Bartonella spp. Infections in Rodents of Cambodia, Lao PDR, and Thailand: Identifying Risky Habitats

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Abstract

This study investigated the type of environmental habitat that may explain the infection of 1176 individuals from 17 rodent species by *Bartonella* species in seven sites in Cambodia, Lao PDR, and Thailand. No effects of host sex and host maturity on the level of individual infection by all *Bartonella* spp., but significant effects of locality, season, and host species were observed. The patterns differed when investigating the three more prevalent *Bartonella* species. For *B. rattimassiliensis*, season and habitat appeared to be significant factors explaining host infection, with higher levels of infection in wet season and lower levels of infection in rain-fed field, dry field, and human settlement habitats compared to forest habitat. The infection by *B. queenslandensis* was found to vary, although not significantly, with season and locality, and *Bartonella* n. sp. (a species mostly associated with *Mus* spp.) was found to be more prevalent in the wet season and dry field habitat compared to forest habitat. We discuss these results in relation to rodent habitat specificity.

Key Words: Rodent—*Bartonella* spp.—Habitat—Southeast Asia.

Introduction

MEMBERS OF THE GENUS *Bartonella* are Gram-negative bacteria belonging to the class Alphaproteobacteria. Several species have been implicated as causing human diseases, ranging with short-term fever to severe endocarditis. Reports of *Bartonella* infections in humans have dramatically increased in Southeast Asian countries (Bhengsi et al. 2010, Kosoy et al. 2010, Pachirat et al. 2011, Bai et al. 2012). In Thailand, studies have reported human infections with *B. elizabethae*, *B. henselae*, *B. tamiae*, *B. rattimassiliensis*, *B. tribocorum*, and *B. vinsonii* subsp. *arupensis* (Kosoy et al. 2008, Paitoonpong et al. 2008, Kosoy et al. 2010). However, the identification of rodent reservoirs and particularly the role played by habitats in their infection are investigated far less (Castle et al. 2004, Bai et al. 2009, Jiyipong et al. 2012).

Southeast Asia is a recognized hotspot of both biodiversity at threat (Wilcove et al. 2013) and emerging infectious diseases (Coker et al. 2011), with biodiversity loss identified as a likely explanatory factor for the increase in zoonotic disease outbreaks in the region (Morand et al. 2014). Ongoing land use changes that characterize Southeast Asian countries may affect the transmission of rodent-borne diseases, and among others of *Bartonella* species, and then the risk of transmission to humans. The investigation of rodent infection in different habitats at different locations in Southeast Asia makes it possible to evaluate the particular effect of habitat, taking into account the influence of season and species.

The aim of this study was to determine the type of environmental habitat that may explain the infection of rodents by *Bartonella* species. For this we used a subset of the screening data of Jiyipong et al. (2012), who investigated the diversity of *Bartonella* infections from rodents and shrews that were

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trapped from seven localities (and four major habitats) in Cambodia, Lao PDR, and Thailand. Three zoonotic species, *B. elizabethae*, *B. rattimassiliensis*, and *B. tribocorum*, were found in the study of Jiyipong et al. (2012).

Material and Methods

Trapping protocol

Seven different localities were chosen in three countries (Thailand, Cambodia, and Lao PDR), as offering a representative overview of the various ecosystems that are affected by land use changes (see map in Jiyipong et al. 2012). These sampling sites were part of the CERoPath project (www.ceropath.org). Four main habitats were investigated in each locality. At each site, 30 lines of 10 traps were installed over four nights targeting three different habitats, *i.e.*, forests, nonflooded lands (agricultural lands such as orchards, dry rice field, cassava field, or noncultivated land such as bush), and flooded-irrigated agricultural lands (*i.e.*, paddy rice fields), for a total of 1200 night-traps and for each season (wet and dry). Villages and isolated houses, which corresponded to a fourth habitat category, the human settlement, were also sampled using cage-traps distributed to residents (with around 300 hundred traps, corresponding to similar trapping pressure as the other habitats).

Pictures, a habitat description, and coordinates of the trap lines are available in the “research/study” areas and “research/protocols” sections of the CERoPath project web site (www.ceropath.org). Two trapping sessions were realized per locality at the wet and at the dry season characterized according to the average rainfall recorded during the month of trapping and the former month, and provided by the Global Precipitation Climatology Centre (GPCC, <http://gpcc.dwd.de>). The trapping sessions were conducted during the years 2008–2009. For logistical reasons, some localities were investigated in wet season one year and the dry season the other year.

Rodents were identified on the basis of their morphology or using species-specific primers and/or barcoding assignment (Chaval et al. 2010). Complete data for animals used as a reference for barcoding assignment can be consulted in the “Barcoding Tool/RodentSEA” section of the CERoPath project web site (www.ceropath.org).

Rodents were euthanized and dissected to collect blood and organs following the CERoPath protocols (Pagès et al. 2010, Herbreteau et al. 2011) (www.ceropath.org), which respect animal care, health security for field parasitologists, and quality data handling. Blood samples were collected by cardiocentesis, and stored at -80°C before shipment on dry ice to the URMITE CNRS-IRD UMR laboratory in Marseille, France.

Bartonella infection and identification

In the study of Jiyipong et al. (2012), DNA of blood samples was extracted from 1341 individuals, belonging to 19 rodent and shrew species, and screened using real-time PCR targeting the 16S–23S ribosomal RNA intergenic spacer region (internal transcribed spacer, ITS). Blood samples were also tested by culture method on Columbia agar supplemented with 5% sheep blood and incubated at 37°C in 5% CO_2 for up to 4 weeks. A single colony for each positive

sample was picked, and its DNA was extracted and identified species using standard PCR amplification and a sequencing targeting two housekeeping genes (*gltA* and *rpoB*) and the ITS fragment (Roux and Raoult 1995, La Scola et al. 2003). Species were identified by comparing sequence data with the sequences of the *Bartonella* reference strains, which were retrieved from GenBank using ClustalW (see Jiyipong et al. 2012).

We limited our analyses to the 1176 individuals (of 1341) that were trapped according to the standardized protocol (excluding the individuals trapped by local hunters) and of 17 (19) rodent species that were identified to species level (and removing shrew species). Table 1 summarizes the species and number of rodents by locality and habitat where *Bartonella* species were found.

Statistical analysis

We performed generalized linear models (GLM), using a binomial distribution of individual host infection and logit function, to identify the likely variables that might explain the infection of rodents by *Bartonella* spp. in the R software. Selection of the best model was based on the Akaike information criterion (AIC) using host species, habitat, locality, season, maturity, and sex as independent variables. These localities represented a variety of habitats in relation to human pressures and land usage. Habitats were ranked as: (1) Forests and mature plantations, (2) nonflooded lands or fields (shrubby wasteland, young plantations, orchards), (3) rain-fed and irrigated lowland paddy rice fields (cultivated floodplain), and (4) settlement and households (in villages or city), which corresponded to an increasing gradient of human-dominated habitats.

We performed GLM analyses on all *Bartonella* spp., and on each of the three more prevalent species: *Bartonella* n. sp. (a new species mostly found associated with humans; see Jiyipong et al. 2012), *B. rattimassiliensis*, and *B. queenslandensis*. For the three prevalent species, only individuals from the host species reported infected were used in the analyses (see Table 1).

Results

Of the 1176 individuals, 112 were found infected by *Bartonella* spp. (8.7 %).

Factors of rodent infection by Bartonella species

We used the AIC to compare logistic regression models used to explain individual rodent infection. There were no effects of host sex and host maturity on the level of individual infection by all *Bartonella* spp., but a significant effect of locality, season, and host species (Table 2). Three localities showed higher host infection—Loei in Thailand, Luang Prabang in Lao PDR, and Sihanouk in Cambodia—with no effect of habitat. Rodents were more infected in the wet season (Table 3; $p < 0.0001$), and two species, *Maxomys surifer* (a forest species) and *Rattus exulans* (a domestic species) were significantly less infected by *Bartonella* spp. ($p < 0.0001$).

The patterns differed when investigating the three more prevalent *Bartonella* species. For *B. rattimassiliensis*, season and habitat appeared to be significant factors explaining host

TABLE 1. LIST AND NUMBER OF HOST SPECIES COLLECTED IN SEVEN LOCALITIES OF CAMBODIA, LAO PDR, AND THAILAND, WITH NUMBER OF INDIVIDUALS FROM RODENT SPECIES TRAPPED IN FOUR MAIN HABITATS (FOREST, RAIN-FED LANDS, NONFLOODED OR DRY LANDS, SETTLEMENT) AND INFECTED BY *BARTONELLA* SPECIES^a

Country	Locality	Habitat	Host species	n	<i>Bartonella</i> <i>n. sp.</i>	B. rattimassiliensis	B. queenslandensis	B. tribocorum	B. coopersplainsensi	B. elizabethae	B. phoceensis
Thailand	Buriram	Forest	<i>M. cookii</i>	1							
		Rain-fed	<i>R. tanezumi</i>	5		3					
			<i>B. indica</i>	2							
			<i>Bandicota savilei</i>	21							
			<i>M. caroli</i>	13							
			<i>M. cervicolor</i>	25							
			<i>R. argentiventer</i>	2							
			<i>R. exulans</i>	1							
			<i>R. sakaretensis</i>	2							
			<i>R. tanezumi</i>	9					1		1
			<i>B. indica</i>	1							
		Dry land	<i>R. tanezumi</i>	6		2					
		Settlement	<i>R. exulans</i>	67							
			<i>R. tanezumi</i>	13							
	Loie	Forest	<i>B. berdmorei</i>	1							
			<i>M. cookii</i>	4	2						
			<i>N. fulvescens</i>	5							
		Rain-fed	<i>M. caroli</i>	3	1						
			<i>M. cervicolor</i>	2	2						
			<i>R. sakaretensis</i>	35							
		Dry land	<i>B. savilei</i>	2							
			<i>B. berdmorei</i>	2							
			<i>B. bowersi</i>	1							
			<i>M. surifer</i>	4							
			<i>M. caroli</i>	2	1						
			<i>M. cervicolor</i>	18	7						
			<i>M. cookii</i>	6	2						
			<i>N. fulvescens</i>	1							
			<i>R. tanezumi</i>	1							
	Nan	Settlement	<i>R. exulans</i>	18				1		1	
		Forest	<i>B. indica</i>	6							
			<i>B. berdmorei</i>	1							
			<i>B. bowersi</i>	1							
			<i>M. cookii</i>	2	1						
			<i>R. tanezumi</i>	1							
		Rain-fed	<i>B. indica</i>	32			2	1			
			<i>M. caroli</i>	3							
			<i>M. cookii</i>	3							
			<i>R. tanezumi</i>	6							

(continued)

TABLE 1. (CONTINUED)

Country	Locality	Habitat	Host species	n	Bartonella <i>n. sp.</i>	B. rattimassiliensis	B. queenslandensis	B. tribocorum	B. coopersplainsensis	B. elizabethae	B. phoceensis
Cambodia	Mondolkiri	Dry land	<i>B. indica</i>	3							
			<i>B. berdmorei</i>	1							
			<i>M. caroli</i>	1							
			<i>M. cervicolor</i>	3							
			<i>M. cookii</i>	15							
		Settlement	<i>R. tanezumi</i>	7			1				
			<i>B. indica</i>	3							
			<i>B. berdmorei</i>	5			1			1	
			<i>B. bowersi</i>	1							
			<i>R. exulans</i>	50							
	Forest		<i>R. tanezumi</i>	4		1		1			
			<i>B. berdmorei</i>	1							
			<i>Leopoldamys edwardsi</i>	2							
			<i>M. surifer</i>	31							
			<i>N. fulvescens</i>	7			1				
			<i>R. tanezumi</i>	12		1	1				
			<i>B. indica</i>	1							
			<i>B. savilei</i>	32		4			2		
			<i>R. exulans</i>	1							
			<i>R. tanezumi</i>	1			1				
			<i>B. indica</i>	2							
			<i>B. savilei</i>	37		1					
			<i>B. berdmorei</i>	3							
			<i>M. surifer</i>	2							
			<i>N. fulvescens</i>	2							
			<i>R. tanezumi</i>	7			1				
			<i>R. exulans</i>	45							
			<i>R. tanezumi</i>	19		2					
			<i>B. berdmorei</i>	1							
			<i>M. surifer</i>	23			1				
			<i>N. fulvescens</i>	1							
			<i>R. argentiventer</i>	1							
			<i>R. tanezumi</i>	6		1					
			<i>B. berdmorei</i>	2							
			<i>R. argentiventer</i>	14		1				1	
			<i>R. exulans</i>	2							
			<i>R. norvegicus</i>	3							
			<i>R. tanezumi</i>	25							
			<i>B. berdmorei</i>	3			1				
			<i>M. surifer</i>	33							
			<i>R. argentiventer</i>	5							

(continued)

TABLE 1. (CONTINUED)

Country	Locality	Habitat	Host species	n	Bartonella <i>n. sp.</i>	B. rattimassiliensis	B. queenslandensis	B. tribocorum	B. coopersplainsensi	B. elizabethae	B. phoceensis
Lao PDR	Champasak	Settlement	<i>R. exulans</i>	4							
			<i>R. tanezumi</i>	16		1	3				
			<i>M. surifer</i>	4							
			<i>R. argentiventer</i>	19			1				
	Forest	Rain-fed	<i>R. exulans</i>	61			1				2
			<i>R. norvegicus</i>	18							
			<i>R. tanezumi</i>	25				1			
			<i>B. berdmorei</i>	1		2	3				
			<i>M. surifer</i>	1							
			<i>R. tanezumi</i>	3							
			<i>B. indica</i>	1							
			<i>B. savilei</i>	14			1				
	Dry land	Settlement	<i>B. berdmorei</i>	1							
			<i>M. caroli</i>	1							
			<i>R. exulans</i>	16							
			<i>R. sakaretensis</i>	5							
Luang Prabang	Forest	Settlement	<i>R. tanezumi</i>	1							
			<i>B. sakaretensis</i>	3							
			<i>R. tanezumi</i>	1							
			<i>M. surifer</i>	2							
	Rain-fed	Dry land	<i>N. fulvessens</i>	1							
			<i>R. exulans</i>	81							
			<i>R. tanezumi</i>	7							
			<i>M. cookii</i>	3							
	Settlement	Rain-fed	<i>R. andamanensis</i>	3		1					
			<i>R. nitidus</i>	2							
			<i>R. tanezumi</i>	35		5		3			
			<i>M. caroli</i>	2							
	Dry land	Settlement	<i>M. cookii</i>	2	1						
			<i>R. nitidus</i>	3							
			<i>R. tanezumi</i>	3							
			<i>B. indica</i>	5							
	Settlement	Rain-fed	<i>B. berdmorei</i>	1			1				
			<i>B. bowersi</i>	2							
			<i>L. edwardsi</i>	1							
			<i>M. caroli</i>	10	1						
	Dry land	Settlement	<i>M. cookii</i>	48	16						
			<i>R. nitidus</i>	1							
			<i>R. tanezumi</i>	5		4	1			1	
			<i>M. caroli</i>	5							
	Settlement	Rain-fed	<i>R. andamanensis</i>	2							
			<i>R. tanezumi</i>	10							
			<i>R. andamanensis</i>	2							
			<i>R. tanezumi</i>	10							

^aThese data are extracted from Jiyipong et al. (2012).

TABLE 2. COMPARISON OF MODELS USED TO TEST THE EFFECT OF SEVERAL INDEPENDENT VARIABLES (LOCALITY, HABITAT, SEASON, SEX, AGE, AND SPECIES OF RODENTS) ON INDIVIDUAL RODENT INFECTION (GLM WITH LOGIT FUNCTION) IN EIGHT SITES IN THAILAND, LAO PDR, AND CAMBODIA

Dependent variables	Model ranks	AIC
All <i>Bartonella</i> spp.	Province + season + species	609.9
	Province + season + habitat + species	611.3
	Province + season + habitat + sex + species	613.2
	Province + season + habitat + sex + maturity + species	617.0
<i>B. rattimassiliensis</i>	Season + habitat	229.7
	Season + habitat + sex	231.3
	Season + habitat + sex + maturity	233.4
	Province + season + habitat + sex + maturity	236.8
<i>B. queenslandensis</i>	Province + season	232.2
	Province	232.3
	Province + season + habitat	233.0
	Province + season + habitat + sex	233.3
	Province + season + habitat + sex + maturity	235.0
<i>B. musii</i>	Season + habitat	117.0
	Province + season + habitat	177.1
	Province + season + habitat + maturity	177.4
	Province + season + habitat + sex + maturity	178.2

Models are ranked from the least to the most supported according to corrected Akaike information criteria (AIC). For *B. rattimassiliensis*, *B. queenslandensis*, and *B. musii* only individuals from rodent species reported infected were used in the analyses (see Table 1). GLM, generalized linear model.

infection (Table 2), with higher levels of infection in the wet season and lower levels of infection in a rainfed field, dry field, and human settlement compared to forest habitat (Table 3; $p=0.04$). The infection by *B. queenslandensis* was found related to season and locality (Table 2) but not significantly (Table 3; $p>0.05$). Finally, *Bartonella* n. sp. was found more prevalent in wet season and in dry field habitat compared to forest habitat (Tables 2 and 3; $p<0.001$ and $p<0.0001$, respectively).

Discussion

Species of *Bartonella* showed a great variability in their host specificity with *B. queenslandensis* presenting a low host

specificity by infecting nine host species and five genera, followed by *B. rattimassiliensis* found in three species and two genera and *Bartonella* n. sp. in four species and two genera, although this last species seems to infect preferentially the three species of *Mus* investigated by Jiyipong et al. (2012).

The prevalence of infection reported here (8.7%; see also Jiyipong et al. 2012) is lower than those currently observed in natural populations of rodents with range from 50% to 70% according to the reviews of Kosoy et al. (2004a, b). Such a lower prevalence could be related to the high rodent species richness observed in these localities and/or to their low population densities (Blasdel et al. 2012), although accurate rodent population densities were lacking.

TABLE 3. GENERALIZED LINEAR MODEL OF RODENT INFECTION BY *BARTONELLA* WITH BINOMIAL DISTRIBUTION AND LOGIT LINK FUNCTION (LOG- LIKELIHOOD TYPE 1 TEST) AT SEVEN SITES IN THAILAND, LAO PDR, AND CAMBODIA. SELECTION OF THE BEST MODEL USING AKAIKE INFORMATION CRITERION

Dependent variable	Variables	Category	Estimate (SD)	p Values	Log ratio chi squared (df)	p values (> chi squared)
All <i>Bartonella</i> spp.	Locality Buriram versus	Loei	2.35 (0.52)	<0.0001		
		Luang Prabang	1.67 (0.49)	0.0007		
		Sihanouk	1.57 (0.49)	0.001	39.8 (6)	<0.0001
	Season dry versus	Season wet	0.72 (0.28)	0.01	7.0 (1)	<0.0001
	Species <i>B. indica</i> versus	<i>M. surifer</i>	-2.59 (1.19)	0.03		
		<i>R. exulans</i>	-1.87 (0.76)	0.01	92.9 (12)	<0.0001
<i>B. rattimassiliensis</i>	Season dry versus	Season wet	0.89 (0.44)	0.04	4.4 (1)	0.04
	Habitat forest versus	Rain fed field	-1.12 (0.51)	0.02		
		Settlement	-1.66 (0.61)	0.006		
		Dry field	-0.88 (0.52)	0.09	8.2 (3)	0.04
<i>B. queenslandensis</i>	Season dry versus	Season wet	-0.20 (0.10)	0.16	2.1 (1)	0.14
<i>Bartonella</i> n. sp.	Season dry versus	Season wet	2.58 (1.04)	0.01	12.8 (1)	0.0003
	Habitat forest versus	Dry fields	1.66 (0.63)	0.008	28.9 (3)	<0.0001

Significant categories (p values <0.05) among selected variables given in Table 2 are given with estimate and standard deviation. SD, standard deviation; df, degrees of freedom.

Although *Bartonella* infection may vary among localities, season appears to be a major factor for host infection, with an increase of infection during the wet season. We did not observe any influence of host sex as most other studies that investigated the epidemiology of *Bartonella* in rodent populations (Morway et al. 2008, Meheretu et al. 2013). Published studies showed that season may influence (Fichet-Calvet et al. 2000, Morway et al. 2008) or not (Morway et al. 2008) the prevalence of *Bartonella*. We found a higher prevalence in the wet season, which may be related to the arthropod vector populations that can be enhanced during the wet season. However, studies have shown that vector abundance did not appear important for the dynamics of *Bartonella* (Telfer et al. 2007, Meheretu et al. 2013), emphasizing that host densities are crucial for ectoparasite exchange between hosts and *Bartonella* infection (Telfer et al. 2007). Moreover, information on the abundance and diversity of ectoparasites on rodents is still missing. Moreover, depending on the *Bartonella* and host species, transmission may occur through intermediate hosts such as ticks, fleas, sand flies, and mosquitoes (Parola et al. 2003, Boulouis et al. 2005, Billeter et al. 2008, Chomel and Kasten 2010, Kabeya et al. 2010).

Rodent species living in close proximity with humans, such as *R. exulans* and *Rattus tanezumi*, host several *Bartonella* species. However, the levels of rodent infection in human settlement are significantly lower, particularly for the infection of the house rat *R. exulans*. Lower infection could be explained by a lower prevalence of ectoparasites in houses, although data are missing, as mentioned previously. Dry fields, which are preferential habitats of *Mus* species, showed higher level of infection by *Bartonella* n. sp. than forest habitats. Finally, the zoonotic *B. rattimassiliensis* appeared to preferentially infect the rodents from forests compared to all other habitats (i.e., rain-fed fields, dry fields, and human settlement), with *R. tanezumi* being the main infected host and reservoir for this *Bartonella* species.

Several rodent species investigated here show relatively strong habitat preferences: *Rattus norvegicus* and *R. exulans* in settlements; *Rattus argentiventer*, *R. sakeratensis*, *Bandicota indica*, and *Mus caroli* in rain-fed fields; *Mus cookii* and *Berylmys berdmorei* in nonflooded lands; and *Maxomys surifer* and *Leopoldamys edwardsi* in forests (Ivanova et al. 2012, Palmeirim et al. 2014). Some species show lower habitat preferences, including *Niviventer fulvescens*, which were found in forests or other non-flooded lands. Finally, *R. tanezumi*, demonstrates more generalist tendencies and was trapped in a variety of habitats, including households (Palmeirim et al. 2014). Our study confirms that if several rodent species can be reservoirs of zoonotic *Bartonella*, the generalist and synanthropic species such as *R. tanezumi* appear to be reservoirs of all detected *Bartonella*. *R. tanezumi* can be found in forest, which seems a likely habitat that favors the transmission of *B. rattimassiliensis*, particularly in the wet season. However, as this rodent species can be found in all habitats (Palmeirim et al. 2014), it may potentially enhance transmission among all habitats.

The ongoing land use changes in Southeast Asia, with increasing biodiversity loss, habitat fragmentation, and zoonotic outbreaks (Morand et al. 2014) may likely favor the population dynamics of synanthropic rodent species (Bordes et al. 2013), which in turn may affect the epidemiology of

Bartonella species on the risk of transmission to humans (Herbreteau et al. 2012, Bordes et al. 2013).

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Author Disclosure Statement

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