was the most frequently reported serogroup (23% of positive animals), followed by Icterohaemorrhagiae (15%), Canicola and Hebdomadis (9% each) [55].

Poultry and wild birds

Everard *et al.* [55] showed that 11% (16/144) of the chickens tested had a positive serological reaction against *Leptospira*. Fifty per cent of the reactions were against serogroup Shermani, while 25% were against serogroup Hebdomadis. Eight ducks and geese were also tested but were negative. No leptospiral antibodies were found in the American black vulture *Coragyps atratus* [55].

NEW CALEDONIA

Micromammals

In 1985–1986, a study based on culture showed that 61·1% (11/18) of rats (*R. rattus*, *R. norvegicus*, *R. exulans*) excreted leptospires in their urine [59]. A complementary study identified the leptospires shed in urine of rats as belonging to serogroups Icterohaemorrhagiae and Canicola [60].

Domestic carnivores

In 1985–1986, Brethes *et al.* [60] reported that 59·25% (48/81) of canids in New Caledonia were seropositive, of which 39·6% (19/48) had antibodies against serogroup Icterohaemorrhagiae. In the particular area of Bourail (a 'hot-spot' of human leptospirosis in New Caledonia), 63% (29/46) of dogs were seropositive, of which 55% (16/29) were against Icterohaemorrhagiae. Predominance of serogroup Icterohaemorrhagiae in canids was confirmed in 1999 by the Laboratoire Territorial de Diagnostic Vétérinaire (LTDV) whose results reported serological evidence of a high circulation of serogroup Canicola in dogs [61].

Livestock

All cattle sampled (15 animals) in the area of Bourail in 1985–1986 were positive by MAT [60]. A subsequent survey in 1990 on the entire New Caledonian cattle assessed the seroprevalence at 58·3% (204/350), with 74·6% (85/114) of the surveyed herds having at least one positive animal [62]. Serogroups Sejroe, Tarassovi and Pomona were circulating in New Caledonian cattle [60, 62], with a prevalence of 59·3%, 19·6% and 7·8% among the positive animals, respectively [62]. In 2007, the annual report of the LTDV confirmed the predominance of serovars hardjo (Sejroe) and sejroe (Sejroe) in cattle [10].

In 1985–1986, 58·3% (21/36) of pigs were found to be seropositive for leptospirosis. By MAT, sera reacted principally against serogroup Pomona and secondly against Icterohaemorrhagiae [59].

Antibodies against serovar hardjo (Sejroe) were found in the Rusa deer [60].

Equines

In 1983, MAT results showed that the dominant serogroups in horses in New Caledonia were Canicola and Pomona [63]. In 1986, the dominant serogroup was Icterohaemorrhagiae: 17/18 of the horses sampled in the area of Bourail were seropositive, of which nine were against Icterohaemorrhagiae [60]. Icterohaemorrhagiae was still prevailing in horses in 1996 [64]. However, since 1996, inclusion of serogroups Pyrogenes and Hurtsbridge in the MAT panel of strains demonstrated the high circulation of these serogroups in positive horses, with a frequency of 29·3% and 18·8%, respectively, in 1996 [64]; 18·7% and 43·2%, respectively, in 1998 [65]; and 52·3% and 32·1%, respectively, in 1999 [61].

A serological survey conducted on the donkeys of Maré (Loyalty Islands) in 1999 proved that 97% (38/39) of the sampled animals had antibodies against *Leptospira*. The dominant serogroups were Hurtsbridge and Pyrogenes [61].

HAWAII

Micromammals and mongooses

In the 1950s and 1960s, the study of Wallace *et al.* [66] on Hawaiian rats *R. norvegicus, R. rattus, R. hawaiiensis* (= *R. exulans*), mice and mongooses reported that 45% (558/1238) of these mammals had antibodies against *Leptospira*. A survey conducted between 1959 and 1961 on 1281 mammals (same species as cited above) [67] showed that mice and *R. norvegicus* populations were highly infected, with respectively 66·7% (26/39) and 32·4% (165/510) seropositive by MAT and 79·5% (31/39) and 60·2% (307/510) renal carriers. They were followed by the mongoose with 28·6% (36/126) seropositive, and 14·3% (18/126) renal carriers. The serological prevalence in *R. rattus* was lower with 19·7% (72/366) seropositive contrasting with the high rate of renal carriage (43·7%, 160/366) in this species [67]. Cultures of kidney tissues proved the renal carriage of serovar icterohaemorrhagiae (Icterohaemorrhagiae) in all the species [66, 67]. Serovar ballum (Ballum) was only recovered in *R. rattus* [66]. One isolate of the serogroup Australis was obtained in *R. norvegicus*, while serogroups Canicola and Sejroe were isolated from the mongoose only [67]. Another survey was conducted in Hawaii between 1969 and 1973 on 2982 animals of the same species [68] and the following seroprevalences were found: 34·0% (419/1234) positive in *R. rattus*, 61·4% (137/223) in *R. norvegicus*, 17·8% (166/932) in *R. exulans*, 43·2% (41/95) in *M. musculus* and 28·8% (136/473) in *H. auropunctatus* [68]. Cultures of kidneys showed that serogroup Icterohaemorrhagiae was predominant in *R. norvegicus* (91·4% of positives, 85/93), while 58·7% (24/41) of the identified cultures recovered from mice were from serogroup Ballum and 59·7% (43/72) of those recovered from mongooses were from serogroup Sejroe. Serogroups Icterohaemorrhgiae and Ballum were isolated from all rat species and mice, but not from mongooses, while Sejroe was isolated only from mongooses [68].

Marine mammals

A serological study on the endemic monk seals of Hawaii *Monachus schauinslandi* (order Carnivora, family Phocidae) showed that leptospirosis was circulating in this population and that monk seals had positive titres against serovars bratislava (Australis), hardjo (Sejroe), icterohaemorrhagiae (Icterohaemorrhagiae) and pomona (Pomona) [69].

Livestock

Serovars hardjo (Sejroe) and bataviae (Bataviae) were identified by MAT in cattle on Kauai island in 1987 [70].

FRENCH POLYNESIA

Livestock

In 1988, Raust [71] published the results of a serological survey showing that 15·5% (23/148) of dairy cattle were seropositive and that the dominant serovar was hardjo (Sejroe) in 43% of those positive, followed by serovar tarassovi (Tarassovi) in 14% and serovar sejroe (Sejroe) in 10%. A health control conducted in 1997 in cattle confirmed the results of 1988 [72].

In 1988, 32% (37/115) [71] to 39% (140/360) [65] of pigs were seropositive by MAT. Both studies reported icterohaemorrhagiae (Icterohaemorrhagiae) as the most prevalent serovar in this species (22·6% of positive pigs for the former, 96% for the latter). The first study also identified pomona (Pomona, 18%), bratislava (Australis, 16·7%), canicola (Canicola, 10·8%), cynopteri (Cynopteri, 9·9%) and autumnalis (Autumnalis, 7·1%) as circulating serovars in pigs [71].

Equines

Only five horses were tested during the survey of Raust in 1988 [71], and all were seropositive. Serovars pomona (Pomona), australis (Australis) and icterohaemorrhagiae (Icterohaemorrhagiae) were identified in this species.

LA RÉUNION

Micromammals

In 2007, a serological survey on tenrecs *Tenrec ecaudatus* (order Lipotyphla, family Tenrecidae) showed a seroprevalence of 92% (34/37) in this species with all sera predominantly reacting against serogroup Icterohaemorrhagiae [73].

Domestic carnivores

Two serosurveys conducted in a dog pound in 1977–1979 [74] and 1978–1983 [75] showed that 40% (58/142 and 60/150, respectively) of the stray dogs were seropositive by MAT. In the former study, serogroups Canicola and Icterohaemorrhagiae were found in 69% (40/58) and 26% (15/58), respectively, of the seropositive dogs [74] while in the latter study 16% of those seropositive had antibodies against Icterohaemorrhagiae [75].

Livestock

In 1978–1979, two simultaneous serological studies showed similar results with 29% (452/1582) [76] and 32% (337/1063) [74] of cattle having a positive serological titre. Serogroups Hebdomadis and Sejroe each represented 25% of the seropositive reactions [74, 76], serogroup Icterohaemorrhagiae accounted for 12–13% [75, 77], Pomona 12% [76], Autumnalis 10–12% [74, 76], Ballum 5% [76], Australis, Bataviae and Grippotyphosa 4·5% each, and Canicola 0·5% [76]. In La Réunion, serogroups Sejroe and Hebdomadis were recognized as a major cause of abortion in dairy cattle [77].

A sampling conducted in 1979 at a slaughter-house revealed a limited circulation of leptospires in swine, with 5% (3/57) of pigs seropositive and circulation of serogroups Autumnalis and Hebdomadis [74]. Currently, field data indicate a high seroprevalence rate in reproduction swine: a serological follow-up of 13 pig farms between 2001 and 2008 showed that each year 6–29% of the tested sera were positive (Dr P. André, personal communication).

Equines

At the end of the 1970s, there were four riding schools in La Réunion, accounting for about 150 horses. In this equine population, 10–20 cases of leptospirosis occurred throughout the year [77]. In 1979, two serological surveys [74, 76] revealed that 69% (100/145) to 71% (121/171) of the horses were seropositive. Eleven different serogroups were serologically identified in horses and the predominant serogroup was Autumnalis (30–34% of positive reactions), while Icterohaemorrhagiae was found in 14–18% of positive animals [74, 76]. In 1983, Mollaret *et al.* [75] confirmed that 12% of horses were serologically reactive against serogroup Icterohaemorrhagiae. Moutou [74] pointed out that the prevailing serogroup differed among the riding school of origin: Icterohaemorrhagiae in the riding school of St-Denis, Australis in the riding schools of St-Gilles and Tampon, Ballum in horses of Bras Panon. Nevertheless, in 1990, following a clinical outbreak of leptospirosis in the riding school of Tampon, 22 horses were tested. All were seropositive for Icterohaemorrhagiae (Dr A. Michault, personal communication). Thus if leptospirosis is highly prevalent in horses in La Réunion without systematic clinical expression of the disease, serogroup Icterohaemorrhagiae could be responsible for clinical outbreaks.

MAYOTTE

Micromammals and wild fauna

The 19 rats sampled in 1991 were all seronegative by MAT [78].

In the same year, the circulation of serovar hardjo (Sejroe) was shown in two out of ten tenrecs *T. ecaudatus* and in the only fruit bat *Pteropus seychellensis* (order Chiroptera, family Pteropodidae) caught. Antibodies against serogroup Pyrogenes and serovar wolffi (Sejroe) were also found in the tenrec, while antibodies against serovar icterohaemorrhagiae (Icterohaemorrhagiae) were found in small Indian civets *Viverricula indica* (order Carnivora, family Viverridae) [78].

Domestic carnivores

MAT results showed the circulation of serovar icterohaemorrhagiae (Icterohaemorrhagiae) in dogs [78].

Livestock

At the beginning of the 1990s, zebus, goats and dogs were highly infected, with 85% (34/40), 70% (7/10) and 83% (5/6) seropositive, respectively. In zebus, serovars identified by MAT were canicola (Canicola), grippotyphosa (Grippotyphosa), sejroe (Sejroe), each accounting for 23·5% of the seropositives, then ballum (Ballum, 11·7%), Pyrogenes (8·8%), wolffi (Sejroe, 5·8%) and australis (Australis, 2·9%). In goats, serovars were icterohaemorrhagiae, wolffi (each accounting for 28·6% of seropositives), canicola, ballum and grippotyphosa (14·3% each) [78].

DISCUSSION

Origin of the serovars

Introduction of animal species in a region induces introduction of simultaneous pathogens. So, originally, the presence of leptospiral serovars circulating on each island was linked with the history of the human colonization and the shipping importations of animals by the Europeans [20, 28, 79]. Nevertheless, serovars circulating on a colonized island are different from those of the colonizing country. Even if no study has compared mainland and tropical islands, we know that serovars carried by rats, mice and hedgehogs (*Erinaceus europaeus*) in New Zealand are not the same as those carried by the same species in

Great Britain, the country from where they were imported during colonization [80]. Thus, the few serogroups of leptospires circulating in animals on an island are specific to the animals which have colonized the island and could maintain themselves in this typical environment. Serovars present on tropical islands are generally circulating worldwide but each island represents a unique ecosystem, the limited panel of serovars found in each insular area is absolutely island specific.

The case of vaccinated animals

The most commercially available vaccines against leptospirosis are for dogs and are directed against serogroups Icterohaemorrhagiae and Canicola. Consequently, the presence of seropositive domestic dogs [50] and the presence of both these serogroups in high proportions in populations of healthy dogs [60, 61] could be partly explained by the vaccination measures currently practised in the majority of the presented islands. Nevertheless, a study in Trinidad showed that vaccination did not have any significant effect on *Leptospira* infection as similar prevalence of infections were detected for both vaccinated (5·3%) and non-vaccinated dogs (7·7%) [57]. Moreover, Hathaway *et al.* [80] showed that agglutinins induced by the vaccine disappear within weeks of administration [81]. Consequently, the seropositive dogs detected in the different studies were essentially due to exposure to field serovars of *Leptospira* sp.

Carrier state and immune response

In Hawaii the rate of renal infection in *R. norvegicus, R. rattus* and *M. musculus* is significantly higher than the serological prevalence in each species [67]. The same observation was reported in the rodent population of Terceira Island (Azores) [9] and in *R. norvegicus* caught in Brazil [7, 38]. Duration of immunity is not known in field rats, but after infection in carrier animals, leptospires are subsequently cleared from all organs except the renal tubules [82]. Thus, in the absence of re-infection, carrier animals may be serologically negative, thus the carrier state may not be detected in MAT-positive animals. In contrast, other studies showed that the serological prevalence in rats is higher than the renal carriage [8]. Consequently, serology is often not clear, as MAT-negative bacteriologically proved carriers may be encountered [2].

Diversity of hosts and serovars in insular areas

In insular areas of volcanic origin like La Réunion, Mayotte, Hawaii, Martinique, Guadeloupe and French Polynesia, the mammalian diversity is generally poor and leptospires have a limited choice in mammalian hosts compared to the larger choice offered by continental countries like Guyana [83], Peru [84], Brazil [85], or larger islands, e.g. New Zealand [80] or Australia [86]. In consequence, bacteria concentrate themselves in abundant species, susceptible but generally non-sensitive, living most frequently in an anthropic environment, and which are perfect to play the role of reservoir and spreader of bacteria. On these islands, this role is played most frequently by alien species, e.g. rats and mice, or even mongooses and dogs.

Almost all knowledge on leptospirosis is related to infection in mammals but the finding of *Leptospira* in amphibians and reptiles [45, 46], which live in moist or wet environments, and birds [55], leads to questions about the role of these species, if any, in the carriage and maintenance of foci of leptospirosis.

Comparison with mainland

The seroprevalence of leptospirosis in animals seems to be higher in small islands than in mainland or larger islands but the number of circulating serovars is lower. In fact, the diversity of serovars in a region may be correlated on the one hand directly with the faunistic diversity of the area (number of potential hosts) and on the other with its environmental diversity [8]. For example, in Australia, which can be considered as the nearest 'mainland' from New Caledonia, the prevalence of leptopsirosis in the dog population is 1·9% (18/956) [87], which is markedly inferior to the prevalence in New Caledonian dogs (59·25%) [60]. Nevertheless, although only two serovars are described in the New Caledonian canids [60, 61], 11 are found in Australian dogs [87]. An other example can be found in Trinidad which has a greater mammal species diversity (about 100 mammalian species) than the neighbouring island of Grenada (15 mammalian species): 80 isolates of *L. interrogans* were reported in Trinidad to infect humans, domestic and wild animals, and only 20 were reported in Grenada [88]. The hypothesis is reinforced by the situation in the temperate Azorean islands (North Atlantic ocean) where three serovars are described in the four rodents and insectivorous mammal species present, while six serovars are counted among the 21 micromammals in Portugal [51, 89].

Adaptation of the serovars to insular ecosystems

When a serovar is introduced within a new ecosystem, it finds an ecological niche that may be different from the one it uses in its native environment. Indeed, one animal species, living in two different countries/islands within two different ecosystems, may offer two distinct ecological niches for leptospires [80, 90]. Generally, in a geographical region an equilibrium is established in which there is an 'adaptation' of a serogroup to a reservoir species [4, 74]. Thus, the Indian mongoose (*H. auropunctatus*) is considered as a reservoir for serogroups Sejroe, Icterohaemorrhagiae and Canicola in Hawaii [67, 68], serogroup Sejroe in Oahu island [91], serogroups Icterohaemorrhagiae, Sejroe and Australis in Guadeloupe [51, 52], serogroup Canicola in Trinidad [13, 19] and serovars copenhageni (Icterohaemorrhagiae), atchafalaya (Tarassovi) and brasiliensis (Bataviae) in Grenada [19]. Moreover, in La Réunion, Moutou [74] reported that the dominant serogroup identified by serology in horses differed according to the riding school in which the animals lived, i.e. according to the geographical zone of the island.

Lastly, it should be noted that phenomena of speciation by adaptation to a particular host in a small biotope can lead to the appearance of new serovars, e.g. serovar bim (Autumnalis) in dogs on Barbados [48] or atchafalaya (Tarassovi) in Grenadian mongooses [19], or even serovar lanka (Louisiana) in Trinidad [19].

Evolution of seroprevalence

Few studies report a follow-up of the seroprevalence of leptospirosis in animal species. A survey was conducted between 1959 and 1961 on five species of wild mammals in Hawaii [67] and another survey on the same species was conducted between 1969 and 1973 [68] (see earlier results): comparison between the two studies shows that (i) serogroups of *Leptospira* sp. isolated by culture in each animal species were the same but the relative distribution of the serovars per species was different and (ii) the serogroup Sejroe was emergent in the mongoose. Furthermore, the respective densities of the rodents and mongooses have changed in Hawaii, with an increase of the populations of *R. rattus, R. exulans* and mongooses, while the populations of *R. norvegicus* and mice decreased. In consequence, although in the 1960s *R. norvegicus* and the mouse were the main reservoirs of leptospires in Hawaii, in 1973 *R. rattus* represented the main bacterial reservoir. Therefore, the epidemiology of the disease had changed in Hawaii, switching from a peridomestic animal reservoir (*R. norvegicus* and mouse) to a more rural reservoir (*R. rattus* and mongoose) [68].

Different examples show that the seroprevalence of leptospirosis in one species seems to be quite stable over time. In 1971–1972 and in 1983, two serosurveys proved that the seroprevalence assessed by MAT in mongooses in Grenada did not evolve over 10 years with a prevalence of 35% [13] and 36%, respectively [19]. Moreover, prevalence of antibodies did not change much in Trinidadian mongooses over 6 years, with 33·3–51·1% seropositive in 1976 [13], whereas in 1983, 48% of the mongooses sampled were seropositive [19]. In La Réunion two serosurveys conducted in the same dog pound at two distinct periods (1977–1979 [74] and 1978–1983 [75]) showed that 40% (58/142 and 60/150, respectively) of the stray dogs were seropositive by MAT. Similarly for French Polynesia the seroprevalence in cattle did not evolve between 1988 and 1997 [65].

Nevertheless, an exception can be found in the population of pigs in La Réunion in which the seroprevalence seemed to increase significantly over 30 years going from 5% of pigs seropositive in 1979 to 6–29% at 7 years follow-up conducted between 2001 and 2008. Three hypothesis can be put forward: (i) the survey of Moutou [74] underestimated the prevalence of the disease in swine, either because of a too small sample size or because the animals sampled were too young; (ii) the disease has greatly evolved in La Réunion, with a 'burst' occurring during the last 30 years; (iii) changes in the methods of farming, going from small family pig farms to battery industrial breeding farms could have induced an evolution in the prevalence of leptospirosis in pigs. Thus, higher animal density could favour the maintenance and transmission of the disease inside farms, and the gathering of fattening animals born in different reproductive farms, or in a growing farm could favour the spread of the disease between sites. Moreover the seroprevalence and consequences of the disease are different when considering breeding sows or grower animals [92].

Meteorological factors

In tropical regions, high rainfall is the main climatic factor of maintenance of leptospires in the environment and of their transmission to exposed animals and humans [93, 94]. A survey conducted in Hawaii between 1969 and 1973 showed that the sero-prevalence rates in rodents and mongooses were higher on the Eastern coast (where rainfall is high) than on the Western part of the island [68]. In North America, a statistical positive correlation was also demonstrated between prevalence of infection in dogs and rainfall [95]. Moreover, in 2002–2003 and 2003–2004 the Caribbean region had two successive years of the El Niño phenomenon, which resulted in an increase in rainfall and probably in a proliferation of rodents which modified the epidemiology of human leptospirosis in Guadeloupe. In consequence, not only was there an increase in the total number of human cases observed in this island, but also the number of cases due to serogroup Ballum, a mouse-associated serogroup [8, 9] increased [96].

Nevertheless, cyclones do not appear to be linked with an increase in the number of human cases in La Réunion (Dr A. Michault, personal communication), nor in Guadeloupe [96]. It is likely that these intense climatic phenomena are responsible for the leaching of the environmental reservoirs and the destruction of the habitats of the micromammals considered as reservoirs [96].

CONCLUSION

This paper reviews the current knowledge on animal leptospirosis in small tropical islands and shows that the specificity of the host–serovar relation is greatly dependent of a specific insular ecosystem. However, the interpretation of the serological results and comparison between islands might be hazardous for two main reasons: (i) data are mainly stemmed from sero-epidemiological surveys that include a variable number of species and individuals, and (ii) methods of analysis and thresholds of positivity differ between studies.

Nonetheless, leptospirosis appears endemic in the majority of the animal species. If the status of domestic or peri-domestic (rats, mongooses, mice) animals against leptospirosis has been well studied in insular areas, the wild fauna has been investigated less so. The interest of the scientific community in animal leptospirosis in these regions is modest thus far, and available data are often poor, mainly due to the fact that research is concentrated on the human disease. This paper stresses the need for more research in this field and highlights that studies on fauna have to be done at the island scale. Identification of the prevailing serovars and of their animal reservoirs is essential to understand the particular epidemiology of leptospirosis on each island and advise measures of prevention for humans. Furthermore, the economic cost of human and animal leptospirosis in these islands is not negligible [97]. Because molecular tools are more powerful than serology and because they allow the establishment of stronger epidemiological links between strains circulating in animals and those inducing disease in humans, the use of genotyping techniques needs to be incorporated into epidemiological studies of *Leptospira* sp. in insular areas in order to generate more meaningful and translational data.

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Political and population information on countries has been extracted from Wikipedia via the internet and is not necessarily accurate.

DECLARATION OF INTEREST

None.

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