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# Assessment of data on vector and host competence for Japanese encephalitis virus: A systematic review of the literature

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ABSTRACT

Japanese encephalitis virus (JEV) is a virus of the *Flavivirus* genus that may result in encephalitis in human hosts. This vector-borne zoonosis occurs in Eastern and Southeastern Asia and an intentional or inadvertent introduction into the United States (US) would have major public health and economic consequences. The objective of this study was to gather, appraise, and synthesize primary research literature to identify and quantify vector and host competence for JEV, using a systematic review (SR) of the literature.

After defining the research question, we performed a search in selected electronic databases and journals. The title and abstract of the identified articles were screened for relevance using a set of exclusion and inclusion criteria, and relevant articles were subjected to a risk of bias assessment, followed by data extraction.

Data were extracted from 171 peer-reviewed articles. Most studies were observational studies (59.1%) and reported vector competence (60.2%). The outcome measures reported pertained to transmission efficiency, host preference, and vector susceptibility to infection within vector competence; and susceptibility to infection within host competence. Regarding vector competence, the proportion of JEV infection reported across all 149 mosquito species in all observational studies ranged from 0 to 100%. In experimental studies, infection, dissemination, and transmission rates varied between 0 and 100%. Minimum infection rates (MIR) varied between 0 and 333.3 per 1000 mosquitoes. Maximum likelihood estimation (MLE) values ranged from 0 to 53.8 per 1000 mosquitoes. The host species in which mosquitoes mostly fed consisted of pigs and cattle (total of 84 blood meals taken by mosquitoes from each of these host species). As for host competence, the proportion of JEV infection varied between 0 (in rabbits, reptiles, and amphibians) and 88.9% (cattle).

This SR presents comprehensive data on JEV vector and host competence, which can be used to quantify risks associated with the introduction of JEV into the US.

## 1. Introduction

Japanese encephalitis (JE) is a mosquito-transmitted disease that may result from infection by the Japanese encephalitis virus (JEV), an arbovirus (arthropod-borne virus) of the *Flavivirus* genus. Virus transmission extends from Southeastern Asia to the Western Pacific islands. Japanese encephalitis virus is among the most important causes of encephalitis worldwide, with approximately 68,000 JE human cases occurring every year, particularly in children (Campbell et al., 2011; Weaver and Barrett, 2004). The mechanism of transmission is based on interactions between vectors (over 30 species of mosquitoes) and hosts (pigs and ardeid birds) that maintain an enzootic cycle not yet fully understood (Le Flohic et al., 2013).

According to previous work (Le Flohic et al., 2013), JEV can easily shift between the domestic and the wild cycles, with no viral adaptation needed, if competent hosts and vectors are present, which is consistent with the observed geographical expansion of the virus to contiguous regions. This expansion puts the more than three billion people who live in currently JE-endemic countries at risk of infection (Le Flohic et al., 2013). The spread of JE is also related to the exponential human population growth in the affected regions, the increase in the number of pig production systems, and the changes in land usage and agricultural

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practices. Changes in agricultural practices are related to an increase in rice production, leading to more opportunities for mosquito breeding, as rice paddy fields are a suitable and prolific habitat for the development of mosquito vector populations (Erlanger et al., 2009; Mackenzie et al., 2004).

The most competent JEV vectors are *Culex* mosquitoes, such as *Culex tritaeniorhynchus, Culex annulirostris*, *Culex annulus*, *Culex fuscocephala*, *Culex gelidus*, *Culex sitiens*, and the *Culex vishnui* species complex, which are widely distributed over the JEV-endemic areas, thus contributing to further maintaining the transmission cycle. Regarding vertebrate host species, the most competent amplifying and reservoir hosts are wild ardeid birds, especially egrets (*Egretta garzetta*) and herons (*Nycticorax nycticorax*), and pigs, both feral and domestic. The rise in intensive pig farming observed in East and Southeast Asia over the past decades also contributes to JEV transmission, as it increases the number of susceptible vertebrate hosts available (Le Flohic et al., 2013).

To date and despite many reviews describing the susceptibility of hosts, vectors, and environmental parameters that can sustain the introduction of the virus and its further spread in JEV-free countries, such as the United States (US), the role of different vectors and hosts, and their competence, has not been quantitatively evaluated (Huang et al., 2015; Nemeth et al., 2012; Nett et al., 2012; Reeves and Hammon, 1946).

Furthermore, other authors (Lord et al., 2015) refer to the fact that the basis of our current knowledge about the JEV transmission cycle was established during the initial research in the 1950s in Japan, and that it reflected the context of the region and time period when it was carried out. Japanese encephalitis virus transmission should therefore be reconsidered for other regions where the transmission context differs from the one first described in Japan. Limited evidence supporting the need for viral adaptation between different cycles, as well as recent evidence that vector-free transmission between pigs without the intervention of arthropod vectors is possible (Ricklin et al., 2016), further reiterate knowledge gaps. A better understanding of the relative importance of vectors and hosts will determine optimal mitigation strategies, such as JEV vaccination or insect vector control, but will depend on the accurate assessment of parameters that include vector and host abundance, mosquito host preference, and vector competence for JEV (Lord et al., 2015; Le Flohic et al., 2013).

Globalization and increasing international travel create additional opportunities for the introduction of exotic pathogens into new regions of the globe. In the US, specifically, the rapid spread of the West Nile virus after its introduction in 1999, and the inability of the public health services to control the outbreaks and prevent the establishment of the disease raised an important issue regarding the emergence of exotic vector-borne diseases in the country. Agencies responsible for the prevention and control of the introduction of foreign pathogens and the timely response to potential outbreaks, should they occur, require comprehensive information regarding the previously mentioned parameters, of which vector and host competence play a major role (Huang et al., 2015; Nemeth et al., 2012; Nett et al., 2012; Reeves and Hammon, 1946).

A systematic review (SR) of the literature provides a replicable, transparent, and reliable method of identifying, assessing, and summarizing available evidence on a research question, with reduced bias (Sargeant and O'Connor, 2014; Sargeant et al., 2006). The objective of this study was therefore to identify research gaps and information regarding vector and host competence for JEV worldwide, using a systematic review of the literature.

## 2. Materials and methods

Steps of the SR consisted of posing a research question, searching the literature, conducting a relevance screening, extracting data, assessing the risk of bias, as well as analyzing and presenting the extracted data.

### 2.1. Research question

The original research question was as follows: Which vectors and hosts are competent for Japanese encephalitis virus transmission in the United States?

Due to the low number of publications originating from the US, the research question and search were refined to include peer-reviewed literature worldwide.

Because the research question was related to descriptive parameters (competence of vectors and hosts), rather than interventions, we used a PO (population, outcome) question format to define the research question (O'Connor et al., 2014b). Population (P) referred to vectors and hosts, while outcomes (O) concerned competence, in terms of transmission efficiency, host preference, and susceptibility to infection.

The working team was comprised of four reviewers (AO, LE, ES, NC), each participating in different steps of the review.

We followed the protocols and guidelines for performing systematic reviews in veterinary medicine (O'Connor et al., 2014a; O'Connor et al., 2014b; Sargeant and O'Connor, 2014; Sargeant et al., 2006), and the Cochrane group's guidelines (adapted) to conduct the risk of bias assessment (Higgins and Green, 2011).

### 2.2. Searching the literature

The search was restricted to the English language, without limitations to year of publication, and was performed using eight electronic databases and journals. The journals included in the search (Armed Forces Pest Management Board, The American Journal of Tropical Medicine and Hygiene, Journal of the American Mosquito Control Association, and Vector-Borne and Zoonotic Diseases) were selected based on the relevance of the topics covered, which are aligned with our research question. Databases were accessed in March and April 2016 and the search terms were related to the PO components. A complete list of the search terms, and their combinations, used for each database and journal is available in S1 Appendix (supplementary materials).

A hand-search was also used to identify additional articles cited in the reference list of nine articles considered as key publications by the reviewers based on a priori identification of relevant articles (Huang et al., 2014; Le Flohic et al., 2013; Misra and Kalita, 2010; Erlanger et al., 2009; Nett et al., 2012; van den Hurk et al., 2009a; Mackenzie et al., 2004; Weaver and Barrett, 2004; Solomon et al., 2000). Only peer-reviewed articles were considered for further evaluation. All articles were given a unique number that was kept throughout the SR for identification purposes.

### 2.3. Relevance screening

To determine their relevance, the title and abstract of all identified articles were subjected to a set of inclusion and exclusion criteria comprised of language, time period, population, study type, outcome measures, and location fields. A detailed description of the inclusion and exclusion criteria is included in Table 1.

Based on this set of criteria, we created a relevance screening tool composed of six questions, using an Excel® (Microsoft Corp., Redmond WA, 2013) spreadsheet. The first five questions were deemed crucial to establish relevance, and based on the answers to those questions, the abstracts were considered relevant or not.

The first version of the tool was pre-tested by three reviewers (AO, LH, NC) using 10 abstracts. After reviewing the sources of disagreement, we improved the tool and performed a second testing using the same 10 abstracts and three new ones.

Two reviewers (AO, LH) working independently performed the final relevance screening, and compared the answers for conflict resolution. When both reviewers determined that the abstract was not relevant, it was not considered further in the SR. The two reviewers resolved all

**Table 1**
Relevance screening criteria for inclusion and exclusion of articles.

| | Inclusion/ exclusion criteria |
|---|---|
| **Language** | English/ other than English |
| **Time period** | No restrictions (any time period) |
| **Type of population** | Vectors (mosquitoes, other insects) and/or Hosts (vertebrate[a] hosts)/vectors other than insects and non-vertebrate hosts |
| **Study type** | Challenge trial (laboratory and field), field studies (e.g., trapping, capture), observational or experimental studies/non-primary research (thesis) and literature reviews |
| | Vector AND/OR Host Competence to JEV[b] |
| **Outcomes and outcome measures** | Transmission efficiency, feeding patterns, host preference, infectiousness, susceptibility to infection, incubation time, duration of viremia/ vector and/or host competence for other Flaviviruses transmitted by ticks[c] |
| **Type of evidence** | Peer-reviewed articles/ non-peer reviewed articles, conference proceedings, thesis dissertations, and other non-peer reviewed publications |
| **Location** | Any country – |

[a] Vertebrate hosts are those with a backbone or spinal column (mammals, birds, reptiles, amphibians, and fishes).

[b] Vector competence is related to the ability of mosquitoes to become infected with JEV and transmit the virus. Transmission efficiency, host preference, and susceptibility to infection are outcome measures that provide information on vector competence (Golnar et al., 2015). Host competence is related to the vertebrate host's ability to develop viremia and transmit the virus to a mosquito that feeds on that host. Susceptibility to infection is the outcome measure providing information on host competence (Golnar et al., 2015).

[c] Tick-borne Flaviviruses were not included (such as the causative agents of tick-borne encephalitis, Kyasanur Forest disease, Alkhurma disease or Omsk hemorrhagic fever) but other mosquito-borne Flaviviruses were (West Nile, St. Louis Encephalitis, yellow fever, dengue fever, Zika).

conflicts by consensus, and a third reviewer (NC) intervened whenever the first two reviewers were not able to reach consensus. The relevance screening process and conflict resolution were completed by June 27th, 2016.

Following this process, we downloaded all full articles whose abstracts were considered relevant. A second relevance screening was performed by two reviewers (AO, ES), after appraisal of the full articles. This second relevance screening aimed at resolving uncertainties raised in the first screening for some articles, and sorting relevant articles into two categories: competence of hosts and/or vectors for JEV and competence of hosts and/or vectors for other *Flavivirus*. Articles pertaining to the second category (competence of hosts and/or vectors for other *Flavivirus* other than JEV) were not considered further. Again, reviewers resolved all conflicts by consensus, consulting a third reviewer (NC) whenever consensus could not be reached.

Fig. 1 presents a flowchart of the relevance screening tool, including all questions and possible answers.

### 2.4. Data extraction

Similar to the relevance screening step, a data extraction tool was created to guide data extraction from the relevant papers.

A pre-testing of five relevant articles was performed by two reviewers (AO, ES) in a first version of the tool, which was improved according to the flaws observed during this process. Conflicts were resolved by consensus or by the intervention of a third reviewer (NC) when consensus could not be reached.

The data were extracted and incorporated into an Excel® (Microsoft Corp., Redmond WA, 2013) spreadsheet. Information extracted consisted of general information about the article, which included the identification number, authors, year of publication, title, journal, population type (vector or host), and study type (observational or experimental). Data related to host and vector competence in experimental and observational studies were extracted and pertained to the outcome measures of interest: transmission efficiency, host preference, and susceptibility to infection. A detailed description of the outcome measures extracted from the articles is summarized in Table 2.

In observational studies, we also extracted data pertaining to the methods used to capture vectors, which included manual passive (aspirations) or active (sweep or drop nets) methods; and mechanical visual (use of visual attractants like UV or white light) or olfactory (use of olfactory attractants like CO2 and other lures, such as octanol) methods.

The diagnostic methods recorded for measuring vector-related outcomes varied and included real-time reverse transcription PCR, reverse transcription PCR, antigen-capture enzyme assays (e.g., ELISA), and virus isolation (using cell culture techniques, insect bioassays, immunofluorescence assays, hemagglutination inhibition tests, or neutralization tests). These methods were used exclusively or in different combinations.

As for hosts, diagnostic methods reported aimed at detecting antibodies using ELISA or immunochromatography, hemagglutination inhibition assays, neutralization tests (e.g., plaque reduction neutralization test), and virus isolation, exclusively or combined.

Studies could contribute to more than one population type (vector and host) and/or study type component (observational and experimental). For this reason, data from articles containing information on more than one type or component were split into multiple entries, according to the type of information they included, but maintaining the same unique identification number that linked those entries to the article from which they originated. Therefore, an article could have multiple entries under the same identification number.

Regarding taxonomy, mosquito species were recorded as reported in the source articles.

### 2.5. Assessment of the risk of bias

Following the Cochrane Review Handbook guidelines (Higgins and Green, 2011), we created a tool for each type of study design (observational and experimental) to assess the risk of bias in articles from which data were extracted (Tables 3 and 4), using eight criteria for each. These criteria aimed to address internal and external validity of the relevant studies. Criteria were designed to objectively determine if the study question, study population, inclusion and exclusion criteria, study period, study area, exposures, outcomes, and bias, were reported and/or defined for observational studies. Similarly, criteria pertaining to study question, study population, intervention, experimental conditions, experimental setting, randomization, blinding, and outcomes, were assessed for experimental studies.

We determined three levels of risk of bias for the articles being evaluated: low risk of bias, which is defined as the article having plausible bias that is unlikely to seriously alter the results; high risk of bias, defined as plausible bias that seriously weakens confidence in the results; and unclear risk of bias, defined as plausible bias that raises some doubt regarding the results of the study (Higgins and Green, 2011).

To assign articles a low, high, or unclear risk of bias, we established key domains that determined to which risk category each article belonged (Tables 3 and 4). Key domains pertained to questions considered critical by the authors for the overall risk of bias, given the relative importance of the different domains. A low risk of bias was assigned to the articles with a low risk of bias in all key domains; a high risk of bias was attributed when at least one key domain had a high risk of bias; and finally, an unclear risk of bias was assigned to articles with at least one unclear key domain.

The risk of bias assessment tool was pre-tested by two reviewers (AO, NC) working independently in a set of 10 articles, with all

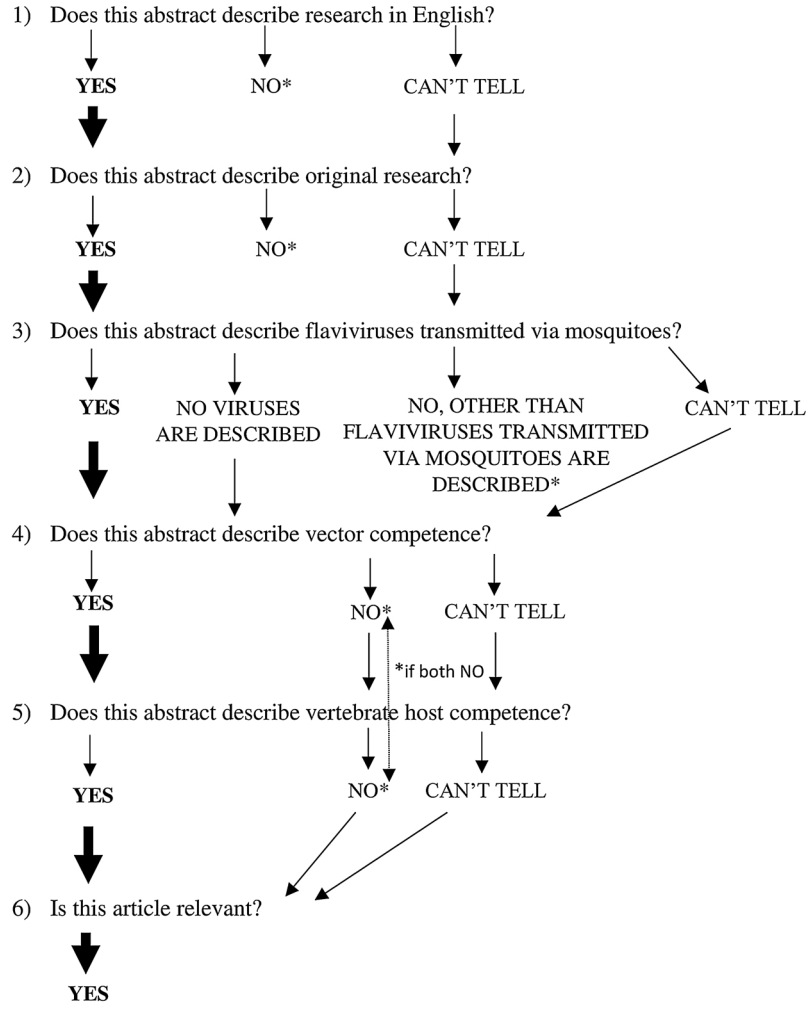


**Fig. 1.** Flowchart depicting questions and potential answers in the relevance screening tool.

**Table 2**
Outcome measures documented and extracted.

| Competence related to: | Transmission efficiency[a] | Host preference | Susceptibility to infection |
|---|---|---|---|
| **Vectors** | Infection rate,[b] dissemination rate[c] and transmission rate[d] | Host species preference[e] | Proportion of JEV infection,[f] minimum infection rate[h] and maximum likelihood estimation[i] |
| **Hosts** | – | – | Proportion of JEV infection[g] |

[a] Administration routes included: oral feeding (pledgets/membranes or hosts), intrathoracic inoculation, or vertical transmission (parents infected either intrathoracically or by oral feeding).

[b] Infection rate is the sum of individual/pool of mosquitoes that are JEV-positive divided by the total number of mosquitoes/pools tested in experimental studies.

[c] Dissemination rate is the proportion of mosquitoes with virus in their legs, irrespective to their infection status (Golnar et al., 2015).

[d] Transmission rate is the proportion of mosquitoes with a disseminated infection that transmit the virus during refeeding (Golnar et al., 2015).

[e] Host preference is the host species from which mosquito blood meals originated.

[f] Proportion of JEV infection is the total of positive mosquito pools divided by the total number of pools tested (observational studies).

[g] Proportion of positive vertebrate hosts is the sum of positive samples divided by the sum of samples tested.

[h] Minimum infection rate (MIR) is the ratio of positive mosquito pools to the total number of mosquitoes in the sample (assumption: only one infected individual is present in a positive pool) (Bustamante and Lord, 2010).

[i] Maximum likelihood estimation (MLE) is the proportion (parameter of a binomial distribution) of infected mosquitoes that maximizes the likelihood of pools of a specific size being positive (Bustamante and Lord, 2010).

**Table 3**
Risk of bias assessment in observational studies – criteria, outcomes and key domains.

| Criteria (description) | Outcome | Notes |
|---|---|---|
| 1. Study question[a] (is the study question clearly defined?) | Yes/ No/ Not reported | *Not reported*: study question is unclear/ poorly defined. |
| 2. Study population[a] (is the study population properly described?) | Yes/ No/ Partially | **KEY DOMAIN** *Study population*: vertebrate hosts (age, breed, gender, location) and mosquito populations (age, species, gender) clearly reported. *Partially*: some information is provided. |
| 3. Inclusion/exclusion criteria[a] (are inclusion and exclusion criteria properly described?) | Yes/ No/ Not reported | *Not reported*: criteria are unclear/ poorly defined. |
| 4. Study period[b] (was time/duration (month/year/season) of the study reported?) | Yes/ No/ Partially | **KEY DOMAIN** *Partially:* some information is provided. |
| 5. Study area[b] (was the area (country/region) of the study reported?) | Yes/ No/ Partially | **KEY DOMAIN** *Partially*: some information is provided. |
| 6. Exposures[a] (are exposures clearly defined and reported?) | Yes/ No/ Not defined | *Not defined:* exposures are reported but poorly defined. |
| 7. Outcomes[a] (are outcome measures clearly defined and reported?) | Yes/ No/ Not defined | **KEY DOMAIN** *Not defined:* outcome measures are reported but poorly defined. |
| 8. Bias[a] (was bias reported and controlled for in the statistical analyses?) | Yes/ No/ Not controlled for | *Not controlled for*: bias is reported but controlling for bias is unclear/ not reported. |

[a] Criteria assessing internal validity.
[b] Criteria assessing external validity.

remaining articles being assessed by one reviewer (AO).

Different entries from the same article were assessed individually for their risk of bias. Thus, for instance, data from an article containing both observational and experimental components for vector competence were assessed twice for their risk of bias (one for each of the study type components).

### 2.6. Data analysis

A descriptive summary of results, presented in tabular form, was performed using Stata-SE 12.0 (StataCorp., College Station TX, USA) and the pivot tables function in Excel® (Microsoft Corp., Redmond WA, 2013).

Data presentation for proportion of JEV infection in vectors were organized alphabetically by species and by author and year of publication. Minimum infection rates and MLE values were organized by author and year of publication and then alphabetically by mosquito species. Data regarding transmission efficiency were presented by days post infection (DPI), by author and year of publication, and alphabetically by mosquito species. As for proportion of JEV infection in host

**Table 5**
Search results by database source.

| Database/ journal | Originals (total)[a] |
|---|---|
| Web of Science | 112 |
| PubMed | 129 |
| Armed Forces Pest Management Board | 68 |
| The American Journal of Tropical Medicine and Hygiene | 33 |
| Journal of Medical Entomology | 126 |
| Journal of the American Mosquito Control Association | 139 |
| Vector-Borne and Zoonotic Diseases | 15 |
| Google Scholar | 180 |
| Hand Search | 1,053 |
| Total | 1855 |
| Eliminated (duplicates or non-primary research) | 450 |
| Selected | 1405 |

[a] Originals refer to abstracts identified as unique during the literature search (including duplicates).

**Table 4**
Risk of bias assessment in experimental studies – criteria, outcomes and key domains.

| Criteria (description) | Outcome | Notes |
|---|---|---|
| 1. Study question[a] (is the study question clearly defined?) | Yes/ No/ Not reported | *Not reported:* study question is unclear or poorly defined. |
| 2. Study population[a] (is the study population properly described?) | Yes/ No/ Partially | **KEY DOMAIN** *Study population:* vertebrate hosts (age, breed, gender, location) and mosquito populations (age, species, gender) clearly reported. *Partially:* some information is provided. |
| 3. Intervention[a] (is intervention clearly defined (dose, route, viral strain, incubation period, with details sufficient for assessment and reproducibility)?) | Yes/ No/ Not reported | **KEY DOMAIN** *Not reported:* information concerning intervention is unclear or poorly defined. |
| 4. Experimental conditions (challenge trials)[b] (are results generalizable?) | Yes/ No/ Not applicable | E.g., infection by oral feeding = yes *vs* intrathoracic in vector studies = no; infection by mosquito bite = yes *vs* needle in host studies) = no |
| 5. Experimental setting (controlled trials)[b] (are results generalizable?) | Yes/ No/ Not applicable | E.g., cage = yes *vs* farm/slaughterhouse = no |
| 6. Randomization[a] (is randomization performed and defined?) | Yes/ No/ Not defined | **KEY DOMAIN** *Not defined:* evidence that randomization is performed but poorly defined. |
| 7. Blinding[a] (is blinding performed and defined?) | Yes/ No/ Not defined | *Not defined:* evidence of blinding that is poorly defined. |
| 8. Outcomes[a] (are outcome measures clearly defined and reported?) | Yes/ No/ Not defined | **KEY DOMAIN** *Not defined:* outcome measures are reported but poorly defined. |

[a] Criteria assessing internal validity.
[b] Criteria assessing external validity.

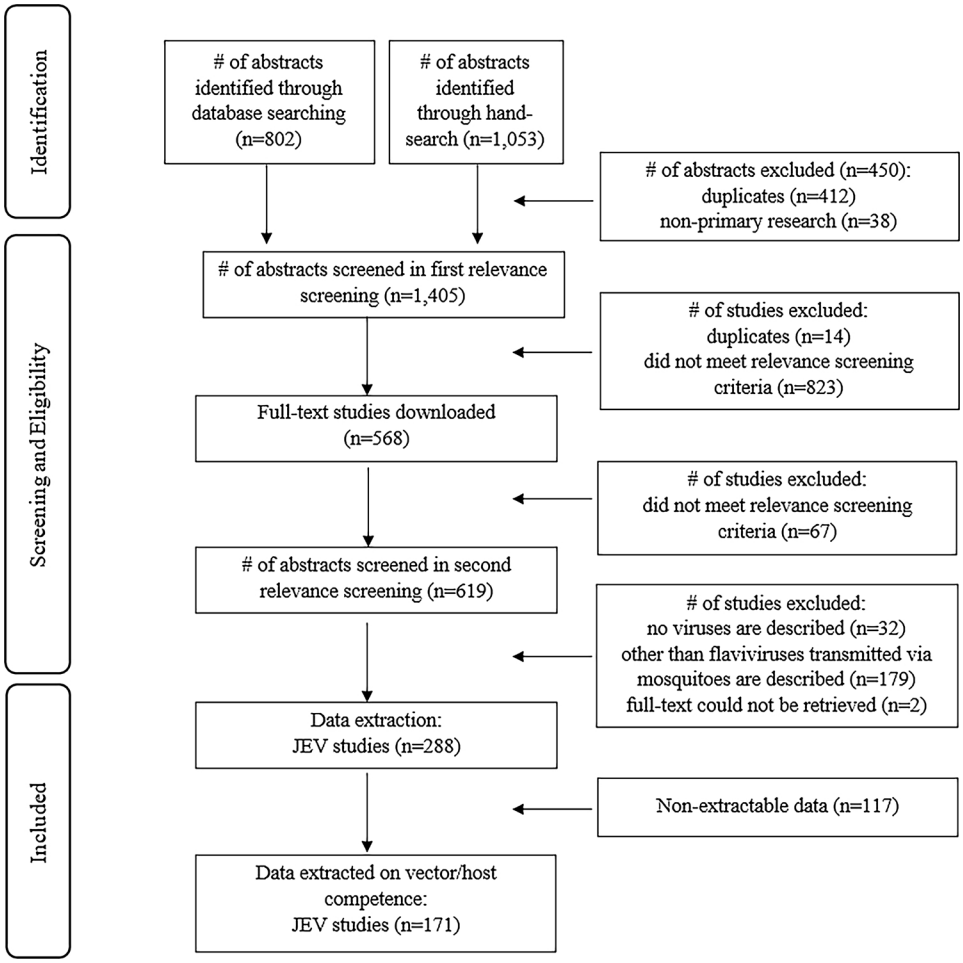


**Fig. 2.** Flowchart of the articles identified, screened, and included for data extraction.

species and mosquito host preferences, data from all articles were combined and presented by vertebrate host species.

## 3. Results

### 3.1. Searching the literature and relevance screening

We identified a total of 1855 abstracts, 450 of which were duplicates or non-primary research (non-peer reviewed articles, conference proceedings, thesis dissertations, and other non-peer reviewed publications), leading to a final selection of 1405 abstracts, which were downloaded for assessment of relevance (Table 5).

During the relevance screening process 14 more abstracts were identified as duplicates, leading to a total of 1391 abstracts that were screened for relevance and subjected to conflict resolution. A total of 568 abstracts were considered relevant.

During the process of downloading the 568 full-text articles, 67 were excluded for not meeting the inclusion criteria, mainly due to not fulfilling the language (full-text not in English) and study type (literature reviews) criteria.

The second relevance screening further narrowed down relevant studies to 288, however, during data extraction, 116 more articles were excluded for not having extractable data, resulting in a final number of 171 articles, which we then assessed for the risk of bias and from which we extracted data. A complete flowchart of the articles identified, screened, and included for data extraction is presented in Fig. 2.

### 3.2. Data extraction

#### 3.2.1. Characteristics of the studies

The study characteristics of the 171 articles included in the final SR, including their source (author and year of publication) are summarized in Table 6.

Most studies were observational (59.1%) and reported vector competence (60.2%). Seven articles (4.1%) had both an experimental and an observational component and 18 (10.6%) reported more than one population type (Table 6).

The year of publication ranged from 1946 to 2016, with half of the articles (n = 85) published after 1992.

The countries represented in all studies were: Vietnam, Taiwan, China, Nepal, Saipan (Mariana islands), South Korea, Indonesia, India, Malaysia, Thailand, Australia, Papua New Guinea, Japan, Australia, Bangladesh, Sri Lanka, Myanmar, USA, Singapore, Guam (US), and Saipan (US). Only two articles reported information from continental US.

#### 3.2.2. Outcome measures: vector competence

Data on proportion of JEV infection in vectors extracted from articles reporting positive mosquito pools are depicted in Table 7. A complete list of results from all mosquito species reported across all studies is available in the supplementary materials (S1 Table).

The proportion of JEV infection, reported in a total of 149 mosquito species, across all observational studies ranged from 0 to 100%. For *Culex tritaeniorhynchus,* one of the most important vector species, the

**Table 6**
Source of relevant articles by type of study design and outcome (n = 171), ordered chronologically.

| | Number of articles | Source |
|---|---|---|
| **Study design** | | |
| Experimental | 63 | Reeves and Hammon (1946), Hurlbut (1950), Hurlbut (1951), Rosenberg et al. (1953), Morris et al. (1955), Gresser et al. (1958), Buescher et al. (1959c), Scherer and Smith (1960), Gould et al. (1962), Gould et al. (1964), Sulkin et al. (1964), Sulkin et al. (1966), Doi et al. (1967), Kodama et al. (1968), Nathanson and Cole (1970), Doi, 1970, Igarashi et al. (1972), Muangman et al. (1972), Takahashi (1976), Doi et al. (1977), Dhanda et al. (1977), Soman et al. (1977), Rosen et al. (1978), Rosen et al. (1980), Rosen (1981), Sasaki et al. (1982), Takahashi (1982), Boyle et al. (1983), Oya et al. (1983), Banerjee et al. (1984), Rosen and Shroyer (1985), Rosen et al. (1985), Leake and Johnson (1987), Yamamoto et al. (1987), Hayakawa (1988), Rosen (1988), Ilkal et al. (1988), Takashima and Rosen (1989), Rosen et al. (1989b), Ilkal et al. (1994), Weng et al. (1997), Samuel et al. (1998), Weng et al. (2000), Mwandawiro et al. (2000), Mourya and Mishra (2000), van den Hurk et al. (2003b), Turell et al. (2006a), Turell et al. (2006b), van den Hurk et al. (2007), Johnson et al. (2009), van den Hurk et al. (2009b), Kramer et al. (2011), Bosco-Lauth et al. (2011), Nemeth et al. (2012), Huber et al. (2014), Nicholson et al. (2014), Sudeep et al. (2015), Huang et al. (2015), Mackenzie-Impoinvil et al. (2015), Ricklin et al. (2016), Do et al. (2016). |
| Observational | 101 | Hammon et al. (1958), Buescher et al. (1959a), Scherer et al. (1959a), Buescher et al. (1959b), Scherer et al. (1959c), Konno et al. (1966), Pennington and Phelps (1968), Cates and Detels (1969), Dandawate et al. (1969), Wada et al. (1970), Yamada et al. (1971), Gould et al. (1973), Self et al. (1973), Okuno et al. (1973), Mitchell et al. (1973), Johnsen et al. (1974), van Peenen and Joseph (1975), Fukumi et al. (1975), Wada et al. (1975), Wang (1975), Benenson et al. (1975), Chakravarty et al. (1975), Hayashi et al. (1975), Ura (1976), Simpson et al. (1976), Hsu et al. (1978), Khan and Banerjee (1980), Khan et al. (1981), Rodrigues et al. (1981), Burke et al. (1985), Olson et al. (1985), Thein et al. (1988), Takashima et al. (1988), Rosen et al. (1989a), Takashima et al. (1989), Somboon et al. (1989), Mourya et al. (1989), Dhanda et al. (1989), Mani et al. (1991), Reuben et al. (1992), Gingrich et al. (1992), Peiris et al. (1992), Mitchell et al. (1993), Peiris et al. (1993), Paul et al. (1993), Tan et al. (1993), Pant et al. (1994), Tadano et al. (1994), Bhattacharyya et al. (1995), Nga et al. (1995), Hanna et al. (1996), Khan et al. (1997), Vythilingam et al. (1997), Gajanana et al. (1997), Dhanda et al. (1997), Ritchie et al. (1997), Weng et al. (1999), Hanna et al. (1999), Victor et al. (2000), Johansen et al. (2000), Johansen et al. (2001), van den Hurk et al. (2001a), van den Hurk et al. (2001b), See et al. (2002), van den Hurk et al. (2003a), Turell et al. (2003), Johansen et al. (2003), Bryant et al. (2005), Weng et al. (2005), Arunachalam et al. (2005), Das et al. (2005), Nitatpattana et al. (2005), Thenmozhi et al. (2006), van den Hurk et al. (2006), Hasegawa et al. (2008), Tewari et al. (2008), Samuel et al. (2008), Johansen et al. (2009), Sun et al. (2009), Arunachalam et al. (2009), Ohno et al. (2009), Nemeth et al. (2010), Konishi et al. (2010), Tiawsirisup and Nuchprayoon (2010), Kim et al. (2011), Nitatpattana et al. (2011), Chanyasanha et al. (2011), Li et al. (2011), Thakur et al. (2012), Feng et al. (2012), Upadhyayula et al. (2012), Hall-Mendelin et al. (2012), Tiawsirisup et al. (2012), Kumari et al. (2013), Seo et al. (2013), Liu et al. (2013), Borah et al. (2013), Lindahl et al. (2013), Su et al. (2014), Kim et al. (2015), Cha et al. (2015). |
| Both | 7 | Sabin (1947), Scherer et al. (1959b), Buescher et al. (1959d), Hurlbut (1964), Doi et al. (1983), Chen et al. (2000), Saito et al. (2009). |
| **Reporting of** | | |
| Vector competence | 103 | Reeves and Hammon (1946), Hurlbut (1950), Hurlbut (1951), Rosenberg et al. (1953), Buescher et al. (1959b), Gould et al. (1962), Hurlbut (1964), Konno et al. (1966), Doi et al. (1967), Cates and Detels (1969), Dandawate et al. (1969), Doi, 1970, Igarashi et al. (1972), Muangman et al. (1972), Mitchell et al. (1973), Gould et al. (1973), Wang (1975), van Peenen and Joseph (1975), Fukumi et al. (1975), Wada et al. (1975), Hayashi et al. (1975), Takahashi (1976), Doi et al. (1977), Rosen et al. (1978), Hsu et al. (1978), Rosen et al. (1980), Rosen (1981), Khan et al. (1981), Takahashi (1982), Rosen and Shroyer (1985), Rosen et al. (1985), Burke et al. (1985), Olson et al. (1985), Leake and Johnson (1987), Yamamoto et al. (1987), Hayakawa (1988), Rosen (1988), Takashima and Rosen (1989), Somboon et al. (1989), Rosen et al. (1989a), Rosen et al. (1989b), Takashima et al. (1989), Mourya et al. (1989), Dhanda et al. (1989), Gingrich et al. (1992), Peiris et al. (1992), Mitchell et al. (1993), Tan et al. (1993), Pant et al. (1994), Bhattacharyya et al. (1995), Hanna et al. (1996), Weng et al. (1997), Vythilingam et al. (1997), Gajanana et al. (1997), Dhanda et al. (1997), Ritchie et al. (1997), Samuel et al. (1998), Weng et al. (1999), Weng et al. (2000), Mwandawiro et al. (2000), Mourya and Mishra (2000), Victor et al. (2000), Johansen et al. (2000), Johansen et al. (2001), van den Hurk et al. (2001a), van den Hurk et al. (2003a), van den Hurk et al. (2003b), Turell et al. (2003), Johansen et al. (2003), Bryant et al. (2005), Weng et al. (2005), Das et al. (2005), Nitatpattana et al. (2005), Thenmozhi et al. (2006), van den Hurk et al. (2006), Turell et al. (2006a), Turell et al. (2006b), van den Hurk et al. (2007), Samuel et al. (2008), Tewari et al. (2008), Johansen et al. (2009), Johnson et al. (2009), Sun et al. (2009), Arunachalam et al. (2009), Tiawsirisup and Nuchprayoon (2010), Kramer et al. (2011), Kim et al. (2011), Li et al. (2011), Feng et al. (2012), Upadhyayula et al. (2012), Tiawsirisup et al. (2012), Seo et al. (2013), Borah et al. (2013), Lindahl et al. (2013), Huber et al. (2014), Nicholson et al. (2014), Su et al. (2014), Sudeep et al. (2015), Huang et al. (2015), Mackenzie-Impoinvil et al. (2015), Kim et al. (2015). |
| Host competence | 50 | Morris et al. (1955), Gresser et al. (1958), Hammon et al. (1958), Scherer et al. (1959a), Buescher et al. (1959a), Scherer et al. (1959c), Buescher et al. (1959c), Scherer and Smith (1960), Sulkin et al. (1964), Sulkin et al. (1966), Kodama et al. (1968), Pennington and Phelps (1968), Nathanson and Cole (1970), Self et al. (1973), Johnsen et al. (1974), Benenson et al. (1975), Simpson et al. (1976), Ura (1976), Dhanda et al. (1977), Soman et al. (1977), Khan and Banerjee (1980), Rodrigues et al. (1981), Sasaki et al. (1982), Boyle et al. (1983), Oya et al. (1983), Banerjee et al. (1984), Ilkal et al. (1988), Thein et al. (1988), Takashima et al. (1988), Mani et al. (1991), Paul et al. (1993), Peiris et al. (1993), Ilkal et al. (1994), Tadano et al. (1994), Nga et al. (1995), Hanna et al. (1999), See et al. (2002), Hasegawa et al. (2008), Ohno et al. (2009), Nemeth et al. (2010), Konishi et al. (2010), Bosco-Lauth et al. (2011), Nitatpattana et al. (2011), Chanyasanha et al. (2011), Nemeth et al. (2012), Thakur et al. (2012), Kumari et al. (2013), Liu et al. (2013), Cha et al. (2015), Ricklin et al. (2016). |
| More than one category | 18 | Sabin (1947), Buescher et al. (1959d), Scherer et al. (1959b), Gould et al. (1964), Wada et al. (1970), Yamada et al. (1971), Okuno et al. (1973), Chakravarty et al. (1975), Doi et al. (1983), Reuben et al. (1992), Khan et al. (1997), Chen et al. (2000), van den Hurk et al. (2001a,b), Arunachalam et al. (2005), van den Hurk et al. (2009b), Saito et al. (2009), Hall-Mendelin et al. (2012), Do et al. (2016). |

proportion of positive pools also ranged from 0 to 100% across all 44 articles that reported results for this species. The countries where mosquitoes were captured and tested for JEV infection belonged to Southeast Asia, including Australia, Bangladesh, China, India, Indonesia, Japan, Malaysia, Saipan (Mariana islands), South Korea, Sri Lanka, Taiwan, Thailand, and Vietnam.

Minimum infection rates from observational studies were reported in 16 studies in 28 species and 10 countries. Minimum infection rates varied between 0 per 1000 mosquitoes in several species and 333.3 per 1000 mosquitoes in *Culex gelidus*. Information related to MIR is presented in Table 8.

Maximum likelihood estimation values from observational studies

**Table 7**
Proportion of JEV infection in positive mosquito pools (in observational studies only) by mosquito species (ordered alphabetically), and by reference, and country of origin, ordered from highest to lowest proportion of JEV infection.[a]

| Mosquito species | Reference | Country | Positive pools/Total pools tested[b] | Proportion positive pools (%) |
|---|---|---|---|---|
| *Aedes (Cancraedes)* sp. | Vythilingam et al. (1997) | Malaysia | 1/19 | 5.26 |
| *Aedes albopictus* | Weng et al. (1999) | Taiwan | 20/39 | 51.28 |
| | Su et al. (2014) | Taiwan | 1/25 | 4.00 |
| *Aedes butleri* | Vythilingam et al. (1997) | Malaysia | 4/79 | 5.06 |
| *Aedes lineatopennis* | Vythilingam et al. (1997) | Malaysia | 1/6 | 16.67 |
| *Aedes scutellaris* | van den Hurk et al. (2003b) | India | 1/1 | 100.00 |
| *Aedes vexans* | Weng et al. (1999) | Taiwan | 1/3 | 33.33 |
| | Su et al. (2014) | Taiwan | 3/32 | 9.38 |
| *Aedes vexans nipponii* | Fukumi et al. (1975) | Japan | 4/44,926 | 0.01 |
| *Aedes vexans nocturnus* | Weng et al. (2005) | Taiwan | 1/9 | 11.11 |
| *Anopheles annullaris* | Olson et al. (1985) | Indonesia | 1/28 | 3.57 |
| *Anopheles kochi* | Tan et al. (1993) | Indonesia | 2/28 | 7.14 |
| *Anopheles minimus* | Su et al. (2014) | Taiwan | 1/7 | 14.29 |
| *Anopheles peditaeniatus* | Mourya et al. (1989) | India | 1/133 | 0.75 |
| *Anopheles sinensis* | Su et al. (2014) | Taiwan | 6/419 | 1.43 |
| | Feng et al. (2012) | China | 3/14,170 | 0.02 |
| *Anopheles subpictus* | Thenmozhi et al. (2006) | India | 98/982 | 9.98 |
| | Mourya et al. (1989) | India | 1/87 | 1.15 |
| | Dhanda et al. (1997) | India | 1/163 | 0.61 |
| *Anopheles tessellatus* | Su et al. (2014) | Taiwan | 2/31 | 6.45 |
| *Anopheles vagus* | Tan et al. (1993) | Indonesia | 3/93 | 3.23 |
| | Olson et al. (1985) | Indonesia | 1/42 | 2.38 |
| *Armigeres subalbatus* | Weng et al. (1999) | Taiwan | 8/20 | 40.00 |
| | Su et al. (2014) | Taiwan | 3/30 | 10.00 |
| | Tan et al. (1993) | Indonesia | 3/114 | 2.63 |
| | Chen et al. (2000) | Taiwan | 1/123 | 0.81 |
| | Feng et al. (2012) | China | 2/394 | 0.51 |
| | Fukumi et al. (1975) | Japan | 1/11,666 | 0.01 |
| *Coquillettidia crassipes* | van den Hurk et al. (2003b) | India | 2/3 | 66.67 |
| *Culex* spp. | Tewari et al. (2008) | India | 59/2,816 | 2.10 |
| *Culex annulirostris* | van den Hurk et al. (2003b) | India | 2368/3,197 | 74.07 |
| | Ritchie et al. (1997) | Australia | 8/134 | 5.97 |
| | Hanna et al. (1996) | Australia | 8/2,871 | 0.28 |
| *Culex annulus* | Wang (1975) | Taiwan | 220/223 | 98.65 |
| | Weng et al. (1999) | Taiwan | 1/3 | 33.33 |
| | Su et al. (2014) | Taiwan | 9/79 | 11.39 |
| | Okuno et al. (1973) | Taiwan | 6/91 | 6.59 |
| | Hsu et al. (1978) | Taiwan | 31/703 | 4.41 |
| | Cates and Detels (1969) | Taiwan | 3/174 | 1.72 |
| *Culex bitaeniorhynchus* | van den Hurk et al. (2003b) | India | 7/10 | 70.00 |
| | Seo et al. (2013) | South Korea | 1/26 | 3.85 |
| | Kim et al. (2011) | South Korea | 1/45 | 2.22 |
| | Tan et al. (1993) | Indonesia | 1/85 | 1.18 |
| *Culex fuscanus* | Weng et al. (1999) | Taiwan | 1/2 | 50.00 |
| *Culex fuscocephala* | Wang (1975) | Taiwan | 353/359 | 98.33 |
| | Su et al. (2014) | Taiwan | 3/19 | 15.79 |
| | Vythilingam et al. (1997) | Malaysia | 2/76 | 2.63 |
| | Gajanana et al. (1997) | India | 6/305 | 1.97 |
| | Dhanda et al. (1989) | India | 1/85 | 1.18 |
| | Mourya et al. (1989) | India | 2/257 | 0.78 |
| | Gould et al. (1973) | Thailand | 2/142,375 | < 0.01 |
| *Culex fuscocephalus* | van Peenen and Joseph (1975) | Indonesia | 1/12 | 8.33 |
| | Hsu et al. (1978) | Taiwan | 19/282 | 6.74 |
| | Tan et al. (1993) | Indonesia | 3/185 | 1.62 |
| *Culex gelidus* | Samuel et al. (2008) | India | 56/64 | 87.50 |
| | van den Hurk et al. (2003b) | India | 13/16 | 81.25 |
| | van Peenen and Joseph (1975) | Indonesia | 2/12 | 16.67 |
| | Vythilingam et al. (1997) | Malaysia | 12/224 | 5.36 |
| | Mourya et al. (1989) | India | 4/127 | 3.15 |
| | Gajanana et al. (1997) | India | 5/194 | 2.58 |
| | Tewari et al. (2008) | India | 4/177 | 2.26 |
| | Upadhyayula et al. (2012) | India | 12/590 | 2.03 |
| | Arunachalam et al. (2009) | India | 11/594 | 1.85 |
| | Gould et al. (1973) | Thailand | 3/11,495 | 0.03 |
| | Peiris et al. (1992) | Sri Lanka | 4/13,043 | 0.03 |
| *Culex orientalis* | Kim et al. (2015) | South Korea | 5/83 | 6.02 |
| *Culex palpalis* | van den Hurk et al. (2003b) | India | 57/69 | 82.61 |
| *Culex pipiens* | Seo et al. (2013) | South Korea | 4/64 | 6.25 |
| | Kim et al. (2015) | South Korea | 1/264 | 0.38 |
| | Buescher et al. (1959b) | Australia | 2/1,490 | 0.13 |
| *Culex pipiens fatigans* | Wang (1975) | Taiwan | 65/66 | 98.48 |
| *Culex pipiens pallens* | Fukumi et al. (1975) | Japan | 2/2,783 | 0.07 |
| *Culex pipiens quinquefasciatus* | Tan et al. (1993) | Indonesia | 10/333 | 3.00 |

(*continued on next page*)

**Table 7** (*continued*)

| Mosquito species | Reference | Country | Positive pools/Total pools tested[b] | Proportion positive pools (%) |
|---|---|---|---|---|
| *Culex pseudovishnui* | Dhanda et al. (1989) | India | 3/81 | 3.70 |
| | Borah et al. (2013) | India | 3/107 | 2.80 |
| | Mourya et al. (1989) | India | 1/112 | 0.89 |
| | Fukumi et al. (1975) | Japan | 8/21,012 | 0.04 |
| *Culex quinquefasciatus* | van den Hurk et al. (2003b) | India | 7/8 | 87.50 |
| | Weng et al. (1999) | Taiwan | 7/31 | 22.58 |
| | Nitatpattana et al. (2005) | Thailand | 2/25 | 8.00 |
| | Mourya et al. (1989) | India | 1/18 | 5.56 |
| | Su et al. (2014) | Taiwan | 2/74 | 2.70 |
| | Vythilingam et al. (1997) | Malaysia | 1/48 | 2.08 |
| *Culex rubithoracis* | Weng et al. (2005) | Taiwan | 4/22 | 18.18 |
| *Culex sitiens* | Weng et al. (1999) | Taiwan | 2/2 | 100.00 |
| | van den Hurk et al. (2003b) | India | 3/8 | 37.50 |
| | Weng et al. (2005) | Taiwan | 1/34 | 2.94 |
| | Johansen et al. (2001) | Australia | 42/25,292 | 0.17 |
| | Hall-Mendelin et al. (2012) | Australia | 17/39,698 | 0.04 |
| | van den Hurk et al. (2006) | Australia | 1/22,833 | < 0.01 |
| *Culex tritaeniorhynchus* | Wang (1975) | Taiwan | 110/110 | 100.00 |
| | Weng et al. (1999) | Taiwan | 97/294 | 32.99 |
| | Kim et al. (2011) | South Korea | 50/207 | 24.15 |
| | Seo et al. (2013) | South Korea | 29/121 | 23.97 |
| | Su et al. (2014) | Taiwan | 468/2,242 | 20.87 |
| | Victor et al. (2000) | India | 2/10 | 20.00 |
| | Buescher et al. (1959b) | Australia | 307/2,400 | 12.79 |
| | Konno et al. (1966) | Japan | 16/153 | 10.46 |
| | Weng et al. (2005) | Taiwan | 95/1,061 | 8.95 |
| | Hayashi et al. (1975) | Japan | 19/216 | 8.80 |
| | Borah et al. (2013) | India | 19/281 | 6.76 |
| | Hsu et al. (1978) | Taiwan | 18/267 | 6.74 |
| | Das et al. (2005) | India | 1/15 | 6.67 |
| | Okuno et al. (1973) | Taiwan | 6/91 | 6.59 |
| | Dhanda et al. (1997) | India | 7/163 | 4.29 |
| | Vythilingam et al. (1997) | Malaysia | 24/731 | 3.28 |
| | van Peenen and Joseph (1975) | Indonesia | 3/93 | 3.23 |
| | Tewari et al. (2008) | India | 13/429 | 3.03 |
| | Dhanda et al. (1989) | India | 3/117 | 2.56 |
| | Arunachalam et al. (2009) | India | 19/951 | 2.00 |
| | Upadhyayula et al. (2012) | India | 19/972 | 1.95 |
| | Tan et al. (1993) | Indonesia | 3/165 | 1.82 |
| | Gajanana et al. (1997) | India | 58/4,128 | 1.41 |
| | Mourya et al. (1989) | India | 3/272 | 1.10 |
| | Li et al. (2011) | China | 1/97 | 1.03 |
| | Turell et al. (2003) | South Korea | 14/4,281 | 0.33 |
| | Olson et al. (1985) | Indonesia | 1/596 | 0.17 |
| | Pant et al. (1994) | India | 1/753 | 0.13 |
| | Sun et al. (2009) | China | 12/14,840 | 0.08 |
| | Fukumi et al. (1975) | Japan | 435/598,434 | 0.07 |
| | Feng et al. (2012) | China | 15/37,119 | 0.04 |
| | Rosen et al. (1989a) | Taiwan | 165/524,290 | 0.03 |
| | Peiris et al. (1992) | Sri Lanka | 4/17,436 | 0.02 |
| | Gould et al. (1973) | Thailand | 8/182,940 | < 0.01 |
| *Culex univittattus* | Dhanda et al. (1989) | India | 1/29 | 3.45 |
| *Culex vishnui* | Borah et al. (2013) | India | 7/198 | 3.54 |
| | Gajanana et al. (1997) | India | 22/1,080 | 2.04 |
| | Tewari et al. (2008) | India | 42/2,203 | 1.91 |
| | Mourya et al. (1989) | India | 2/290 | 0.69 |
| | Dandawate et al. (1969) | India | 2/5,553 | 0.04 |
| *Culex whitmorei* | van den Hurk et al. (2003b) | India | 2/2 | 100.00 |
| | Dhanda et al. (1989) | India | 1/20 | 5.00 |
| | Mourya et al. (1989) | India | 1/132 | 0.76 |
| | Peiris et al. (1992) | Sri Lanka | 1/167 | 0.60 |
| *Mansonia indiana* | Dhanda et al. (1997) | India | 1/163 | 0.61 |
| *Mansonia septempunctata* | van den Hurk et al. (2003b) | India | 4/14 | 28.57 |
| *Mansonia uniformis* | van den Hurk et al. (2003b) | India | 11/11 | 100.00 |
| | Su et al. (2014) | Taiwan | 1/19 | 5.26 |
| | Dhanda et al. (1997) | India | 3/163 | 1.84 |
| | Mourya et al. (1989) | India | 2/281 | 0.71 |
| *Ochleratus normanensis* | van den Hurk et al. (2003b) | India | 100/310 | 32.26 |
| *Ochleratus vigilax* | van den Hurk et al. (2003b) | India | 3/3 | 100.00 |
| *Ochleratus vittiger* | van den Hurk et al. (2003b) | India | 1/1 | 100.00 |
| *Ochlerotatus vigilax* | Johansen et al. (2001) | Australia | 1/3,073 | 0.03 |
| *Verrallina funerea* | van den Hurk et al. (2003b) | India | 3/5 | 60.00 |

[a] A complete list of all mosquito species (n = 149) across all observational studies (n = 58) is available in S1 Table (supplementary materials).

[b] Mosquito pools = 1 to 800 mosquitoes.

**Table 8**
Minimum infection rates (MIR), standard errors (SE), and ranges reported across all observational studies (n = 16), by reference and by mosquito species (ordered alphabetically).

| Reference | Mosquito species[a] | MIR[b] | SE | MIR Range |
|---|---|---|---|---|
| Olson et al. (1985) | *Anopheles annullaris* | 4.00 | – | – |
| | *Anopheles vagus* | 0.37 | – | – |
| | *Culex tritaeniorhynchus* | 0.01 | – | – |
| Gingrich et al. (1992) | *Culex gelidus* | 0.17–0.21 | – | – |
| | *Culex tritaeniorhynchus* | 0.09–0.1 | – | – |
| Peiris et al. (1992) | *Aedes* spp. | 0.23 | – | – |
| | *Culex fuscocephala* | 0.06–0.23 | – | – |
| | *Culex gelidus* | 0.06–0.23 | – | – |
| | *Culex pseudovishnui* | 0.06–0.23 | – | – |
| | *Culex tritaeniorhynchus* | 0.06–0.23 | – | – |
| | *Culex whitmorei* | 0.23 | – | – |
| | *Mansonia uniformis* | 0.23 | – | – |
| | *Mansonia uniformis* | 0.06 | – | – |
| Dhanda et al. (1997) | *Culex tritaeniorhynchus* | 0.00 | – | – |
| Gajanana et al. (1997) | *Culex fuscocephala* | 0.39 | 0.32 | – |
| | *Culex gelidus* | 0.52 | 0.46 | – |
| | *Culex tritaeniorhynchus* | 0.28 | 0.08 | – |
| | *Culex vishnui* | 0.41 | 0.18 | – |
| Vythilingam et al. (1997) | *Culex tritaeniorhynchus* | 0.1-5.6 | – | – |
| Johansen et al. (2000) | *Culex sitiens subgroup* | 0.01–0.02 | – | – |
| Johansen et al. (2001) | *Culex sitiens group* | 1.70 | – | – |
| | *Ochlerotatus vigilax* | 0.30 | – | – |
| Turell et al. (2003) | *Culex tritaeniorhynchus* | 2.6–13.2 | – | – |
| Weng et al. (2005) | *Aedes albopictus* | 0.00 | – | – |
| | *Aedes penghuensis* | 0.00 | – | – |
| | *Aedes subalbatus* | 0.00 | – | – |
| | *Aedes vexans nocturnus* | 16.40 | – | – |
| | *Anopheles sinensis* | 0.00 | – | – |
| | *Anopheles tessellatus* | 0.00 | – | – |
| | *Culex annulus* | 0.00 | – | – |
| | *Culex fuscanus* | 0.00 | – | – |
| | *Culex quinquefasciatus* | 0.00 | – | – |
| | *Culex rubithoracis* | 30.80 | – | – |
| | *Culex sitiens* | 1.70 | – | – |
| | *Culex tritaeniorhynchus* | 3.30 | – | – |
| | *Mansonia uniformis* | 0.00 | – | – |
| | *Mimomyia luzonensis* | 0.00 | – | – |
| Thenmozhi et al. (2006) | *Anopheles subpictus* | 0–12.5 | – | – |
| Tewari et al. (2008) | *Culex* spp. | 0–0.59 | – | – |
| Feng et al. (2012) | *Anopheles sinensis* | 0.21 | – | – |
| | *Armigeres subalbatus* | 5.08 | – | – |
| Hall-Mendelin et al. (2012) | *Culex sitiens subgroup* | 0.04–1.61 | – | – |
| Upadhyayula et al. (2012) | *Culex gelidus* | 0–333.3 | – | – |
| | *Culex tritaeniorhynchus* | 0–3.43 | – | – |
| Borah et al. (2013) | *Culex pseudovishnui* | 0.20 | – | 0.00–2.10 |
| | *Culex tritaeniorhynchus* | 0.90 | – | 0.00–4.30 |
| | *Culex vishnui* | 0.40 | – | 0.00–2.90 |

[a] Mosquito pools = 1 to 500 mosquitoes.

[b] Minimum infection rates per 1000 mosquitoes (presented as an average MIR or range of MIR values depending on how it was reported in the studies). Minimum infection rate (MIR) is defined as the ratio of the number of positive mosquito pools to the total number of mosquitoes in the sample, assuming that only one infected individual is present in a positive pool (Bustamante and Lord, 2010).

**Table 9**
Maximum likelihood estimation (MLE) and 95% confidence intervals (CI) reported across all observational studies (n = 6), by reference and by mosquito species (ordered alphabetically).

| Reference | Mosquito species[a] | MLE[b] | 95% CI |
|---|---|---|---|
| van den Hurk et al. (2006) | *Culex sitiens* | 0.04 | – |
| Arunachalam et al. (2009) | *Culex gelidus* | 0.56 | 0.29–0.97 |
| | *Culex tritaeniorhynchus* | 0.63 | 0.34–1.07 |
| Kim et al. (2011) | *Aedes vexans nipponii* | 0.90 | – |
| | *Culex pipiens pallens* | 9.70 | – |
| Lindahl et al. (2013) | *Culex quinquefasciatus* | 1.30 | 0.10–6.30 |
| | | 1.20 | 0.20–3.80 |
| | *Culex tritaeniorhynchus* | 1.60 | 0.40–4.40 |
| | | 0.90 | 0.40–1.80 |
| Seo et al. (2013) | *Culex bitaeniorhynchus* | 2.80 | – |
| | *Culex pipiens* | 5.60 | – |
| | *Culex tritaeniorhynchus* | 11.80 | – |
| Su et al. (2014) | *Aedes aegypti* | 0.00 | 0.00–499.14 |
| | *Aedes albopictus* | 19.44 | 1.30–88.53 |
| | | 0.00 | 0.00–22.75 |
| | *Aedes penghuiensis* | 0.00 | 0.00–10.46 |
| | *Aedes vexans* | 29.65 | 1.91–139.58 |
| | | 9.75 | 1.79–32.33 |
| | *Anopheles ludlowae* | 0.00 | 0.00–793.45 |
| | *Anopheles minimus* | 53.78 | 3.38–230.59 |
| | *Anopheles sinensis* | 2.05 | 0.77–4.50 |
| | | 5.33 | 0.34-25.44 |
| | *Anopheles tessellatus* | 4.81 | 0.33-23.37 |
| | | 2.75 | 0.16–13.24 |
| | *Armigeres subalbatus* | 17.34 | 4.83–45.72 |
| | | 0.00 | 0.00–56.26 |
| | *Coquillettidia crassipes* | 0.00 | 0.00–35.54 |
| | *Culex annulus* | 26.29 | 13.89–46.52 |
| | | 1.41 | 0.08–6.76 |
| | *Culex bitaeniorhynchus* | 0.00 | 0.00–37.88 |
| | *Culex brevipalpis* | 0.00 | 0.00–793.45 |
| | *Culex fuscanus* | 0.00 | 0.00–499.14 |
| | | 0.00 | 0.00–793.49 |
| | *Culex fuscocephala* | 7.77 | 2.17-20.82 |
| | *Culex mimeticus* | 0.00 | 0.00–793.45 |
| | *Culex murrelli* | 0.00 | 0.00–53.12 |
| | *Culex nigropunctatus* | 0.00 | 0.00–160.75 |
| | *Culex quinquefasciatus* | 1.64 | 0.30–5.38 |
| | | 0.00 | 0.00–26.51 |
| | *Culex rubithoracis* | 0.00 | 0.00–42.44 |
| | *Culex sitiens* | 0.00 | 0.00–0.60 |
| | *Culex tritaeniorhynchus* | 7.68 | 6.97–8.45 |
| | | 2.10 | 1.60–2.72 |
| | *Mansonia uniformis* | 18.14 | 1.06–90.71 |
| | | 0.00 | 0.00–146.56 |
| | *Ochlerotatus albolateralis* | 0.00 | 0.00–793.45 |
| | *Ochlerotatus togoi* | 0.00 | 0.00–793.45 |
| | *Uranotenia macfarlanei* | 0.00 | 0.00–793.45 |

[a] Mosquito pools = 1 to 200 mosquitoes.

[b] Maximum likelihood estimation per 1000 mosquitoes. Maximum likelihood estimation (MLE) represents the proportion of infected mosquitoes that maximizes the likelihood of the number of pools of a specific size to be virus positive, where the proportion is the parameter of a binomial distribution (Bustamante and Lord, 2010).

were reported in 6 studies, in 30 mosquito species and 5 countries, ranging from 0 per 1000 mosquitoes in different species to 53.8 per 1000 mosquitoes in *Anopheles minimus*. Results are presented in Table 9.

In experimental studies, infection, dissemination, and transmission rates from 50 different mosquito species and 30 studies varied between 0 and 100%. *Culex quinquefasciatus* and *Ochlerotatus detritus* were the mosquito species reported having up to 100% dissemination rates, while the species reported as having 100% transmission rates were *Culex tritaeniorhynchus*, *Culex gelidus*, *Mansonia uniformis*, and *Ochlerotatus purpureus*. JEV infection, dissemination, and transmission rates for 14 days post-infection (DPI), or the closest to 14 DPI, are reported in Table 10 and a complete list of all results is available in the supplementary materials (S2 Table).

**Table 10**
JEV infection, dissemination, and transmission rates for 14 days post infection (DPI) or the closest to 14 DPI (most frequently reported incubation period) across all experimental studies reporting incubation period (n = 30), by reference and by mosquito species (ordered alphabetically).

| Reference | Mosquito Name | DPI[g] | Proportion infected[a] | Infection rate (%)[b] | Proportion disseminated[c] | Dissemination rate (%)[d] | Proportion transmitted[e] | Transmission rate (%)[f] | Mosquitoes/pool |
|---|---|---|---|---|---|---|---|---|---|
| Reeves and Hammon (1946) | *Aedes dorsalis* | 16 | 1/31 | 3.23 | – | – | – | – | – |
| | *Aedes nigromaculis* | 8–14 | 4/217 | 1.84 | – | – | – | – | – |
| | *Aedes varipalpus* | 6–14 | 0/153 | 0.00 | – | – | – | – | – |
| | *Aedes vexans* | 8–27 | 0/98 | 0.00 | – | – | – | – | – |
| | *Anopheles maculipennis freeborni* | 0–16 | 0/119 | 0.00 | – | – | – | – | – |
| | *Culex pipiens molestus* | 7–20 | 3/216 | 1.39 | – | – | – | – | – |
| | *Culex pipiens (pipiens)* | 20 | 2/15 | 13.33 | – | – | – | – | – |
| | *Culex quinquefasciatus* | 11–25 | 4/664 | 0.60 | – | – | – | – | – |
| | *Culex tarsalis* | 6–10 | 2/165 | 1.21 | – | – | – | – | – |
| | *Culiseta incidens* | 8–14 | 3/74 | 4.05 | – | – | – | – | – |
| | *Culiseta inornata* | 10–20 | 3/82 | 3.66 | – | – | – | – | – |
| Hurlbut (1950) | *Culex quinquefasciatus* | 6 | 5/5 | 100.00 | – | – | – | – | – |
| Gresser et al. (1958) | *Culex tritaeniorhynchus* | 18 | 7/8 | 87.50 | – | – | – | – | – |
| Gould et al. (1962) | *Culex gelidus* | 6–21 | – | – | – | – | 1/13 | 8.00 | – |
| Gould et al. (1964) | *Culex gelidus* | 6 | – | – | – | – | 0/13 | 0.00 | – |
| | *Culex tritaeniorhynchus* | 6 | – | – | – | – | 1/29 | 3.45 | – |
| Hurlbut (1964) | *Aedes albopictus* | 14 | 0/10 | 0.00 | – | – | – | – | – |
| | *Culex tritaeniorhynchus* | 14 | 4/26 | 15.38 | – | – | – | – | – |
| Doi et al. (1967) | *Culex tritaeniorhynchus* | 15 | 6/6 | 100.00 | – | – | – | – | – |
| Doi, 1970 | *Culex pipiens* | 14 | 2/5 | 40.00 | – | – | – | – | – |
| | *Culex tritaeniorhynchus* | 15 | 9/9 | 100.00 | – | – | – | – | – |
| Muangman et al. (1972) | *Culex fuscocephala* | 10 | 19/20 | 95.00 | – | – | 1/10 | 10.00 | – |
| | *Culex tritaeniorhynchus* | 10 | 20/20 | 100.00 | – | – | 0/10 | 0.00 | – |
| Doi et al. (1977) | *Culex pipiens fatigans* | 10–14 | 0/17 | 0.00 | – | – | – | – | – |
| | *Culex pipiens pallens* | 10–14 | 0/23 | 0.00 | – | – | – | – | – |
| | *Culex pseudovishnui* | 10–14 | 0/19 | 0.00 | – | – | – | – | – |
| | *Culex tritaeniorhynchus* | 10–14 | 8/9 | 88.90 | – | – | – | – | – |
| Takahashi (1982) | *Culex tritaeniorhynchus* | 10–14 | 19/20 | 95.00 | – | – | 19/19 | 100.00 | – |
| Rosen and Shroyer (1985) | *Toxorhynchites amboinensis* | 14 | 5/5 | 100.00 | – | – | – | – | – |
| | *Toxorhynchites brevipalpis* | 14 | 5/5 | 100.00 | – | – | – | – | – |
| | *Toxorhynchites rutilus* | 14 | 5/5 | 100.00 | – | – | – | – | – |
| | *Toxorhynchites Splendens* | 14 | 5/5 | 100.00 | – | – | – | – | – |
| | *Toxorhynchites Theobaldi* | 14 | 5/5 | 100.00 | – | – | – | – | – |
| Rosen (1988) | *Aedes albopictus* | 9–10 | 0/26 | 0.00 | – | – | – | – | ≤100 |
| Takashima and Rosen (1989) | *Aedes japonicus* | 1–20 | 18/20 | 90.00 | – | – | 3/4 | 75.00 | – |
| | *Aedes vexans nipponii* | 1–20 | 3/12 | 25.00 | – | – | – | – | – |
| | *Culex pipiens pallens* | 1–20 | 3/10 | 30.00 | – | – | – | – | – |
| | *Culex tritaeniorhynchus* | 1–20 | 15/15 | 100.00 | – | – | 6/6 | 100.00 | – |
| Weng et al. (1997) | *Aedes albopictus* | 14 | – | – | – | – | 5/13 | 38.46 | – |
| Samuel et al. (1998) | *Culex tritaeniorhynchus* | 12–14 | 17/26 | 65.40 | – | – | 3/19 | 15.79 | – |
| Weng et al. (2000) | *Culex pipiens molestus* | 7 | – | – | – | – | 3/3 | 100.00 | – |
| | *Culex tritaeniorhynchus* | 13 | – | – | – | – | 6/6 | 100.00 | – |
| Chen et al. (2000) | *Aedes aegypti* | 14 | 0/6 | 0.00 | – | – | – | – | – |
| | *Aedes albopictus* | 14 | 7/15 | 46.67 | – | – | – | – | – |
| | *Armigeres subalbatus* | 14 | 7/8 | 87.50 | – | – | – | – | – |
| | *Culex quinquefasciatus* | 14 | 2/5 | 40.00 | – | – | – | – | – |
| Mourya and Mishra (2000) | *Culex pseudovishnui* | 10 | 6/10 | 60.00 | – | – | – | – | – |
| | *Culex tritaeniorhynchus* | 10 | 8/10 | 80.00 | – | – | – | – | – |
| | *Culex vishnui* | 10 | 4/10 | 40.00 | – | – | – | – | – |
| van den Hurk et al. (2003b) | *Aedes aegypti* | 14–15 | 16/60 | 26.67 | 0/60 | | 15/60 | 25.00 | – |
| | *Coquillettidia xanthogaster* | 14–15 | 4/36 | 11.11 | – | – | 1/15 | 6.67 | – |

(*continued on next page*)

**Table 10** (*continued*)

| Reference | Mosquito Name | DPI[g] | Proportion infected[a] | Infection rate (%)[b] | Proportion disseminated[c] | Dissemination rate (%)[d] | Proportion transmitted[e] | Transmission rate (%)[f] | Mosquitoes/pool |
|---|---|---|---|---|---|---|---|---|---|
| | *Culex annulirostris* | 14 | 36/36 | 100.00 | 23/36 | 63.89 | 13/16 | 81.25 | – |
| | *Culex gelidus* | 14–15 | 4/4 | 100.00 | – | – | 1/1 | 100.00 | – |
| | *Culex quinquefasciatus* | 14–15 | 51/55 | 92.73 | – | – | 14/23 | 60.87 | – |
| | *Culex sitiens* | 14 | 33/36 | 92.00 | 4/36 | 11.11 | 10/15 | 66.67 | – |
| | *Mansonia septempunctata* | 9 | 16/24 | 66.67 | 0/24 | 0.00 | 13/24 | 54.17 | – |
| | *Mansonia uniformis* | 14–15 | 1/1 | 100.00 | 0/1 | 0.00 | 1/1 | 100.00 | – |
| | *Ochlerotatus kochi* | 14–15 | 6/28 | 21.43 | – | – | 0/8 | 0.00 | – |
| | *Ochlerotatus normanensis* | 14-15 | 0/1 | 0.00 | 0/1 | 0.00 | 0/1 | 0.00 | – |
| | *Ochlerotatus notoscriptus* | 13–14 | 13/48 | 27.00 | 4/48 | 8.33 | 3/11 | 27.27 | – |
| | *Ochlerotatus purpureus* | 14-15 | 2/2 | 100.00 | 0/2 | 0.00 | 2/2 | 100.00 | – |
| | *Ochlerotatus vigilax* | 14–15 | 1/9 | 11.11 | – | – | 1/8 | 12.50 | – |
| | *Verrallina carmenti* | 14–15 | 0/2 | 0.00 | 0/2 | 0.00 | 0/2 | 0.00 | – |
| | *Verrallina funerea* | 14–15 | 43/75 | 57.33 | – | – | 3/18 | 16.67 | – |
| Turell et al. (2006b) | *Culex pipiens pallens* | 12 | 0/40 | 0.00 | – | – | – | – | – |
| | *Culex tritaeniorhynchus* | 12 | 10/10 | 100.00 | – | – | – | – | – |
| Turell et al. (2006a) | *Culex pipiens* | 16–17 | 28/50 | 56.00 | – | 26.00 | – | – | – |
| van den Hurk et al. (2007) | *Culex annulirostris Skuse* | 13 | 22/23 | 95.65 | – | – | – | 96.00 | – |
| | *Culex gelidus* | 13 | 20/25 | 80.00 | – | – | – | 12.00 | – |
| Johnson et al. (2009) | *Culex annulirostris* | 12 | 20/25 | 80.00 | 14/56 | 25.00 | 3/12 | 25.00 | – |
| | *Culex gelidus* | 12 | 22/23 | 96.00 | 22/96 | 22.92 | 22/96 | 23.00 | – |
| van den Hurk et al. (2009b) | *Culex annulirostris* | 5 | 1/4 | 25.00 | – | – | – | – | – |
| Kramer et al. (2011) | *Aedes notoscriptus* | 14 | 0/39 | 0.00 | – | – | – | – | – |
| | *Culex pipiens* | 14 | 5/50 | 10.00 | 2/5 | 40.00 | 0/5 | 0.00 | – |
| | *Culex quinquefasciatus* | 14 | 6/36 | 16.67 | 0/6 | 0.00 | – | – | – |
| | *Opifex fuscus* | 14 | 37/50 | 74.00 | 26/37 | 70.27 | 0/37 | 0.00 | – |
| Huber et al. (2014) | *Aedes japonicus japonicus* | 0–14 | 3/3 | 100.00 | – | – | – | – | – |
| Nicholson et al. (2014) | *Aedes albopictus* | 14 | – | – | – | 16.00 | – | 16.00 | – |
| Huang et al. (2015) | *Culex quinquefasciatus* | 14 | 22/26 | 84.60 | 7/14 | 50.00 | – | – | – |
| Mackenzie-Impoinvil et al. (2015) | *Culex quinquefasciatus* | 14 | 20/32 | 62.00 | 18/32 | 56.25 | 2/32 | 6.25 | – |
| | *Ochlerotatus detritus* | 14 | 25/32 | 78.00 | 29/32 | 90.63 | 1/32 | 3.13 | – |

[a] Proportion infected represents the number of positive infected mosquitoes divided by the total number of mosquitoes tested.

[b] Infection rate consists of an estimate of the prevalence of infection in a mosquito population (Bustamante and Lord, 2010).

[c] Proportion disseminated represents the number of positive mosquitoes with disseminated infection divided by the total number of mosquitoes tested.

[d] Dissemination rate refers to the proportion of mosquitoes containing virus in their legs, regardless of their infection status (Golnar et al., 2015).

[e] Proportion transmitted consists of number of positive mosquitoes that transmit the virus divided by the total number of mosquitoes tested.

[f] Transmission rate is defined as the proportion of mosquitoes with a disseminated infection that transmit the virus after refeeding (Golnar et al., 2015).

[g] When more than one trial on the same mosquito species and DPI was reported, the first result is shown (please refer to S2 Table in the supplementary materials for a complete list of results).

**Table 11**
Proportion of JEV infection in host species reported across all observational studies (n = 33) and mosquito host preferences (all mosquito species) across all observational studies (n = 16), by host species.

| Proportion of JEV infection in host species | | | | Mosquito host preferences | |
|---|---|---|---|---|---|
| Host species | Reference[a] | Proportion infected[b] | Proportion positive (%) | Reference[c] | Bloodmeals[d] |
| Bats | Hammon et al. (1958), Johnsen et al. (1974). | 2/56 | 3.57 | Reuben et al. (1992), Tiawsirisup et al. (2012). | 13 |
| Birds | Nemeth et al. (2010), Khan and Banerjee (1980), Takashima et al. (1989), Rodrigues et al. (1981), Hammon et al. (1958), Paul et al. (1993), Buescher et al. (1959a), Johnsen et al. (1974). | 17/3,041 | 0.56 | Johansen et al. (2009), Reuben et al. (1992), Hurlbut (1964), van den Hurk et al. (2003a), Hall-Mendelin et al. (2012), Wang (1975), Mitchell et al. (1973), van den Hurk et al. (2001b). | 74 |
| Cattle | Peiris et al. (1993), Sabin (1947), Hammon et al. (1958), Johnsen et al. (1974). | 573/644 | 88.98 | Johansen et al. (2009), Reuben et al. (1992), Hurlbut (1964), Arunachalam et al. (2005), Gould et al. (1973), Self et al. (1973), van den Hurk et al. (2003a), Samuel et al. (2008), Hall-Mendelin et al. (2012), Wang (1975), Somboon et al. (1989), Pennington and Phelps (1968), Mitchell et al. (1973). | 84 |
| Chickens | Peiris et al. (1993), Khan and Banerjee (1980), Hanna et al. (1996), Mani et al. (1991), Sabin (1947), Hammon et al. (1958), Paul et al. (1993), Hayashi et al. (1975), Johnsen et al. (1974). | 52/920 | 5.65 | Reuben et al. (1992), Somboon et al. (1989), Pennington and Phelps (1968). | 22 |
| Ducks | Peiris et al. (1993), Khan and Banerjee (1980), Paul et al. (1993), Johnsen et al. (1974). | 113/298 | 37.92 | Reuben et al. (1992), Samuel et al. (2008). | 13 |
| Ardeid birds | Khan and Banerjee (1980), Rodrigues et al. (1981), Buescher et al. (1959a), Buescher et al. (1959b), Scherer et al. (1959a). | 891/3,001 | 29.69 | Reuben et al. (1992) | 12 |
| Pigs | Thakur et al. (2012), Hurlbut (1964), Kumari et al. (2013), Cha et al. (2015), Konishi et al. (2010), Liu et al. (2013), Nitatpattana et al. (2011), Peiris et al. (1993), Self et al. (1973), Thein et al. (1988), Ura (1976), Tadano et al. (1994), Borah et al. (2013), Lindahl et al. (2013), Takashima et al. (1989), Chanyasanha et al. (2011), Burke et al. (1985), Hanna et al. (1996), Okuno et al. (1973), Li et al. (2011), Hanna et al. (1999), Peiris et al. (1992), Hammon et al. (1958), Paul et al. (1993), Hayashi et al. (1975), Johnsen et al. (1974), Konno et al. (1966), Nga et al. (1995), Scherer et al. (1959b), Scherer et al. (1959c), Simpson et al. (1976), Takashima et al. (1988), Yamada et al. (1971). | 4,281/20,942 | 20.44 | Johansen et al. (2009), Reuben et al. (1992), Hurlbut (1964), Arunachalam et al. (2005), Gould et al. (1973), Self et al. (1973), van den Hurk et al. (2003a), Samuel et al. (2008), Hall-Mendelin et al. (2012), Wang (1975), Somboon et al. (1989), Pennington and Phelps (1968), Mitchell et al. (1973), van den Hurk et al. (2001b). | 84 |
| Rabbits | Peiris et al. (1993) | 0/69 | 0.00 | Reuben et al. (1992) | 12 |
| Reptiles and amphibians | Hammon et al. (1958), Doi et al. (1983). | 0/494 | 0.00 | – | – |
| Wild Pigs | See et al. (2002), Ohno et al. (2009), Hayashi et al. (1975). | 32/47 | 68.09 | – | – |
| Cats and dogs | Peiris et al. (1993), Hanna et al. (1996), Hammon et al. (1958), Paul et al. (1993), Johnsen et al. (1974). | 3/287 | 85.37 | van den Hurk et al. (2003a), Hall-Mendelin et al. (2012), Wang (1975), Pennington and Phelps (1968), Mitchell et al. (1973), van den Hurk et al. (2001b). | 73 |
| Sheep and Goats | Paul et al. (1993), Peiris et al. (1993), Sabin (1947), Hammon et al. (1958), Hayashi et al. (1975). | 103/386 | 26.68 | Samuel et al. (2008), Pennington and Phelps (1968). | 8 |
| Sylvatic mammals | Saito et al. (2009), Ohno et al. (2009). | 239/1,183 | 20.20 | – | – |
| Horses and donkeys | Hanna et al. (1996), Mani et al. (1991), Sabin (1947), Hammon et al. (1958). | 34/54 | 62.96 | Reuben et al. (1992), Self et al. (1973), van den Hurk et al. (2003a), Hall-Mendelin et al. (2012), Pennington and Phelps (1968), van den Hurk et al. (2001b). | 57 |
| Rats | Hammon et al. (1958) | 0/26 | 0.00 | Hall-Mendelin et al. (2012) | 7 |

[a] Articles pertaining to JEV infection in hosts (observational studies reporting host competence).
[b] Proportion positive is the number of positive vertebrate hosts divided by the total number of vertebrate hosts tested (results combined from a total of 33 articles).
[c] Articles pertaining to mosquito host preferences (observational studies reporting vector competence).
[d] Number of blood meals taken from hosts by mosquitoes (mosquito host preferences) – results combined from 16 articles.

Concerning mosquito host preference, mosquitoes preferred to feed on pigs and cattle (84 blood meals taken from each of these species by mosquitoes, corresponding to 14 and 13 observational studies, respectively), followed by cats and dogs (73 blood meals taken from cats and dogs by mosquitoes in 6 observational studies), and horses and donkeys (57 blood meals taken from these species by mosquitoes in 6 observational studies). Mosquito host preferences in all observational studies are depicted in Table 11 (columns on the right).

There was only one experimental study reporting host feeding preferences (Mwandawiro et al., 2000). This study reported data from three mosquito species: *Culex gelidus*, *Culex tritaeniorhynchus*, and *Culex vishnui*. Mosquitoes were released in nets where pigs, cows, or both host species were present, marked with a fluorescent dye, and then tested to reveal the origin of the blood meals. Results showed that mosquitoes preferred to feed on cows, rather than pigs (Mwandawiro et al., 2000).

#### 3.2.3. Outcome measures: host competence

Regarding JEV infection in vertebrate host species, reported in 33 observational studies, proportions varied between 0 and 88.9%. Information pertained to 13 countries: Nepal, India, South Korea, USA, China, Japan, Sri Lanka, Myanmar, Thailand, Australia, Guam (US), Saipan (US), and Vietnam. The total number of host species categories represented was 15 and included: pigs, birds, sylvatic mammals, cattle, sheep and goats, cats and dogs, chickens, ducks, rabbits, herons, horses and donkeys, wild pigs, bats, rats, and reptiles and amphibians. Host species tested but JEV-negative included rabbits, reptiles, and amphibians. Host species reporting the highest JEV infection proportions were cattle (88.9%) and cats and dogs (85.4%).

Detailed information on proportion of JEV infection in host species across all observational studies is presented in Table 11.

### 3.3. Assessment of the risk of bias

The number of entries corresponding to studies that did not report or control for bias was 188, while 6 entries included information on bias reporting but not control. Seventeen entries did report and control for bias. Nevertheless, all observational studies had a low risk of bias.

Experimental studies were all considered having a high risk of bias and articles with both observational and experimental components all had a low risk of bias.

The key domain that contributed to all articles reporting experimental studies being considered as having a high risk of bias was the randomization criterion, as none of the entries defined randomization or provided evidence of having performed randomization. One entry also did not define the outcome measures, though it reported them. Furthermore, and despite not being considered as a key domain, 73 entries did not define or perform blinding.

## 4. Discussion

This study is the first SR evaluating vector and host competence for JEV that compiles the body of evidence on vector transmission efficiency and host preference along with data on vector and host susceptibility to infection.

Data on vector and host competence outcomes for JEV are very broad varying, depending on the specific outcome, from 0 to 100% across different genera and species, making it difficult to interpret and contrast. This is typical for most arboviruses where only a small number of species are important vectors. Nevertheless, by gathering information on JEV infection from various mosquito species and a large number of articles, this SR provides a comprehensive resource of mosquito species and their reported JEV infection. This review also demonstrates that similar to other JE group viruses, JEV is invasive to a number of mosquito species of medical and veterinary importance and known disease vectors of other arboviruses. Moreover, this SR provides a better understanding of the geographical distribution of the information available regarding vector competence, revealing that data are more readily available on countries where JE is prevalent, as expected, and pointing to the need of conducting similar studies in other countries where hosts and vectors are present and thus may be potentially at risk.

It is important to highlight that variation across studies may result from between-study and within-study variation. Within-study variation is associated with random sampling error, while between-study variation is considered to be related to the study characteristics, although other factors may be involved. Unexplained variation is usually incorporated into random-effects models in meta-analyses, the statistical analysis of individual studies for integrating the findings of a SR (Dohoo et al., 2009).

Despite being referred to as rates, however, we note that infection, dissemination, and transmission rates are actually proportions, as a rate is a ratio in which the denominator is the number of subject-time units at risk, mosquito-time units at risk in these examples, which is not the case, as no time component is involved (Dohoo et al., 2009). However, because this is the common terminology used to refer to these measures, particularly among entomologists, we used it across this manuscript.

Data on JEV infection were reported most frequently in *Culex tritaeniorhynchus* (44 articles), which is in line with our current understanding of this species being the most significant JEV vector, playing a paramount role in the transmission dynamics of the disease (Weaver and Barrett, 2004; Le Flohic et al., 2013; van den Hurk et al., 2009a; Mackenzie et al., 2004; Solomon et al., 2000). However, previous research (Lord et al., 2016) proposes that sampling design of JEV studies, which tend to be based on capturing mosquitoes from around cattle sheds at dusk, may influence the observed dominance of *Culex tritaeniorhynchus* as the primary JEV vector reported in the literature. In fact, our results show a great variability for the proportion of JEV infection in *Culex tritaeniorhynchus* among all observational studies, with infection proportions as low as 0 and as high as 100% (Table 7). This variability is likely due to differences in data collection, study design and reporting, sample size, methods used for testing mosquito infection, as well as the sensitivity and specificity of those methods, geographical regions and environmental factors specific to those regions. Even within the same geographical region there may be differences in climate or weather (within and among seasons) that could explain some effect on the variability of the observed outcomes.

Furthermore, the highest values for MIR in observational studies belong to mosquito species other than *Culex tritaeniorhynchus*: *Culex gelidus* (333.3 per 1000 mosquitoes), *Culex vishnui* (0.4 per 1000 mosquitoes), and *Culex rubithoracis* (30.8 per 1000 mosquitoes) (Table 8). Accordingly, MLE values were the highest in *Anopheles minimus* (53.8 per 1000 mosquitoes), *Aedes vexans* (29.7 per 1000 mosquitoes), and *Culex annulus* (26.3 per 1000 mosquitoes) (Table 9). Additionally, other authors (Bustamante and Lord, 2010) point to evidence that supports that infection in vectors is not always a straightforward indicator of risk and that other indicators, such as mosquito population size (vector abundance), age, and climatic conditions, should be taken into account for assessing the risk of arbovirus transmission.

In experimental studies, results on JEV infection, dissemination, and transmission rates are also very broad, ranging from 0 to 100% in different mosquito species and days post-infection, across all articles (Table 10). For *Culex tritaeniorhynchus*, for instance, JEV infection rates varied between 0 and 100%, although the lowest infection rates pertained to 1 DPI, time at which mosquitoes have probably not developed infection yet. Transmission rates for *Culex tritaeniorhynchus* varied, again, between 0 and 100%, as well as for other mosquito species reported. Data about transmission efficiency are therefore variable across experimental studies.

Transmission experiments are important, as they lead to a better understanding of which factors determine the mosquito's ability to acquire, maintain, and transmit the virus (virus competence), thus clarifying the mechanisms under which mosquitoes become infected,

disseminate infection, and transmit the virus to hosts. JEV causes a persistent and amplifying infection in the mosquito, a priori requirements for midgut penetration, which results in diffused infection of the insect vector (i.e. dissemination).

Furthermore, it is important to stress that in observational studies mosquito-related outcomes are measured in terms of pools of mosquitoes (with variable number of mosquitoes per pool, up to 800), while in experimental studies mosquitoes are tested individually, except for three studies reporting vertical transmission that used pools of mosquitoes with sizes up to 120. This distinction is important as it contributes to the variability reported across outcomes, especially in observational studies, where the number of mosquitoes per pool varies greatly.

Regarding host preference of vectors, information extracted revealed that mosquitoes preferred to feed on pigs and cattle, according to the number of blood meals originated from those species (Table 11). Nonetheless, poor mixing of hosts and mosquitoes across the spatial areas where mosquitoes are captured may be a source of bias leading to a potential overestimation of the proportion of blood meals taken from certain species (Lord et al., 2015). Therefore, reported feeding patterns may depend on the availability of hosts, rather than the actual feeding preference of mosquitoes, as some species of mosquitoes just feed on certain animals while others are more opportunistic. Furthermore, trap placement to collect blood fed mosquitoes for the observational studies may be biasing these studies, as few traps are placed in trees or on the water where wading birds are most frequently present.

The importance of host feeding preferences, based on the only experimental study included in this SR reporting this outcome (Mwandawiro et al., 2000) is questionable, because the hosts' surface area or biomass are not considered when analyzing the results. Results showing that mosquitoes preferred to feed on cows, rather than pigs, may reflect that mosquitoes simply chose to feed on the larger animal which has higher surface area and volume available (Tuno et al., 2017).

Regarding host competence, pigs were not the host species with the highest proportion of JEV, as it would be expected because pigs are considered the main amplifying host for JEV (Le Flohic et al., 2013; van den Hurk et al., 2009a; Mackenzie et al., 2004; Solomon et al., 2000). In fact, across all observational studies, the proportion of JEV positive pigs was 20.4%, which is low compared to cattle (88.9%) or cats and dogs (85.4%). Proportion of JEV infection in ardeid birds was also lower than in other species (29.7%) (Table 11). Because host competence is not a constant parameter though, assuming constant proportions of JEV infection in hosts may lead to failure in recognizing regional differences due to environmental or ecological factors that are not being taken into consideration when accounting for transmission potential of competent species (Lord et al., 2015).

An evaluation of the risk of bias allows us to determine whether the study has asked the appropriate question (external validity: generalizability of study findings) and it answered the question correctly (internal validity: the study is free from bias). As such, we can better appraise if the results from included studies are valid. The fact that all experimental studies (n = 63) had a high risk of bias is related to the fact that a randomization criterion was considered to be a key domain for determining that a study had a low risk of bias. Randomization is considered an important criterion in experimental studies, as an inadequate randomization may lead to non-comparable experimental groups, which, in turn, may lead to selection bias (Higgins and Green, 2011). However, due to the nature of the experimental studies included in this SR, mostly challenge trials performed in a small sample of subjects, randomization was not performed or reported in these articles. For this reason, none of the experimental studies passed the randomization criterion, which would otherwise lead to a low risk of bias. Although all experimental studies were deemed to have high risk of bias, this assessment did not warrant exclusion of these studies. However, it is important to consider the potential of bias (due to lack of randomization and/or blinding) arising from these studies when interpreting their results.

In observational studies, on the other hand, all studies had a low risk of bias, because all of them successfully met the key domain criteria established for observational studies. The bias criterion was not met by most of the articles, as authors either did not report or did not control for bias (e.g., selection bias) in the design or analysis stages, but because this was not considered to be a key domain in the assessment of the risk of bias, it did not influence the final assessment. Reporting and controlling for bias was not considered a key domain for determining the risk of bias in observational studies, as it is usually difficult to assess and it constitutes an important source of heterogeneity between studies, according to the Cochrane Review Handbook guidelines (Higgins and Green, 2011).

Outcome measures for vector and host competence of JEV had a large variability in terms of values reported across all studies included in this SR, which constitutes a major limitation of this study.

Differences in study methodology, data collection, detection methods, data reporting, and results presentation were in part responsible for this variability and constituted a challenge when combining and summarizing the data. Furthermore, geographical diversity and environmental factors related to differences in the locations where studies were performed also determined the variability found across articles. Nevertheless, the large amount of information retrieved substantially contributed to further our understanding on the role that different vectors and hosts have on the epidemiology of JEV. Moreover, the span of the research question posed in the beginning of this study played a major role on the large amount of data collected and their variability, making it challenging to compare and contrast studies, as data were collected under different field or experimental conditions, outcomes were measured using different methods and also differed in terms of sample size. In addition, the specifics of each study in terms of design were often lacking or not presented in sufficient detail, also failing to report measures of variability around point estimates (e.g., standard errors, variance, confidence intervals), preventing the possibility of extrapolation and of being able to extract and summarize their data. As an example of extrapolation challenges, data regarding JEV infection on vectors from observational studies are preferred to data from experimental studies, because in general, challenge trials, in which conditions are artificially controlled by researchers, although may have higher internal validity, they have limited external validity. Moreover, in observational studies, methods employed for measuring and testing mosquito infection, including the number of mosquitoes per pool tested and diagnostic tests, along with their sensitivity and specificity, vary. Due to the likely heterogeneity (within and between-study variability) of the data extracted, we did not attempt to summarize the data quantitatively (to calculate summary effect sizes) in this work, though meta-analyses of specific outcomes have been pursued and are published elsewhere (Oliveira et al., 2017). Variability of the data was also evident when summarizing the actual proportions of JEV infection in vectors (both in experimental and observational studies) that ranged from 0 to 100%. The same occurred when examining infection, dissemination, and transmission rates in mosquitoes in experimental studies (values varying between 0 and 100%) and was likely related to the small sample size of some of these studies. Some of the 100% dissemination and transmission rates were calculated for sample sizes of one mosquito, erroneously leading to high rates for some mosquito species.

The large quantity of articles from which data were extracted (n = 171) is a strength of this SR, as well as the assessment of the risk of bias of the primary articles, which allowed for a critical appraisal of their internal and external validity, thus providing information regarding the relevance and validity of the extracted information.

Future efforts for combining the results from this SR include performing meta-analyses for some of the outcome measures of interest, some of which have already been published (Oliveira et al., 2017). This type of analyses is crucial for obtaining quantitative estimates to be

inputted into risk assessment models.

This SR presents comprehensive data on competent vectors and hosts in JEV endemic and epidemic countries, which may lead to a better understanding of the paths of introduction of JEV and other arboviruses in the US and other relevant JEV-free regions, such as South America. Vector abundance, along with climatic conditions and availability of hosts, are important factors in arbovirus transmission (Bustamante and Lord, 2010). In the US, specifically, mosquito size populations should be taken into account when assessing JEV transmission, as availability and abundance of vectors have a strong implication on the transmission potential of JEV. Data on vector and host competence can be used to generate parameters to quantitatively evaluate the potential role arthropods and vertebrate hosts may play in the transmission of transboundary foreign vector-borne diseases.

These efforts will ultimately support future surveillance actions and public health interventions for predicting the risk of introduction and maintaining the JEV-free status of the US. Similarly, data obtained from this study can help populate risk models to predict risk and determine the effectiveness of mitigation strategies for other foreign mosquito-borne disease threats in the US.

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## Disclosures

No conflict of interest, financial or other, exists.

## Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.prevetmed.2018.03.018.

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