SCIENTIFIC DATA

DATA DESCRIPTOR

Received: 6 March 2019 Accepted: 16 August 2019 Published online: 30 September 2019

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

Samson Leta¹, Eyerusalem Fetene¹, Tesfaye Mulatu², Kebede Amenu¹, Megarsa Bedasa Jaleta¹, Tariku Jibat Beyene^{1,3}, Haileleul Negussie¹, Darren Kriticos ^{6,5} & Crawford W. Revie₆

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. pulicaris^{7,10}. The 1998 incursion and emergence of bluetongue virus in Southern and Eastern Europe were manly 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 horses^{4,11}. 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

¹Addis Ababa University, College of Veterinary Medicine and Agriculture, P. O. Box 34, Bishoftu, Ethiopia. ²National Animal Health Diagnostic and Investigation Centre (NAHDIC), P. O. Box 04, Sebeta, Ethiopia. ³Center for Outcome Research and Epidemiology, Kansas State University, Manhattan, Kansas, USA. ⁴Commonwealth Scientific and Industrial Research Organisation (CSIRO), GPO Box 1700, Canberra, ACT 2601, Australia. ⁵InSTePP, University of Minnesota, St. Paul, MN, USA. ⁶Department of Computing and Information Sciences, University of Strathclyde, Livingstone Tower (14.01), 26 Richmond Street, Glasgow, G1 1XQ, Scotland, UK. Correspondence and requests for materials should be addressed to S.L. (email: samiwude@gmail.com)

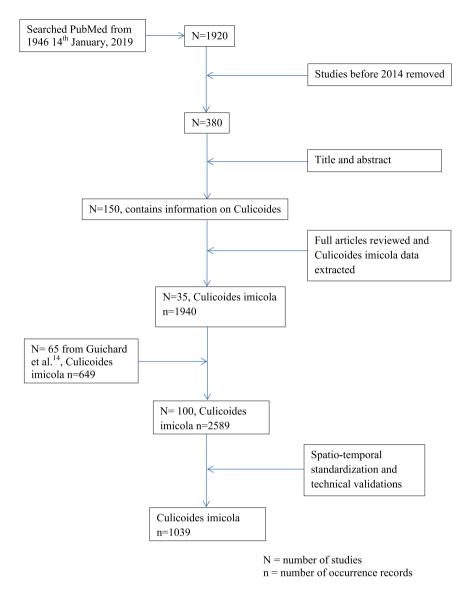


Fig. 1 Flow chart of literature search and data extraction.

doubled. Thus, it is important and timely to expand the effort of Guichard *et al.*¹⁴ and update the global Culicoides occurrence record. With these research gaps in mind, this study compiled the global occurrences of *C. imicola* based on the dataset provided by Guichard *et al.*¹⁴ and literature published since 1st 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 14th January 2019, which resulted in a collection of 1 920 articles. However, a geo-database of 649 occurrences of C. imicola compiled by Guichard et al.¹⁴ from 65 articles^{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 1st January 2014 till 14th January 2019^{4,6,79-111} was combined with existing data points obtained from Guichard et al.¹⁴ for the period 1959 to 2014. The search retrieved a total of 380 articles published since 1st 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 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

Attribute	Column #	Column name	Unit	Note	
Reference	1	Reference	_	Author names and publication year of the article from which the occurrence record is extracted	
Site location	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).	
	6	Site name		Name of the site where the occurrence lies	
	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)	
Year		Year		Year of C. imicola occurrence	

Table 1. Description of attributes and columns in the dataset.

.....

name, year of data collection and other information, and confirmed *C. imicola* occurrences within these articles were entered into the database. Occurrences were classified as confirmed when the article clearly stated the presence of the vector at a specific time in a specific location.

Geo-coding of data. The occurrence coordinates (longitude and latitude) of *C. imicola* was extracted from each articles 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)¹¹² 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 Figshare¹¹³. 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 $5 \text{ km} \times 5 \text{ km}$ 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 spThin¹¹⁴ 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 world¹¹⁵⁻¹¹⁷, 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.

Continent (UN region 2)	Region (UN region 1)	Number of <i>C. imicola</i> before technical validation	Number of <i>C. imicola</i> after technical validation
	Eastern Africa	104	84
	Middle Africa	10	10
Africa	Northern Africa	86	81
	Southern Africa	153	96
	Western Africa	71	40
	Caribbean	0	0
Americas	Central America	0	0
Americas	Northern America	0	0
	South America	0	0
	Central Asia	0	0
	Eastern Asia	2	2
Asia	South-Eastern Asia	20	18
	Southern Asia	5	5
	Western Asia	100	63
	Eastern Europe	0	0
Europe	Northern Europe	0	0
Europe	Southern Europe	1998	615
	Western Europe	40	25
	Melanesia	0	0
Oceania	Micronesia	0	0
Oceania	Australia and New Zealand	0	0
	Polynesia	0	0
Total		2589	1039

Table 2. Culicoides imicola occurrence records by UN region.

.....

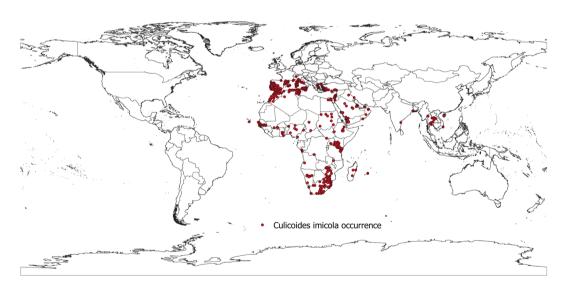


Fig. 2 Map of occurrence points for Culicoides imicola.

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.

Code Availability

There is no custom code produced during the collection and validation of this dataset.

References

- Venter, G. J., Groenewald, D. M., Paweska, J. T., Venter, E. H. & Howell, P. G. Vector competence of selected South African Culicoides species for the Bryanston serotype of equine encephalosis virus. *Med. Vet. Entomol.* 13, 393–400 (1999).
- Paweska, 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).
- Braverman, 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).
- 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).
- 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).
- 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).
- 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 2. PLoS One 7, e32601 (2012).
- 9. Zientara, S. *et al.* Novel bluetongue virus in goats, Corsica, France, 2014. *Emerg. Infect. Dis.* **20**, 2123–2125 (2014).
- Maclachlan, N. J. Bluetongue: history, global epidemiology, and pathogenesis. *Prev. Vet. Med.* 102, 107–111 (2011).
 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).
- Balenghien, 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, e112491 (2014).
- 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).
- Braverman, 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).
- Bravermann, Y., Boorman, J., Kremer, M. & Delecolle, J.-C. Faunistic list of Culicoides (Diptera, Ceratopogonidae) from Israel. Cah. O.R.S.T.O.M., séries Entomol. médicale Parasitol. 14, 179–185 (1976).
- Braverman, 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).
- 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).
- 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).
- Capela, R., Sousa, C., Pena, I. & Caeiro, V. Preliminary note on the distribution and ecology of Culicoides imicola in Portugal. Med. Vet. Entomol. 7, 23–26 (1993).
- Chaker, E. et al. Note faunistique sur les Culicoides (Diptera, Ceratopogonidae) du gouvernorat de monastir (Tunisie). Parasite 12, 359–361 (2005).
- Clastrier, J. & Wirth, W. W. Notes sur les Cératopogonidés. XIV. Cératopogonidés de la region éthiopienne (2). Arch. l'Institut Pasteur d'Algerie 39, 302–337 (1961).
- 24. Cornet, M. The Culicoides (Diptera Ceratopogonidae) of West Africa (first note). Cah. ORSTOM, Série Entomol. Médicale Parasitol. 7, 341-364 (1969).
- Dallas, J. F. et al. Phylogenetic status and matrilineal structure of the biting midge, Culicoides imicola, in Portugal, Rhodes and Israel. Med. Vet. Entomol. 17, 379–87 (2003).
- 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).
- 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 Madagascan Ceratopogonidae. Rev Entomol Mocambaise 4, 34-64 (1961).
- Delecolle, 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).
- Dik, B., Yağci, Ş. & Linton, Y. M. A review of species diversity and distribution of Culicoides Latreille, 1809 (Diptera: Ceratopogonidae) in Turkey. J. Nat. Hist. 40, 32–34 (2006).
- 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).
- 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).
- Goldarazena, 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).
- Ghonaim, M. F., Fadl, H. H., Ibrahim, A. W. A. & Ali, A. An annotated checklist of the ceratopogonidae (Diptera) of egypt. Orient. Insects 35, 247–258 (2001).
- 36. Glick, J. I. Culicoides biting midges (Diptera: Ceratopogonidae) of Kenya. J. Med. Entomol. 27, 85-195 (1990).
- Bailly-Choumara, H. & Kremer, M. Second contribution to the study of the Culicoides of Morocco (Diptera, Ceratopogonidae). Cah. ORSTOM, Ser. Entomol. Medicale Parasitol. 8, 383–391 (1970).
- Hammami, S., Bouzid, M., Hammou, F., Fakhfakh, E. & Delecolle, J. C. Occurrence of Culicoides spp. (Diptera: Ceratopogonidae) in Tunisia, with emphasis on the bluetongue vector Culicoides imicola. *Parasite* 15, 179–181 (2008).
- Herniman, K. A. J., Boorman, J. P. T. & Taylor, W. P. Bluetongue virus in a Nigerian dairy cattle herd: 1. Serological studies and correlation of virus activity to vector population. J. Hyg. (Lond). 90, 177–193 (1983).
- Hilali, M. et al. Culicoides midges (Ceratopogonidae) in some localities of Saudi Arabia and their veterinary significance. Vet. Arh. 73, 285–294 (2003).

- Itoua, A. & Cornet, M. Les Ceratopogonidae (Diptera) du Mayombe congolais: Revue taxonomique des especes de genre Culicoides Latreille. 1809. Cah. O.R.S.T.O.M., ser. Ent. med. Parasitol. 24, 233–250 (1986).
- Khamala, C. P. M. Ecological distribution of East African Culicoides Latreille (Dipt., Ceratopogonidae) as shown by light-traps. Bull. Entomol. Res. 60, 549–557 (1971).
- Kitaoka, S., Kaneko, K. & Shinonaga, S. Survey on blood-sucking Culicoides species in Ife, Nigeria. J. Aichi Med. Univ. Assoc. 12, 454–458 (1984).
- Kremer, M. Culicoides (Diptera: Ceratopogonidae) de la région éthiopienne et particulièrement d'Angola (lle note) (espèces, nouvelles, redescription et chorologie). Publicações Cult. da Cia. Diam. Angola 84, 79–107 (1972).
- Labuschagne, K., Gerber, L. J., Espie, I. & Carpenter, S. Culicoides biting midges at the National Zoological Gardens of South Africa. Onderstepoort J. Vet. Res. 74, 343–347 (2007).
- Linton, Y. M. et al. Phylogenetic analysis of the mitochondrial cytochrome oxidase subunit I gene of five species of the Culicoides imicola species complex. Med. Vet. Entomol. 16, 139–146 (2002).
- Meiswinkel, R. Afrotropical Culicoides: a redescription of C. (Avaritia) imicola Kieffer, 1913 (Diptera: Ceratopogonidae) with description of the closely allied C. (A.) bolitinos sp. nov. reared from the dung of the African buffalo, blue wildebeest and cattle in South A. Onderstepoort J. Vet. Res. 56, 23–39 (1989).
- Baylis, M., El Hasnaoui, H., Bouayoune, H., Touti, J. & Mellor, P. S. The spatial and seasonal distribution of African horse sickness and its potential Culicoides vectors in Morocco. *Med. Vet. Entomol.* 11, 203–212 (1997).
- Meiswinkel, R. The 1996 outbreak of African horse sickness in South Africa-the entomological perspective. Arch. Virol. Suppl. 14, 69–83 (1998).
- Mellor, P. S., Osborne, R. & Jennings, D. M. Isolation of bluetongue and related viruses from Culicoides spp. in the Sudan. J. Hyg. (Lond). 93, 621–628 (1984).
- Miranda, M. A. *et al.* Presence in the Balearic Islands (Spain) of the midges Culicoides imicola and Culicoides obsoletus group. *Med. Vet. Entomol.* 17, 52–54 (2003).
- 52. Mohammed, M. E. H. & Mellor, P. S. Further studies on bluetongue and bluetongue-related orbiviruses in the Sudan. *Epidemiol. Infect.* **105**, 619–632 (1990).
- Mushi, E. Z., Isa, J. F. W., Chabo, R. G., Binta, M. G. & Kapaata, R. W. Culicoides (Diptera: Ceratopogonidae) associated with horses at Mogoditshane, Gaborone, Botswana. Vet. Res. Commun. 22, 295–297 (1998).
- Musuka, G. N., Mellor, P. S., Meiswinkel, R., Baylis, M. & Kelly, P. J. Prevalence of Culicoides imicola and other species (Diptera: Ceratopogonidae) ateight sites in Zimbabwe: to the editor. J. S. Afr. Vet. Assoc. 72, 62–63 (2001).
- Navai, S. & Mesghali, A. Ceratopogonidae (Diptera) of Iran: II. More records of Culicoides Latreille, 1809. J. Nat. Hist. 2, 241–246 (1968).
- Nevill, H. & Nevill, E. M. A survey of the Culicoides (Diptera: Ceratopogonidae) of the Umlalazi Nature Reserve in Zululand, South Africa, with notes on two species biting man. Onderstepoort J. Vet. Res. 62, 51–58 (1995).
- Nolan, D. V., Dallas, J. F., Mordue Luntz, A. J. & Mordue, A. J. Molecular taxonomy and population structure of a Culicoides midge vector. Vet. Ital 40, 352–359 (2004).
- Nolan, D. V. et al. Incursion and range expansion in the bluetongue vector Culicoides imicola in the Mediterranean basin: a phylogeographic analysis. Med. Vet. Entomol. 22, 340–351 (2008).
- Boorman, J. & Mellor, P. S. Culicoides vectors of bluetongue and African horse sickness viruses in Mauritius. Med. Vet. Entomol. 6, 306–306 (1992).
- Ortega, M. D. & Holbrook, F. R. Presence of Culicoides imicola (Diptera: Ceratopogonidae) in Jaen, Spain. J. Am. Mosq. Control Assoc. 10, 463–463 (1994).
- Ortega, M. D., Lloyd, J. E., Frederick Holbrook, eNo. R. & Holbrook, F. R. Seasonal and geographical distribution of Culicoides imicola Kieffer (Diptera: Ceratopogonidae) in southwestern Spain. J. Am. Mosq. Control Assoc. 13, 227–232 (1997).
- 62. Patakakis, M. J. et al. Distribution of Culicoides in Greece. J. Vector Ecol. 34, 243-251 (2009).
- 63. Ortega, M. D., Mellor, P. S., Rawlings, P. & Pro, M. J. The seasonal and geographical distribution of Culicoides imicola, C. pulicaris group and C. obsoletus group biting midges in central and southern Spain. In *African* Horse Sickness (eds Mellor, P. S., Baylis, M., Hamblin, C., Calisher, C. H. & Mertens, P. P. C.) 85–91 (Springer Vienna, 1998).
- Rawlings, P. et al. The relationship between climate and the distribution of Culicoides imicola in Iberia. In African Horse Sickness (eds Mellor, P. S., Baylis, M., Hamblin, C., Calisher, C. H. & Mertens, P. P. C.) 93–102 (Springer Vienna, 2011).
- Sarto i Monteys, V., Ventura, D., Pages, N., Aranda, C. & Escosa, R. Expansion of Culicoides imicola, the main bluetongue virus vector in Europe, into Catalonia, Spain. Vet. Rec. 156, 415–417 (2005).
- Sebastiani, F. et al. Molecular differentiation of the Old World Culicoides imicola species complex (Diptera, Ceratopogonidae), inferred using random amplified polymorphic DNA markers. Mol. Ecol. 10, 1773–1786 (2001).
- 67. Szadziewski, R. Ceratopogonidae (Diptera) from Algeria. VI. Culicoides Latr. Pol. Pismo Entomol. 54, 163-182 (1984).
- Taylor, W. P., Busaidy, S. Al, Mellor, P. S., al Busaidy, S. M. & Mellor, P. S. Bluetongue in the Sultanate of Oman, a preliminary epidemiological study. *Epidemiol. Infect.* 107, 87–97 (1991).
- 69. Venter, G. J. *et al.* Culicoides (Diptera:Ceratopogonidae) associated with livestock in the Onderstepoort area, Gauteng, South Africa as determined by light-trap collections. *Onderstepoort J. Vet. Res.* **63**, 315–325 (1996).
- 70. Boorman, J. & van Harten, A. Vectors of African horse sickness in the Cape Verde Islands. Vet. Rec. 131, 56 (1992).
- Venter, G. J., Nevill, E. M. & Van der Linde, T. C. Geographical distribution and relative abundance of stock-associated Culicoides species (Diptera: Ceratopogonidae) in southern Africa in relation to their potential as viral vectors. Onderstepoort J. Vet. Res. 63, 25–38 (1996).
- 72. Walker, A. R. Seasonal fluctuations of Culicoides species (Diptera: Ceratopogonidae) in Kenya. *Bull. Entomol. Res.* **67**, 217–233 (1977).
- 73. Wirth, W. W. & Hubert, A. A. The Culicoides of Southeast Asia (Diptera: Ceratopogonidae). Memoirs of the American Entomological Institute (1989).
- 74. Yu, Y.-X. Ceratopogonidae of China: Insecta, Diptera. (Military Medical Science Press, 2005).
- 75. Howarth, F. Biosystematics of the Culicoides of Laos (Diptera: Ceratopogonidae). Int. J. Entomol. 27, 1–96 (1985).
- Boorman, J. Culicoides (Diptera: Ceratapogonidae) of the Arabian Peninsula with Notes on their Medical and Veterinary Importance. Fauna Saudi Arab. 10, 160–224 (1989).
 - Braverman, Y. & Linley, J. R. Effect of light trap height on catch of Culicoides (Diptera: Ceratopogonidae) in Israel. J. Med. Entomol. 30, 1060–1063 (1993).
 - Braverman, Y. & Phelps, R. J. Species composition and blood-meal identification in samples of Culicoides (Diptera: Ceratopogonidae) collected near Salisbury, Zimbabwe in 1976–77. J. Entomol. Soc. South. Afr. 44, 315–323 (1981).
- Foxi, C. et al. Role of different Culicoides vectors (Diptera: Ceratopogonidae) in bluetongue virus transmission and overwintering in Sardinia (Italy). Parasites and Vectors 9, 440 (2016).
- Goffredo, M. et al. Orbivirus detection from Culicoides collected on African horse sickness outbreaks in Namibia. Vet. Ital. 51, 17–23 (2015).
- Gordon, S. J. G. et al. The occurrence of Culicoides species, the vectors of arboviruses, at selected trap sites in Zimbabwe. Onderstepoort J. Vet. Res. 82, e1–e8 (2015).

- 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).
- 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).
- Jacquet, S. et al. Range expansion of the Bluetongue vector, Culicoides imicola, in continental France likely due to rare windtransport events. Sci. Rep. 6, 27247 (2016).
- Liebenberg, 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).
- 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).
- 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).
- 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).
- 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).
- 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).
- Page, P. C., Labuschagne, K., Venter, G. J., Schoeman, J. P. & Guthrie, A. J. 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).
- 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).
- Ramilo, D. W., Nunes, T., Madeira, S., Boinas, F. & 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).
- 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).
- 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).
- 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).
- 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, 2435–2443 (2014).
- Bakhoum, 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., Mezhoud, H., Babba, 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).
- 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. J. S. Afr. Vet. Assoc. 85, e1–e5 (2014).
- Talavera, S. et al. Revealing potential bridge vectors for BTV 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 & kettle (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. Debrah, L. B. et al. Epidemiology of Mansonella perstans in the middle belt of Ghana. Parasit. Vectors 10, 15 (2017).
- Del Río, R. *et al.* Detrimental effect of cypermethrin treated nets on Culicoides populations (Diptera; Ceratopogonidae) and nontargeted fauna in livestock farms. *Vet. Parasitol.* 199, 230–234 (2014).
- 110. Diarra, M. *et al.* Seasonal dynamics of \emph{Culicoides} (Diptera: Ceratopogonidae) biting midges, potential vectors of {Africa} n 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. *Parasites and Vectors* **8**, 39 (2015).
- 112. FAO. The Global Administrative Unit Layers (GAUL): Technical Aspects. Food Agric. Organ. United Nations, EC-FAO Food Secur. Program. (2008).
- 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).
- Aiello-Lammens, M. E., Boria, R. A., Radosavljevic, A., Vilela, B. & Anderson, R. P. spThin: An R package for spatial thinning of species occurrence records for use in ecological niche models. *Ecography (Cop.)*. 38, 541–545 (2015).
- 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).

Acknowledgements

Data from France were collected through the French surveillance network for *Culicoides* funded by the French Ministry for Agriculture (Dgal) and coordinated by Cirad, Montpellier (T. Balenghien, C. Garros, T. Baldet) and we would like to extend our acknowledgment for them.

Author Contributions

S.L. 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

Competing Interests: The authors declare no competing interests.

Publisher's note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons license, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons license, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons license and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this license, visit http://creativecommons.org/licenses/by/4.0/.

The Creative Commons Public Domain Dedication waiver http://creativecommons.org/publicdomain/zero/1.0/ applies to the metadata files associated with this article.

© The Author(s) 2019