Updating the global occurrence of Culicoides imicola, a vector for emerging viral diseases

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Culicoides imicola is the main vector transmitting viruses causing animal diseases such as Bluetongue, African Horse Sickness, and Schmallenberg. It has become widely distributed, with reports from South Africa to southern Europe, and from western Africa to southern China. This study presents a global compendium of Culicoides imicola occurrence between 1943 and 2018, reflecting the most recently compiled and harmonized global dataset derived from peer-reviewed literature. The procedures used in producing the data, as well as the geo-coding methods, database management and technical validation procedures are described. The study provides an updated and comprehensive global database of C. imicola occurrence, consisting of 1 039 geo-coded records from 50 countries. The datasets can be used for risk mapping of the diseases transmitted by C. imicola as well as to develop the global habitat suitability for the vector.

Background & Summary

Culicoides imicola Kieffer (Diptera: Ceratopogonidae) is a globally widespread species that vectors the agents of many important viral diseases of veterinary importance such as Bluetongue1–3, African Horse Sickness (AHS)4,5, and Schmallenberg6. Bluetongue (BT) is a viral disease that affects ruminants and the etiological agent has at least 27 different serotypes7–9. Historically, BT was enzootic in tropical regions of the world, but in recent years it has expanded its distribution markedly. The disease has become a concern in areas that experience a temperate climate, particularly in Europe. This expanding disease distribution is mainly facilitated by northward distribution of the infected Culicoides species mainly C. imicola and availability of competent and efficient vectors such as C. obsoletus and C. pulicaris7,10. The 1998 incursion and emergence of bluetongue virus in Southern and Eastern Europe were mainly associated with C. imicola, while the 2006 incursion of Northern and Western Europe7 was mainly associated with C. obsoletus and C. pulicaris.

AHS is native to sub-Saharan Africa4. It is an infectious disease considered to be the most lethal viral disease of equines, especially in horses4,11. The recent emergence of the two Culicoides-borne diseases (BT and Schmallenberg) in Europe has raised a concern for the potential introduction and further spread of AHS virus in temperate parts of the world as well11.

Although C. obsoletus and C. pulicaris are considered as main vectors for Schmallenberg, experimental infection on field collected C. imicola provided evidence of high efficiency for Schmallenberg virus infection and transmission by C. imicola as well6. Schmallenberg virus is a very recently emerged virus first identified in North Rhine-Westphalia, Germany, during the summer of 201112 and since then it has spread across Europe causing congenital deformities in the offspring of infected adult ruminants13.

The recent emergence of Culicoides-borne diseases highlights large knowledge gaps on the biology and ecology of the vectors. Since the emergence of BT and Schmallenberg virus, Culicoides surveillance efforts have

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doubled. Thus, it is important and timely to expand the effort of Guichard et al.\textsuperscript{14} and update the global Culicoides occurrence record. With these research gaps in mind, this study compiled the global occurrences of \textit{C. imicola} based on the dataset provided by Guichard et al.\textsuperscript{14} and literature published since 1\textsuperscript{st} January 2014 and created the largest currently available standardized up-to-date georeferenced global dataset for the vector, containing 1 039 occurrence records.

**Methods**

**Literature search and data extraction.** PubMed (http://www.ncbi.nlm.nih.gov) was searched using the term ‘Culicoides imicola’ OR ‘Ceratopogonidae’. Automatic inclusion of all pseudonyms in the searches was guaranteed by using the Medical Subject Headings (MeSH) term technology of the PubMed citation archive (http://www.nlm.nih.gov/mesh). The literature search was last updated on 14\textsuperscript{th} January 2019, which resulted in a collection of 1 920 articles. However, a geo-database of 649 occurrences of \textit{C. imicola} compiled by Guichard et al.\textsuperscript{14} from 65 articles\textsuperscript{5,15–78} covering 1943 to 2010 (1959 to 2014 by publication year) was obtained from the authors. Thus, in this study a literature search for the period 1\textsuperscript{st} January 2014 till 14\textsuperscript{th} January 2019\textsuperscript{4,6,79–111} was combined with existing data points obtained from Guichard et al.\textsuperscript{14} for the period 1959 to 2014. The search retrieved a total of 380 articles published since 1\textsuperscript{st} January 2014 and the titles and abstracts of those articles were screened and those not fitting the criteria: 1) no mention of the vector species; and 2) data from experimental study were removed. After literature searching and initial selections, 150 eligible full-text articles were downloaded and examined in detail to filter those meeting the following criteria: 1) the coordinates of field sites were reported or could be retrieved from Google earth using the reported location information, and 2) occurrence of \textit{C. imicola} was reported. Therefore, each entry was checked for site coordinates, occurrence of the target species, and other information if available. Subsequently, the geo-location of the vector was extracted from a total of 35 articles meeting all the criteria (Fig. 1). Each article was thoroughly reviewed and all important information was extracted: site location, site
In Fig. 2 the global geographical distribution of *C. imicola* as well. In Fig. 2 the global geographical distribution of *C. imicola* was reduced down to 1,039. Within a global grid only one record was retained and the number of times to repeat the thinning process was set (Table 1) in the dataset. The spatial thinning procedure was provided under technical validation section. In the data, the rows represent a single occurrence record (one or more entries (before technical validations) and 1,039 entries (after technical validations) with information in 8 columns.

**Geo-coding of data.** The occurrence coordinates (longitude and latitude) of *C. imicola* was extracted from each article and whenever the coordinates were not provided in the articles or supporting information of the articles, the study site name together with all contextual information as well as alternative spelling of site name was used to determine its coordinates using Google Earth (http://www.google.co.uk/intl/en_uk/earth). When two locations have the same name and different geolocations, both the location name and occurrence coordinates were provided. All data points were then linked to the FAO Global Administrative Unit Layer (GAUL) system (http://www.fao.org/geonetwork) by using a join attributes by location tool in QGIS Version 3.4 (https://qgis.org/).

**Data Records**

R (https://cran.r-project.org/), QGIS (https://qgis.org/), Mendeley Desktop http://www.mendeley.com/, and Microsoft Excel were the software packages used to manage, store and analyze the database. The dataset is saved in a comma-delimited (.csv) format and can be imported into a variety of Statistical and GIS software programs. The data records described in this paper are publicly and freely available on Figshare. There are 2,589 entries (before technical validations) and 1,039 entries (after technical validations) with information in 8 columns (Table 1) in the dataset. The spatial thinning procedure was provided under technical validation section. In the data, the rows represent a single occurrence record (one or more *C. imicola* occurrences in the same unique location within a single calendar year). The fields contained in the database are described in Table 1.

**Technical Validation**

To ensure the accuracy and validity of the occurrence records, a technical validation was performed. Firstly, a 5 km × 5 km resolution landcover raster was used to ensure all occurrences were positioned on a valid land pixel. Based on the reported coordinates some sites (n = 96) fell on water bodies. This was probably due to the precision of the longitude and latitude values since these sites were all in peri-coastal locations. Thus, from 2,589 occurrence points 96 were removed from the database.

Further, as the database was compiled from different sources and over many years, it was important to standardize the data entries such that identical locations which may have been geo-positioned slightly differently were given the same unique identifier. The present dataset is heavily clustered in Europe and Southern Africa, with a high degree of aggregation in Spain, Portugal, Italy and South Africa compared to elsewhere. Consequently, it was important to spatially thin the occurrence records. The spatial thinning was performed using R package spThin with the use of the following parameters: “thin.par” (the distance between occurrence records in kilometers) and “reps” (the number of times to repeat the thinning process). In the thinning process, the distance (in kilometers) between occurrence records was set to 5 km (meaning if occurrence records lay within the same 5 km × 5 km pixel within a global grid only one record was retained) and the number of times to repeat the thinning process was set at 100. As a result, the 2,493 occurrence points were reduced down to 1,039.

The resulting database consists of 2,589 (before technical validations) and 1,039 (after technical validations) geo-positioned occurrences of *C. imicola* spanning 50 countries worldwide, disaggregated by continent, region, and country (Table 2). The data before technical validations includes the 96 occurrence points that fell on water bodies as well. In Fig. 2 the global geographical distribution of *C. imicola* is displayed.

**Usage Notes**

The database described here can be used to investigate the spatial and temporal distribution of *C. imicola*. The data are most appropriate for applications at global and continental scales. It is known that *C. imicola* and the diseases transmitted by the vector were previously known to be a problem of Africa. However, due to the recent spread of the species to Europe and other parts of the world, this data could support improved modelling of new locations at high-risk of experiencing the occurrence of the vector as well as the diseases transmitted by it.

| Attribute | Column # | Column name | Unit | Note |
|-----------|----------|-------------|------|------|
| Reference | 1        | Reference   |      | Author names and publication year of the article from which the occurrence record is extracted. |
| 2         | UNREGION2 | —           |      | The name of UN region 2 within which the occurrence lies (Global Administrative Unit Layers (GAUL) system). |
| 3         | UNREGION1 | —           |      | The name of the UN region 1 within which the occurrence lies (Global Administrative Unit Layers (GAUL) system). |
| 4         | Country  | —           |      | Name of the country within which the occurrence lies (Global Administrative Unit Layers (GAUL) system). |
| 5         | Site     | —           |      | Name of the site where the occurrence lies (Global Administrative Unit Layers (GAUL) system). |
| 6         | Site     | Site name   |      | Name of site name. |
| 7         | Longitude| Degree East/West |      | The longitudinal coordinate of the occurrence point (WGS1984 Datum). |
| 8         | Latitude | Degree North/South |      | The latitudinal coordinate of the occurrence point (WGS1984 Datum). |

**Table 1.** Description of attributes and columns in the dataset.
The database after technical validations could be used to develop suitability and risk maps at global, continental, and regional scales. On the other hand, for local scale suitability and risk mapping, the database before technical validations could be used.

There are differences in the number of published studies and the availability of occurrence data by continent and region. Continental and regional biases in the density of occurrence records are apparent, and likely reflect differences in the level of surveillance. Due to the recent occurrence of Bluetongue and Schmallenberg viruses in Europe, substantial numbers of surveys have been conducted in Europe, and thus large numbers of recent occurrence records were from Europe. Many occurrence records were also obtained from Southern Africa. From 1 550 points thinned from the database during validations, 1 440 (92.9%) is from Southern Europe and Southern Africa. Thus, researchers using the technically unvalidated database would need to take into account geographical sampling bias.

| Continent (UN region 2) | Region (UN region 1) | Number of *C. imicola* before technical validation | Number of *C. imicola* after technical validation |
|-------------------------|----------------------|---------------------------------------------------|-------------------------------------------------|
| Africa                  | Eastern Africa       | 104                                               | 84                                              |
|                         | Middle Africa        | 10                                                | 10                                              |
|                         | Northern Africa      | 86                                                | 83                                              |
|                         | Southern Africa      | 153                                               | 96                                              |
|                         | Western Africa       | 71                                                | 40                                              |
| Americas                | Caribbean            | 0                                                 | 0                                               |
|                         | Central America      | 0                                                 | 0                                               |
|                         | Northern America     | 0                                                 | 0                                               |
|                         | South America        | 0                                                 | 0                                               |
| Asia                    | Central Asia         | 0                                                 | 0                                               |
|                         | Eastern Asia         | 2                                                 | 2                                               |
|                         | South-Eastern Asia   | 20                                                | 18                                              |
|                         | Southern Asia        | 5                                                 | 5                                               |
|                         | Western Asia         | 100                                               | 63                                              |
| Europe                  | Eastern Europe       | 0                                                 | 0                                               |
|                         | Northern Europe      | 0                                                 | 0                                               |
|                         | Southern Europe      | 1998                                              | 615                                             |
|                         | Western Europe       | 40                                                | 25                                              |
| Oceania                 | Melanesia            | 0                                                 | 0                                               |
|                         | Micronesia           | 0                                                 | 0                                               |
|                         | Australia and New Zealand | 0                          | 0                                               |
|                         | Polynesia            | 0                                                 | 0                                               |
| Total                   |                      | 2589                                              | 1039                                            |

**Table 2.** *Culicoides imicola* occurrence records by UN region.

**Fig. 2** Map of occurrence points for Culicoides imicola.
References

1. Venter, G. J., Groenewald, D. M., Pawska, J. T., Venter, E. H. & Howell, P. G. Vector competence of selected South African Culicoides species for the Brushtick serotype of equine encephalitis virus. Med. Vet. Entomol. 13, 393–409 (1999).

2. Pawska, J. T., Venter, G. J. & Mellor, P. S. Vector competence of South African Culicoides species for bluetongue virus serotype 1 (BTV-1) with special reference to the effect of temperature on the rate of virus replication in C. Imicola and C. Bolitinos. Med. Vet. Entomol. 16, 10–21 (2002).

3. Bravermann, Y., Barzilai, E., Frish, K. & Rubina, M. Bluetongue virus isolation from pools of Culicoides spp in Israel during the years 1981 to 1983. Prog. Clin. Biol. Res. 178, 191–193 (1985).

4. De Waal, T., Liebenberg, D., Venter, G. J., Mienie, C. M. & van Hamburg, H. Detection of African horse sickness virus in Culicoides imicola pools using RT-qPCR. J. Vector Ecol. 41, 179–185 (2016).

5. Venter, G. J. et al. African horse sickness epidemiology: vector competence of south African Culicoides species for virus serotypes 3, 5 and 8. Med. Vet. Entomol. 14, 245–250 (2000).

6. Pages, N. et al. Schmallenberg virus detection in Culicoides biting midges in Spain: First laboratory evidence for highly efficient infection of Culicoides of the Obsoletus complex and Culicoides imicola. Transbound. Emerg. Dis. 65, e1–e6 (2018).

7. Wilson, A. J. & Mellor, P. S. Bluetongue in Europe: past, present and future. Philos. Trans. R. Soc. Lond. B. Biol. Sci. 364, 2669–2681 (2009).

8. Maan, N. S. et al. Identification and differentiation of the twenty six bluetongue virus serotypes by RT-PCR amplification of the serotype-specific genome segment 1. PLoS One 7, e32501 (2012).

9. Zientara, S. et al. Novel bluetongue virus in goats, Corsica, France. 2014. Emerg. Infect. Dis. 20, 2123–2125 (2014).

10. Mbalachlan, N. J. Bluetongue: history, global epidemiology, and pathogenesis. Prev. Vet. Med. 102, 107–111 (2011).

11. Sanchez-Matamoros, A., Sanchez-Vizcaino, J. M., Rodriguez-Prieto, V., Iglesias, E. & Martinez-Lopez, B. Identification of Suitable Areas for African Horse Sickness Virus Infections in Spanish Equine Populations. Transbound. Emerg. Dis. 63, 564–573 (2016).

12. Hoffmann, B. et al. Novel orthobunyavirus in cattle, Europe, 2011. Emerg. Infect. Dis. 18, 469–472 (2012).

13. Balenghienn, T. et al. The emergence of Schmallenberg virus across Culicoides communities and ecosystems in Europe. Prev. Vet. Med. 116, 360–369 (2014).

14. Guichard, S. et al. Worldwide niche and future potential distribution of Culicoides imicola, a major vector of bluetongue and African horse sickness viruses. PLoS One 9, e12491 (2014).

15. Alahmed, A. M., Kheir, S. M. & Al Khereiji, M. A. Distribution of Culicoides Latreille (Diptera: Ceratopogonidae) in Saudi Arabia. J. Entomol. 7, 227–234 (2010).

16. Bravermann, Y., Chechik, F. & Mullens, B. The interaction between climatic factors and bluetongue outbreaks in Israel and the eastern Mediterranean, and the feasibility of establishing bluetongue-free zones. Isr. J. Vet. Med. 56, 99–109 (2001).

17. Bravermann, Y., Boorman, J., Kremer, M. & Delecolle, J.-C. Faunistic list of Culicoides (Diptera, Ceratopogonidae) from Israel. Cah. ORSTOM. Sér. Entomol. Médicale Parasitol. 14, 179–185 (1976).

18. Bravermann, Y. Preferred landing sites of Culicoides species (Diptera: Ceratopogonidae) on a horse in Israel and its relevance to summer seasonal recurrent dermatitis (sweet itch). Equine Vet. J. 20, 426–429 (1988).

19. Cagienard, A., Griot, C., Mellor, P. S., Denison, E. & Stärk, K. D. Bluetongue vector species of Culicoides in Switzerland. Med. Vet. Entomol. 20, 239–247 (2006).

20. Capela, R. et al. Spatial distribution of Culicoides species in Portugal in relation to the transmission of African horse sickness and bluetongue viruses. Med. Vet. Entomol. 17, 165–177 (2003).

21. Capela, R., Sousa, C., Pena, I. & Caíro, V. Preliminary note on the distribution and ecology of Culicoides imicola in Portugal. Med. Vet. Entomol. 7, 23–26 (1993).

22. Chaker, E. et al. Note faunistique sur les Culicoides (Diptera, Ceratopogonidae) du gouvernorat de monastir (Tunisie). parasites 12, 359–361 (2003).

23. Clastrier, J. & Wirth, W. W. Notes sur les Cératopogonidés de la région éthiopienne (2). Arch. de l'Institut Pasteur d’Algerie 39, 302–337 (1961).

24. Cornet, M. The Culicoides (Diptera Ceratopogonidae) of West Africa (first note). Cah. ORSTOM. Sér. Entomol. Médicale Parasitol. 34, 314–364 (1969).

25. Dallas, J. et al. Phylogenetic status and matrineline structure of the biting midge, Culicoides imicola, in Portugal, Rhodes and Israel. Med. Vet. Entomol. 17, 379–407 (2003).

26. al-Busaidy, S. M. & Mellor, P. S. Epidemiology of bluetongue and related orbiviruses in the Sultanate of Oman. Epidemiol. Infect. 106, 167–178 (1991).

27. Davies, F. G. Bluetongue studies with sentinel cattle in Kenya. J. Hyg. (Lond) 80, 197–204 (1978).

28. De Meillon, B. Diptera (Nematocera): Ceratopogonidae. In South African Animal Life (eds Hanstrom, B., Brinck, P. & Rudebeck, G.) 326–355 (1956).

29. De Meillon, B. The Madagasicr Ceratopogonidae. Rev. Entomol. Mocambique 4, 34–64 (1961).

30. Delec scale, J.-C. & De La Rocque, S. Contribution à l'étude des Culicoides de Corse. Liste des espèces recensées en 2000. Bull. la Société Entomol. Fr. 107, 371–379 (2002).

31. Dìk, B., Yaqış, Ş. & Linton, Y. M. A review of species diversity and distribution of Culicoides Latreille (Diptera: Ceratopogonidae) in Turkey. J. Nat. Hist. 40, 32–34 (2006).

32. Dyce, A. L. & Wirth, W. W. Reappraisal of some Indian Culicoides species in the subgenus Avaritia (Diptera: Ceratopogonidae). Int. J. Entomol. 25, 221–225 (1983).

33. Gerry, A. A. C. et al. Biting rates of Culicoides midges (Diptera: Ceratopogonidae) on sheep in northeastern Spain in relation to midge capture using UV light and carbon dioxide-baited traps. J. Med. Entomol. 46, 615–624 (2009).

34. Goldfarazena, A. et al. First record of Culicoides imicola, the main vector of bluetongue virus in Europe, in the Basque Country (northern Spain), Vet. Rec. 162, 820–821 (2008).

35. Ghoneim, T. et al. A Concluded List of the Culicoides spp (Diptera) in Egypt. Oriental Insects 35, 247–258 (2001).

36. Glick, J. J. Culicoides biting midges (Diptera: Ceratopogonidae) of Kenya. J. Med. Entomol. 27, 85–195 (1990).

37. Bally-Charouma, H. & Kremer, M. Second contribution to the study of the Culicoides of Morocco (Diptera, Ceratopogonidae). Cah. ORSTOM. Sér. Entomol. Médicale Parasitol. 8, 383–391 (1970).

38. Hamammi, S., Bouzid, M., Hammou, F., Fakhfakh, E. & Delec scale, J. C. Occurrence of Culicoides spp. (Diptera: Ceratopogonidae) in Tunisia, with emphasis on the bluetongue vector Culicoides imicola. Parasitol. 15, 179–181 (2008).

39. Herrnman, K. A. J., Boorman, J. P. T. & Taylor, W. P. Bluetongue virus in a Nigerian dairy cattle herd: I. Serological studies and correlation of virus activity to vector population. J. Hyg. (Lond). 90, 177–193 (1983).

40. Hiilali, M. et al. Culicoides midges (Ceratopogonidae) in some localities of Saudi Arabia and their veterinary significance. Vet. Arh. 73, 285–294 (2003).
82. Harrup, L. E. et al. DNA barcoding and surveillance sampling strategies for Culicoides biting midges (Diptera: Ceratopogonidae) in southern India. Parasit. Vectors 9, 461 (2016).

83. Jacquet, S. et al. Colonization of the Mediterranean basin by the vector biting midge species Culicoides imicola: an old story. Mol. Ecol. 24, 5707–5725 (2015).

84. Jacquet, S. et al. Range expansion of the Bluetongue vector, Culicoides imicola, in continental France likely due to rare wind-transport events. Sci. Rep. 6, 27247 (2016).

85. Liewen, D. et al. Culicoides species composition and environmental factors influencing African horse sickness distribution at three sites in Namibia. Acta Trop. 163, 70–79 (2016).

86. Magliano, A. et al. Indoor and outdoor winter activity of Culicoides biting midges, vectors of bluetongue virus, in Italy. Med. Vet. Entomol. 32, 70–77 (2018).

87. Martinez-DE LA Puente, J. et al. First molecular identification of the vertebrate hosts of Culicoides imicola in Europe and a review of its blood-feeding patterns worldwide: implications for the transmission of bluetongue disease and African horse sickness. Med. Vet. Entomol. 31, 333–339 (2017).

88. Mayo, C. et al. The prevalence of Culicoides spp. in 3 geographic areas of South Africa. Vet. Ital. 52, 281–289 (2016).

89. Arenas-Montes, A. et al. Spatial-temporal Trends and Factors Associated with the Bluetongue Virus Seropositivity in Large Game Hunting Areas from Southern Spain. Transbound. Emerg. Dis. 63, e339–46 (2016).

90. Meloni, G. et al. Combined larvicidal and adulticidal treatments to control Culicoides biting midges (Diptera: Ceratopogonidae): Results of a pilot study. Vet. Parasitol. 257, 28–33 (2018).

91. Muñoz-Muñoz, F. et al. Phenotypic differentiation and phylogenetic signal of wing shape in western European biting midges, Culicoides spp., of the subgenus Avaritia. Med. Vet. Entomol. 28, 319–329 (2014).

92. Onyango, M. G. et al. Delineation of the population genetic structure of Culicoides imicola in East and South Africa. Parasit. Vectors 8, 660 (2015).

93. Page, P. C., Labuschagne, K., Venter, G. J., Schoeman, J. P. & Guthrie, A. J. A. Efficacy of alphacypermethrin-treated high density polyethylene mesh applied to jet stalls housing horses against Culicoides biting midges in South Africa. Vet. Parasitol. 210, 84–90 (2015).

94. Pages, N. et al. First detection of Wolbachia-infected Culicoides (Diptera: Ceratopogonidae) in Europe: Wolbachia and Cardinium infection across Culicoides communities revealed in Spain. Parasites and Vectors 10, 582 (2017).

95. Ramilo, D. W., Nunes, T., Madeira, S., Ribeiro, R. & da Fonseca, I. P. Geographical distribution of Culicoides (Diptera: Ceratopogonidae) in mainland Portugal: Presence/absence modelling of vector and potential vector species. PLoS One 12, e0180606 (2017).

96. Ribeiro, R. et al. Spatial and temporal distribution of Culicoides species in mainland Portugal (2005–2010). Results of the Portuguese Entomological Surveillance Programme. PLoS One 10, e0124019 (2015).

97. Sambou, M. et al. Comparison of matrix-assisted laser desorption ionization-time of flight mass spectrometry and molecular biology techniques for identification of Culicoides (Diptera: Ceratopogonidae) biting midges in senegal. J. Clin. Microbiol. 53, 410–418 (2015).

98. Sghaier, S. et al. New species of the genus Culicoides (Diptera Ceratopogonidae) for Tunisia, with detection of Bluetongue viruses in vectors. Vet. Ital. 53, 357–366 (2017).

99. Slama, D. et al. Biting midges monitoring (Diptera: Ceratopogonidae: Culicoides Latreille) in the governate of Monastir (Tunisia): Species composition and molecular investigations. Parasitol. Res. 113, 2433–2443 (2014).

100. Bakhour, M. T. et al. Foraging range of arthropods with veterinary interest: New insights for Afrotropical Culicoides biting midges (Diptera: Ceratopogonidae) using the ring method. Acta Trop. 157, 59–67 (2016).

101. Slama, D., Haouas, N., Mezroud, H., Babha, H. & Chaker, E. Blood meal analysis of culicoides (Diptera: Ceratopogonidae) in central Tunisia. PLoS One 10, e0120528 (2015).

102. Venail, R. et al. How do species, population and active ingredient influence insecticide susceptibility in Culicoides biting midges (Diptera: Ceratopogonidae) of veterinary importance? Parasites and Vectors 8, 439 (2015).

103. Venter, G. J. et al. Culicoides species abundance and potential over-wintering of African horse sickness virus in the Onderstepoort area, Gauteng, South Africa. J. S. Afr. Vet. Assoc. 85, e1–e6 (2014).

104. Venter, G. J., Labuschagne, K., Boikanyo, S. N. B. & Morey, L. Assessment of the repellent effect of citronella and lemon eucalyptus oil against South African Culicoides species. Vet. Parasitol. 201, 5707–5725 (2015).

105. Talavera, S. et al. Revealing potential biting vectors for BV and SBV: a study on Culicoides blood feeding preferences in natural ecosystems in Spain. Med. Vet. Entomol. 32, 35–40 (2018).

106. Bellis, G. et al. Revision of the culicoides (Avaritia) imicola complex khamala & kettie (Diptera: Ceratopogonidae) from the Australasian region. Zootaxa 3768, 401–427 (2014).

107. Blanda, V. et al. Geo-statistical analysis of Culicoides spp. distribution and abundance in Sicily, Italy. Parasit. Vectors 11, 78 (2018).

108. Debbar, L. B. et al. Epidemiology of Mansowella perstans in the middle belt of Ghana. Parasit. Vectors 10, 13 (2017).

109. Del Río, R. et al. Detrimental effect of cypermethrin treated nets on Culicoides populations (Diptera: Ceratopogonidae) and non-targeted fauna in livestock farms. Vet. Parasitol. 199, 230–234 (2014).

110. Diarra, M. et al. Seasonal dynamics of lemp(Culicoides) (Diptera: Ceratopogonidae) biting midges, potential vectors of African horse sickness and bluetongue viruses in the Niayes area of Senegal. Parasit. Vectors 7, 147 (2014).

111. Fall, M. et al. Culicoides (Diptera: Ceratopogonidae) midges, the vectors of African horse sickness virus - A host/vector contact study in the Niayes area of Senegal. Parasit. Vectors 8, 39 (2015).

112. FAO. The Global Agricultural Unit Levels (GAUL): Technical Aspects. Food Agric. Organ. United Nations, EC-FAO Food Secur. Program. (2008).

113. Leta, S. et al. The global compendium of Culicoides imicola occurrence, a Major Vector of Bluetongue, Schmallenberg, and African Horse Sickness Viruses. figshare. https://doi.org/10.6084/m9.figshare.c.4407773 (2019).

114. Aiello-Lammens, M. E., Boria, R. A., Radosavljevic, A., Vilela, B. & Anderson, R. P. sp’thin: An R package for spatial thinning of species occurrence records for use in ecological niche models. Ecology (Cop.) 138, 541–545 (2015).

115. Tatem, A. J. et al. Prediction of bluetongue vector distribution in Europe and north Africa using satellite imagery. Vet. Microbiol. 97, 13–29 (2003).

116. Baylis, M., Caminade, C., Turner, J. & Jones, A. E. The role of climate change in a developing threat: the case of bluetongue in Europe. Rev. Sci. Tech. 36, 467–478 (2017).

117. Purse, B. V. et al. Climate change and the recent emergence of bluetongue in Europe. Nature reviews. Microbiology 3, 171–181 (2005).

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Author Contributions
S.L. conceived and designed the research, and drafted the manuscript with critical input from K.A., C.R., DK., T.J., T.M. and H.N. and approval from all authors. E.F. and S.L. extracted and compiled the data. S.L. and E.F., M.B. performed database standardization and technical validation.

Additional Information
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