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Molecular detection of *Rickettsia* species and host associations of *Laelaps* mites (Acari: Laelapidae) in Taiwan

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Abstract

Various rickettsiae have recently been detected in *Laelaps* mites (Acari: Laelapidae), which are common ectoparasites of rodents; however, investigations on this topic remain very scarce, particularly in Asia. In the present study, shrews and rodents were trapped from 2006 to 2010 in eight lowland regions of Taiwan (< 500 m in elevation) to collect associated *Laelaps* mites, from which *Rickettsia*—a group of emerging pathogens—were detected and identified by assaying the *gltA* and *ompB* genes. A total of 853 *Laelaps* mites of at least four species were collected from a sample of 1004 small mammals that included one shrew and 10 rodent species. *Rattus losea* was the most common species (44.9% of total hosts) and hosted the highest percentage of mites (76.6% of total mites). *Laelaps nuttalli* was the most abundant mite species (51.7% of total mites), followed by *Laelaps echidninus* (24.2%), *Laelaps sedlaceki* (23.1%), and *Laelaps myonyssognathus* (0.2%). Notably, *Rickettsia* species with the highest similarity to spotted fever group (SFG) rickettsiae were identified from seven of the 72 pools of *Laelaps* mites. The presence of SFG rickettsiae in hematophagous *Laelaps* mites, particularly including species that are closely associated with commensal rodents in frequent contact with humans, calls for further investigation on the competence of *Laelaps* mites in transmitting rickettsiae.

Keywords Vector-borne diseases · Host–parasite association · Laelapine mite · Small mammals

Introduction

Small mammals, including rodents and shrews, are typically infested with a variety of ectoparasites, including fleas, lice, mites, and ticks. Some of these ectoparasites are capable of transmitting causative agents of diseases to humans, with these being more

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thoroughly studied by researchers. Most prominent among these are hard ticks (Acari: Ixo-didae), which can transmit human diseases such as anaplasmosis, babesiosis, Lyme bor-reliosis, spotted fever, and tick-borne encephalitis (Dantas-Torres et al. 2012). Fleas also receive great attention for their central role as vectors of *Bartonella*, flea-borne spotted fever, murine typhus, and plague (Bitam et al. 2010). In comparison, the potential role of mites (Acari) in transmitting diseases remains relatively understudied (Reeves et al. 2006) and most research has been focused on rickettsialpox (caused by *Rickettsia akari* Huebner) and scrub typhus (caused by *Orientia tsutsugamushi* Tamura et al.) that are transmitted by the house mouse mite (*Liponyssoides sanguineus* Hirst, Dermanyssidae) and chigger mites (Trombiculidae), respectively (Elliott et al. 2019; Paddock 2020).

Mites of the genus *Laelaps* (Mesostigmata: Laelapidae) are common ectoparasites of small mammals, particularly rodents (Jameson 1965). Although some neotropical lae-lapines might not feed on blood (Martins-Hatano et al. 2002), other species such as *Lae-laps echidninus* and *Laelaps nuttalli* are hematophagous parasites of humans and rodents (Wharton and Cross 1957; Jameson 1965; Krantz and Walter 2009) that might be capa-ble of transmitting diseases among wild animals and humans (Wharton and Cross 1957; Valiente Moro et al. 2005). However, studies on *Laelaps* mites and their role as dis-ease vectors remain very limited, despite some rickettsiae having recently been detected (though vector competence in pathogen transmission was not demonstrated) in *Laelaps* mites. These included *Anaplasma platys* and *Anaplasma phagocytophilum* in *Laelaps* spp. (Reeves et al. 2006), and *Rickettsia helvetica* and *Rickettsia felis* in *Laelaps agilis* (Miťková et al. 2015; Radzijevskaja et al. 2018).

Notably, studies of *Laelaps* mites in Taiwan remain scarce. The only research that has focused on this group of ectoparasites in Taiwan listed the rodent host and geographic occurrence of eight *Laelaps* species (Jameson 1965). Tsai et al. (2010) identified *Bar-tonella* species in shrews and rodents trapped near animal farms and their associated fleas and lice in Taiwan but did not detect *Bartonella* in 38 adult *L. echidninus* and 41 pools of nymphal *Laelaps* mites. Related studies in other Asian countries are also fragmentary. The host associations of *Laelaps* mites have been documented in Asiatic Russia (Vinar-ski and Korallo-Vinarskaya 2016), Bangladesh (Fuehrer et al. 2012), China (Guo et al. 2013), Indonesia (Durden and Page 1991), Laos and Vietnam (Allred 1970), and Malaysia (Ahamad et al. 2013).

Spotted fever group (SFG) rickettsioses are transmitted by ectoparasites infective of *Rickettsia* species. Hard ticks are the primary vectors, though some *Rickettsia* species are also transmitted by fleas and mites (Raoult and Roux 1997; Parola et al. 2005). Recent decades have witnessed the emergence of many novel *Rickettsia* species, whereas human cases of SFG rickettsioses have continuously appeared in previously unrecognized regions (Raoult and Roux 1997; Perlman et al. 2006; Parola et al. 2013).

Although *Rickettsia* species have previously been identified in *Laelaps* mites (Miťková et al. 2015; Radzijevskaja et al. 2018), similar investigations remain scarce, particularly in Asia. Tay et al. (2014) had attempted but failed to detect rickettsiae in *Laelaps* mites in Malaysia. The first aim of the present study was to detect *Rickettsia*-related species in *Laelaps* mites in Taiwan to assess their potential significance for transmitting rickettsiae. Moreover, knowledge regarding the relative contribution of distinct host species in sup-porting parasites is fundamental for disease mitigation by controlling certain hosts; there-fore, the secondary aim of this study was to systematically investigate and compare the extent of *Laelaps* mite infestation among small mammal hosts in different parts of Taiwan. To our knowledge, this is the first study to detect *Rickettsia* in *Laelaps* mites in Taiwan while also systematically assessing their hosts. Importantly, the results of this study will

contribute to the general understanding of *Laelaps* mites and their potential importance as disease vectors.

Materials and methods

Small mammal trapping and collection of mites

This present study was part of a research effort to investigate *Rickettsia* infections in small mammals and associated ectoparasites in rural lowland Taiwan (<500 m in elevation, Kuo et al. 2015a, b; Wang et al. 2020; for more details on the trapping and handling of small mammals in this study, refer to Kuo et al. 2015a). Briefly, from 2006 to 2010, small mammals (shrews and rodents) were trapped at three counties in eastern Taiwan (Yilan: 121.7378° E, 24.7021° N; Hualien: 121.6112° E, 23.9911° N; Taitung: 121.1438° E, 22.7613° N), three counties in western Taiwan (Taoyuan: 121.2300° E, 24.9554° N; Taichung: 120.6736° E, 24.1477° N; Kaoping: 120.3014° E, 22.6273° N), and two counties located in Taiwan's offshore islets (Kinmen: 118.4171° E, 24.4414° N, Penghu: 119.5833° E, 23.5833° N) (Fig. 1). In each county, 80 Sherman traps (26.5×10×8.5 cm) and 80 mesh traps (27×16×13 cm) were deployed in agricultural fields or rural villages for at
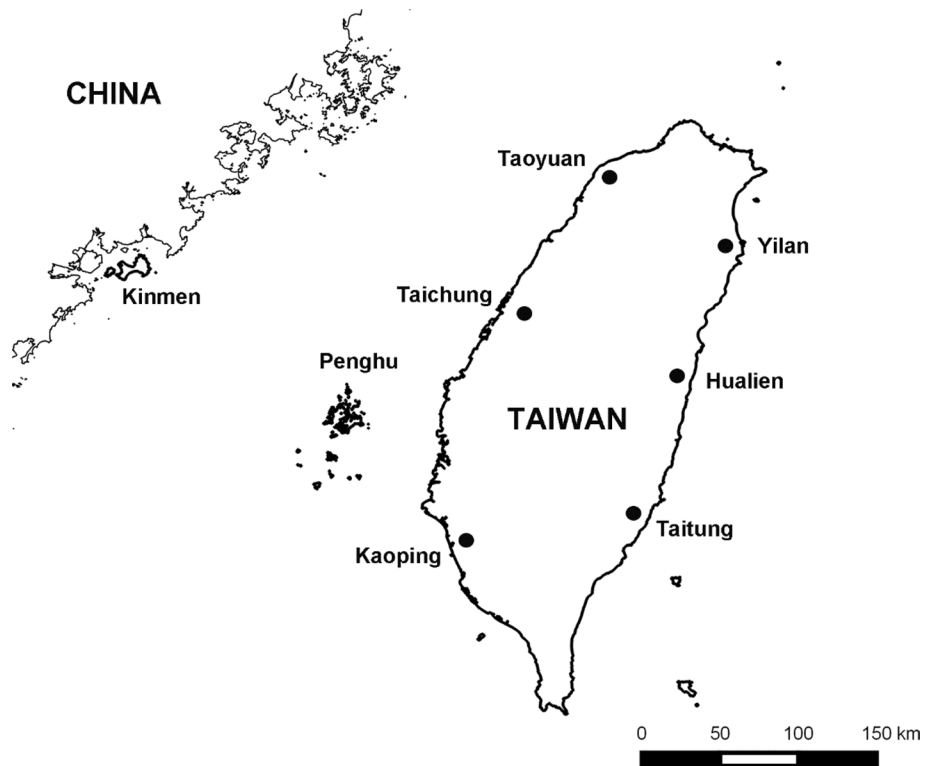

Fig. 1 Study sites for the trapping of shrews and rodents and collecting of associated *Laelaps* mites (Acari: Laelapidae) in lowland Taiwan from 2006 to 2010

least two different seasons (spring: March to May; summer: June to August; fall: September to November; winter: December to February) and baited with sweet potato smeared with peanut butter. Trapped small mammals were euthanized with an overdose of Zoletil 50 (Virbac SA, Carros, France). *Laelaps* mites were brushed off from hosts above a plastic pan until no mites could be found and collected with forceps, then preserved in 70% ethanol and stored at − 70 °C for subsequent molecular investigation. Small mammals and *Laelaps* mites were morphologically identified to species following Lin (1980) and Jameson (1965), respectively.

Detection of *Rickettsia* species in mites

Laelaps mites were pooled for the detection of *Rickettsia*, with each pool containing five mites that typically belong to the same species and were collected from the same host individual. If this could not be achieved, mites of different species or from different host individuals were combined for a pool of five mites (approximately 20% of samples). For each county, mites of all present species were included in the assay except for one mite species with only two individuals, and each county included up to 10 pools. Mite DNA was extracted using a QIAamp DNA Mini Kit (Qiagen, Hilden, Germany) after sterilized mite specimens were ground in a solution containing 180 ml SPG buffer [3.0 mM KH_2PO_4 (Merck), 7.2 mM K_2HPO_4 (Merck), 40 mM L-glutamic acid (Sigma), 218 mM sucrose (Sigma)] and 20 ml proteinase K (Sigma), and vortexed at 56 °C overnight. Mites were detected of *Rickettsia* presence with nested polymerase chain reaction (PCR) following Kuo et al. (2015a), which targeted the genes encoding the 120- to 135-kDa outer membrane protein B (*ompB*; outer primer pair: ompB OF, 5′-GTA ACC GGA AGT AAT CGT TTC GTA A-3′; ompB OR, 5′-GCT TTA TAA CCA GCT AAA CCA CC-3′; inner primer pair: ompB SFG IF, 5′- GTT TAA TAC GTG CTG CTA ACC AA-3′; ompB SFG/TG IR, 5′- GGT TTG GCC CAT ATA CCA TAA G-3′; ompB TG IF, 5′-AAG ATC CTT CTG ATG TTG CAA CA-3′; 426 bp) and citrate synthase (*gltA*; outer primer pair: RpCS.877p, 5′-GGG GGC CTG CTC ACG GCG G-3′; RpCS.1258n, 5′-AAT GCA AAA AGT ACA GTG AAC A-3′; inner primer pair: RpCS.896, 5′-GGC TAA TGA AGC AGT GAT AA-3′; RpCS.1233n, 5′-GCG ACG GTA TAC CCA TAG C-3′; 338 bp). Laboratory *Rickettsia rickettsii* DNA and DEPC-treated water were used as positive and negative controls, respectively. *R. rickettsii* DNA was prepared from *R. rickettsii* antigens coated in a *R. rickettsii* IFA substrate slide (product code IF0101; Focus Technologies) and extracted using a QIAamp DNA Mini Kit. Samples were deemed positive for *Rickettsia* presence when either the *ompB* or *gltA* gene was detected. *Rickettsia* species in positive samples were identified by purifying the PCR products using a QIAquick Gel Extraction Kit and then sequencing once in each direction. The sequencing was performed by a commercial company (Mission Biotech, Taipei, Taiwan). DNA nucleotide sequences were assessed using the Basic Local Alignment Search Tool (http://www.ncbi.nlm.nih.gov) for any resemblance to known *Rickettsia* species. However, due to the limited number of genes detected and the very small fragments sequenced, only broad category of rickettsiae (e.g. SFG rickettsiae) instead of precise *Rickettsia* species was reported in this study.

Data analysis

The difference in mite load (mean mites per host individual) among host species, study sites, and seasons was investigated with a negative binomial generalized linear model

(NBGLM) to account for overdispersion of data, and a significant difference was evaluated based on the 95% Wald confidence interval. These procedures were implemented in SPSS Statistics v.19.0 (IBM Corporation). We used EpiTools Epidemiological Calculators (Sergeant 2018) to estimate mean and 95% confidence interval (CI) of individual-level (per mite) prevalence of *Rickettsia* infection in mites with a frequentist approach assuming perfect test, with confidence intervals calculated based on binomial theory following Cowling et al. (1999).

Results

Host association of *Laelaps* mites

We captured a total of 1,004 small mammals that included one shrew and ten rodent species (Table 1). The most common species was *Rattus losea* (44.9% of total mammals captured), followed by *Suncus murinus* (21.1%) and *Mus caroli* (13.3%). *Rattus losea* also hosted the highest percentage of mites (76.6% of total mites), followed by *M. caroli* (11.5%), whereas only 0.8% of mites were collected from *S. murinus* despite the commonness of this shrew species (Table 1). Upon excluding the non-representative *Niviventer coninga* due to its small sample size (two individuals), the exotic *Rattus exulans* exhibited a higher mite load (an average of 1.76 mites per individual) than most other species except for *Rattus norvegicus* (mean = 1.70), *R. losea* (1.45), and *M. caroli* (0.73) (NBGLM, all $P < 0.05$). Among all host species, *R. exulans* also had a higher prevalence of infestation (52.0%) (Table 1).

Laelaps mite fauna and geographical and seasonal variation

A total of 853 *Laelaps* mites of at least four species were collected (Table 2). *Laelaps nuttalli* was the most abundant species, constituting over half of the collected mites (51.7%). This species was followed by equally abundant *L. echidninus* and *Laelaps sedlaceki*, each accounting for approximately one-quarter of the mites (24.2 and 23.1%, respectively). In contrast, *Laelaps myonyssognathus* was rare, with only two individuals collected (0.2%). The three most common species (*L. echidninus*, *L. nuttalli*, and *L. sedlaceki*) can be found on most small mammal species (seven, nine, and six, respectively), whereas *L. myonyssognathus* was only collected from *R. losea* (Table 1).

Geographically, *L. nuttalli* and *L. echidninus* were generally common in different parts of Taiwan. On the other hand, *L. sedlaceki* occurred mainly on the main island of Taiwan and was uncommon on offshore islets. Moreover, the rare *L. myonyssognathus* was observed in western Taiwan only (Table 2). The mite load on *R. losea*, the primary small mammal host, varied considerably among regions (NBGLM, Wald's $\chi^2 = 86.4$, $P < 0.001$; range 0.43 to 3.05), with lower loads occurring in Yilan (mean = 0.43) in eastern Taiwan and Kaoping (0.59) in western Taiwan (all $P < 0.05$) (Table 2). There was also a seasonal variation in mite load on *R. losea* (NBGLM, Wald's $\chi^2 = 17.5$, $P < 0.005$), with higher and lower loads in the fall (mean = 2.04) and winter (0.62), respectively (Fig. 2a). Likewise, load of *L. echidninus* and *L. nuttalli* was generally higher and lower in the fall and winter, respectively (Fig. 2b, c); however, load of *L. sedlaceki* was higher in the spring but lower in the fall (Fig. 2d).

Table 1 Total number of captures of each shrew and rodent species at eight study sites in lowland Taiwan from 2006 to 2010, as well as prevalence of *Laelaps* mite infestation (% infested individuals), *Laelaps* mite load (mean [± SE] no. mites per host individual), total *Laelaps* mites collected, and *Laelaps* mite species identified from each host species

Mammal species	No. mammals (% of total)	Prevalence of mite infestation (%)	Mite load*	No. mites (% of total)	Infested mite species (no. mites)
Shrew					
Suncus murinus	212 (21.1)	2.4	0.03 ± 0.02[a]	7 (0.8)	*L. echidninus* (2); *L. nuttalli* (5)
Rodent					
Apodemus agrarius	20 (2.0)	15.0	0.35 ± 0.25[ad]	7 (0.8)	*L. echidninus* (2); *L. nuttalli* (5)
Bandicota indica	55 (5.5)	7.3	0.09 ± 0.05[a]	5 (0.6)	*L. nuttalli* (5)
Callosciurus erythraeus	2 (0.2)	0	0[b]	0 (0)	
Mus caroli	134 (13.3)	25.4	0.73 ± 0.17[cd]	98 (11.5)	*L. nuttalli* (93); *L. sedlaceki* (1); *Laelaps* spp. (4)
Mus musculus	45 (4.5)	6.7	0.07 ± 0.04[a]	3 (0.4)	*L. nuttalli* (3)
Niviventer coninga	2 (0.2)	50.0	5.00 ± 5.00[ac]	10 (1.2)	*L. echidninus* (6); *L. sedlaceki* (4)
Rattus exulans	25 (2.5)	52.0	1.76 ± 0.60[c]	44 (5.2)	*L. echidninus* (10); *L. nuttalli* (31); *L. sedlaceki* (3)
Rattus losea	451 (44.9)	29.3	1.45 ± 0.19[c]	653 (76.6)	*L. echidninus* (181); *L. nuttalli* (288); *L. sedlaceki* (179); *L. myonyssognathus* (2); *Laelaps* spp. (3)
Rattus norvegicus	10 (1.0)	30.0	1.70 ± 1.48[cd]	17 (2.0)	*L. echidninus* (4); *L. nuttalli* (4); *L. sedlaceki* (9)
Rattus tanezumi	48 (4.8)	10.4	0.19 ± 0.10[a]	9 (1.1)	*L. echidninus* (1); *L. nuttalli* (7); *L. sedlaceki* (1)
Total	1004	20.2	0.85 ± 0.09	853	*L. echidninus* (206); *L. nuttalli* (441); *L. sedlaceki* (197); *L. myonyssognathus* (2); *Laelaps* spp. (7)

*Means followed by a different letter are significantly different (negative binomial generalized linear model: $P < 0.05$)

Table 2 Total number of *Laelaps* mites and mite load (mean [±SE] no. mites per host individual) on the primary host *Rattus losea* collected from shrews and rodents at each study site of Taiwan from 2006 to 2010

Study site	Mite species						Mite load on *R. losea* (no. hosts)*
	L. echidninus	*L. nuttalli*	*L. sedlaceki*	*L. myonyssognathus*	*Laelaps* spp.	Overall	
Eastern Taiwan							
Yilan	18	14	18	0	0	50	0.43±0.14 (91)[a]
Hualien	19	87	13	0	0	119	2.05±0.89 (19)[b]
Taitung	25	46	19	0	0	90	3.05±1.28 (19)[b]
Western Taiwan							
Taoyuan	43	66	97	1	4	211	1.57±0.42 (116)[b]
Taichung	19	22	32	0	0	73	1.77±0.53 (31)[b]
Kaoping	8	30	12	1	3	54	0.59±0.21 (44)[a]
Offshore islets							
Kinmen	28	77	6	0	0	111	1.48±0.38 (75)[b]
Penghu	46	99	0	0	0	145	2.55±0.88 (56)[b]
Overall	206	441	197	2	7	853	1.45±0.19 (451)

*Means followed by a different letter are significantly different (negative binomial generalized linear model: $P < 0.05$)
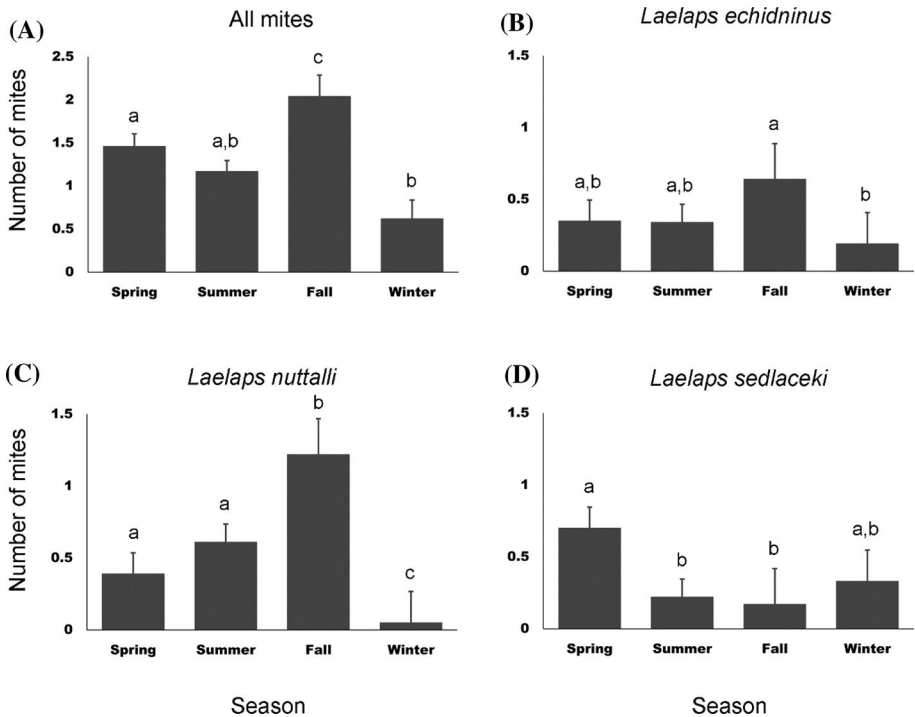
Fig. 2 Seasonal difference in the mean (+ SE) number of *Laelaps* mites collected from *Rattus losea* in lowland Taiwan from 2006 to 2010. **a** Mites of all species; **b** *Laelaps echidninus*; **c** *Laelaps nuttalli*; **d** *Laelaps sedlaceki*. Means within a panel capped with different letters are significantly different, based on the 95% Wald confidence interval

Detection of *Rickettsia* in *Laelaps* mites

In total 72 pools of *Laelaps* mites were examined for the presence of *Rickettsia*. The positivity rates per pool were 4.2 and 9.7% based on the *ompB* and *gltA* genes, respectively (Table 3), whereas positivity rates per mite were 0.85% (95% CI 0.17–2.46%) and 2.02% (0.81–4.13%), respectively. The positivity rate was higher in Taoyuan and Penghu for the *ompB* gene, and it was higher in Hualien, Taitung, and Kinmen for the *gltA* gene. For the *ompB* gene, three DNA sequences that matched the closest in GenBank (99.0–99.2% similarity) to SFG rickettsiae were each detected from *L. echidninus*, *L. sedlaceki*, and a pool of *L. echidninus* and *L. nuttalli* (GenBank Accession Numbers MT611477–MT611479); for the *gltA* gene, four sequences with the highest similarity to SFG rickettsiae (99.3–100% similarity) were each detected from *L. echidninus*, *L. nuttalli* (2×), and *L. sedlaceki* (MT611473-MT611476) (Table 3). All of the mites with *Rickettsia* species detected were collected from *R. losea*.

Table 3 Positivity rate for *Rickettsia* species infection and *Rickettsia* species identification in pools of *Laelaps* mites for each study site in Taiwan from 2006 to 2010

Study site	Positivity rate (%) for *ompB* gene	*Rickettsia* spp. detected (no. detections from mite species)	Positivity rate (%) for *gltA* gene	*Rickettsia* spp. detected (no. detections from mite species)	Laelapine mite species assayed (no. pools)
Eastern Taiwan					
Yilan	0 (0 out of 8)	–	0 (0 out of 8)	–	*L. echidninus* (2); *L. nuttalli* (1); *L. sedlaceki* (1); *L. echidninus*+*L. sedlaceki* (4)
Hualien	0 (0 out of 10)	–	10 (1 out of 10)[a]	–	*L. nuttalli* (6); *L. echidninus*+*L. nuttalli* (1); *L. echidninus*+*L. sedlaceki* (2); *L. echidninus*+*L. nuttalli*+*L. sedlaceki* (1)
Taitung	0 (0 out of 10)	–	30 (3 out of 10)	SFG rickettsiae[b] (1 *L. echidninus*; 1 *L. nuttalli*; 1 *L. sedlaceki*)	*L. echidninus* (3); *L. nuttalli* (4); *L. sedlaceki* (1); *L. echidninus*+*L. sedlaceki* (1); *L. nuttalli*+*L. sedlaceki* (1)
Western Taiwan					
Taoyuan	20 (2 out of 10)	SFG rickettsiae (1 *L. echidninus*; 1 *L. sedlaceki*)	0 (0 out of 10)	–	*L. echidninus* (2); *L. nuttalli* (3); *L. sedlaceki* (5)
Taichung	0 (0 out of 7)	–	0 (0 out of 7)	–	*L. echidninus* (2); *L. nuttalli* (2); *L. sedlaceki* (3)
Kaoping	0 (0 out of 7)	–	0 (0 out of 7)	–	*L. nuttalli* (3); *L. sedlaceki* (1); *L. echidninus*+*L. nuttalli* (2); *L. echidninus*+*L. sedlaceki* (1)
Offshore islets					
Kinmen	0 (0 out of 10)	–	30 (3 out of 10)[a]	SFG rickettsiae (1 *L. nuttalli*)	*L. echidninus* (3); *L. nuttalli* (6); *L. sedlaceki* (1)
Penghu	10 (1 out of 10)	SFG rickettsiae (1 *L. echidninus*+*L. nuttalli*)	0 (0 out of 10)	–	*L. echidninus* (2); *L. nuttalli* (7); *L. echidninus*+*L. nuttalli* (1)
Overall	4.2 (3 out of 72)	SFG rickettsiae (3)	9.7 (7 out of 72)	SFG rickettsiae (4)	

Each pool contained five mites typically belonging to the same species and collected from the same host individual, or mites of different species or from different host individuals were combined for a pool of five mites. These mites with *Rickettisa* species detected were all collected from *Rattus losea*

[a]Some *Rickettsia* detected but could not be sequenced successfully

[b]Spotted fever group rickettsiae

Discussion

In addition to the *R. felis* and *R. helvetica* that were detected in *L. agilis* in Europe (Miťková et al. 2015; Radzijevskaja et al. 2018), we identified *Rickettsia* species closely related to the SFG rickettsiae in *Laelaps* mites for the first time in Asia. Moreover, these *Rickettsia* species were largely detected in *L. echidninus* and *L. nuttalli*, which are known to bite humans (Wharton and Cross 1957). However, due to that only fragments of *gltA* and *ompB* genes were identified, further definitive confirmation of *Rickettsia* species is required. Additionally, SFG rickettsiae are primarily transmitted by ticks (Parola et al. 2013). Therefore, it is more likely that the rickettsiae detected in the present study were contained in blood meals ingested by the mites rather than mites being infective and capable of transmitting these pathogens. For example, prevalence of *Rickettsia* infection in the small mammal hosts during our parallel studies on *Rickettsia* detection in Taiwan was high (Kuo et al. 2015a) although these *Rickettsia*-positive mites were not derived from the same small mammal hosts examined for the presence of *Rickettsia*. The non-concordance in detection of SFG rickettsiae based on *gltA* and *ompB* genes, respectively, also suggests that the concentration of rickettsiae in these mites might be too low for successful amplification by both gene targets simultaneously. In this context, it cannot be excluded that *Laelaps* mites might define alternative transmission routes for some of these *Rickettsia* species. For example, although fleas are the primary competent vectors of *R. felis*, this pathogen can also be successfully cultivated in tick and mosquito-derived cell lines (Reif and Macaluso 2009). Therefore, the presence of tick-borne rickettsiae warrants further investigation on the competence of hematophagous *Laelaps* mites in transmitting *Rickettsia* species, which has never been investigated to date.

A total of eight *Laelaps* mite species have previously been recorded in Taiwan (Jameson 1965). These include the four species that were also collected for the present study in lowland areas (<500 m in elevation; *Laelaps prognathous* in Jameson (1965) considered a junior synonym of *L. myonyssognathus* by Mitchell (1968)). The other four species (*L. agilis*, *Laelaps clethrionomydis*, *Laelaps traubi*, and *Laelaps turkestanicus*) were collected from rodents residing at elevations >900 m (Jameson 1965); therefore, it is not surprising that they were not discovered in the present study.

Among the four species, *L. nuttalli* was the most abundant, observed in all study sites, and collected from most small mammal species—except from the uncommon *Callosciurus erythraeus* and *N. coninga* (Tables 1 and 2). In Taiwan, *L. nuttalli* can reach an elevation of 900 m (Jameson 1965). *L. nuttalli* is also a common ectoparasite of commensal rodents in most parts of the world, including Africa, America, Asia, and the Indian Ocean and Pacific islands, being distributed from sea level to >3000 m in elevation (Allred 1969). This species has also been found on bats (Ahamad et al. 2013). In the present study, *Rickettsia* species with the highest similarity to SFG rickettsiae have been detected in *L. nuttalli* which is also closely associated with commensal rodents that have frequent contact with humans, thus highlighting that the medical importance of this widely distributed mite species is worthy of further investigation. Similarly, *L. echidninus* is also a cosmopolitan ectoparasite of commensal rodents (Durden and Page 1991). Jameson (1965) only found this species on introduced or domestic *Rattus* rats but not on native rodents. Instead, we identified *L. echidninus* on seven host species, including *N. coninga*, which is native and endemic to Taiwan, thereby revealing a wider host range than previously considered. Likewise, *L. sedlaceki* was previously found only on *N. coninga* (Jameson 1965); however, it was also collected from another five host species in the current study (largely *Rattus* rats), which is

similar to what has been observed in Borneo and New Guinea (Strandtmann and Mitchell 1963; Ng et al. 2017). In addition, species with the highest resemblance to SFG rickettsiae have also been identified in both *L. echidninus* and *L. sedlaceki*, once again underscoring the importance of assaying their competence for disease transmission. Lastly, *L. myonyssognathus* was the least common species in the present study, being found only on the abundant *R. losea* in western Taiwan, which is consistent with previous research (Jameson 1965); however, its hosts included at least nine shrew and rodent species in its distribution from East to South Asia (Mitchell 1968).

Over 75% of *Laelaps* mites were collected from *R. losea*, thus indicating that this common rodent is important in sustaining *Laelaps* mite populations. We have also identified *R. losea* as the primary host of ticks, chigger mites, and fleas in lowland Taiwan (Kuo et al. 2015b, c; Wang et al. 2020). Together, these studies demonstrate the prominent role of *R. losea* in supporting arthropod disease vectors in rural lowland Taiwan, which suggests that this species could be targeted when disease control measures are required. Interestingly, we also observed that *R. exulans* had a higher *Laelaps* mite burden similar to what has been reported in Indonesia (Durden and Page 1991) and Hawaii (Mitchell 1964). In Taiwan, *R. exulans* is an invasive species that is currently present only in Hualien (eastern Taiwan). This locally abundant rodent was found to serve only a minor role in supporting chigger mites due to its low chigger mite burden (Kuo et al. 2011). On the contrary, the higher *Laelaps* mite burden identified in this study suggests that the invasive *R. exulans* could be a competent host and its presence could augment the population of *Laelaps* mites, which subsequently increases the mite burden of other coexisting native rodents; such so-called "parasite spillback" effect can arise when invasion of a competent host increases the parasite load in native hosts by supporting a large number of local parasites (Kelly et al. 2009). Therefore, further validation of the importance of *R. exulans* in this context is recommended.

Compliance with ethical standards

Conflict of interest The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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