

Review



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Robust evidence for bats as reservoir hosts is lacking in most African virus studies: a review and call to optimize sampling and conserve bats

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Africa experiences frequent emerging disease outbreaks among humans, with bats often proposed as zoonotic pathogen hosts. We comprehensively reviewed virus–bat findings from papers published between 1978 and 2020 to evaluate the evidence that African bats are reservoir and/or bridging hosts for viruses that cause human disease. We present data from 162 papers (of 1322) with original findings on (1) numbers and species of bats sampled across bat families and the continent, (2) how bats were selected for study inclusion, (3) if bats were terminally sampled, (4) what types of ecological data, if any, were recorded and (5) which viruses were detected and with what methodology. We propose a scheme for evaluating presumed virus–host relationships by evidence type and quality, using the contrasting available evidence for Orthoebolavirus versus Orthomarburgvirus as an example. We review the wording in abstracts and discussions of all 162 papers, identifying key framing terms, how these refer to findings, and how they might contribute to people’s beliefs about bats. We discuss the impact of scientific research communication on public perception and emphasize the need for strategies that minimize human–bat conflict and support bat conservation. Finally, we make recommendations for best practices that will improve virological study metadata.

1. Introduction

Viral spillover from wildlife to humans is a global threat [1–3]. Despite their significance, identification of reservoir hosts, transmission mechanisms and conditions, and pathogenicity remain unknown for most viruses. Several human diseases hypothesized to have originated in bats have devastating effects, as exemplified by the 2019–2023 ongoing COVID-19 pandemic and re-emerging Ebola virus outbreaks [4–7]. Intense, ongoing global surveillance for bat viruses is generating a rapidly growing body of the literature [8]. However, heterogeneity of field and laboratory methods, a paucity of data on bat biology and ecology, and a lack of surveillance in other mammalian groups that may play a role in spillover, have limited reliable assignment of reservoir host status (bat and otherwise) and hamper our understanding of complex multi-host transmission and spillover dynamics.

Many outbreaks of emerging diseases occur in Africa, which has a unique, diverse and ecologically important assemblage of bat species [9,10]. Unlike the well-characterized and well-known Australian and SE Asian *Henipavirus–Pteropus* flying fox systems [11,12], and with the exception of comprehensive work on the African *Orthomarburgvirus–Rousettus aegyptiacus* system [13–28], the disease ecology of African bats is understudied, especially in light of African bat biodiversity and the size of the continent. Herein, we review published field studies on African bat viruses, summarizing and analysing the work published through 2020 to evaluate the types and quality of data available, trends in species and localities sampled, knowledge gaps and conservation concerns, and to make recommendations for best practices that will improve virological study metadata.

2. African bats and virus research

(a) Literature review and data analysis

We analysed data from peer-reviewed primary research articles published through 2020 for which bats were captured in Africa for viral surveillance. We used the search terms ‘bat OR bats OR Chiroptera’ AND ‘virus OR viral OR virological’ AND ‘Africa OR ‘each African country name in English or country name variant’ (electronic supplementary material, figure S1) in a Web of Science (all database) search, repeated in French, yielding a total of 1322 papers (two from French search). We also included older primary data from seven studies used in 11 modelling papers from this period. In total, 162 papers met our study inclusion criteria, published between 1978 and 2020 (electronic supplementary material, text S1). This dataset, analysed alongside our current understanding of African bat systematics and ecology, provided a snapshot in time of African bat viral research from which we were able to describe the nature of these studies in detail (figure 1). Data on (1) numbers of species and individuals sampled across bat families and the continent; (2) how bats were selected for study; (3) whether they were terminally sampled; (4) whether ecological data were recorded; and (5) which viruses were detected and with what methodology, were manually extracted. We focus on four viral families most relevant to humans: *Coronaviridae*, *Paramyxoviridae*, *Rhabdoviridae* and *Filoviridae*, list other viral findings, and propose a schematic approach to evaluating the quality of the evidence underlying putative bat–virus relationships, using the contrasting available evidence base for *Orthoebolavirus* versus *Orthomarburgvirus* as an example. Our findings are placed in the context of numbers of known and suspected human infections and fatalities from African zoonoses associated with bats. Finally, we review the wording in abstracts and discussions of all 162 papers. We identify several key framing terms, how these refer to findings, and how they might contribute to people’s beliefs about bats. In the light of the fear of bats as sources of viral spillovers, we discuss the impact of scientific research communication on public perception and emphasize the need for strategies that minimize human–bat conflict.

(b) Species and guilds of bats sampled and their numbers

In total, 167 bat species from 11 of 13 bat families recorded in Africa were sampled (table 1 and figure 1a; electronic supplementary material, figure S2), representing 742 unique species–study combinations. Thirty-six of these species (21.6%) are of conservation concern and/or data deficient by the criteria of the International Union for Conservation of Nature (IUCN) ([30]; table 1). In 118 genus–study combinations, only the genus was identified (20 genera), in 10 studies (at least some) bats remained unidentified (figure 1b) and 16 publications listed only virus-positive bats, suggesting that greater than 167 species were likely sampled. Based on data from 70.4% (114/162) of the studies, at least 80 241 individual bats were captured; 15 studies failed to indicate numbers of captured bats (9.3%; figure 1c). Almost half (48.6%; ≥ 39 018 individuals) were lethally sampled, as reported in 51.9% of papers (84/162; figure 1c). Twenty-two studies (12.3%) did not report the fate of all bats (19.7% or 15 817 individual bats).

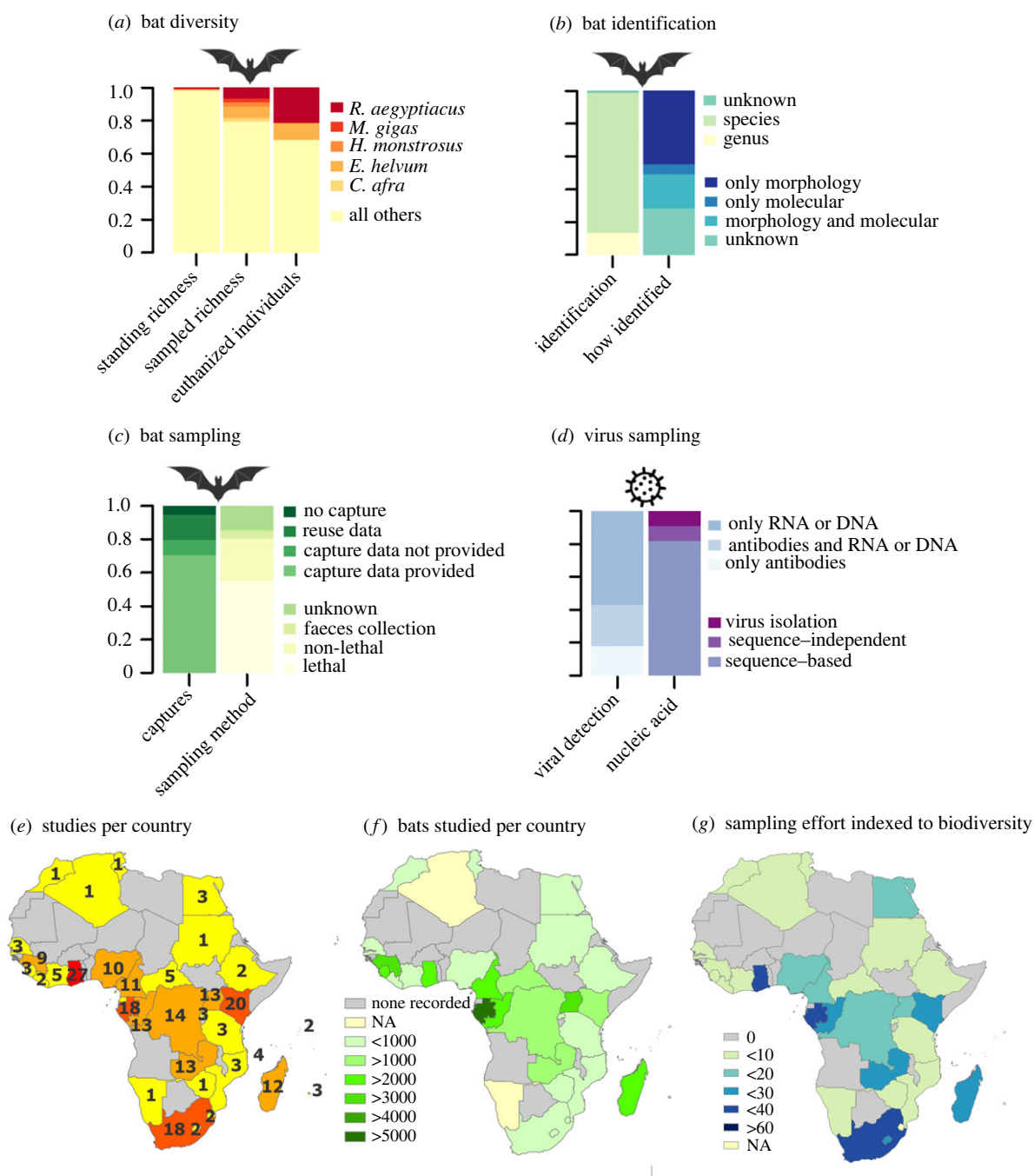


Figure 1. Summaries of review findings (162 papers; 1978–2020). (a) Bat diversity, proportion of five most frequently sampled species relative to standing species richness (first bar) and total sampling effort (out of 742 species–study combinations) (second bar), and the proportion of the two most frequently sampled species being euthanized (third bar). (b) Bat identification, proportion of samples where bats were identified to the genus or species level, or not at all (first bar), and whether morphology and/or molecular methods were used (second bar). (c) Bat sampling, proportion of studies that did or did not provide capture data (first bar), and how captured bats were sampled: lethal, non-lethal (i.e. blood, skin, urine, oral or rectal swab), faeces (roost collected) or unknown (sample type not given) (second bar). (d) Virus sampling, proportion of studies by detection type (first bar), and by type of evidence (second bar). (e) Number of bat virological studies recorded from each African country. (f) Number of bats recorded to have been studied by country (number of bats in Algeria and Namibia not available, numbers are nearest estimates as some studies included more than one country and did not delineate provenance). (g) Viral sampling efforts normalized by species-level bat biodiversity (no. studies/no. species \times 100).

Our analysis revealed biases in sampled species, study sites and data collection. Although some studies aimed to assess viral diversity across multiple taxa, many focused on a subset, including synanthropic species, which may pose a greater risk for viral spillover. Thus, it is not surprising that the gregarious and conspicuous fruit bats *R. aegyptiacus* and *Eidolon helvum* were heavily studied (46 and 52 studies). The largest African fruit bat *Hypsignathus monstrosus*, one of three species from which *Orthoebolavirus zairensis* (EBOV) RNA has been detected [31] was sampled in 21 studies. The insectivorous free-tailed bat *Mops condylurus* (18 studies),

the cave-roosting sheath-tailed bat *Coleura afra*, a large leaf-nosed bat, *Macronycteris gigas* and the small molossid *Mops pumilus* (17 studies each), were also more often sampled than others. Fifty-three species were each sampled only once. When comparing the observed number of studies in which each species (742 species–study combinations) has been reported to the number expected if species (standing richness or sampled richness) were randomly sampled, significant biases were detected (Kolmogorov–Smirnov statistic between observed and expected null distributions, $p < 0.0001$). Fruit bats were overrepresented in the studies

Table 1. Overview of 167 bat species sampled in 162 virus–bat research papers from Africa through 2020. Species identifications adopted from the original studies; nomenclature follows current taxonomy. For each family, number of species sampled relative to the total number of African species in that family is listed. Additionally, taxa only identified to genus or family are indicated and sampled bats may include cryptic species. Bat species are grouped alphabetically within their taxonomic families. Data include: (1) no. of non-lethal studies for that species; (2) no. of lethal studies for that species; (3) whether the species inhabits caves, either obligatory ‘+’, facultatively ‘(+)’ or not known ‘?’ but most species in its taxonomic group are cave-roosting; (4) IUCN Red List category when other than Least Concern (DD, data deficient; NT, near threatened; VU, vulnerable; EN, endangered; na, not assessed). Species that were only sampled once are highlighted in bold.

bat family/bat species	no. non-lethal studies	no. lethal studies	cave	IUCN Red List category	bat family/bat species	no. non-lethal studies	no. lethal studies	cave	IUCN Red List category
Pteropodidae (29/43 species sampled, plus: 4 genus only, 1 family only)									
<i>Casinycteris argymnis</i>	4				<i>Afronycteris helios</i>	3			DD
C. ophiodon	1			NT	<i>A. nana</i>	1	9		
<i>Eidolon dupreanum</i>	4		(+)	VU	<i>Eptesicus hottentotus</i>	3		(+)	
<i>E. helvum</i>	18	34		NT	<i>E. isabellinus</i>	1		(+)	
Epomophorus anselli	1			DD	Glauconycteris alboguttata	1			
<i>E. crypturus</i>	1	1			<i>G. argentata</i>	3			
E. dobsonii	1				<i>G. beatrix</i>	1	1		
<i>E. gambianus</i>	7	5			G. egeria	1	1		DD
<i>E. labiatus</i> ^a	4	7			G. poensis	1			
<i>E. minimus</i>	2				<i>G. variegata</i>	1	2		
<i>E. pusillus</i>	3	8			Hypsugo muscivulus	1	1		DD
<i>E. wahlbergi</i>	1	6			<i>Kerivoula argentata</i>	2			
<i>Epomops buettikoferi</i>	6	1			K. cuprosa	1	1		DD
<i>E. franqueti</i>	5	10			<i>K. lanosa</i>	1	1		
<i>Hypsignathus monstrosus</i>	7	14			Laephotis botswanae	1	1		
Megaloglossus azagnyi	1				<i>L. capensis</i>	5			
<i>M. woermanni</i> ^b	1	10			L. malagasyensis	1	1		VU
<i>Myonycteris angolensis</i> ^c	4	11	(+)		L. matroka	1	1		
<i>M. torquata</i> ^d	1	11			L. robertsi	1	1		DD
<i>Nanonycteris veldkampii</i>	5	2			L. wintoni	1	1		
Plerotes anchietae	1			DD	<i>L. zuluensis</i>	1	3		
Pteropus niger	1			EN	<i>Mimetillus maloneyi</i>	3			
<i>P. rufus</i>	3	2		VU	<i>Myotis bocagii</i>	1	3		
P. seychellensis	1				<i>M. goudoti</i>	2	2	(+)	
<i>Rousettus aegyptiacus</i>	5	41	+		M. punicus	1	1	(+)	NT
<i>R. madagascariensis</i>	3	2	+	NT	<i>M. tricolor</i>	1	3	+	
R. obliviosus	1		+	VU	M. welwitschii	1	1	(+)	

(Continued.)

Table 1. (Continued.)

bat family/bat species	no. non-lethal studies	no. lethal studies	cave	IUCN Red List category	bat family/bat species	no. non-lethal studies	no. lethal studies	cave	IUCN Red List category
<i>Scatonycteris zenkeri</i> ^e	1	1			Neoromicia bemaity		1		
<i>Stenonycteris lanosus</i>	2	1	+		N. somalica		1		
<i>Epomops</i> sp.	2				<i>Nycticeinops crassulus</i>	1	1		
<i>Epomophorus</i> sp.	2	1			<i>N. schlieffeni</i>	1	3		
<i>Megalopterus</i> sp.	1				<i>Pipistrellus cf. hesperidus</i>	1	3		
<i>Myonycteris</i> sp.	1				P. inexpectatus	1			DD
Pteropodidae sp.	1				<i>P. kuhlii</i> ^k	3	2		
Rhinopomatidae (1/3 species sampled)					<i>P. nanulus</i>	1	3		
Rhinopoma microphyllum		1	+		P. raceyi		1		DD
Hipposideridae (11/21 species sampled, plus: 1 genus only)					<i>Pipistrellus rusticus</i>	1	2		
<i>Doryrhina cyclops</i>	2	6			<i>Pseudoromicia brunnea</i>	1	1		NT
<i>Hipposideros abae</i>	2		+		<i>P. tenuipinnis</i>	1	6		
<i>H. beatus</i>	1	2			<i>P. tenuipinnis/rendalli</i>		2		
<i>H. caffer</i> ^f	3	7	(+)		<i>Scotoecus hirundo</i>	1	1		
<i>H. fuliginosus</i> ^g	1	5	(+)		<i>Scotophilus dinganii</i> ^l	1	7		
<i>H. jonesi</i>	1	1	+	NT	<i>S. leucogaster</i> ^l	3	4		
<i>H. ruber</i> ^f	3	11	(+)	na	S. marovaza		1		
<i>Macronycteris commersonii</i> ^l	1	11	(+)	NT	<i>S. nigrita</i> ^l	2	3		
<i>M. gigas</i>	2	15	(+)		<i>S. nux</i>	2	2		
<i>M. vittatus</i>	1	3	(+)	NT	<i>S. viridis</i> ^l	2	2		
<i>Hipposideros caffer/ruber</i>	1	1			Vansonia rueppelli		1	(+)	
<i>Hipposideros</i> sp.	3	10			<i>Hypsugo</i> sp.		1		
Nycteridae (7/13 species sampled, plus: 1 genus only)					<i>Kerivoula</i> sp.	1	2		
Nycteris arge		1			<i>Myotis</i> sp.	1	4		
N. gambiensis		1	(+)		<i>Neoromicia</i> sp.	2	5		
N. grandis		1			<i>Nycticeinops</i> sp.		1		
<i>N. hispida</i>	2	5			<i>Pipistrellus</i> sp.	1	9		
N. macrotis		1	(+)		<i>Scotoecus</i> sp.	1	4		
<i>N. major</i>	1	1		DD	<i>Scotophilus</i> sp.	1	4		
<i>N. thebaica</i>	4	5	+		Vespertilionidae sp.	1	1		
<i>Nycteris</i> sp.	3	9							

(Continued.)

Table 1. (Continued.)

bat family/bat species	no. non-lethal studies	no. lethal studies	cave	IUCN Red List category	bat family/bat species	no. non-lethal studies	no. lethal studies	cave	IUCN Red List category
Megadermatidae (2/2 species sampled)									
<i>Cardioderma cor</i>	1	6	(+)		Emballonuridae (7/12 species sampled, plus: 1 genus only)	3	14	+	
<i>Lavia frons</i>	2	1			<i>Coleura afra</i>				
Rhinonycteridae (5/7 species sampled)									
Clootis perivali									
	1	1	+		C. kibomalandy		1	+	DD
Paratriaenops furculus									
	1	5	(+)		Paremballonura tiavato		1	(+)	
<i>Triaenops afer</i>	1	5	(+)		Saccolaimus peii		1		
<i>T. menamena</i>	2	2	+		<i>Taphozous hildegardeae</i>		2	+	EN
<i>T. persicus</i>	5	5	(+)		<i>T. mauritanus</i>	2	4	(+)	
					<i>T. perforatus</i>	2	1	(+)	
					<i>Taphozous sp.</i>	1	5		
Molossidae (26/44 species sampled, plus: 2 genus only, 1 family only)^m									
Mops aloysiabauidae									
<i>M. ansorgei</i>	1	3	(+)		<i>Rhinolophus alycyone</i>	1	3		
<i>M. atsinanana</i>	2	2	(+)		<i>R. blasii</i>		2	+	
M. brachypterus	1	2			<i>R. chirosoi</i> ^s	2	4	(+)	
<i>M. chapini</i>	4	14			R. danarensis		1	+	
M. congicus	1	1			<i>R. darlingi</i> ^f	1	3	+	
<i>M. condylurus</i>	1	1			<i>R. denti</i> ^f		3	+	
M. demonstrator	2	2			<i>R. eloquens</i> ^f	1	2	+	NT
<i>M. leucogaster</i> ⁿ	2	2			R. euryale	1		+	
<i>M. leucostigma</i>	1	2	(+)		<i>R. ferrumequinum</i>	1	1	+	
<i>M. major</i>	1	2			<i>R. fumigatus</i> ^f	3	1	+	
<i>M. midas</i>	3	3			<i>R. hildebrandtii</i> ^f		6	(+)	
<i>M. nanulus</i>	2	2			R. hipposideros		1	+	
M. niveiventer	1	15			<i>R. landeri</i> ^f	2	7	+	
<i>M. pumilus</i>	2	2			<i>R. simulator</i> ^f		4	+	
<i>M. pusillus</i> ^o	1	2			R. smithersi		1	+	NT
M. russatus	1	2			R. swinnyi ^f		1	+	
<i>M. thersites</i>	2	2			<i>Rhinolophus sp.</i>	3	14		
<i>Mormopterus acetabulosus</i>	1	1	+	EN	Miniopteridae (15/24 species sampled, plus: 1 genus only)ⁿ				
<i>M. francoismoutoui</i>	1	1	(+)		Miniopterus aelleni		1	+	
<i>M. jugularis</i>	2	2	(+)		<i>M. africanus</i>		4	+	
					<i>M. cf. ambohitrensis</i>		2	?+	

(Continued.)

Table 1. (Continued.)

bat family/bat species	no. non-lethal studies	no. lethal studies	cave	IUCN Red List category	bat family/bat species	no. non-lethal studies	no. lethal studies	cave	IUCN Red List category
<i>Myotis whiteleyi</i>	1				<i>M. fraterculus</i>		1	(+)	
<i>Otomops madagascariensis</i>		2	+		<i>M. gleni</i>		2	+	
<i>O. martienseni</i> ^q	3	11	(+)	NT	<i>M. griffithsi</i>		1	+	DD
<i>Sauromys petrophilus</i>		3	+		<i>M. griveaudi</i>		3	+	DD
<i>Tadarida aegyptiaca</i>	1	3	+		<i>M. inflatus</i>		8	+	
<i>Mops</i> sp.	7	6			<i>M. maghrebensis</i>	1		+	NT
<i>Tadarida</i> sp.	1	1			<i>M. majori</i>		1	+	
Molossidae sp.	1				<i>M. minor</i>	1	5	(+)	DD
					<i>M. mossambicus</i>	1		+	na
Cistugidae (0/2 species sampled)					<i>M. natalensis</i>		3	+	
Myzopodidae (0/2 species sampled)					<i>M. schreibersi</i> ^l	2	4	+	(NT/na)
					<i>M. sororculus</i>		2	+	
unidentified 'bat'		10			<i>Miniopterus</i> sp.	1	8		

^aProbably *Epomophorus minor*.^bIncludes *Megalossus azagayi*.^cOften as *Lissonycteris angolensis*.^dIncludes *Myonycteris leptodon*.^eIncludes *Scatonycteris occidentalis* and *Scatonycteris bergmansi*.^fMight include other *Rhinolophus* spp.^gSpecies group with high cryptic diversity.^hHigh cryptic diversity across genus.ⁱIncludes *Macronycteris gigas* and *Macronycteris vittatus*.^jProbably including *Miniopterus villiersi*.^kAs *Pipistrellus deserti*, and as *Pipistrellus aegyptius* (in [29]).^lMight include other *Scotophilus* spp.^mTaxonomically unresolved.ⁿProbably *Chaerephon pumilus*.^oProbably including *Chaerephon pumilus*.^pMight include *Otomops harrisoni*

we reviewed (35.6%), given that they only represent 13.3% of the 334 recognized African bat species (table 1). Sampling of the cave-dwelling *R. aegyptiacus* is explained by its role as a Marburg virus reservoir; this species was lethally sampled in 41 of 46 studies (greater than 8334 individuals). *Eidolon helvum* is tree-roosting and found in large and conspicuous colonies, which may partly explain its disproportionate sampling; 34 of the 52 studies performed lethal sampling (greater than 3992 individuals). High viral diversity has been documented in *E. helvum*, including novel viruses with evolutionary relationships to human pathogens (electronic supplementary material, tables S3, S4, S5b, S6). Yet, we found no documentation of spillover from this species, and whether comparable sampling effort would detect similar numbers of viruses in other species remains unknown.

Gregarious bat species, including cave-dwelling bats, do not appear to harbour more viruses than other bats [32,33], but might be more likely to share viruses with co-roosting species [33]. Of the 114 studies that provided information on study sites (70.4%), cave and cave-like habitats were preferred and sampled in 66 studies (57.9%). Accordingly, 46.1% of sampled species are cave-roosting. Indeed, caves may be opportunistically targeted for the ease of access to large numbers of bats, which has significant conservation implications given the sensitive nature of cave ecosystems [34]. Disturbance, including bat removal, may have unforeseeable consequences for local cave-dwelling bat colonies and ecosystem functioning, particularly when it leads to abandonment. Cave disturbance can also affect viral transmission dynamics: Marburg virus prevalence in *R. aegyptiacus* increased after a mass extermination triggered by the mineworker fears [35]. In the remaining 48 of the 114 studies that provided site information, bats were captured in forest and savanna habitats, agricultural lands, human settlements and non-natural situations (e.g. animal markets).

Data about life history (population estimates, reproductive patterns, age), movement ecology, and habitat use (including co-roosting) are crucial for understanding viral dynamics and the role of bats as reservoir hosts, and for the assessment of spillover risk [36–44]. This information was largely absent in the reviewed studies. Transmission risk may be predicted by ecological data and exacerbated in disturbed habitats [12,45], yet many studies did not report ecological data about captured species (77.8%), or the study site (29.6%). Life-history parameters such as reproductive cycles influence virus infection dynamics, and gradual loss of maternal immunity among young bats increases the number of susceptible individuals [14,15]. Population estimates and identifying the proportion of naive individuals with longitudinal data are thus important to understand viral maintenance and infection dynamics; a recent paper published after our meta-analysis cut-off date that details longitudinal sampling for coronaviruses in *Eidolon helvum* illustrates the strength of this approach [46]. We encourage gathering more comprehensive data on target species and provide a data collection framework (figure 2; electronic supplementary material, figure S9) that will facilitate context-specific goals and priority establishment for bat–virus studies.

(c) Importance of correct bat species identification

Many authors justify their taxonomic focus by naming ‘bats’ as important sources of emerging diseases. Correct bat species identification is key to reliable and reproducible studies on

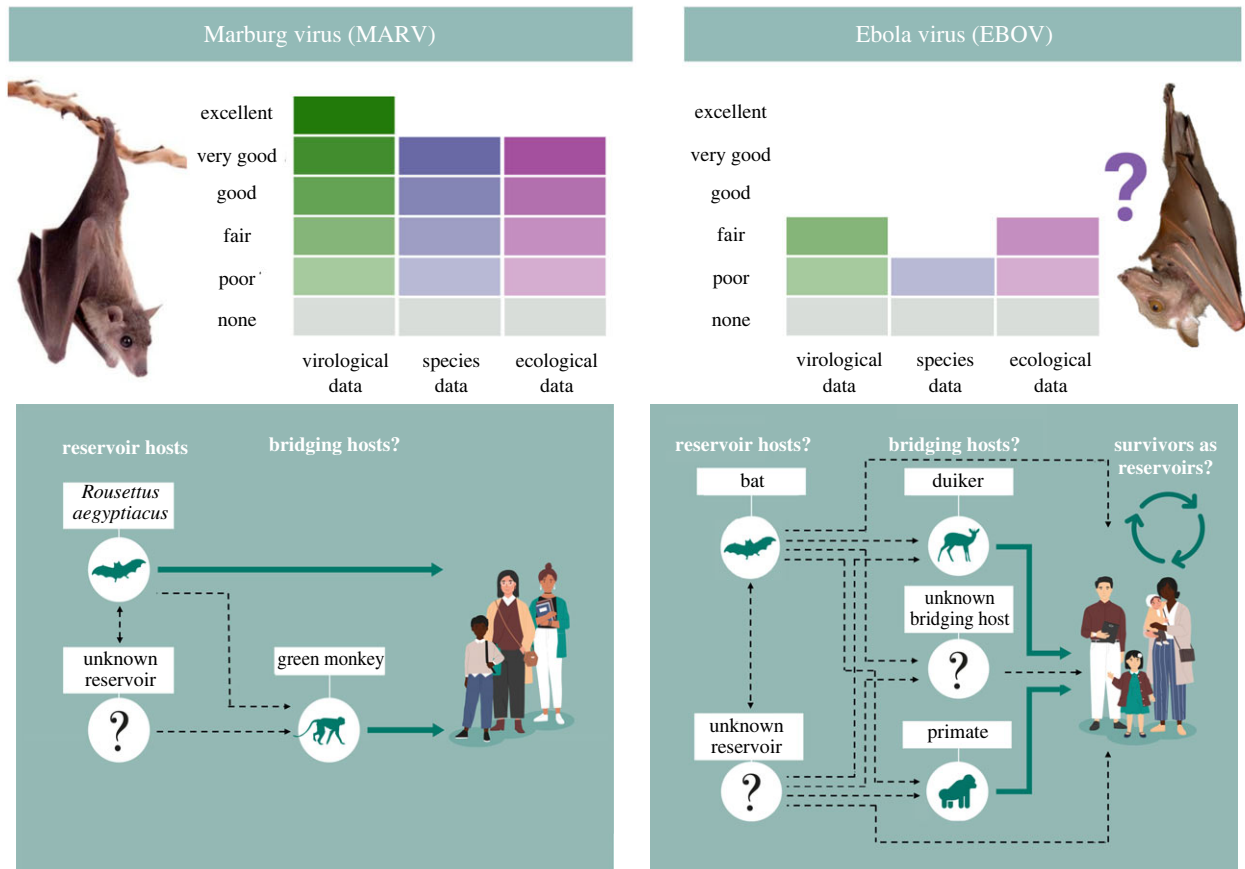
bat viruses. Assignment to the correct taxonomic suborders (Yinptero- and Yangochiroptera) instead of the still widely used but long-recognized incorrect ‘Mega’- and ‘Microchiroptera’ [49–52]; understanding of the basic phylogenetic relationships of bats, and identification at the species level, are important for any co-evolutionary conclusions about virus transmission between different bat families/species [53,54]. Likewise, correct usage of viral names is important [55], noting that significant viral taxonomic standardization has just occurred, resulting in the adoption of binomial nomenclature and many name changes.

Identifying (African) bats is not trivial due to cryptic diversity and the frequent lack of comprehensive and up-to-date keys. As many as 324 named bat species (and counting) are recognized in Africa [56,57]. In the 15 years since the last benchmark compilation of bat diversity [58], at least 47 species have been described for Africa based on new species discoveries and resolution of high cryptic diversity (e.g. [51,59–64]). Therefore, including descriptions of morphological, ecological, acoustic and genetic traits as necessary to describe a species, should be mandatory in future studies (figure 2). As was demonstrated in the multimammate mouse–Lassa Fever virus system and in the bat clade that includes Rhinolophidae and Hipposideridae, with ties to SARS-related CoVs, taxonomically knowing your host is critically important [54,65].

Forty-six studies in our database (28.4%) did not describe how bats were identified (figure 1b). Of the remaining studies, 72 used only morphology (44.4%), 10 only molecular methods (6.2%) and 34 both morphology and genetics (21.0%). Only two of all studies using morphology (1.9%) provided relevant measurements (e.g. forearm length), and 22 studies compared vouchers with museum specimens or cited identification keys (20.8%). The used identification keys, Rosevear [66], Bergmans [67–69] and Patterson & Wehala [70], provide a solid basis for morphological identification by experienced scientists, but these keys are partly outdated due to the numerous taxonomic updates since their publication. Because reference sequences are not available for all bat species, and many species-level errors exist in databases such as GenBank [71,72], DNA barcoding alone often does not allow identification to species level [61,63]. Eight of the 29 studies using DNA barcoding only identified specimens that tested positive for viruses (27.6%). Finally, in 128 bat–study combinations (14.7%), bats were identified only to genus (figure 1b), which, in fact, is preferable when species identification is uncertain.

Misidentifications and outdated species assignments are likely common in the reviewed papers, but often only evident to bat experts. Yet, species identification is of great importance for follow-up investigations, especially when a particular bat is determined to host a virus of interest. We argue for cross-disciplinary teams between virologists and bat taxonomists, ecologists, regional experts and in-country scientists [73] (often affiliated with natural history museums [74]), to ensure proper species assignment and provide metadata needed for assigning bat–virus relationships (figure 2). If the goals of a particular study require lethal sampling, investigators should adhere to ‘extended specimen’ holistic practices in which multiple types of samples and data are collected for each animal, should deposit their sampled bats in museums where they can be archived in perpetuity [74–77], and should link respective voucher specimens to pathogen studies in museum databases and in publications. In the rare instance that a bat

(a) assess quality of types of available data and address gaps as appropriate



(b) follow recommended sampling standards

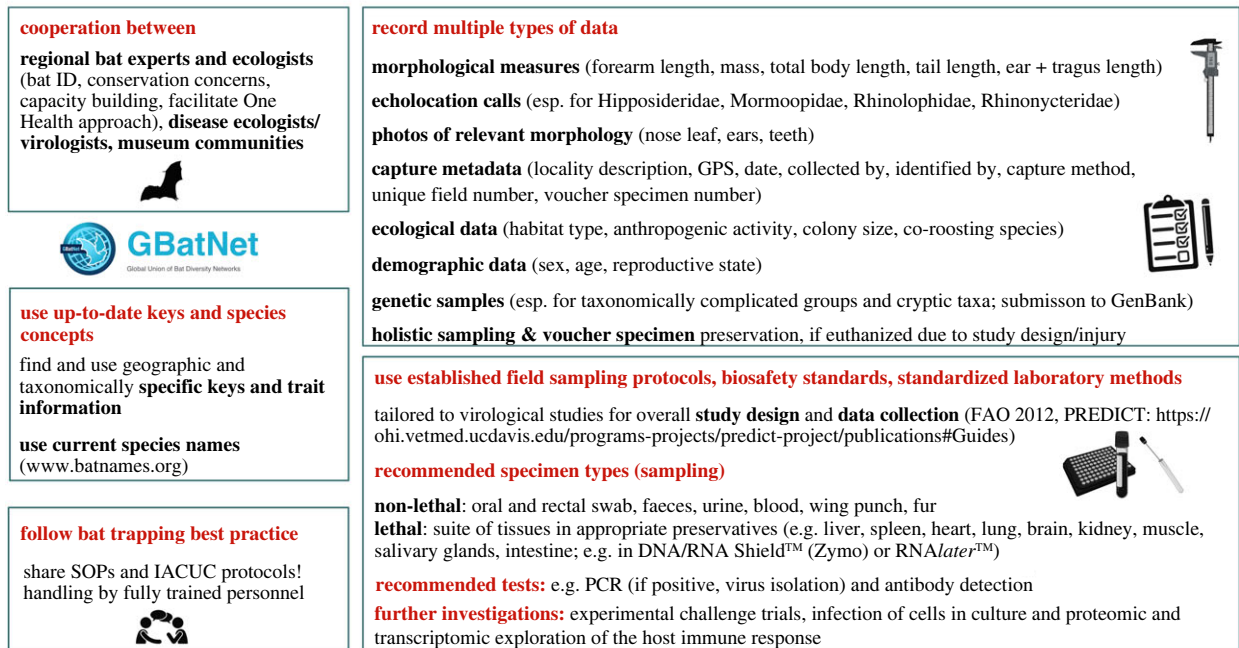


Figure 2. (a) Schematic approach to assess available knowledge on specific virus–host relationships (adapted from [47,48]). How well a system has been described is a function of: green: virological data (longitudinal/repeated versus one-off studies; virus isolated/full genomes obtained versus short sequences/inconclusive serology; choice of methods; experimental studies), blue: bat species data (accuracy of species identification; quantity and quality of collected data; sampling strategy), and purple: ecological/environmental metadata (description of habitat, roost site, colony size, life history data); examples shown are for filoviruses, indicating inadequate data on the putative host status of a given bat for EBOV (e.g. for virological data, no EBOV has yet been isolated from any bat, bat species data—confirmation of any bat species as a host is lacking) and high confidence for MARV. See electronic supplementary material, figure S9 for a more schematic illustration allowing qualitative scoring. (b) Recommended best practices for bat sampling and identification. Figure created using BioRender.com; *Epomops franqueti* image modified from photo 303584, (c) Jakob Fahr, some rights reserved (CC BY-NC), iNaturalist. *Rousettus aegyptiacus* modified from iStock photo.

inadvertently dies or is severely injured during sampling intended to be non-lethal, they should be vouchered, increasing the value of the data collected.

(d) Virus detection methods and associated challenges

Studies in our database focused on detecting RNA/DNA ($n = 91$), antibodies ($n = 29$), or both ($n = 40$; figure 1*d*), providing evidence of exposure to (but not necessarily replication of) a pathogen. Eleven studies detected RNA/DNA with next generation sequencing and 13 attempted virus isolation (figure 1*d*), 10 successfully. Most (96.75%) viral RNA/DNA detections in African bats are based on PCR amplification of specific partial sequences of conserved gene regions [78], which is efficient yet intrinsically biased, and provides little information on formal viral taxonomic placement or on infectivity, virulence or spillover potential. Serology yields higher prevalence as it indicates both current and past infection [5,79], but methods vary widely and cross-reactivity is problematic [16,80–82]. Virus isolation indicates replication and, depending on the sample type, strongly suggests shedding and intra-specific transmission, indicating host competence [83]. Indeed, isolation from non-terminal samples (urine, faeces, saliva, blood), themselves likely spillover routes, provides strong support for reservoir status. However, as illustrated in the filovirus discussion below, viral detection by PCR, serology and viral isolation are but pieces of evidence of variable quality through which host status can be suggested. As recently reviewed by others (e.g. [84–95]), identifying and studying reservoir hosts is not straightforward and ‘target’, ‘source’ and ‘maintenance’ populations may vary. Layered on top of other types of evidence, experimental challenge trials provide the strongest indication that a particular species is a confirmed reservoir host. Additional studies, including infection of cells in culture and proteomic and transcriptomic exploration of the host immune response (e.g. the display of immune tolerance) provide further support for host status and understanding the dynamics of infection [23,95,96].

(e) Geospatial sampling biases

Geospatial analysis of our dataset demonstrates significant scientific efforts in South Africa, Kenya, Ghana and Gabon (figure 1*e*), with many countries lacking published data. Sheer numbers of bats recorded from each country also varied widely in ways not reflective of relative country size, with the largest number of bats sampled in Gabon (figure 1*f*). Not surprisingly, bat viral survey locations appear to be at least practically driven by geopolitical and capacity considerations. At the family, genus, and especially species level, bat biodiversity in Africa is highly concentrated in equatorial, tropical sub-Saharan Africa [56]. Our geographical analysis (figure 1*g*) demonstrates that greater effort is required in many countries, especially those with zero sampling effort to date.

3. African bats and virus families important to human health

Viruses with clear importance to human health are generally clustered within four viral families: *Corona*-, *Paramyxo*-, *Rhabdo*- and *Filoviridae*, although evidence for viruses in many other lineages exists (table 2; electronic supplementary material,

tables S3 and S8). Definitive evidence for direct spillover from bat to human or spillover via a bridging host [152] between African bats and humans only exists for *Sosuga*, Marburg and Duvenhage virus. For the majority of viruses detected in African bats (22% of bat viral sequences worldwide through 2020), there is no documented human infection. Recent modelling studies have shown sampling effort to be the most important predictor of bat infection [91,153] (electronic supplementary material, text S6), reminding us that the absence of evidence may be heavily biased by which species are sampled.

The 24 African coronavirus studies we analysed reported RNA sequences related to human-relevant viruses, i.e. SARSr-CoV, MERSr-CoV, HCoV-NL63 and HCoV-229E (table 2; electronic supplementary material, text S3, table S3). Paramyxovirus RNA was detected in 45 African bat species (electronic supplementary material, text S4, table S4*a,b*). Nine studies reported potential zoonotic *Orthoparamyxovirinae* members, mainly in fruit bat species and based on serology or RNA sequences, with no documented spillover. Four studies detected sequences related to human mumps and to parainfluenza virus 2 and 4. Within this same viral subfamily (*Rubulavirinae*), *Sosuga* virus was initially isolated from a wildlife biologist and subsequently identified by PCR and full genome sequencing from *R. aegyptiacus* [136,154], whose host status is strongly supported by experimental infection studies [155]. *Rabies virus* (RABV) and the 16 rabies-related *Lyssavirus* species in the family *Rhabdoviridae* cause the fatal disease rabies. Due to very low RNA detectability outside of brain tissue, most surveillance studies prefer serology (electronic supplementary material, text S5, table S5*a,b*). In Africa, rabies-related lyssaviruses have each generally been associated with a different bat species, yet knowledge on lyssavirus epidemiology and ecology in African bats is highly limited [156].

The greatest attention to bat viruses in Africa has focused on filoviruses. Of the four genera encountered in bats, only two occur in Africa (*Orthoebolavirus* and *Orthomarburgvirus*). *Orthomarburgvirus* is restricted to Africa and contains Marburg (MARV) and Ravn virus. *Orthoebolaviruses* occur in Africa and Southeast Asia (electronic supplementary material, text S6, table S6*a–d*). They include six species: EBOV, Bundibugyo, Sudan, Tai Forest, Reston and Bombali [157]. Both the orthomarburg- and several orthoebolaviruses cause high mortality rates in humans (table 2). In our dataset, sampling for the *Filoviridae* was done in 23.5% ($n = 38$) of the 162 studies, and accounted for nearly one-third (29.0%) of all confirmed captures ($n = 24\,875$) and almost half of lethally sampled bats ($n = 19\,089$). Sampling efforts for orthomarburg- ($n = 17\,750$) and orthoebolaviruses combined ($n = 18\,574$) are similar, but the results and associated information content could hardly differ more (figure 2*a*; electronic supplementary material, text S6).

(a) Contrasting examples: information on bats as reservoir hosts of Marburg and Ebola virus

The first detection of MARV RNA and antibodies in bats [158] was followed 2 years later by virus isolation from *R. aegyptiacus* [17]; epidemiological ties to caves directed early efforts towards this populous cave-dwelling bat [28]. Isolation has subsequently been successfully repeated [13,14,18,26,35,159]. That *R. aegyptiacus* is a reservoir host of MARV [159] is based on: (1) high genetic similarity between

Table 2. Zoonotic viruses with known or potential relation to human disease and evidence for a bat origin or potential relation to African bats.

virus family	virus genus/ subfamily	virus	number of human infections/fatalities	zoonotic source of human infection	virus evidence from bats	bat-human transmission shown	references
Coronaviridae	<i>Alphacoronavirus</i>	HCov-229E	unknown, mostly mild respiratory disease	possibly camelids (endemic in humans)	possible evolutionary origin in hippo- bats (PCR evidence)	no	[97–103]
		HCov-NL63	unknown, mostly mild respiratory disease	unknown (endemic in humans)	possible evolutionary origin in rhinonycterid or hipposiderid bats (PCR evidence)	no	[98,100,104]
Filoviridae	<i>Orthomarburgvirus</i>	Marburg virus	498/397 (1967–2023)	non-human	<i>R. aegyptiacus</i> , considered as reservoir host based on PCR and virus isolation	yes	[15,17,18,21,22,26,105– 107]
		Ebola, Bundibugyo, Sudan, Tai Forest virus	34 849/15 343 (1976– 2023)	non-human primates, duiker, possibly bats	natural reservoir unknown; PCR positives (<i>E.</i> <i>franqueti</i> , <i>H. monstrosus</i> , <i>M. torquata</i>), serological evidence from several African bats	no	[21,31,80,82,105,108– 122]
Flaviviridae	<i>Orthoflavivirus</i>	Dengue-2 virus	estimated 400 million per year/40 000 per year	mosquitoes	serological evidence from <i>M. pumilus</i> , <i>M.</i> <i>condylurus</i> , <i>E. labiatus</i>	no	[123,124]
		West Nile virus	56 569/2773 (1999– 2022)	mosquitoes	serological evidence from <i>E. helvum</i> and <i>E.</i> <i>labiatus</i>	no	[124,125]
Nairoviridae	<i>Orthonaïrovirus</i>	Yellow fever virus	estimated 200 000 per year/30 000 per year	mosquitoes	serological evidence from <i>R. aegyptiacus</i>	no	[124,126]
		Crimean Congo haemorrhagic fever virus or CCHF-like viruses	estimated 10 000– 15 000 per year/500 per year	ticks, livestock	serological evidence in 10 African bat species for CCHFV or a closely related virus belonging to the CCHFV serotype	no	[127–131]
Orthomyxoviridae	<i>Alphainfluenzavirus</i>	Dugbe virus	unknown, moderate clinical manifestation	ticks, livestock	serological evidence from <i>C. afro</i>	no	[131,132]
		Avian influenza A (H9)	H9N2 caused > 100 infections and small number of deaths	poultry	serological evidence for avian influenza H9 in <i>E. helvum</i>	no	[133–135]

(Continued.)

Table 2. (Continued.)

virus family	virus genus/ subfamily	virus	number of human infections/fatalities	zoonotic source of human infection	virus evidence from bats	bat–human transmission shown	references
Paramyxoviridae	Orthorubulavirus	Sosuga virus	1/0	<i>R. aegyptiacus</i>	<i>R. aegyptiacus</i> (PCR evidence)	yes	[136]
	Pararubulavirus	Achimota virus 1 & 2	3 of 443 seropositive for AchPV2	unknown	serological evidence for both viruses in <i>E. helvum</i>	no	[137]
Phenuiviridae	Phlebovirus	Rift Valley fever virus	4641/957 (2000–2016); no systematic surveillance	mosquitoes, livestock	serological evidence from <i>R. aegyptiacus</i> , <i>E. labiatus</i> , virus isolation from <i>L. frons</i> , <i>H. caffer</i> , <i>Myotis</i> sp.	no	[124,131,138,139]
	Ledantevirus	Kumasi rhabdovirus	6 of 163 seropositive	possibly <i>E. helvum</i>	KRV isolated from <i>E. helvum</i>	possibly	[140]
Rhabdoviridae	Lyssavirus	Mokola virus	2/2	unknown	never isolated from bats; serological evidence uncertain (cross reaction with Lagos bat virus); other potential reservoirs are African shrews and insectivorous rodents	no	[141–146]
	Lyssavirus	Duvenhage virus	3/3	African bats	African bats (e.g. virus isolation from <i>N. thebaica</i>)	yes	[141,147–150]
Spennareoviridae	Orthoreovirus	Pteropine orthoreovirus	infections may be common in Southeast Asia, no known deaths	Asian <i>Pteropus</i> sp.	Asian <i>Pteropus</i> sp., African <i>Myonycteris angolensis ruwenzorii</i> (PCR evidence)	yes	[151]
	Alphavirus	Babanki virus	unknown	mosquitoes	serological evidence from <i>E. labiatus</i> , <i>R. aegyptiacus</i>	no	[124]

bat and human virus isolates (99.3%; [13]); (2) serological findings of MARV-specific antibodies [17,21,22,159]; (3) seasonal infection peaks that match spillover to humans [14,19], and (4) experimental infection of *R. aegyptiacus* without overtly apparent symptoms [15,159], with a transcriptional host response that indicates immunological tolerance [23], and with oral, faecal and urine virus shedding [15,24,159–161], likely the spillover route [20,25]. The relation between MARV and *R. aegyptiacus* as a reservoir host is based on high-quality virological, species and ecological/environmental information content (figure 2a), and has the highest scientific support of all bat–virus relationships in the 162 reviewed papers. Nevertheless, several other bat species also tested positive for MARV (electronic supplementary material, table S6b–d; [21,22,80,159]), interpreted as incidental spillover between bat species [159]. Given that PCR and serological evidence for MARV exists in two insectivorous bat species (*Miniopterus inflatus* and *Rhinolophus eloquens*) (electronic supplementary material, table S6b; [22]), further research on the role of these and other (likely cave-roosting) species is needed.

By contrast, *Orthoebolavirus* nucleic acid detections in bats are rare, with no virus isolation (figure 2b; electronic supplementary material, text S6, table S6c). Efforts have largely focused on EBOV within fruit bats (based upon early detection in *Epomops franqueti*, *Hypsignathus monstrosus*, and *Myonycteris torquata* [31,162]), with additional sampling in a variety of other bats and vertebrates [91,116,157,163]. A partial EBOV genome was reported in 2019 in the popular press from *Miniopterus inflatus* in Liberia [164] (which is likely the West African *M. nimbae*, newly described several months later [165]). Remarkably, RNA detection of the recently discovered Bombali virus [157], which is probably not human-relevant [166,167], has been PCR-confirmed five times [168–171] in two species of free-tailed bats (erroneously ‘fruit bats’ in [167]) across four countries. Other links between bats and orthoebolaviruses are largely based on serology (electronic supplementary material, table S6d; [163,172,173]).

Early experimental infection studies with EBOV demonstrated replication with seroconversion in all three bat species tested (*Mops condylurus*, *M. pumilus* and *Epomophorus wahlbergi*), with viral shedding in the faeces in *E. wahlbergi* [174]. Infection of *R. aegyptiacus* with five viruses in the genus *Orthoebolavirus* (except Bombali) resulted in injection-site replication only, except for Sudan virus, which replicated without shedding [160]; *R. aegyptiacus* is a dead-end host for these orthoebolaviruses. Additional evidence for bats as reservoir hosts for orthoebolaviruses comes from cell line studies, which suggest differential susceptibility of bat species to infection [175,176], including *E. helvum*, whose cells are refractory to viral entry [175,177]. In particular, immune tolerance of EBOV and Bombali virus has been documented in *Mops condylurus* [176,178,179], which displays little histopathology when infected [171]. This body of evidence, along with modelling studies (electronic supplementary material, text S6), point to forest-dwelling bats as likely *Orthoebolavirus* reservoir hosts. However, more recent studies indicate a more complex scenario with potential bridging hosts and environmental influences, highlighting the need for multidisciplinary approaches [153,180–189]. Direct transmission of EBOV from bats to humans has been posited in two theoretical scenarios [112,162], without evidence. By contrast, there is convincing

evidence for EBOV spillover from symptomatic great apes and potentially duikers to humans [190–194] (figure 2a; electronic supplementary material, text S6). Importantly, spillovers have exclusively been documented within the distribution ranges of chimpanzees and bonobos (electronic supplementary material, text S6, figure S6), which may have had contact with the natural reservoir(s) of EBOV [195,196] when feeding at the same fruit trees, through consuming infected animals [197] or even through contact with aquatic or semi-aquatic reservoir hosts [198]. Molecular evidence from recent EBOV outbreaks suggests a human survivor origin rather than zoonotic transmission [199,200], raising the possibility that some previous outbreaks (including the 2013 West African outbreak) are not from spillover [201]. Recent findings continue to support bats as key players in the EBOV story, but the epidemiology is complex and many gaps remain in our understanding (figure 2a; electronic supplementary material, text S6).

4. Communication of virological findings in bats and conservation implications

‘When a man is hated in the village, he will be accused of raising dust even when he jumps into a pool of water’ - Ugandan proverb

Bats are important ecosystem service providers and many, including African species, are under significant threat (e.g. habitat encroachment and loss, degradation, hunting, etc.) [9,10,202]. Bats are already widely perceived to be dangerous [203] and the perception that spillover from bats poses a significant risk to humans increases the threat of culling or roost site destruction. For example, portrayal of ‘bats’ as a definitive spillover source of orthoebolaviruses is common across the surveyed literature, with consequences for public perception, conservation, as well as other research sectors [204] and during outbreaks, epidemiological messaging runs the risk of characterizing bats as ‘epidemic villains’ [204–206].

Precision and tone of language and data interpretation are critical, especially expressions such as ‘public health concern’, ‘threat to humans’, ‘spillovers with fatal consequences’, or ‘reservoirs of many recently emerged zoonotic viruses’, all of them present in the reviewed literature. At times, indirect evidence was used to infer scenarios and in the most extreme cases, authors linked viruses to bats simply based on their presence in an area [162,207]. In our reviewed papers, 53.1% of the abstracts explicitly framed bats as a threat to human wellbeing; only 19.1% explicitly stated the contrary and the rest made no statement. This pattern recurred in the discussions (dangerous: 62.3%, non-dangerous: 0.8%). Potential transmission pathways were rarely specified in the abstract (6.1%), and only occasionally addressed in the discussion (32.1%). Numbers of human deaths were only reported in a single abstract and 7.4% of discussions, and ecosystem services barely at all (three abstracts and 4.9% of discussions). Only one study expressed concern about misguided consequences for bats.

The strengths and weaknesses of specific scientific findings are difficult to understand for scientists, and even more so for the public. Disease-related speculation not supported by strong evidence but shaped by bat–virus catchphrases lacking scientific integrity undermines decades of conservation efforts [208]. Careful, scientifically correct

wording is crucial for how results are disseminated to and by the press [209,210], informing the press and the public about the relation of bats and viruses based on scientific information content, while considering the challenges of contextualizing scientific findings from a non-expert audience perspective. Fortunately, efforts aimed at mitigating bat–human interactions can successfully balance bat conservation and human health [159]. Indeed, conservation efforts that target habitat preservation are linked to spillover prevention [12,211–213]. Balanced messaging to prevent extirpation and promote conservation needs to be delivered through awareness raising campaigns, targeting and led by local communities and authorities [155,214–220].

5. Conclusion and recommendations

Despite the large body of the literature and intensive research efforts, evidence for links between African bats and human-relevant disease is sparse. Few examples of bat surveillance efforts translate into the frequently declared goal, i.e. the prediction or prevention of spillover. Considering the risks emerging zoonotic diseases pose, a taxonomically broad One Health approach at the human–animal–ecosystem interface, with multidisciplinary and local team members, should be deployed (figure 2b). Efforts to identify potential bridging hosts of bat-borne viruses and to identify human behaviour that fosters spillover are needed. Additionally, it is crucial to explicitly distinguish between the evolutionary origin of a virus (e.g. *Betacoronaviruses* in bats), and the actual reservoir and/or spillover source. Current global initiatives (e.g. the Global Union of Bat Diversity Networks [221]) are actively working to strengthen, standardize and share research protocols and can connect non-bat experts with potential collaborators around the world. For host–virus systems identified for further study based upon human health risk or other research priorities, assessing the quality and types of available virological, species, and ecological data will facilitate the identification of knowledge gaps and direct subsequent efforts to fill those gaps. Attending to and prioritizing the bat conservation implications of bat–virus studies and the sociological elements at the bat–human interface will be crucial for continued studies of potential zoonoses within the One Health context.

Data accessibility. Data used in this study are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.c866t1gcx> [222]. Supplementary material is available online [223].

References

- Allen T, Murray KA, Zambrana-Torrel C, Morse SS, Rondinini C, Di Marco M, Breit N, Olival KJ, Daszak P. 2017 Global hotspots and correlates of emerging zoonotic diseases. *Nat. Commun.* **8**, 1124. (doi:10.1038/s41467-017-00923-8)
- Jones KE, Patel NG, Levy MA, Storeygard A, Balk D, Gittleman JL, Daszak P. 2008 Global trends in emerging infectious diseases. *Nature* **451**, 990–993. (doi:10.1038/nature06536)
- Morens DM, Folkers GK, Fauci AS. 2004 The challenge of emerging and re-emerging infectious diseases. *Nature* **430**, 242–249. (doi:10.1038/nature02759)
- Khan SA, Imtiaz MA, Islam MM, Tanzin AZ, Islam A, Hassan MM. 2022 Major bat-borne zoonotic viral epidemics in Asia and Africa: a systematic review and meta-analysis. *Vet. Med. Sci.* **8**, 1787–1801. (doi:10.1002/vms3.835)
- Wang L-F, Anderson DE. 2019 Viruses in bats and potential spillover to animals and humans. *Curr. Opin. Virol.* **34**, 79–89. (doi:10.1016/j.coviro.2018.12.007)
- Zhou P *et al.* 2020 A pneumonia outbreak associated with a new coronavirus of probable bat origin. *Nature* **579**, 270–273.
- Dobson AP *et al.* 2020 Ecology and economics for pandemic prevention. *Science* **369**, 379–381. (doi:10.1126/science.abc3189)
- Gibb R, Albery GF, Mollentze N, Eskew EA, Brierley L, Ryan SJ, Seifert SN, Carlson CJ. 2022 Mammal virus diversity estimates are unstable due to accelerating discovery effort. *Biol. Lett.* **18**, 20210427. (doi:10.1098/rsbl.2021.0427)

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9. Ramírez-Francel LA, García-Herrera LV, Losada-Prado S, Reinoso-Flórez G, Sánchez-Hernández A, Estrada-Villegas S, Lim BK, Guevara G. 2022 Bats and their vital ecosystem services: a global review. *Integr. Zool.* **17**, 2–23. (doi:10.1111/1749-4877.12552)
10. Aziz SA *et al.* 2021 The critical importance of Old World fruit bats for healthy ecosystems and economies. *Front. Ecol. Evol.* **9**, 641411. (doi:10.3389/fevo.2021.641411)
11. Bruno L, Nappo MA, Ferrari L, Di Lecce R, Guarnieri C, Cantoni AM, Corradi A. 2022 Nipah virus disease: epidemiological, clinical, diagnostic and legislative aspects of this unpredictable emerging zoonosis. *Animals (Basel)* **13**, 159. (doi:10.3390/ani13010159)
12. Eby P, Peel AJ, Hoegh A, Madden W, Giles JR, Hudson PJ, Plowright RK. 2022 Pathogen spillover driven by rapid changes in bat ecology. *Nature* **613**, 1–5. (doi:10.1038/s41586-022-05506-2)
13. Towner JS *et al.* 2009 Isolation of genetically diverse Marburg viruses from Egyptian fruit bats. *PLoS Pathog.* **5**, e1000536. (doi:10.1371/journal.ppat.1000536)
14. Amman BR *et al.* 2012 Seasonal pulses of Marburg virus circulation in juvenile *Rousettus aegyptiacus* bats coincide with periods of increased risk of human infection. *PLoS Pathog.* **8**, e1002877. (doi:10.1371/journal.ppat.1002877)
15. Pawęska JT, Van Vuren PJ, Kemp A, Storm N, Grobelaar AA, Wiley MR, Palacios G, Markotter W. 2018 Marburg virus infection in Egyptian rousette bats, South Africa, 2013–2014. *Emerg. Infect. Dis.* **24**, 1134–1137. (doi:10.3201/eid2406.172165)
16. Schuh AJ, Amman BR, Sealy TS, Flietstra TD, Guito JC, Nichol ST, Towner JS. 2019 Comparative analysis of serologic cross-reactivity using convalescent sera from filovirus-experimentally infected fruit bats. *Sci. Rep.* **9**, 6707. (doi:10.1038/s41598-019-43156-z)
17. Towner JS *et al.* 2007 Marburg virus infection detected in a common African bat. *PLoS ONE* **2**, e764. (doi:10.1371/journal.pone.0000764)
18. Storm N, Jansen Van Vuren P, Markotter W, Paweska JT. 2018 Antibody responses to Marburg virus in Egyptian rousette bats and their role in protection against infection. *Viruses* **10**, 73. (doi:10.3390/v10020073)
19. Hayman DTS. 2015 Biannual birth pulses allow filoviruses to persist in bat populations. *Proc. R. Soc. B* **282**, 20142591. (doi:10.1098/rspb.2014.2591)
20. Adjemian J *et al.* 2011 Outbreak of Marburg hemorrhagic fever among miners in Kamwenge and Ibanda Districts, Uganda, 2007. *J. Infect. Dis.* **204**, S796–S799. (doi:10.1093/infdis/jir312)
21. Pourrut X, Souris M, Towner J, Rollin P, Nichol S, Gonzalez J-P, Leroy E. 2009 Large serological survey showing cocirculation of Ebola and Marburg viruses in Gabonese bat populations, and a high seroprevalence of both viruses in *Rousettus aegyptiacus*. *BMC Infect. Dis.* **9**, 159. (doi:10.1186/1471-2334-9-159)
22. Swanepoel R *et al.* 2007 Studies of reservoir hosts for Marburg virus. *Emerg. Infect. Dis.* **13**, 1847–1851. (doi:10.3201/eid1312.071115)
23. Guito JC *et al.* 2021 Asymptomatic infection of Marburg virus reservoir bats is explained by a strategy of immunoprotective disease tolerance. *Curr. Biol.* **31**, 257–270. (doi:10.1016/j.cub.2020.10.015)
24. Amman BR *et al.* 2015 Oral shedding of Marburg virus in experimentally infected Egyptian fruit bats (*Rousettus aegyptiacus*). *J. Wildl. Dis.* **51**, 113–124. (doi:10.7589/2014-08-198)
25. Amman BR, Schuh AJ, Albariño CG, Towner JS. 2021 Marburg virus persistence on fruit as a plausible route of bat to primate filovirus transmission. *Viruses* **13**, 2394. (doi:10.3390/v13122394)
26. Amman BR *et al.* 2020 Isolation of Angola-like Marburg virus from Egyptian rousette bats from West Africa. *Nat. Commun.* **11**, 510. (doi:10.1038/s41467-020-14327-8)
27. Schuh AJ, Amman BR, Sealy TK, Spengler JR, Nichol ST, Towner JS. 2017 Egyptian rousette bats maintain long-term protective immunity against Marburg virus infection despite diminished antibody levels. *Sci. Rep.* **7**, 8763. (doi:10.1038/s41598-017-07824-2)
28. Pigott DM, Golding N, Mylne A, Huang Z, Weiss DJ, Brady OJ, Kraemer MU, Hay SI. 2015 Mapping the zoonotic niche of Marburg virus disease in Africa. *Trans. R. Soc. Trop. Med. Hyg.* **109**, 366–378. (doi:10.1093/trstmh/trv024)
29. El Taweel E, Kandeil A, Barakat A, Alfarooq Rabiee O, Kayali G, Ali MA. 2020 Diversity of astroviruses circulating in humans, bats, and wild birds in Egypt. *Viruses* **12**, 485. (doi:10.3390/v12050485)
30. International Union for Conservation of Nature and Natural Resources. 2023 IUCN Red List of Threatened Species. See <https://www.iucnredlist.org/en> (accessed 2 August 2023).
31. Leroy EM *et al.* 2005 Fruit bats as reservoirs of Ebola virus. *Nature* **438**, 575–576. (doi:10.1038/438575a)
32. Luis AD, O'shea TJ, Hayman DTS, Wood JLN, Cunningham AA, Gilbert AT, Mills JN, Webb CT. 2015 Network analysis of host–virus communities in bats and rodents reveals determinants of cross-species transmission. *Ecol. Lett.* **18**, 1153–1162. (doi:10.1111/ele.12491)
33. Willoughby A, Phelps K, Consortium P, Olival K. 2017 A comparative analysis of viral richness and viral sharing in cave-roosting bats. *Diversity* **9**, 35. (doi:10.3390/d9030035)
34. Furey N, Racey P. 2016 Conservation ecology of cave bats. In *Bats in the Anthropocene: conservation of bats in a changing world* (eds C Voigt, T Kingston), pp. 463–500. Cham, Switzerland: Springer.
35. Amman BR *et al.* 2014 Marburgvirus resurgence in Kitaka Mine bat population after extermination attempts, Uganda. *Emerg. Infect. Dis.* **20**, 1761–1764. (doi:10.3201/eid2010.140696)
36. Carlson CJ *et al.* 2021 The future of zoonotic risk prediction. *Phil. Trans. R. Soc. B* **376**, 20200358. (doi:10.1098/rstb.2020.0358)
37. Guyton JA, Brook CE. 2015 African bats: conservation in the time of Ebola. *Therya* **6**, 69–88. (doi:10.12933/therya-15-244)
38. Han BA, Schmidt JP, Alexander LW, Bowden SE, Hayman DT, Drake JM. 2016 Undiscovered bat hosts of filoviruses. *PLoS Negl. Trop. Dis.* **10**, e0004815. (doi:10.1371/journal.pntd.0004815)
39. Reed Hranac C, Marshall JC, Monadjem A, Hayman DTS. 2019 Predicting Ebola virus disease risk and the role of African bat birthing. *Epidemics* **29**, 100366. (doi:10.1016/j.epidem.2019.100366)
40. Seltmann A, Corman V, Rasche A, Drosten C, Czirkák GÁ, Bernard H, Struebig M, Voigt C. 2017 Seasonal fluctuations of astrovirus, but not coronavirus shedding in bats inhabiting human-modified tropical forests. *EcoHealth* **14**, 272–284. (doi:10.1007/s10393-017-1245-x)
41. Guy C, Ratcliffe JM, Mideo N. 2020 The influence of bat ecology on viral diversity and reservoir status. *Ecol. Evol.* **10**, 5748–5758. (doi:10.1002/ece3.6315)
42. Albery GF, Eskew EA, Ross N, Olival KJ. 2020 Predicting the global mammalian viral sharing network using phylogeography. *Nat. Commun.* **11**, 2260. (doi:10.1038/s41467-020-16153-4)
43. Albery GF *et al.* 2021 The science of the host–virus network. *Nat. Microbiol.* **6**, 1483–1492. (doi:10.1038/s41564-021-00999-5)
44. Nieto-Rabiela F, Suzán G, Wiratsudakul A, Rico-Chávez O. 2018 Viral metacommunities associated to bats and rodents at different spatial scales. *Community Ecol.* **19**, 168–175. (doi:10.1556/168.2018.19.2.9)
45. Becker DJ *et al.* 2022 Optimising predictive models to prioritise viral discovery in zoonotic reservoirs. *Lancet Microbe* **3**, e625–e637. (doi:10.1016/S2666-5247(21)00245-7)
46. Montecino-Latorre D *et al.* 2022 Seasonal shedding of coronavirus by straw-colored fruit bats at urban roosts in Africa. *PLoS ONE* **17**, e0274490. (doi:10.1371/journal.pone.0274490)
47. Guyatt GH, Oxman AD, Schunemann HJ, Tugwell P, Knottnerus A. 2011 GRADE guidelines: a new series of articles in the *Journal of Clinical Epidemiology*. *J. Clin. Epidemiol.* **64**, 380–382. (doi:10.1016/j.jclinepi.2010.09.011)
48. Guyatt GH, Oxman AD, Vist GE, Kunz R, Falck-Ytter Y, Alonso-Coello P, Schunemann HJ, Group GW. 2008 GRADE: an emerging consensus on rating quality of evidence and strength of recommendations. *BMJ* **336**, 924–926. (doi:10.1136/bmj.39489.470347.AD)
49. Amador LI, Moyers Arévalo RL, Almeida FC, Catalano SA, Giannini NP. 2018 Bat systematics in the light of unconstrained analyses of a comprehensive molecular supermatrix. *J. Mammal Evol.* **25**, 37–70. (doi:10.1007/s10914-016-9363-8)
50. Kruskop SV, Artyushin IV. 2021 Chiropteran (Chiroptera; Mammalia) taxonomy in light of modern methods and approaches. *Rus. J. Theriol.* **20**, 111–128. (doi:10.15298/rusjtheriol.20.2.01)
51. Almeida FC, Simmons NB, Giannini NP. 2020 A species-level phylogeny of Old World fruit bats with a new higher-level classification of the family Pteropodidae. *Am. Museum Novitates* **3950**, 1–24. (doi:10.5531/sd.sp.39)
52. Teeling EC, Springer MS, Madsen O, Bates P, O'Brien SJ, Murphy WJ. 2005 A molecular phylogeny for bats illuminates biogeography and the fossil record.

- Science* **307**, 580–584. (doi:10.1126/science.1105113)
53. Puechmaille SJ *et al.* 2021 Misconceptions and misinformation about bats and viruses. *Int. J. Infect. Dis.* **105**, 606–607. (doi:10.1016/j.ijid.2021.02.097)
 54. Foley NM, Thong VD, Soisook P, Goodman SM, Armstrong KN, Jacobs DS, Puechmaille SJ, Teeling EC. 2015 How and why overcome the impediments to resolution: lessons from rhinolophid and hipposiderid Bats. *Mol. Biol. Evol.* **32**, 313–333. (doi:10.1093/molbev/msu329)
 55. Zerbini FM *et al.* 2022 Differentiating between viruses and virus species by writing their names correctly. *Arch. Virol.* **167**, 1231–1234. (doi:10.1007/s00705-021-05323-4)
 56. Van Cakenberghe V, Seamark EC. 2021 *African Chiroptera Report*. Pretoria, Republic of South Africa: AfricanBats NPC.
 57. Simmons N, Cirranello A. 2020 Bat species of the world: a taxonomic and geographic database. See <https://batnames.org/> (accessed July 2020).
 58. Simmons NB. 2005 Order Chiroptera. In *Mammal species of the world: a taxonomic and geographic reference, vol. 1* (eds DE Wilson, DM Reeder), pp. xxxviii+743. Baltimore, MD: John Hopkins University Press.
 59. Vallo P, Guillén-Servent A, Benda P, Pires DB, Koubek P. 2008 Variation of mitochondrial DNA in the *Hipposideros caffer* complex (Chiroptera: Hipposideridae) and its taxonomic implications. *Acta Chiropterol.* **10**, 193–206. (doi:10.3161/150811008X414782)
 60. Demos TC, Webala PW, Kerbis Peterhans JC, Goodman SM, Bartonjo M, Patterson BD. 2019 Molecular phylogenetics of slit-faced bats (Chiroptera: Nycteridae) reveal deeply divergent African lineages. *J. Zool. System. Evol. Res.* **00**, 1–14. (doi:10.1111/jzs.12313)
 61. Dool SE *et al.* 2016 Nuclear introns outperform mitochondrial DNA in inter-specific phylogenetic reconstruction: lessons from horseshoe bats (Rhinolophidae: Chiroptera). *Mol. Phylogenet. Evol.* **97**, 196–212. (doi:10.1016/j.ympev.2016.01.003)
 62. Hutterer R, Decher J, Monadjem A, Astrin J. 2019 A new genus and species of vesper bat from West Africa, with notes on *Hypsugo*, *Neoromicia*, and *Pipistrellus* (Chiroptera: Vespertilionidae). *Acta Chiropterol.* **21**, 1–22. (doi:10.3161/15081109ACC2019.21.1.001)
 63. Nesi N, Kadjo B, Pourrut X, Leroy E, Pongombo Shongo C, Cruaud C, Hassanin A. 2013 Molecular systematics and phylogeography of the tribe Myonycterini (Mammalia, Pteropodidae) inferred from mitochondrial and nuclear markers. *Mol. Phylogenet. Evol.* **66**, 126–137. (doi:10.1016/j.ympev.2012.09.028)
 64. Puechmaille SJ, Allegrini B, Benda P, Gürün K, Šrámek J, Ibañez C, Juste J, Bilgin R. 2014 A new species of the *Miniopterus schreibersii* species complex (Chiroptera: Miniopteridae) from the Maghreb Region, North Africa. *Zootaxa* **3794**, 108–124. (doi:10.11646/zootaxa.3794.1.4)
 65. Gryseels S, Baird SJE, Borremans B, Makundi R, Leirs H, De Bellocq JG. 2017 When viruses don't go viral: the importance of host phylogeographic structure in the spatial spread of arenaviruses. *PLoS Pathog.* **13**, e1006073. (doi:10.1371/journal.ppat.1006073)
 66. Rosevear DR. 1965 *The bats of West Africa*. London, UK: Trustees of the British Museum (Natural History).
 67. Bergmans W. 1990 Taxonomy and biogeography of African fruit bats (Mammalia, Megachiroptera). 3. The genera *Scotonycteris* Matschie, 1894, *Casinycteris* Thomas, 1910, *Pteropus* Brisson, 1762, and *Eidolon* Rafinesque, 1815. *Beaufortia* **40**, 111–177.
 68. Bergmans W. 1997 Taxonomy and biogeography of African fruit bats (Mammalia, Megachiroptera). 5. The genera *Lissonycteris* Andersen, 1912, *Myonycteris* Matschie, 1899 and *Megaloglossus* Pagenstecher, 1885; general remarks and conclusions; annex: key to all species. *Beaufortia* **47**, 11–90.
 69. Bergmans W. 1989 Taxonomy and biogeography of African fruit bats (Mammalia, Megachiroptera). 2. The genera *Micropteropus* Matschie, 1899, *Epomops* Gray, 1870, *Hypsignathus* H. Allen, 1861, *Nanonycteris* Matschie, 1899, and *Plerotes* Andersen, 1910. *Beaufortia* **39**, 89–153.
 70. Patterson BD, Webala PW. 2012 Keys to the bats (Mammalia: Chiroptera) of East Africa. *Fieldiana Life Earth Sci.* **2012**, 1–60. (doi:10.3158/2158-5520-12.6.1)
 71. Leray M, Knowlton N, Ho S-L, Nguyen BN, Machida RJ. 2019 GenBank is a reliable resource for 21st century biodiversity research. *Proc. Natl Acad. Sci. USA* **116**, 22 651–22 656. (doi:10.1073/pnas.1911714116)
 72. Meiklejohn KA, Damaso N, Robertson JM. 2019 Assessment of BOLD and GenBank—their accuracy and reliability for the identification of biological materials. *PLoS ONE* **14**, e0217084. (doi:10.1371/journal.pone.0217084)
 73. Voller S, Chitalu C-CM, Nyondo-Mipando AL, Opobo T, Bangirana CA, Thorogood N, Schellenberg J, Chi P. 2022 'We should be at the table together from the beginning': perspectives on partnership from stakeholders at four research institutions in sub-Saharan Africa. *Int. J. Equity Health* **21**, 1–13. (doi:10.1186/s12939-022-01707-3)
 74. Cook JA *et al.* 2020 Integrating biodiversity infrastructure into pathogen discovery and mitigation of emerging infectious diseases. *BioScience* **70**, 531–534. (doi:10.1093/biosci/biaa064)
 75. Lendemer J *et al.* 2020 The extended specimen network: a strategy to enhance US biodiversity collections, promote research and education. *BioScience* **70**, 23–30. (doi:10.1093/biosci/biz140)
 76. Schindel DE, Cook JA. 2018 The next generation of natural history collections. *PLoS Biol.* **16**, e2006125. (doi:10.1371/journal.pbio.2006125)
 77. Thompson CW *et al.* 2021 Preserve a voucher specimen! The critical need for integrating natural history collections in infectious disease studies. *mBio* **12**, 10–128. (doi:10.1128/mBio.02698-20)
 78. Zhou S, Liu B, Han Y, Wang Y, Chen L, Wu Z, Yang J. 2022 ZOVER: the database of zoonotic and vector-borne viruses. *Nucleic Acids Res.* **50**, D943–D949. (doi:10.1093/nar/gkab862)
 79. Gilbert AT *et al.* 2013 Deciphering serology to understand the ecology of infectious diseases in wildlife. *EcoHealth* **10**, 298–313. (doi:10.1007/s10393-013-0856-0)
 80. Ogawa H *et al.* 2015 Seroepidemiological prevalence of multiple species of filoviruses in fruit bats (*Eidolon helvum*) migrating in Africa. *J. Infect. Dis.* **212**, S101–S108. (doi:10.1093/infdis/jiv063)
 81. Schountz T, Baker ML, Butler J, Munster V. 2017 Immunological control of viral infections in bats and the emergence of viruses highly pathogenic to humans. *Front. Immunol.* **8**, 1098. (doi:10.3389/fimmu.2017.01098)
 82. Brook CE *et al.* 2019 Disentangling serology to elucidate henipa- and filovirus transmission in Madagascar fruit bats. *J. Anim. Ecol.* **88**, 1001–1016. (doi:10.1111/1365-2656.12985)
 83. Mull N, Carlson CJ, Forbes KM, Becker DJ. 2022 Virus isolation data improve host predictions for New World rodent orthohantaviruses. *J. Anim. Ecol.* **91**, 1290–1302. (doi:10.1111/1365-2656.13694)
 84. Wilber MQ, Demarchi J, Fefferman NH, Silk MJ. 2022 High prevalence does not necessarily equal maintenance species: avoiding biased claims of disease reservoirs when using surveillance data. *J. Anim. Ecol.* **91**, 1740–1754. (doi:10.1111/1365-2656.13774)
 85. Haydon DT, Cleaveland S, Taylor LH, Laurenson MK. 2002 Identifying reservoirs of infection: a conceptual and practical challenge. *Emerg. Infect. Dis.* **8**, 1468–1473. (doi:10.3201/eid0812.010317)
 86. Viana M, Mancy R, Biek R, Cleaveland S, Cross PC, Lloyd-Smith JO, Haydon DT. 2014 Assembling evidence for identifying reservoirs of infection. *Trends Ecol. Evol.* **29**, 270–279. (doi:10.1016/j.tree.2014.03.002)
 87. Brook CE, Dobson AP. 2015 Bats as 'special' reservoirs for emerging zoonotic pathogens. *Trends Microbiol.* **23**, 172–180. (doi:10.1016/j.tim.2014.12.004)
 88. Olival KJ, Hayman DT. 2014 Filoviruses in bats: current knowledge and future directions. *Viruses* **6**, 1759–1788. (doi:10.3390/v6041759)
 89. Plowright RK, Peel AJ, Streicker DG, Gilbert AT, Mccallum H, Wood J, Baker ML, Restif O. 2016 Transmission or within-host dynamics driving pulses of zoonotic viruses in reservoir–host populations. *PLoS Negl. Trop. Dis.* **10**, e0004796. (doi:10.1371/journal.pntd.0004796)
 90. Plowright RK, Becker DJ, Mccallum H, Manlove KR. 2019 Sampling to elucidate the dynamics of infections in reservoir hosts. *Phil. Trans. R. Soc. B* **374**, 20180336. (doi:10.1098/rstb.2018.0336)
 91. Crowley D, Becker D, Washburne A, Plowright R. 2020 Identifying suspect bat reservoirs of emerging infections. *Vaccines* **8**, 228. (doi:10.3390/vaccines8020228)

92. Letko M, Seifert SN, Olival KJ, Plowright RK, Munster VJ. 2020 Bat-borne virus diversity, spillover and emergence. *Nat. Rev. Microbiol.* **18**, 461–471. (doi:10.1038/s41579-020-0394-z)
93. Roberts M, Heesterbeek J. 2020 Characterizing reservoirs of infection and the maintenance of pathogens in ecosystems. *J. R. Soc. Interface* **17**, 20190540. (doi:10.1098/rsif.2019.0540)
94. Becker DJ, Washburne AD, Faust CL, Pulliam JRC, Mordecai EA, Lloyd-Smith JO, Plowright RK. 2019 Dynamic and integrative approaches to understanding pathogen spillover. *Phil. Trans. R. Soc. B* **374**, 20190014. (doi:10.1098/rstb.2019.0014)
95. Becker DJ *et al.* 2020 Predicting wildlife hosts of betacoronaviruses for SARS-CoV-2 sampling prioritization. bioRxiv 111344. (doi:10.1101/2020.05.22.111344)
96. Larson PA, Bartlett ML, Garcia K, Chitty J, Balkema-Buschmann A, Towner J, Kugelman J, Palacios G, Sanchez-Lockhart M. 2021 Genomic features of humoral immunity support tolerance model in Egyptian rousette bats. *Cell Rep.* **35**, 109140. (doi:10.1016/j.celrep.2021.109140)
97. Anthony SJ *et al.* 2017 Global patterns in coronavirus diversity. *Virus Evol.* **3**, vex012. (doi:10.1093/ve/vex012)
98. Corman VM, Muth D, Niemeyer D, Drosten C. 2018 Hosts and sources of endemic human coronaviruses. *Adv. Virus Res.* **100**, 163–188. (doi:10.1016/bs.aivir.2018.01.001)
99. Bourgarel M *et al.* 2018 Circulation of Alphacoronavirus, Betacoronavirus and Paramyxovirus in *Hipposideros* bat species in Zimbabwe. *Infect. Genet. Evol.* **58**, 253–257. (doi:10.1016/j.meegid.2018.01.007)
100. Joffrin L *et al.* 2020 Bat coronavirus phylogeography in the Western Indian Ocean. *Sci. Rep.* **10**, 6873. (doi:10.1038/s41598-020-63799-7)
101. Corman VM *et al.* 2015 Evidence for an ancestral association of human coronavirus 229E with bats. *J. Virol.* **89**, 11 858–11 870. (doi:10.1128/JVI.01755-15)
102. Lacroix A *et al.* 2020 Wide diversity of coronaviruses in frugivorous and insectivorous bat species: a pilot study in Guinea, West Africa. *Viruses* **12**, 855. (doi:10.3390/v12080855)
103. Maganga GD *et al.* 2020 Genetic diversity and ecology of coronaviruses hosted by cave-dwelling bats in Gabon. *Sci. Rep.* **10**, 7314. (doi:10.1038/s41598-020-64159-1)
104. Tao Y, Shi M, Chommanard C, Queen K, Zhang J, Markotter W, Kuzmin IV, Holmes EC, Tong S. 2017 Surveillance of bat coronaviruses in Kenya identifies relatives of human coronaviruses NL63 and 229E and their recombination history. *J. Virol.* **91**, e01953-16. (doi:10.1128/JVI.01953-16)
105. Changula K *et al.* 2018 Seroprevalence of filovirus infection of *Rousettus aegyptiacus* bats in Zambia. *J. Infect. Dis.* **218**, S312–S317. (doi:10.1093/infdis/jiy266)
106. Paweska J, Storm N, Markotter W, Paola N, Wiley M, Palacios G, Jansen Van Vuren P. 2020 Shedding of Marburg virus in naturally infected Egyptian rousette bats, South Africa, 2017. *Emerg. Infect. Dis.* **26**, 3051–3055. (doi:10.3201/eid2612.202108)
107. Kajihara M *et al.* 2019 Marburgvirus in Egyptian fruit bats, Zambia. *Emerg. Infect. Dis.* **25**, 1577–1580. (doi:10.3201/eid2508.190268)
108. Maganga GD *et al.* 2014 Bat distribution size or shape as determinant of viral richness in African bats. *PLoS ONE* **9**, e100172. (doi:10.1371/journal.pone.0100172)
109. Muyembe-Tamfum J-J, Mulangu S, Masumu J, Kayembe JMN, Kemp A, Paweska JT. 2012 Ebola virus outbreaks in Africa: past and present. *Onderstepoort J. Vet. Res.* **79**, E1–E8. (doi:10.4102/ojvr.v79i2.451)
110. Paweska J, Storm N, Grobbelaar A, Markotter W, Kemp A, Jansen Van Vuren P. 2016 Experimental inoculation of Egyptian fruit bats (*Rousettus aegyptiacus*) with Ebola virus. *Viruses* **8**, 29. (doi:10.3390/v8020029)
111. Pourrut X, Delicat A, Rollin PE, Ksiazek TG, Gonzalez JP, Leroy EM. 2007 Spatial and temporal patterns of Zaire ebolavirus antibody prevalence in the possible reservoir bat species. *J. Infect. Dis.* **196**, 176–183. (doi:10.1086/520541)
112. Mari Saéz A *et al.* 2014 Investigating the zoonotic origin of the West African Ebola epidemic. *EMBO Mol. Med.* **7**, 17–23. (doi:10.15252/emmm.201404792)
113. World Health Organization (WHO). 2020 Ebola virus disease. See <https://www.who.int/news-room/factsheets/detail/ebola-virus-disease> (accessed 1 April 2023).
114. World Health Organization (WHO). 2022. Ebola virus disease in the Democratic Republic of the Congo. Disease outbreak news. See <https://www.who.int/emergencies/disease-outbreak-news/item/2022-DON377> (accessed 1 September 2022).
115. Breman JG, Johnson KM, Van Der Groen G, Robbins CB, Szczeniowski MV, Ruti K, Webb PA, Meier F, Heymann DL. 1999 A Search for ebola virus in animals in the Democratic Republic of the Congo and Cameroon: ecologic, virologic, and serologic surveys, 1979–1980. *J. Infect. Dis.* **179**, S139–S147. (doi:10.1086/514278)
116. De Nys HM *et al.* 2018 Survey of Ebola viruses in frugivorous and insectivorous bats in Guinea, Cameroon, and the Democratic Republic of the Congo, 2015–2017. *Emerg. Infect. Dis.* **24**, 2228–2240. (doi:10.3201/eid2412.180740)
117. Germain M. 1978 Collection of mammals and arthropods during the epidemic of haemorrhagic fever in Zaire. In *Ebola virus haemorrhagic fever. Proc. of an Int. Colloquium on Ebola Virus Infection and Other Haemorrhagic Fevers*, Antwerp, Belgium, 6–8 December, 1977, pp. 133–135. Amsterdam, The Netherlands: Elsevier.
118. Hassanin A *et al.* 2016 Comparative phylogeography of African fruit bats (Chiroptera, Pteropodidae) provide new insights into the outbreak of Ebola virus disease in West Africa, 2014–2016. *C. R. Biol.* **339**, 517–528. (doi:10.1016/j.crvi.2016.09.005)
119. Hayman DTS, Emmerich P, Yu M, Wang L-F, Suu-Ire R, Fooks AR, Cunningham AA, Wood JLN. 2010 Long-term survival of an urban fruit bat seropositive for Ebola and Lagos bat viruses. *PLoS ONE* **5**, e11978. (doi:10.1371/journal.pone.0011978)
120. Hayman DTS, Yu M, Cramer G, Wang L-F, Suu-Ire R, Wood JLN, Cunningham AA. 2012 Ebola virus antibodies in fruit bats, Ghana, West Africa. *Emerg. Infect. Dis.* **18**, 1207–1209. (doi:10.3201/eid1807.111654)
121. Leroy E, Gonzalez JP. 2012 Filovirus research in Gabon and equatorial Africa: the experience of a research center in the heart of Africa. *Viruses* **4**, 1592–1604. (doi:10.3390/v4091592)
122. Leirs H, Mills JN, Krebs JW, Childs JE, Akaibe D, Woolen N, Ludwig G, Peters CJ, Ksiazek TG. 1999 Search for the Ebola virus reservoir in Kikwit, Democratic Republic of the Congo: reflections on a vertebrate collection. *J. Infect. Dis.* **179**, S155–S163. (doi:10.1086/514299)
123. Centers for Disease Control and Prevention. 2023 Data and Maps | Dengue | CDC. See <https://www.cdc.gov/dengue/statistics-maps/data-and-maps.html> (accessed 24 September 2023).
124. Kading RC *et al.* 2018 Neutralizing antibodies against flaviviruses, Babanki virus, and Rift Valley fever virus in Ugandan bats. *Infect. Ecol. Epidemiol.* **8**, 1439215. (doi:10.1080/20008686.2018.1439215)
125. Centers for Disease Control and Prevention. 2023 Historic Data (1999–2022) | West Nile Virus | CDC. See <https://www.cdc.gov/westnile/statsmaps/historic-data.html> (accessed 24 September 2023).
126. Centers for Disease Control and Prevention. 2019 Global Health - Newsroom - Yellow Fever. See <https://www.cdc.gov/globalhealth/newsroom/topics/yellowfever/index.html> (accessed 24 September 2023).
127. European Centers for Disease Control and Prevention. 2017 Factsheet about Crimean-Congo haemorrhagic fever. See <https://www.ecdc.europa.eu/en/crimean-congo-haemorrhagic-fever/facts/factsheet> (accessed 24 September 2023).
128. Bente DA, Forrester NL, Watts DM, McAuley AJ, Whitehouse CA, Bray M. 2013 Crimean-Congo hemorrhagic fever: history, epidemiology, pathogenesis, clinical syndrome and genetic diversity. *Antiviral Res.* **100**, 159–189. (doi:10.1016/j.antiviral.2013.07.006)
129. Müller MA *et al.* 2016 Evidence for widespread infection of African bats with Crimean-Congo hemorrhagic fever-like viruses. *Sci. Rep.* **6**, 26637. (doi:10.1038/srep26637)
130. Ergonul O. 2006 Crimean-Congo haemorrhagic fever. *Lancet Infect. Dis.* **6**, 203–214. (doi:10.1016/S1473-3099(06)70435-2)
131. Butenko AM. 1996 [Arbovirus circulation in the Republic of Guinea]. *Med. Parazitol (Mosk)* **1**, 40–45.
132. Burt F, Spencer D, Leman P, Patterson B, Swanepoel R. 1996 Investigation of tick-borne viruses as pathogens of humans in South Africa and evidence of Dugbe virus infection in a patient with prolonged thrombocytopenia. *Epidemiol. Infect.* **116**, 353–361. (doi:10.1017/S0950268800052687)
133. Centers for Disease Control and Prevention. 2023 Reported Human Infections with Avian Influenza A

- Viruses | Avian Influenza (Flu). See <https://www.cdc.gov/flu/avianflu/reported-human-infections.htm> (accessed 24 September 2023).
134. Freidl GS *et al.* 2014 Influenza at the animal–human interface: a review of the literature for virological evidence of human infection with swine or avian influenza viruses other than A(H5N1). *Euro. Surveill.* **19**, 20793. (doi:10.2807/1560-7917.es2014.19.18.20793)
 135. Freidl GS *et al.* 2015 Serological evidence of influenza A viruses in frugivorous bats from Africa. *PLoS ONE* **10**, e0127035. (doi:10.1371/journal.pone.0127035)
 136. Amman BR *et al.* 2015 A recently discovered pathogenic paramyxovirus, Sosuga virus, is present in *Rousettus aegyptiacus* fruit bats at multiple locations in Uganda. *J. Wildl. Dis.* **51**, 774–779. (doi:10.7589/2015-02-044)
 137. Baker KS *et al.* 2013 Novel, potentially zoonotic paramyxoviruses from the African straw-colored fruit bat *Eidolon helvum*. *J. Virol.* **87**, 1348–1358. (doi:10.1128/JVI.01202-12)
 138. World Health Organization. 2018 Rift Valley fever. See <https://www.who.int/news-room/fact-sheets/detail/rift-valley-fever> (accessed 24 September 2023).
 139. Fagre AC, Kading RC. 2019 Can bats serve as reservoirs for arboviruses? *Viruses* **11**, 215. (doi:10.3390/v11030215)
 140. Binger T *et al.* 2015 A novel rhabdovirus isolated from the straw-colored fruit bat *Eidolon helvum*, with signs of antibodies in swine and humans. *J. Virol.* **89**, 4588–4597. (doi:10.1128/JVI.02932-14)
 141. Constantine DG. 2009 *Bat rabies and other lyssavirus infections. Circular 1329*. Reston, VA: U.S. Geological Survey
 142. Kgaladi J *et al.* 2013 Diversity and epidemiology of Mokola virus. *PLoS Negl. Trop. Dis.* **7**, e2511. (doi:10.1371/journal.pntd.0002511)
 143. Familusi JB, Moore DL. 1972 Isolation of a rabies related virus from the cerebrospinal fluid of a child with ‘aseptic meningitis’. *Afr. J. Med. Sci.* **3**, 93–96.
 144. Familusi JB, Osunkoya BO, Moore DL, Kemp GE, Fabiyi A. 1972 A fatal human infection with Mokola virus. *Am. J. Trop. Med. Hyg.* **21**, 959–963. (doi:10.4269/ajtmh.1972.21.959)
 145. Wright E, Hayman DT, Vaughan A, Temperton NJ, Wood JL, Cunningham AA, Suu-Ire R, Weiss RA, Fooks AR. 2010 Virus neutralising activity of African fruit bat (*Eidolon helvum*) sera against emerging lyssaviruses. *Virology* **408**, 183–189. (doi:10.1016/j.virol.2010.09.014)
 146. Vora NM *et al.* 2020 Bat and lyssavirus exposure among humans in area that celebrates bat festival, Nigeria, 2010 and 2013. *Emerg. Infect. Dis.* **26**, 1399–1408. (doi:10.3201/eid2607.191016)
 147. World Health Organization (WHO). 2018 WHO expert consultation on rabies: third report. WHO TRS N° 1012. See <https://www.who.int/publications/item/WHO-TRS-1012>.
 148. Markotter W, Monadjem A, Nel LH. 2013 Antibodies against Duvenhage virus in insectivorous bats in Swaziland. *J. Wildl. Dis.* **49**, 1000–1003. (doi:10.7589/2012-10-257)
 149. Melade J, Mcculloch S, Ramasindrazana B, Lagadee E, Turpin M, Pascalis H, Goodman SM, Markotter W, Dellagi K. 2016 Serological evidence of lyssaviruses among bats on Southwestern Indian Ocean Islands. *PLoS One* **11**, e0160553. (doi:10.1371/journal.pone.0160553)
 150. Coertse J, Grobler CS, Sabeta CT, Seamark ECJ, Kearney T, Paweska JT, Markotter W. 2020 Lyssaviruses in insectivorous bats, South Africa, 2003–2018. *Emerg. Infect. Dis.* **26**, 3056–3060. (doi:10.3201/eid2612.203592)
 151. Bennett AJ, Goldberg TL. 2020 Pteropine Orthoreovirus in an Angolan soft-furred fruit bat (*Lissonycteris angolensis*) in Uganda dramatically expands the global distribution of an emerging bat-borne respiratory virus. *Viruses* **12**, 740. (doi:10.3390/v12070740)
 152. Shapiro JT *et al.* 2021 Setting the terms for zoonotic diseases: effective communication for research, conservation, and public policy. *Viruses* **13**, 1356. (doi:10.3390/v13071356)
 153. Schmidt JP, Maher S, Drake JM, Huang T, Farrell MJ, Han BA. 2019 Ecological indicators of mammal exposure to Ebolavirus. *Phil. Trans. R. Soc. B* **374**, 20180337. (doi:10.1098/rstb.2018.0337)
 154. Albariño CG *et al.* 2014 Novel paramyxovirus associated with severe acute febrile disease, South Sudan and Uganda, 2012. *Emerg. Infect. Dis.* **20**, 211–216. (doi:10.3201/eid2002.131620)
 155. Amman BR, Schuh AJ, Sealy TK, Spengler JR, Welch SR, Kirejczyk SGM, Albariño CG, Nichol ST, Towner JS. 2020 Experimental infection of Egyptian rousette bats (*Rousettus aegyptiacus*) with Sosuga virus demonstrates potential transmission routes for a bat-borne human pathogenic paramyxovirus. *PLoS Negl. Trop. Dis.* **14**, e0008092. (doi:10.1371/journal.pntd.0008092)
 156. Coertse J, Geldenhuys M, Le Roux K, Markotter W. 2021 Lagos bat virus, an under-reported rabies-related lyssavirus. *Viruses* **13**, 576. (doi:10.3390/v13040576)
 157. Goldstein T *et al.* 2018 The discovery of Bombali virus adds further support for bats as hosts of ebolaviruses. *Nat. Microbiol.* **3**, 1084–1089. (doi:10.1038/s41564-018-0227-2)
 158. Schuh A, Amman B, Towner JS. 2017 Filoviruses and bats. *Microbiol. Australia* **38**, 12–16. (doi:10.1071/ma17005)
 159. Amman BR, Swanepoel R, Nichol ST, Towner JS. 2017 Ecology of Filoviruses. *Curr. Top. Microbiol. Immunol.* **411**, 23–61. (doi:10.1007/82_2017_10)
 160. Jones MEB, Schuh AJ, Amman BR, Sealy TK, Zaki SR, Nichol ST, Towner JS. 2015 Experimental inoculation of Egyptian rousette bats (*Rousettus aegyptiacus*) with viruses of the Ebolavirus and Marburgvirus genera. *Viruses* **7**, 3420–3442. (doi:10.3390/v7072779)
 161. Schuh AJ *et al.* 2017 Modelling filovirus maintenance in nature by experimental transmission of Marburg virus between Egyptian rousette bats. *Nat. Commun.* **8**, 14446. (doi:10.1038/ncomms14446)
 162. Leroy EM, Epelboin A, Mondonge V, Pourrut X, Gonzalez J-P, Muyembe-Tamfum J-J, Formenty P. 2009 Human ebola outbreak resulting from direct exposure to fruit bats in Luebo, Democratic Republic of Congo, 2007. *Vector-Borne Zoonotic Dis.* **9**, 723–728. (doi:10.1089/vbz.2008.0167)
 163. Lacroix A *et al.* 2021 Investigating the circulation of Ebola viruses in bats during the Ebola virus disease outbreaks in the equateur and North Kivu Provinces of the Democratic Republic of Congo from 2018. *Pathogens* **10**, 557. (doi:10.3390/pathogens10050557)
 164. Scientists Discover Ebola Virus in West African Bat. 2019 *Columbia University Mailman School of Public Health*. See <https://www.publichealth.columbia.edu/news/scientists-discover-ebola-virus-west-african-bat> (accessed 2 August 2023).
 165. Monadjem A, Shapiro JT, Richards LR, Karabulut H, Crawley W, Nielsen IB, Hansen A, Bohmann K, Mourier T. 2020 Systematics of West African *Miniopterus* with the description of a new species. *Acta Chiropterol.* **21**, 237–256. (doi:10.3161/15081109ACC2019.21.2.001)
 166. Bodmer BS *et al.* 2023 *In vivo* characterization of the novel ebolavirus Bombali virus suggests a low pathogenic potential for humans. *Emerging Microbes Infect.* **12**, 2164216. (doi:10.1080/22221751.2022.2164216)
 167. Martell HJ, Masterson SG, Mcgregor JE, Michaelis M, Wass MN. 2019 Is the Bombali virus pathogenic in humans? *Bioinformatics* **35**, 3553–3558. (doi:10.1093/bioinformatics/btz267)
 168. Lebarbenchon C *et al.* 2022 Bombali Ebolavirus in *Mops condylurus* bats (Molossidae), Mozambique. *Emerg. Infect. Dis.* **28**, 2583. (doi:10.3201/eid2812.220853)
 169. Forbes KM *et al.* 2019 Bombali virus in *Mops condylurus* bat, Kenya. *Emerg. Infect. Dis.* **25**, 955–957. (doi:10.3201/eid2505.181666)
 170. Karan LS *et al.* 2019 Bombali virus in *Mops condylurus* bats, Guinea. *Emerg. Infect. Dis.* **25**, 1774. (doi:10.3201/eid2509.190581)
 171. Kareinen L *et al.* 2020 Range expansion of Bombali virus in *Mops condylurus* bats, Kenya, 2019. *Emerg. Infect. Dis.* **26**, 3007. (doi:10.3201/eid2612.202925)
 172. Seifert SN *et al.* 2022 Zaire ebolavirus surveillance near the Bikoro region of the Democratic Republic of the Congo during the 2018 outbreak reveals presence of seropositive bats. *PLoS Negl. Trop. Dis.* **16**, e0010504. (doi:10.1371/journal.pntd.0010504)
 173. Djomsji D *et al.* 2022 Dynamics of antibodies to Ebolaviruses in an *Eidolon helvum* bat colony in Cameroon. *Viruses* **14**, 560. (doi:10.3390/v14030560)
 174. Swanepoel R, Leman PA, Burt FJ, Zachariades NA, Braack LE, Ksiazek TG, Rollin PE, Zaki SR, Peters CJ. 1996 Experimental inoculation of plants and animals with Ebola virus. *Emerg. Infect. Dis.* **2**, 321–325. (doi:10.3201/eid0204.960407)
 175. Hoffmann M, Hernández MG, Berger E, Marzi A, Pöhlmann S. 2016 The glycoproteins of all filovirus species use the same host factors for entry into bat

- and human cells but entry efficiency is species dependent. *PLoS ONE* **11**, e0149651. (doi:10.1371/journal.pone.0149651)
176. Edenborough KM *et al.* 2019 Dendritic cells generated from *Mops condylurus*, a likely filovirus reservoir host, are susceptible to and activated by Zaire Ebolavirus infection. *Front. Immunol.* **10**, 2414. (doi:10.3389/fimmu.2019.02414)
177. Ng M *et al.* 2015 Filovirus receptor NPC1 contributes to species-specific patterns of ebolavirus susceptibility in bats. *eLife* **4**, e11785. (doi:10.7554/eLife.11785)
178. Bokelmann M *et al.* 2020 Utility of primary cells to examine NPC1 receptor expression in *Mops condylurus*, a potential Ebola virus reservoir. *PLoS Negl. Trop. Dis.* **14**, e0007952. (doi:10.1371/journal.pntd.0007952)
179. Bokelmann M *et al.* 2021 Tolerance and persistence of Ebola virus in primary cells from *Mops condylurus*, a potential Ebola virus reservoir. *Viruses* **13**, 2186. (doi:10.3390/v13112186)
180. Rulli MC, Santini M, Hayman DT, D'odorico P. 2017 The nexus between forest fragmentation in Africa and Ebola virus disease outbreaks. *Sci. Rep.* **7**, 41613. (doi:10.1038/srep41613)
181. Koch LK, Cunze S, Kochmann J, Klimpel S. 2020 Bats as putative Zaire ebolavirus reservoir hosts and their habitat suitability in Africa. *Sci. Rep.* **10**, 14268. (doi:10.1038/s41598-020-71226-0)
182. Guégan J-F, Ayouba A, Cappelle J, De Thoisy B. 2020 Forests and emerging infectious diseases: unleashing the beast within. *Environ. Res. Lett.* **15**, 083007. (doi:10.1088/1748-9326/ab8dd7)
183. Guth S, Mollentze N, Renault K, Streicker DG, Visher E, Boots M, Brook CE. 2021 Bats host the most virulent—but not the most dangerous—zoonotic viruses. *Proc. Natl Acad. Sci. USA* **119**, e2113628119. (doi:10.1101/2021.07.25.453574)
184. Lee-Cruz L, Lenormand M, Cappelle J, Caron A, Nys HD, Peeters M, Bourgarel M, Roger F, Tran A. 2021 Mapping of Ebola virus spillover: suitability and seasonal variability at the landscape scale. *PLoS Negl. Trop. Dis.* **15**, e0009683. (doi:10.1371/journal.pntd.0009683)
185. Sundaram M, Schmidt JP, Han BA, Drake JM, Stephens PR. 2022 Traits, phylogeny and host cell receptors predict Ebolavirus host status among African mammals. *PLoS Negl. Trop. Dis.* **16**, e0010993. (doi:10.1371/journal.pntd.0010993)
186. Atherstone C *et al.* 2021 Investigation of Ebolavirus exposure in pigs presented for slaughter in Uganda. *Transbound. Emerg. Dis.* **68**, 1521–1530. (doi:10.1111/tbed.13822)
187. Fischer K, Camara A, Troupin C, Fehling SK, Strecker T, Groschup MH, Tordo N, Diederich S. 2020 Serological evidence of exposure to ebolaviruses in domestic pigs from Guinea. *Transbound. Emerg. Dis.* **67**, 724–732. (doi:10.1111/tbed.13391)
188. Fischer K *et al.* 2018 Serological evidence for the circulation of ebolaviruses in pigs from Sierra Leone. *J. Infect. Dis.* **218**, S305–S311. (doi:10.1093/infdis/jiy330)
189. Olivero J *et al.* 2017 Recent loss of closed forests is associated with Ebola virus disease outbreaks. *Sci. Rep.* **7**, 14291. (doi:10.1038/s41598-017-14727-9)
190. Formenty P, Boesch C, Wyers M, Steiner C, Donati F, Dind F, Walker F, Le Guenno B. 1999 Ebola virus outbreak among wild chimpanzees living in a rain forest of Cote d'Ivoire. *J. Infect. Dis.* **179**, S120–S126. (doi:10.1086/514296)
191. Georges AJ *et al.* 1999 Ebola hemorrhagic fever outbreaks in Gabon, 1994–1997: epidemiologic and health control issues. *J. Infect. Dis.* **179**, S65–S75. (doi:10.1086/514290)
192. Lahm SA, Kombila M, Swanepoel R, Barnes RFW. 2007 Morbidity and mortality of wild animals in relation to outbreaks of Ebola haemorrhagic fever in Gabon, 1994–2003. *Trans. R. Soc. Trop. Med. Hyg.* **101**, 64–78. (doi:10.1016/j.trstmh.2006.07.002)
193. Leendertz SAJ, Wich SA, Ancrenaz M, Bergl RA, Gonder MK, Humle T, Leendertz FH. 2017 Ebola in great apes—current knowledge, possibilities for vaccination, and implications for conservation and human health. *Mammal. Rev.* **47**, 98–111. (doi:10.1111/mam.12082)
194. Rouquet P *et al.* 2005 Wild animal mortality monitoring and human Ebola outbreaks, Gabon and Republic of Congo, 2001–2003. *Emerg. Infect. Dis.* **11**, 283. (doi:10.3201/eid1102.040533)
195. Hayman DTS, Sam John R, Rohani P. 2022 Transmission models indicate Ebola virus persistence in non-human primate populations is unlikely. *J. R. Soc. Interface* **19**, 20210638. (doi:10.1098/rsif.2021.0638)
196. Hayman DTS. 2019 African primates: likely victims, not reservoirs, of Ebolaviruses. *J. Infect. Dis.* **220**, 1547–1550. (doi:10.1093/infdis/jiz007)
197. Walsh PD, Bermejo M, Rodriguez-Teijeiro JD. 2009 Disease avoidance and the evolution of primate social connectivity: Ebola, bats, gorillas, and chimpanzees. In *Primate parasite ecology: the dynamics and study of host–parasite relationships*, pp. 183–198. Cambridge, UK: Cambridge University Press.
198. Leendertz SAJ. 2016 Testing new hypotheses regarding Ebolavirus reservoirs. *Viruses* **8**, 30. (doi:10.3390/v8020030)
199. Keita AK *et al.* 2021 Resurgence of Ebola virus in 2021 in Guinea suggests a new paradigm for outbreaks. *Nature* **597**, 539–543. (doi:10.1038/s41586-021-03901-9)
200. Mbala-Kingebeni P *et al.* 2021 Ebola virus transmission initiated by relapse of systemic Ebola virus disease. *N. Engl. J. Med.* **384**, 1240–1247. (doi:10.1056/NEJMoa2024670)
201. Fairhead J, Leach M, Millimouno D. 2021 Spillover or endemic? Reconsidering the origins of Ebola virus disease outbreaks by revisiting local accounts in light of new evidence from Guinea. *BMJ. Glob Health* **6**, e005783. (doi:10.1136/bmjgh-2021-005783)
202. Frick WF, Kingston T, Flanders J. 2019 A review of the major threats and challenges to global bat conservation. *Ann. N. Y. Acad. Sci.* **1469**, 5–25. (doi:10.1111/nyas.14045)
203. Kingston T. 2016 Cute, creepy, or crispy—how values, attitudes, and norms shape human behavior toward bats. In *Bats in the Anthropocene: conservation of bats in a changing world*, pp. 571–595. Cham, Switzerland: Springer. (doi:10.1007/978-3-319-25220-9_18)
204. Roth E. 2022 How to live safely with bats? Ignorance(s) in post-Ebola risk communication (Guinea, Sierra Leone). In *Sources. Material & Fieldwork in African Studies, Knowing Nature | Savoirs environnementaux* **4**, 39–67.
205. Turcios-Casco MA, Cazzolla Gatti R. 2020 Do not blame bats and pangolins! Global consequences for wildlife conservation after the SARS-CoV-2 pandemic. *Biodivers. Conserv.* **29**, 3829–3833. (doi:10.1007/s10531-020-02053-y)
206. Lynteris C. 2019 *Framing animals as epidemic villains: histories of non-human disease vectors*. Cham, Switzerland: Springer International Publishing.
207. Cyranoski D. 2017 SARS outbreak linked to Chinese bat cave. *Nature* **552**, 15–16. (doi:10.1038/d41586-017-07766-9)
208. López-Baucells A, Rocha R, Fernández-Llamazares Á. 2018 When bats go viral: negative framings in virological research imperil bat conservation. *Mammal. Rev.* **48**, 62–66. (doi:10.1111/mam.12110)
209. López-Baucells A, Revilla-Martín N, Mas M, Alonso-Alonso P, Budinski I, Fraixedas S, Fernández-Llamazares Á. 2023 Newspaper coverage and framing of bats, and their impact on readership engagement. *EcoHealth* **20**, 18–30. (doi:10.1007/s10393-023-01634-x)
210. Cerri J, Mori E, Ancillotto L, Russo D, Bertolino S. 2021 COVID-19, media coverage of bats and related Web searches: a turning point for bat conservation? *Mammal. Rev.* **52**, 16–25. (doi:10.1111/mam.12261)
211. Plowright RK, Reaser JK, Locke H, Woodley SJ, Patz JA, Becker DJ, Oppler G, Hudson PJ, Tabor GM. 2021 Land use-induced spillover: a call to action to safeguard environmental, animal, and human health. *Lancet Planet. Health* **5**, e237–e245. (doi:10.1016/S2542-5196(21)00031-0)
212. Plowright RK, Hudson PJ. 2021 From protein to pandemic: the transdisciplinary approach needed to prevent spillover and the next pandemic. *Viruses* **13**, 1298. (doi:10.3390/v13071298)
213. Keesing F, Ostfeld RS. 2021 Impacts of biodiversity and biodiversity loss on zoonotic diseases. *Proc. Natl Acad. Sci. USA* **118**, e2023540118. (doi:10.1073/pnas.2023540118)
214. Ejtore I, Reeder DM, Matuschewski K, Kityo R, Schaer J. 2022 Negative perception of bats, exacerbated by the SARS-CoV-2 pandemic, may hinder bat conservation in Northern Uganda. *Sustainability* **14**, 16924. (doi:10.3390/su142416924)
215. Macfarlane D, Rocha R. 2020 Guidelines for communicating about bats to prevent persecution in the time of COVID-19. *Biol. Conserv.* **248**, 108650. (doi:10.1016/j.biocon.2020.108650)

216. Tuttle MD. 2017 Fear of bats and its consequences. *J. Bat. Res. Conserv.* **10**, 1–4. (doi:10.14709/BarbJ.10.1.2017.09)
217. Gbogbo F, Kyei MO. 2017 Knowledge, perceptions and attitude of a community living around a colony of straw-coloured fruit bats (*Eidolon helvum*) in Ghana after Ebola virus disease outbreak in West Africa. *Zoonoses Public Health* **64**, 628–635. (doi:10.1111/zph.12357)
218. Ayivor JS, Ohemeng F, Tweneboah Lawson E, Waldman L, Leach M, Ntiamoah-Baidu Y. 2017 Living with bats: the case of Ve Golokuati Township in the Volta Region of Ghana. *J. Environ. Public Health* **2017**, 5938934. (doi:10.1155/2017/5938934)
219. Lawson ET, Ohemeng F, Ayivor J, Leach M, Waldman L, Ntiamoah-Baidu Y. 2017 Understanding framings and perceptions of spillover: preventing future outbreaks of bat-borne zoonoses. *Disaster Prev. Manag. Int. J.* **26**, 396–411. (doi:10.1108/DPM-04-2016-0082)
220. Leach M *et al.* 2019 Local disease-ecosystem-livelihood dynamics: reflections from comparative case studies in Africa. *Phil. Trans. R. Soc. B* **372**, 20160163. (doi:10.1098/rstb.2016.0163)
221. GBatNet – Global Union of Bat Diversity Networks. 2023. See <https://www.gbatnet.org/>.
222. Weber N *et al.* 2023 Data from: Robust evidence for bats as reservoir hosts is lacking in most African virus studies: a review and call to optimize sampling and conserve bats. Dryad Digital Repository. (doi:10.5061/dryad.c866t1gcx)
223. Weber N *et al.* 2023 Robust evidence for bats as reservoir hosts is lacking in most African virus studies: a review and call to optimize sampling and conserve bats. Figshare. (doi:10.6084/m9.figshare.c.6910799.v2)