

2013

A comparison of bats and rodents as reservoirs of zoonotic viruses: are bats special?

Angela D. Luis

Colorado State University

David T. S. Hayman

Colorado State University, d.t.s.hayman@massey.ac.nz

Thomas J. O'Shea

US Geological Survey

Paul M. Cryan

US Geological Survey, cryanp@usgs.gov

Amy T. Gilbert

National Center for Emerging and Zoonotic Infectious Diseases, Amy.T.Gilbert@aphis.usda.gov

See next page for additional authors

Follow this and additional works at: http://digitalcommons.unl.edu/icwdm_usdanwrc



Part of the [Life Sciences Commons](#)

Luis, Angela D.; Hayman, David T. S.; O'Shea, Thomas J.; Cryan, Paul M.; Gilbert, Amy T.; Pulliam, Juliet R. C.; Mills, James N.; Timonin, Mary E.; Willis, Craig K. R.; Cunningham, Andrew A.; Fooks, Anthony R.; Rupprecht, Charles E.; Wood, James L. N.; and Webb, Colleen T., "A comparison of bats and rodents as reservoirs of zoonotic viruses: are bats special?" (2013). *USDA National Wildlife Research Center - Staff Publications*. 1527.

http://digitalcommons.unl.edu/icwdm_usdanwrc/1527

This Article is brought to you for free and open access by the U.S. Department of Agriculture: Animal and Plant Health Inspection Service at DigitalCommons@University of Nebraska - Lincoln. It has been accepted for inclusion in USDA National Wildlife Research Center - Staff Publications by an authorized administrator of DigitalCommons@University of Nebraska - Lincoln.

Authors

Angela D. Luis, David T. S. Hayman, Thomas J. O'Shea, Paul M. Cryan, Amy T. Gilbert, Juliet R. C. Pulliam, James N. Mills, Mary E. Timonin, Craig K. R. Willis, Andrew A. Cunningham, Anthony R. Fooks, Charles E. Rupprecht, James L. N. Wood, and Colleen T. Webb



CrossMark
click for updates

Research

Cite this article: Luis AD, Hayman DTS, O'Shea TJ, Cryan PM, Gilbert AT, Pulliam JRC, Mills JN, Timonin ME, Willis CKR, Cunningham AA, Fooks AR, Rupprecht CE, Wood JLN, Webb CT. 2013 A comparison of bats and rodents as reservoirs of zoonotic viruses: are bats special? *Proc R Soc B* 280: 20122753. <http://dx.doi.org/10.1098/rspb.2012.2753>

Received: 26 November 2012

Accepted: 10 January 2013

Subject Areas:

ecology, health and disease and epidemiology

Keywords:

trait-based approaches, zoonoses, viral richness, reservoir host, spillover, Chiroptera

Author for correspondence:

Angela D. Luis

e-mail: angela.d.luis@gmail.com

Electronic supplementary material is available at <http://dx.doi.org/10.1098/rspb.2012.2753> or via <http://rspb.royalsocietypublishing.org>.

A comparison of bats and rodents as reservoirs of zoonotic viruses: are bats special?

Angela D. Luis^{1,2}, David T. S. Hayman^{1,3,4,5}, Thomas J. O'Shea⁶, Paul M. Cryan⁷, Amy T. Gilbert⁸, Juliet R. C. Pulliam^{2,9,10}, James N. Mills¹¹, Mary E. Timonin¹², Craig K. R. Willis¹², Andrew A. Cunningham⁵, Anthony R. Fooks^{4,13}, Charles E. Rupprecht¹⁴, James L. N. Wood³ and Colleen T. Webb¹

¹Department of Biology, Colorado State University, Fort Collins, CO 80523, USA

²Fogarty International Center, National Institutes of Health, Bethesda, MD 20892, USA

³Disease Dynamics Unit, Department of Veterinary Medicine, University of Cambridge, Cambridge CB3 0ES, UK

⁴Wildlife Zoonoses and Vector-borne Diseases Research Group, Animal Health and Veterinary Laboratories Agency (Weybridge), New Haw, Addlestone, Surrey KT15 3NB, UK

⁵Institute of Zoology, Zoological Society of London, Regent's Park, London NW1 4RY, UK

⁶US Geological Survey (retired), and ⁷US Geological Survey, Fort Collins Science Center, Fort Collins, CO 80526, USA

⁸National Center for Emerging and Zoonotic Infectious Diseases, Centers for Disease Control and Prevention, Atlanta, GA 30333, USA

⁹Department of Biology, and ¹⁰Emerging Pathogens Institute, University of Florida, Gainesville, FL 32611, USA

¹¹Population Biology, Ecology, and Evolution Program, Emory University, Atlanta, GA 30322, USA

¹²Department of Biology and Centre for Forest Interdisciplinary Research, University of Winnipeg, Winnipeg, Manitoba, Canada R3B 2E9

¹³National Consortium for Zoonosis Research, Leahurst, Neston, South Wirral CH64 7TE, UK

¹⁴The Global Alliance for Rabies Control, Manhattan, KS 66502, USA

Bats are the natural reservoirs of a number of high-impact viral zoonoses. We present a quantitative analysis to address the hypothesis that bats are unique in their propensity to host zoonotic viruses based on a comparison with rodents, another important host order. We found that bats indeed host more zoonotic viruses per species than rodents, and we identified life-history and ecological factors that promote zoonotic viral richness. More zoonotic viruses are hosted by species whose distributions overlap with a greater number of other species in the same taxonomic order (sympatry). Specifically in bats, there was evidence for increased zoonotic viral richness in species with smaller litters (one young), greater longevity and more litters per year. Furthermore, our results point to a new hypothesis to explain in part why bats host more zoonotic viruses per species: the stronger effect of sympatry in bats and more viruses shared between bat species suggests that interspecific transmission is more prevalent among bats than among rodents. Although bats host more zoonotic viruses per species, the total number of zoonotic viruses identified in bats (61) was lower than in rodents (68), a result of there being approximately twice the number of rodent species as bat species. Therefore, rodents should still be a serious concern as reservoirs of emerging viruses. These findings shed light on disease emergence and perpetuation mechanisms and may help lead to a predictive framework for identifying future emerging infectious virus reservoirs.

1. Introduction

Emerging infectious diseases threaten global biodiversity and public health [1–3]. Most emerging and re-emerging infectious diseases of humans are zoonoses. Most zoonoses originate in wildlife and are increasing over time [3–5]; however, the relative importance of different groups of wildlife hosts in the emergence of zoonoses remains unclear, as do the mechanisms driving such differences.

Bats (Order Chiroptera) provide considerable ecosystem services, such as arthropod suppression, seed dispersal and pollination, across a vast range of regions and habitats. However, bats are receiving increasing attention as potential reservoirs for zoonotic diseases following recent identification of their involvement with severe acute respiratory syndrome-like coronaviruses, Ebola and Marburg filoviruses, as well as Hendra and Nipah paramyxoviruses [6]. Consequently, there has been repeated speculation that bats may be unique in their potential to harbour zoonotic viruses [6–8]. Traits that may make bats suited to hosting more viruses in general (zoonotic and non-zoonotic) include relatively long lifespans for their body size [9], which may facilitate viral persistence for chronic infections; the reliance of some on prolonged torpor, which can decrease both viral replication and immune function [10,11]; and flight, allowing movement and dispersal over long distances in some species. Additionally, many bat species are gregarious, some living in dense aggregations: for example, some Mexican free-tailed bat (*Tadarida brasiliensis mexicana*) colonies can reach densities of 3000 bats per square metre, in populations of up to a million individuals per roost [12,13]. Roosting sites can house diverse assemblages of multiple bat species [14,15]. High intra- and interspecific contact rates can facilitate rapid transmission of pathogens and large population sizes could sustain acute-immunizing infections. Additionally, there are some traits that may make bats more likely to host zoonotic viruses in particular and/or transmit them to humans. In evolutionary terms, bats are ancient mammals and it has been hypothesized that viruses which evolved in bats may use highly conserved cellular receptors, thus enhancing their ability to transmit viruses to other mammals [6]. Many species of bats have peridomestic habits, roosting in houses and other buildings, as well as trees in dense urban areas, leading to frequent human contact with bat excreta [16–18]. Bat–human contact is also increasing in recent decades owing to habitat encroachment and increased use of bats as bushmeat [17–21]. However, despite the speculation that bats are unusual in their potential to host zoonotic viruses, there are no quantitative comparative analyses to support this hypothesis.

Identifying reservoir species is key to controlling emerging infectious diseases, but there is currently no framework for characterizing the likely role a potential host species may play. Therefore, a general approach is needed for understanding how host–pathogen communities are broadly structured. A growing area of research in ecology relies on trait-based approaches to predict community assembly [22]. These approaches concentrate on traits of species in an attempt to find generalities in species interactions with each other and with the environment. Characterizing which traits are associated with pathogens and their reservoir hosts will contribute to understanding basic disease emergence and perpetuation mechanisms and may help to focus future research and disease mitigation efforts.

In this study, we make a first attempt to quantitatively address the hypothesis that bats are unique hosts of zoonotic viruses, and further, apply a trait-based approach to identify life-history, physiological and ecological traits that correlate with a species' propensity to host zoonotic viruses. Rodents (Order Rodentia) are a suitable comparison group as they are important reservoir hosts of a number of zoonotic viral pathogens with significant impacts on public health [23]. These pathogens include hantaviruses (causing hantavirus

pulmonary syndrome and haemorrhagic fever with renal syndrome; [24]) and arenaviruses (causing, e.g. lymphocytic choriomeningitis, Lassa fever and Argentine, Bolivian, Venezuelan and Brazilian haemorrhagic fevers [25]). Rodents also share a number of characteristics with bats that have been hypothesized to affect reservoir potential; both taxonomic orders are evolutionarily ancient, diverse and include many species with peridomestic habits and species that commonly express torpor. Rodents are more diverse than bats in numbers of species and life-history strategies (the reproduction-longevity trade-off), which enables a more general examination of host correlates for viral richness across taxonomic orders. We also investigate a series of factors that may be important in pathogen sharing, such as host relatedness, geographical overlap and conservation status (which may be important in pathogen sharing, e.g. as in primates [26,27]). Finally, we examine the possibility of increased zoonotic viruses at low latitudes, as Jones *et al.* proposed a link between latitude and risk of zoonotic emergence [3].

In addition to host traits, viral traits affect spillover and emergence of zoonoses: RNA viruses are more likely to emerge than DNA viruses [28], and replication in the cytoplasm was the best predictor of cross-species transmission from livestock to humans [29]. Therefore, we also explore some basic characteristics of viruses found in bats and rodents.

2. Material and methods

(a) Viral data

We compiled databases of viruses in bats or rodents and the species in which each has been detected by searching Thomson Reuters (formerly ISI) Web of Science (<http://apps.webofknowledge.com/>) for each rodent and bat genus 'AND virus' (under 'Topic') through the year 2011. Viruses were grouped at the species level, based on the International Committee on the Taxonomy of Viruses database. Host taxonomy conforms to Wilson & Reader's *Mammal Species of the World* [30]. These databases are included in the electronic supplementary material. Viruses were classified as zoonotic or non-zoonotic; RNA or DNA; replicating in the cytoplasm or nucleus, and whether they consist of a single segment or multiple segments. Viruses and hosts that were not identified to species were not included in the analyses. More than double the number of viruses are known for *Mus musculus* than for any other rodent species, as a consequence of its use as a laboratory animal and the donor of many cell lines. For example, minute virus of mice was discovered as a contaminant in the experimental stock of a different virus when grown in a mouse cell line [31]. Therefore, this host species was removed from analyses, because preliminary analyses identified it as a high leverage point.

(b) Species trait data

For as many host species in our viral database as possible, we compiled data for the following traits (see the electronic supplementary material, table S14 and figures S4–S8): adult body mass, maximum longevity, number of litters per year, litter size, torpor use, migration (bats only), International Union for Conservation of Nature (IUCN) conservation status, species geographical distribution area, latitude of the midpoint (centroid) of the species distribution, number of other species in the same taxonomic order that are sympatric, number of citations on Web of Science. Data were obtained from an online database of mammalian traits (<http://www.utheria.com>) [32] on body mass, maximum longevity, number of litters per year and litter

Table 1. GLM rankings, with the number of zoonotic viruses identified in a species as the response variable (not considering host traits).

model	AICc	d.f.	weight	p-value
~ log(citations) + order	1275.3	410	0.710	$< 10^{-16}$
~ log(citations)*order	1277.1	409	0.290	$< 10^{-16}$
~ log(citations)	1301.5	411	0	$< 10^{-16}$
~ order	1420.2	411	0	0.092
~ 1	1421.0	412	0	

size. Additional values were compiled from the literature (see the electronic supplementary material, table S14 for values and references) and the AnAge database (<http://genomics.senescence.info/species/>) [33]. Torpor expression was treated as a categorical variable with three categories: (i) no evidence of torpor use, (ii) some torpor use, but not true hibernation (minimum body temperature $\geq 11^\circ\text{C}$), and (iii) true hibernation (body temperature $< 11^\circ\text{C}$) [34].

Species sampling intensity was represented by the logged number of Web of Science citations for the binomial species name (and commonly used synonyms) in quotations. IUCN conservation status, species distributions and longitude and latitude coordinates for the centroids of the distributions were obtained from the IUCN website (<http://www.iucnredlist.org/technical-documents/spatial-data>) [35]. The IUCN has seven conservation status categories: least concern, near threatened, vulnerable, endangered, critically endangered, extinct in the wild and extinct. The first three categories described all the bats in our analysis, and 'least concern' and 'vulnerable' described all the rodents in our analysis. Using the shape files from the IUCN website and the command 'over' from the R packages 'sp' and 'rgeos' [36,37], for each species in the analysis, we calculated how many other species in the same taxonomic order had species ranges that overlapped with its own, referred to here as sympatry. This included every species of bat or rodent for which IUCN had distribution shape files (1150 species of bat and 2216 of rodent).

We follow Fleming & Eby [38, p. 157] in defining migration in bats as 'a seasonal, usually two-way movement from one place or habitat to another to avoid unfavorable climatic conditions and/or to seek more favorable energetic conditions'. In most cases, these are regular annual movements that vary with predictable seasonal changes in temperature (for temperate zone bats) or rainfall (tropical bats). We did not consider records of one-way movements or dispersal as evidence for migration. We categorized migratory status of bats as: (i) species that can be broadly categorized as sedentary or only local (approx. less than 100 km) migrants, (ii) species that can be generalized as regional migrants (approx. 100–500 km), and (iii) species that can be categorized as long-distance migrants (greater than 500 km). This information was compiled from the literature, with species reported to be present in an area year-round considered evidence for category 1.

(c) Analysis

We used generalized least squares (GLS) to examine host trait correlates of zoonotic viral richness per host species, while controlling for phylogeny as described below. To examine whether bats host a significantly greater number of zoonotic viruses per host species than rodents, with and without taking into account sampling intensity, we used generalized linear models (GLMs) with negative binomial errors.

Because many life-history traits are correlated, we performed principal components analyses (PCA) on the life-history traits: logged body mass, maximum longevity, number of litters per

year and litter size. We performed three PCAs, one for bats (PC_b), one for rodents (PC_r) and one for the bats and rodents combined (PC_rb). The variables were rescaled to have unit variance before analysis in R using the 'prcomp' function [36], and these principal components were then used in subsequent analyses.

To determine if the number of zoonotic viruses or total number of viruses hosted by a species is significantly correlated to species traits, we performed GLS models for bats and rodents separately, then on the combined bat and rodent data. Because closely related species share traits, we tested for phylogenetic dependence using a GLS framework to allow for correlation structure in the error term. The 'APE' package [39] in R [36] was used to calculate a phylogenetic correlation matrix in which each entry was a pairwise correlation between each pair of species based on their shared branch lengths of a mammalian phylogenetic supertree [40]. The subsets of the phylogenetic tree that we used are shown in the electronic supplementary material, figures S2 and S3. The error term for the GLS was set to this correlation matrix multiplied by an additional parameter, Pagel's λ , that was estimated (using 'optim' in R) to determine the strength of phylogenetic dependence [41,42]. A λ estimate of one indicates that the error structure of the model was directly proportional to the species shared branch lengths. A λ estimate of zero indicates that the error structure of the model was not related to the species shared branch lengths (e.g. phylogeny does not explain any additional variation), and the correlation matrix is not included in the model. Models were ranked by their Akaike information criterion with a correction for finite sample sizes (AICc) values. Correlation coefficients (R) were obtained by using Pearson's product moment correlation comparing the observed number of viruses to model predictions.

Chi-squared (χ^2) tests were used to examine which viral traits, such as type of nucleic acid, genomic segmentation and site of replication were associated with zoonotic infection and taxonomic order.

3. Results

Bats host, on average, significantly more zoonotic viruses per species than rodents (tables 1 and 2). The response variable, zoonotic viral richness (i.e. number of zoonotic viruses per host species), was significantly greater for bats than rodents after controlling for the significant effect of sampling effort (i.e. order and number of citations were in the best model by AICc; table 1). However, as there are approximately twice as many species of rodent as species of bat, the overall number of zoonotic viruses was fewer in bats (61) than in rodents (68). Twenty-four viruses were present in both bats and rodents, of which 21 were zoonotic. Viruses (both zoonotic and non-zoonotic) had a broader host range in bats, averaging 4.51 bat host species per virus, whereas rodent viruses averaged 2.76, which was significantly different by *t*-test ($t = 2.17$, $p = 0.031$; table 2).

Table 2. Summary of the viruses identified.

order	mean no. hosts/virus	total viruses		zoonotic viruses	
		no.	mean/host (range)	no.	mean/host (range)
bats	4.51	137	2.71 (1,15)	61	1.79 (0,12)
rodents	2.76	179	2.48 (1,20)	68	1.48 (0,11)

Species trait data were available for 66 species of bat and 81 species of rodent (out of 413 species totally). This subset of bat and rodent species had 46 and 53 zoonotic viruses, respectively, which accounted for more than 75 per cent of the total number of zoonotic viruses identified in both orders.

(a) Species trait correlates of zoonotic infection in rodents

The first three principal components accounted for 93 per cent of the variance in rodent life-history strategies. PC1_r separated r-selected species (larger litter size, more litters per year, shorter lifespan) from K-selected species (lower reproductive rates and greater mass and longevity; electronic supplementary material, figure S1a *x*-axis and table S1). PC2_r separated reproductive strategies for a given number of offspring per year (litters per year versus litter size; electronic supplementary material, figure S1a *y*-axis and table S1). PC3_r separated species with lower or higher values for all of the life-history traits (bigger, longer lived, higher reproduction; electronic supplementary material, table S1).

Two models tied for the best model by AICc in GLS analyses examining correlates of zoonotic viral richness in rodents (see the electronic supplementary material, table S2). Both models included the logged number of citations and rodent sympatry, with one model containing IUCN conservation status. The number of citations was positively correlated with viral richness. Rodent sympatry was also positively correlated to zoonotic viral richness, i.e. rodent species whose distributions overlapped with a greater number of other rodent species had more zoonotic viruses. Rodents with an IUCN status of 'vulnerable' hosted fewer zoonotic viruses than those listed as 'least concern'. Phylogeny did not explain additional variation: for every model, $\lambda < 1 \times 10^{-11}$. Figure 1a shows the ranking of variables by their Δ AICc values on removal or addition (compared with the best model).

(b) Species trait correlates of zoonotic infection in bats

The first three principal components accounted for 88 per cent of the variance in bat life-history strategies. Negative values of PC1_b indicated species with a greater litter size, and positive values indicated species with higher mass and longevity and more litters per year (see the electronic supplementary material, figure S1b *x*-axis and table S3). PC2_b separated species with more litters per year from those with higher longevity (see the electronic supplementary material, figure S1b *y*-axis and table S3). PC3_b separated species with larger litters and mass from those with higher longevity and litters per year (see the electronic supplementary material, table S3).

The best model examining correlates of viral richness in bats by AICc included (in order of importance by Δ AICc) bat sympatry, the logged number of citations, and PC1_b accounting for 78.7 per cent of the model weight (see the electronic supplementary material, table S4). The positive coefficient of PC1_b in the top ranked model indicated that bats with smaller litter size, larger body mass, greater longevity and more litters per year (see the electronic supplementary material, figure S1b, *x*-axis) are more likely to have more zoonotic viruses. Similar to our findings for rodents, sampling effort and sympatry were positively correlated to zoonotic viral richness. In models that did not include sympatry, phylogeny explained additional variation (λ estimates ranged up to 0.29). For all the models that included sympatry, $\lambda < 0.001$, indicating phylogeny did not explain additional variation once sympatry was taken into account. The importance of the different variables ranked by Δ AICc is shown in figure 1b.

(c) Species trait correlates of zoonotic infection across both bats and rodents

PC1_{rb} of the combined data largely separated bats from rodents and accounted for 51.1 per cent of the variance in life-history traits (see the electronic supplementary material, figure S9 and table S5). PC2_{rb}, PC3_{rb} and PC4_{rb} largely described body mass, litters per year and longevity, and litter size and longevity, respectively (see the electronic supplementary material, figure S9 and table S5).

All four PCs were used in the GLS models that controlled for phylogeny to account for relatively small differences in life-history traits. The best model for the combined data included, in order of importance, citations, taxonomic order, taxon sympatry, the interaction between order and sympatry and torpor use (table 3 and figure 1c). Again, bats hosted more zoonotic viruses per species and the effect of sympatry for bats was 3.9 times higher than for rodents. Torpor use was negatively correlated to zoonotic viral richness (see the electronic supplementary material, table S7), and there was some weight for a negative effect of latitude (table 3). Phylogeny did not explain any additional variation ($\lambda < 0.01$).

(d) Species trait correlates of total viral infections

The species trait correlates of total viral infections were similar to those for zoonotic infections. (see the electronic supplementary material, tables S8–S10.) The best rodent model included citations, rodent sympatry and torpor. The best bat model and the best model for the combined data were the same as for zoonotic viruses.

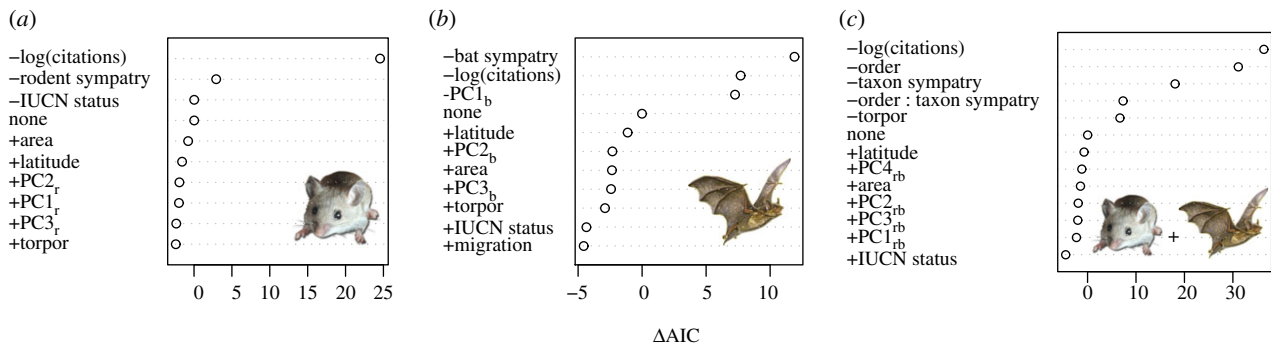


Figure 1. Ranking of variables from the GLS models (with phylogenetic correction) by ΔAICc : the change in AICc values when each variable is individually added (+) or removed (−) from the best model for (a) rodents (best model: number of zoonotic viruses $\sim \log(\text{citations}) + \text{rodent sympatry} + \text{IUCN status}$), (b) bats (best model: number of zoonotic viruses $\sim \log(\text{citations}) + \text{bat sympatry} + \text{PC1}_b$), and (c) combined rodent and bat data (best model: number of zoonotic viruses $\sim \log(\text{citations}) + \text{order} + \text{taxon sympatry} + \text{order:taxon sympatry} + \text{torpor}$; where the colon represents the interaction). (Online version in colour.)

Table 3. A subset of the GLS rankings for rodents and bats together considering species traits. (The response variable is the number of zoonotic viruses identified in a species. λ shows the strength of the phylogenetic correction. See electronic supplementary material, table S6 for full set of models tested. Asterisks (*) indicate the two variables and their interaction and ‘cit.’ indicates logged citations.)

model	AICc	npar	weight	p-value	R	λ
$\sim \text{order} * \text{taxon sympatry} + \text{cit.} + \text{torpor}$	643.2	8	0.366	8.88×10^{-16}	0.66	0
$\sim \text{order} * \text{taxon sympatry} + \text{cit.} + \text{torpor} + \text{latitude}$	643.8	9	0.269	1.55×10^{-15}	0.66	0
$\sim \text{order} * \text{taxon sympatry} + \text{cit.} + \text{PC3}_{rb}$	649.6	7	0.014	1.34×10^{-14}	0.63	0
$\sim \text{order} * \text{taxon sympatry} + \text{cit.}$	649.9	6	0.012	9.77×10^{-15}	0.62	0
$\sim \text{order} + \text{cit.} + \text{taxon sympatry} + \text{torpor}$	650.3	7	0.010	1.80×10^{-14}	0.63	0
$\sim \text{order} + \text{cit.} + \text{taxon sympatry}$	659.3	5	0	5.30×10^{-13}	0.58	0
$\sim \text{order} + \text{cit.} + \text{taxon sympatry} + \text{PC4}_{rb}$	661.1	6	0	2.17×10^{-12}	0.58	0
$\sim \text{order} + \text{cit.} + \text{taxon sympatry} + \text{PC1}_{rb}$	661.4	6	0	2.58×10^{-12}	0.58	0
$\sim \text{order} + \text{cit.} + \text{taxon sympatry} + \text{IUCN}$	663.5	7	0	1.04×10^{-11}	0.58	0
$\sim \text{cit.} + \text{taxon sympatry}$	672.6	4	0	1.93×10^{-10}	0.52	0.001
$\sim \text{order} + \text{cit.}$	680.5	4	0	9.80×10^{-9}	0.47	0
$\sim \text{order} + \text{taxon sympatry}$	686.9	4	0	2.39×10^{-7}	0.44	0
the null (intercept) model	713.2	2	0			0.037

(e) Viral traits associated with zoonotic infection

Using χ^2 tests, we compared zoonotic with non-zoonotic viruses. The zoonotic viruses in our database were much more likely to be RNA viruses ($\chi^2 = 42.7$, $p < 0.001$), have multiple segments ($\chi^2 = 12.3$, $p < 0.001$) and replicate in the cytoplasm ($\chi^2 = 41.8$, $p < 0.001$; electronic supplementary material, table S11), compared with non-zoonotic viruses. From the host perspective, bats harbored a higher proportion of unsegmented genome viruses compared with rodents ($\chi^2 = 6.89$, $p = 0.008$; electronic supplementary material, table S12), but no significant differences were detected in replication site or nucleic acid, and no significant differences were present if comparing only zoonotic viruses of bats and rodents.

4. Discussion

It has been suggested that bats may be unique in hosting many emerging zoonotic viruses [6,7]. We found that bats indeed host a significantly greater number of zoonotic viruses per species compared with rodents. Additionally, using a trait-based approach, we identified important life-history

and ecological predictors of zoonotic viral richness for both bats and rodents, and identified viral traits that were strongly associated with zoonotic infection.

Sympatry within taxonomic order appeared to be the most important host trait associated with zoonotic viral richness, other than sampling effort as reflected in number of citations. In previous studies, sympatry was also found to be an important predictor of sharing of rabies virus variants among bats [43] and viruses among primates [26]. We show that the effect of sympatry was 3.9 times stronger for bats than for rodents. Although there are fewer range overlaps in bats, perhaps a consequence of there being approximately half the number of bat species as rodent species, there appears to be a greater impact on the number of zoonotic viruses per host when sympatry does occur, suggesting that viruses may be transmitted more easily between sympatric bat species than between sympatric rodent species. One possible contributing factor is the level of interspecific contacts among bats when compared with rodents because many bat roosts have a diverse assemblage of bat species [14,15], whereas rodent species typically do not share communal nesting sites. However, high contact rates alone are

insufficient for cross-species transmission because host and/or virus traits also determine the ability of a virus to infect new host species. For example, the level of physiological similarity across sympatric bat species could affect the ability of viruses adapted to any of the sympatric species to spillover into others (which may be why phylogeny was also an important factor in viral sharing of rabies virus variants [43]). The generality of viral infection traits are probably also important and could allow non-specific viruses to take advantage of multiple host species in close contact. Here, we examined viral richness, but further examination of which viruses are shared among which hosts and their characteristics is warranted and may shed more light on this question.

The importance of PC1_b for bats indicated that bat species with smaller litter size, greater body mass, longevity and more litters per year, tended to host more zoonotic viruses. Rodents have a broad range of reproductive strategies, but in bats, litter size is negatively correlated with the number of litters per year (Pearson's product moment correlation, $p = 0.024$). No bat species consistently has more than three offspring per year, but at lower latitudes (less than 20°), there is some variation as to how these offspring are distributed throughout the year. Our analyses suggest that species which spread births over the year host more zoonotic viruses. A potential physiological explanation is the trade-off between immune function and reproduction. Sex hormones can modulate immunocompetence and affect disease resistance genes and behaviour that may make individuals more susceptible to infection [44]. A potential ecological explanation is the replenishment of the susceptible pool from births. Immunizing, horizontally transmitted infections with a high R_0 (basic reproductive number) are vulnerable to 'burn-out' after an epidemic when the number of susceptible hosts drops below the level needed to sustain an epidemic. More litters per year could mean a more continual replenishment of susceptible individuals.

Increased zoonotic viral richness with host longevity is at odds with the 'pace of life' hypothesis, which proposes that short-lived animals put less energy into adaptive immunity in favour of more general immune responses (like broad bacterial recognition), which may make them more competent reservoir hosts [45]. The competency of Lyme disease hosts, for example, seems to follow this pattern [46], but there appears to be mixed evidence for this more generally [47]. This hypothesis also does not consider pathogen traits. Viruses that cause chronic or persistent infections would have higher fitness in a longer-lived host because of the increased infectious period. Therefore, how the pace of a host's life affects reservoir potential may be a function of traits of the virus, host and/or the virus–host interaction.

We hypothesized that torpor use would be positively correlated to viral richness since torpor expression was identified as a key factor in rabies perpetuation in big brown bats (*Eptesicus fuscus*) in Colorado [48], and viral titers can peak upon arousal from hibernation [10]. However, we found torpor was negatively correlated to viral richness. One potential explanation is reduced exposure to viruses owing to lower contact rates during torpor. More research is needed to determine the relationship between torpor, host competence as related to within-host viral persistence and population viral perpetuation processes.

For both bats and rodents, the number of citations was a positive indicator for viruses identified. It is commonly found

that the number of pathogens recorded per species is positively correlated with sampling effort, even for well-studied species [26,49,50], indicating that the current estimates of viral richness are probably substantial underestimates. Hence, there may be many more viruses in both bats and rodents with the potential to spillover into humans. Although distribution area was not in the best models, this could be confounded by the finding that area was positively correlated to the number of citations (see the electronic supplementary material, figure S8)—widespread species are more often studied. Widespread species could also have more contact with humans, perhaps facilitating more frequent spillover of pathogens.

We did not see a significant effect of phylogeny in most models (λ was near zero). However, λ indicates only the amount of residual variation that can be explained by phylogeny after the variables are taken into account. Even though we found little effect of phylogeny in our overall models, when considered individually, all variables examined were correlated to phylogeny to some extent, in at least one of the two groups (see the electronic supplementary material, table S13), suggesting phylogenetic relationships are probably more important than indicated by the models.

Overall, our analyses have explained approximately 43 per cent of the variation seen in zoonotic viral richness among hosts. Although we show that zoonotic viral richness of bats and rodents is significantly different, a majority of the variance in the number of zoonotic viruses per host species is still unexplained, leaving room for multiple alternative explanations. Although sympatry is a good predictor of zoonotic viral richness, our findings suggest high species diversity alone [6] is not the reason for bats hosting a high number of zoonotic viruses. Rodents, the mammalian order with the greatest number of species (twice the number of bat species), were found to host only seven more zoonotic viruses than bats, and rodents host fewer zoonotic viruses per species than bats. It has been hypothesized that because bats are evolutionarily ancient mammals, viruses that evolved with bats may use cellular receptors that have been conserved in mammals, enhancing the ability to transmit to other mammals, including humans [6,51]. However, rodents are evolutionarily older than bats and more closely related to humans [52–54]. If cell receptor evolutionary patterns follow whole genome evolutionary patterns, cell receptors between humans and rodents should be more similar than between humans and bats. While it was beyond the scope of this paper to examine qualitative or quantitative differences in immunity between bats and rodents, such differences may play a role in viral establishment and perpetuation within host populations. We were also unable to address directly the hypothesis that flight helps disperse viruses [6]. However, we found that migration in bats did not predict a higher number of zoonotic viruses. One factor that we were not able to quantify but which is probably important for the ecology and evolution of viruses and other pathogens is the degree of sociality or coloniality of the host. Although many bat species are known to be colonial, a number of species are solitary or nearly so for at least part of the annual cycle. Moreover, the roosting behaviour and social structure of many other species is virtually unknown. Thus, we were not able to quantify coloniality reliably for the species in our analysis at this time, and we recommend future studies incorporate this variable.

The viral traits we found to be associated with zoonotic infection were consistent with those identified by studies

of other taxa. Zoonotic viruses in bats and rodents were overwhelmingly RNA viruses that have multiple segments and replicate in the cytoplasm. These results are similar to those previously published for domestic livestock: for example, the ability to complete replication within the cytoplasm was the single best predictor of whether livestock viruses can infect humans, with a multiple-segmented genome also being a good predictor [29]. Other studies have shown that RNA viruses are more likely to cause emerging infectious diseases than DNA viruses, whether from livestock or from other mammals, such as carnivores [28]. These viral traits shed light on mechanisms of pathogen emergence and spillover. Viruses with RNA and/or multiple-segmented genomes may be more likely to generate genetic diversity with replication, through mutation and reassortment, increasing the chance of zoonotic viral emergence. Additionally, the ability to replicate in the cytoplasm may allow greater chance of spillover to new hosts (including humans) through bypassing the need to interact with the complex cell machinery (which is probably highly host-specific) needed to enter the nucleus for replication.

As this study is based on a large literature search, there are necessarily constraints on inference, given different motivations for, and methods used during studies of both rodent and bat viruses through time. However, our analysis of citations and the interactions between order and citations suggest that the interaction only has 12 per cent weight (see electronic supplementary material, 4th model, table S6), thus suggesting that the effect of sampling effort was not substantially different between the two orders (with the exception of *Mus musculus*, removed from the analyses; see §2). Another potential source of bias may be reports of incidental or spillover hosts that are not important reservoirs but are treated with equal weight in these analyses. Furthermore, although we show that bats have more viruses per species, we cannot say with these analyses which species or orders are likely to be more important in spreading these viruses to humans. Disentangling these factors is difficult at present. Therefore, our results should be viewed with some caution. Recent advances in metagenomic and molecular studies may shed light on some of these issues and alter our understanding of human–rodent and human–bat cross-species transmission [55–57]. Since we did not examine other host groups that are important reservoirs of zoonotic viruses, e.g. primates, ungulates, carnivores and birds, the importance of bats in comparison with other groups remains an open question. We chose rodents as a suitable first comparison because bats and rodents are more similar in life-history traits than other host groups. For example, non-human primates are indeed important reservoir hosts, however, their close phylogenetic relationship with humans, less overlap of life-history traits with bats, and the multiple examples of humans transmitting viruses to primates, such as measles and mumps [58,59] add additional confounding variables. However, further comparative analyses examining a broader range of host groups are warranted.

This study provides evidence that bats are indeed special in at least one regard—they host more zoonotic viruses and more total viruses per species than rodents. However, because there is approximately twice the number of rodent species as bat species, the overall number of zoonotic viruses identified in bats was lower than in rodents. Therefore, rodents should remain a serious concern as reservoirs for future zoonotic disease emergence. This study additionally identifies several specific traits that appear to promote viral richness across taxonomic orders. Given the importance of sympatry in our analysis, future analyses should aim to determine the relative effects of phylogeny and sympatry more broadly in animal reservoirs of emerging zoonoses. Furthermore, our analyses support the theory that traits of zoonotic viruses are also important in determining probability of spillover. Both sympatry and viral traits may act together, with the ability to replicate in the cytoplasm and bypass additional host-specific cell machinery potentially allowing viruses to more easily pass between sympatric species in the same taxonomic order, which could be compounded by increased rates of interspecific contact. Our results, therefore, point to this as a newly hypothesized mechanism to explain, at least in part, how bats host more zoonotic viruses per species. Interspecific transmission may be more prevalent in bats than in rodents (or other orders). This is supported by the most recent molecular studies that indicate there has been a greater number of host switches of paramyxoviruses from bats to other mammals than from rodents, birds, primates, carnivores and cetartiodactyls [55]. Interspecific transmission and spillover is one of the least studied aspects of disease ecology and should therefore be a focus of further studies. Mechanisms of transmission of viruses among bat species may be different than transmission from bats to humans. The mechanisms of interspecific transfer of pathogens, particularly to humans, remain poorly understood, but in some cases are complex and involve intermediate hosts. Gaining understanding of actual mechanisms of such pathogen transfer should be an active area of research in order to develop evidence-based policies to minimize risks, while conserving bats and the irreplaceable ecosystem services they provide.

This work was supported by the Research and Policy for Infectious Disease Dynamics (RAPIDD) program of the Science and Technology Directorate (US Department of Homeland Security) and the Fogarty International Center (National Institutes of Health). D.T.S.H. acknowledges funding from the Wellcome Trust and a David H. Smith post-doctoral fellowship. A.A.C. is partially funded by a Royal Society Wolfson Research Merit award, and J.L.N.W. is supported by the Alborada Trust. C.K.R.W. is funded by a Discovery Grant from the Natural Sciences and Engineering Research Council (NSERC Canada). We thank Dan Horton for useful discussions. The findings and conclusions in this report are those of the authors and the US Geological Survey, but not of the other institutions. Any use of trade product or firm names is for descriptive purposes only and does not imply endorsement by the US Government.

References

1. Daszak P, Cunningham AA, Hyatt AD. 2000 Emerging infectious diseases of wildlife: threats to biodiversity and human health. *Science* **287**, 443–449. (doi:10.1126/science.287.5452.443)
2. Smith KF, Sax DF, Lafferty KD. 2006 Evidence for the role of infectious disease in species extinction and endangerment. *Conserv. Biol.* **20**, 1349–1357. (doi:10.1111/j.1523-1739.2006.00524.x)
3. 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)

4. Taylor LH, Latham SM, Woolhouse MEJ. 2001 Risk factors for human disease emergence. *Phil. Trans. R. Soc. Lond. B* **356**, 983–989. (doi:10.1098/rstb.2001.0888)
5. Woolhouse MEJ, Gowtage-Sequeria S. 2005 Host range and emerging and reemerging pathogens. *Emerg. Infect. Dis.* **11**, 1842–1847. (doi:10.3201/eid1112.050997)
6. Calisher CH, Childs JE, Field HE, Holmes KV, Schountz T. 2006 Bats: important reservoir hosts of emerging viruses. *Clin. Microbiol. Rev.* **19**, 531–545. (doi:10.1128/CMR.00017-06)
7. Dobson AP. 2005 What links bats to emerging infectious diseases? *Science* **310**, 628–629. (doi:10.1126/science.1120872)
8. Misra V, Dumonceaux T, Dubois J, Willis C, Nadin-Davis S, Severini A, Wandeler A, Lindsay R, Artsob H. 2009 Detection of polyoma and corona viruses in bats of Canada. *J. Gen. Virol.* **90**, 2015–2022. (doi:10.1099/vir.0.010694-0)
9. Munshi-South J, Wilkinson GS. 2010 Bats and birds: exceptional longevity despite high metabolic rates. *Ageing Res. Rev.* **9**, 12–19. (doi:10.1016/j.arr.2009.07.006)
10. Dempster G, Grodums EI, Spencer WA. 1966 Experimental Coxsackie B-3 virus infection in *Citellus lateralis*. *J. Cell. Physiol.* **67**, 443–454. (doi:10.1002/jcp.1040670309)
11. Prendergast BJ, Freeman DA, Zucker I, Nelson RJ. 2002 Periodic arousal from hibernation is necessary for initiation of immune responses in ground squirrels. *Am. J. Physiol. Regul. Integr. Comp. Physiol.* **282**, R1054–R1062.
12. Constantine DG. 1967 *Activity patterns of the Mexican free-tailed bat*. University of New Mexico Publications in Biology no. 7. Albuquerque, NM: University of New Mexico Press.
13. Betke M *et al.* 2008 Thermal imaging reveals significantly smaller Brazilian free-tailed bat colonies than previously estimated. *J. Mammal.* **89**, 18–24. (doi:10.1644/07-MAMM-A-011.1)
14. Kuzmin IV, Mayer AE, Niezgoda M, Markotter W, Agwanda B, Breiman RF, Rupprecht CE. 2010 Shimoni bat virus, a new representative of the lyssavirus genus. *Virus Res.* **149**, 197–210. (doi:10.1016/j.virusres.2010.01.018)
15. Kunz TH. 1982 *Ecology of bats*. New York, NY: Plenum Press.
16. Hayman DTS, Fooks AR, Horton D, Suu-Ire R, Breed AC, Cunningham AA, Wood JNL. 2008 Antibodies against Lagos bat virus in Megachiroptera from West Africa. *Emerg. Infect. Dis.* **14**, 926–928. (doi:10.3201/eid1406.071421)
17. O'Shea TJ, Neubaum DJ, Neubaum MA, Cryan PM, Ellison LE, Stanley TR, Rupprecht CE, Pape WJ, Bowen RA. 2011 Bat ecology and public health surveillance for rabies in an urbanizing region of Colorado. *Urban Ecosyst.* **14**, 665–697. (doi:10.1007/s11252-011-0182-7)
18. Plowright RK, Foley P, Field HE, Dobson AP, Foley JE, Eby P, Daszak P. 2011 Urban habituation, ecological connectivity and epidemic dampening: the emergence of Hendra virus from flying foxes (*Pteropus* spp.). *Proc. R. Soc. B* **278**, 3703–3712. (doi:10.1098/rspb.2011.0522)
19. Mickleburgh S, Waylen K, Racey P. 2009 Bats as bushmeat: a global review. *Oryx* **43**, 217–234. (doi:10.1017/S0030605308000938)
20. Kamins AO, Restif O, Ntiemo-Baidu Y, Suu-Ire R, Hayman DTS, Cunningham AA, Wood JNL, Rowcliffe J. 2011 Uncovering the fruit bat bushmeat commodity chain and the true extent of fruit bat hunting in Ghana, West Africa. *Biol. Conserv.* **144**, 3000–3008. (doi:10.1016/j.biocon.2011.09.003)
21. Pulliam JRC *et al.* 2012 Agricultural intensification, priming for persistence and the emergence of Nipah virus: a lethal bat-borne zoonosis. *J. R. Soc. Interface* **9**, 89–101. (doi:10.1098/rsif.2011.0223)
22. McGill BJ, Enquist BJ, Weiher E, Westoby M. 2006 Rebuilding community ecology from functional traits. *Trends Ecol. Evol.* **21**, 178–185. (doi:10.1016/j.tree.2006.02.002)
23. Mills JN. 2006 Biodiversity loss and emerging infectious disease: an example from the rodent-borne hemorrhagic fevers. *Biodiversity* **7**, 9–17. (doi:10.1080/14888386.2006.9712789)
24. Schmaljohn C, Hjelle B. 1997 Hantaviruses: a global disease problem. *Emerg. Infect. Dis.* **3**, 95–104. (doi:10.3201/eid0302.970202)
25. Charrel RN, de Lamballerie X. 2010 Zoonotic aspects of arenavirus infections. *Vet. Microbiol.* **140**, 213–220. (doi:10.1016/j.vetmic.2009.08.027)
26. Davies TJ, Pedersen AB. 2008 Phylogeny and geography predict pathogen community similarity in wild primates and humans. *Proc. R. Soc. B* **275**, 1695–1701. (doi:10.1098/rspb.2008.0284)
27. Altizer S, Nunn CL, Lindenfors P. 2007 Do threatened hosts have fewer parasites? A comparative study in primates. *J. Anim. Ecol.* **76**, 304–314. (doi:10.1111/j.1365-2656.2007.01214.x)
28. Cleaveland S, Laurenson MK, Taylor LH. 2001 Diseases of humans and their domestic mammals: pathogen characteristics, host range and the risk of emergence. *Phil. Trans. R. Soc. Lond. B* **356**, 991–999. (doi:10.1098/rstb.2001.0889)
29. Pulliam JRC, Dushoff J. 2009 Ability to replicate in the cytoplasm predicts zoonotic transmission of livestock viruses. *J. Infect. Dis.* **199**, 565–568. (doi:10.1086/596510)
30. Wilson DE, Reeder DM. 2005 *Mammal species of the world: a taxonomic and geographic reference*, 3rd edn. Baltimore, MD: Johns Hopkins University Press.
31. Crawford LV. 1966 A minute virus of mice. *Virology* **29**, 605–612. (doi:10.1016/0042-6822(66)90284-4)
32. Jones KE *et al.* 2009 PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals. *Ecology* **90**, 2648–2648. (doi:10.1890/08-1494.1)
33. de Magalhães JP, Costa J. 2009 A database of vertebrate longevity records and their relation to other life-history traits. *J. Evol. Biol.* **22**, 1770–1774. (doi:10.1111/j.1420-9101.2009.01783.x)
34. Geiser F, Ruf T. 1995 Hibernation versus daily torpor in mammals and birds: physiological variables and classification of torpor patterns. *Physiol. Zool.* **68**, 935–966.
35. IUCN 2010 IUCN red list of threatened species, version 2010.4. See <http://www.iucnredlist.org>.
36. R Development Core Team 2011 *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
37. Pebesma EJ, Bivand RS. 2005 Classes and methods for spatial data in R. *R News* **5**, 9–13.
38. Fleming T, Eby P. 2003 Ecology of bat migration. In *Bat ecology* (eds TH Kunz, MB Fenton), pp. 156–208. Chicago, IL: University of Chicago Press.
39. Paradis E, Claude J, Strimmer K. 2004 APE: analyses of phylogenetics and evolution in R language. *Bioinformatics* **20**, 289–290. (doi:10.1093/bioinformatics/btg412)
40. Bininda-Emonds OR *et al.* 2007 The delayed rise of present-day mammals. *Nature* **446**, 507–512. (doi:10.1038/nature05634)
41. Pagel M. 1999 Inferring the historical patterns of biological evolution. *Nature* **401**, 877–884. (doi:10.1038/44766)
42. Freckleton RP, Harvey PH, Pagel M. 2002 Phylogenetic analysis and comparative data: a test and review of evidence. *Am. Nat.* **160**, 712–726. (doi:10.1086/343873)
43. Streicker DG, Turmelle AS, Vonnhoff MJ, Kuzmin IV, McCracken GF, Rupprecht CE. 2010 Host phylogeny constrains cross-species emergence and establishment of rabies virus in bats. *Science* **329**, 676–679. (doi:10.1126/science.1188836)
44. Klein SL. 2000 The effects of hormones on sex differences in infection: from genes to behavior. *Neurosci. Biobehav. Rev.* **24**, 627–638. (doi:10.1016/S0149-7634(00)00027-0)
45. Lee KA. 2006 Linking immune defenses and life history at the levels of the individual and the species. *Integr. Comp. Biol.* **46**, 1000–1015. (doi:10.1093/icb/icl049)
46. Keesing F, Brunner J, Duerr S, Killalea M, LoGiudice K, Schmidt K, Vuong H, Ostfeld RS. 2009 Hosts as ecological traps for the vector of Lyme disease. *Proc. R. Soc. B* **276**, 3911–3919. (doi:10.1098/rspb.2009.1159)
47. Martin LB, Weil ZM, Nelson RJ. 2007 Immune defense and reproductive pace of life in *Peromyscus* mice. *Ecology* **88**, 2516–2528. (doi:10.1890/07-0060.1)
48. George DB, Webb CT, Farnsworth ML, O'Shea TJ, Bowen RA, Smith DL, Stanley TR, Ellison LE, Rupprecht CE. 2011 Host and viral ecology determine bat rabies seasonality and maintenance. *Proc. Natl Acad. Sci. USA* **108**, 10 208–10 213. (doi:10.1073/pnas.1010875108)
49. Pedersen AB, Altizer S, Poss M, Cunningham AA, Nunn CL. 2005 Patterns of host specificity and transmission among parasites of wild primates. *Int. J. Parasitol.* **35**, 647–657. (doi:10.1016/j.ijpara.2005.01.005)
50. Turmelle AS, Olival KJ. 2009 Correlates of viral richness in bats (Order Chiroptera). *EcoHealth* **6**, 522–539. (doi:10.1007/s10393-009-0263-8)
51. Wang L-F, Walker PJ, Poon LLM. 2011 Mass extinctions, biodiversity and mitochondrial function: are bats 'special' as reservoirs for emerging viruses?

- Curr. Opin. Virol.* **1**, 1–9. (doi:10.1016/j.coviro.2011.10.013)
52. Simmons NB, Seymour KL, Habersetzer J, Gunnell GF. 2008 Primitive early Eocene bat from Wyoming and the evolution of flight and echolocation. *Nature* **451**, 818–821. (doi:10.1038/nature06549)
 53. dos Reis M, Inoue J, Hasegawa M, Asher RJ, Donoghue PCJ, Yang Z. 2012 Phylogenomic datasets provide both precision and accuracy in estimating the timescale of placental mammal phylogeny. *Proc. R. Soc. B* **279**, 3491–3500. (doi:10.1098/rspb.2012.0683)
 54. Murphy WJ, Pringle TH, Crider TA, Springer MS, Miller W. 2007 Using genomic data to unravel the root of the placental mammal phylogeny. *Genome Res.* **17**, 413–421. (doi:10.1101/gr.5918807)
 55. Drexler JF *et al.* 2012 Bats host major mammalian paramyxoviruses. *Nat. Commun.* **3**, 796. (doi:10.1038/ncomms1796)
 56. Li L, Victoria JG, Wang C, Jones M, Fellers GM, Kunz TH, Delwart E. 2010 Bat guano virome: predominance of dietary viruses from insects and plants plus novel mammalian viruses. *J. Virol.* **84**, 6955–6965. (doi:10.1128/JVI.00501-10)
 57. Donaldson EF, Haskew AN, Gates JE, Huynh J, Moore CJ, Frieman MB. 2010 Metagenomic analysis of the viromes of three North American bat species: viral diversity among different bat species that share a common habitat. *J. Virol.* **84**, 13 004–13 018. (doi:10.1128/JVI.01255-10)
 58. Kilbourn AM, Karesh WB, Wolfe ND, Bosi EJ, Cook RA, Andau M. 2003 Health evaluation of free-ranging and semi-captive orangutans (*Pongo pygmaeus pygmaeus*) in Sabah, Malaysia. *J. Wildl. Dis.* **39**, 73–83.
 59. Bhatt PN, Brandt CD, Weiss R, Fox JP, Shaffer MF. 1966 Viral infections of monkeys in their natural habitat in southern India. II. Serological evidence of viral infection. *Am. J. Trop. Med. Hyg.* **15**, 561.

Supplementary Material

Supplementary Text

In our viral database we note the method of identification, such as isolation, serology (evidence of antibodies), or PCR. Fifteen and eleven viruses were identified in bats and rodents, respectively, solely by serological evidence. It is possible that some of these accounts could list the wrong virus due to antibody crossreactivity. For example, Mokola virus, a (rabies-related) lyssavirus, is one of the viruses listed in our database for which there is only serological evidence for its presence in bats. The virus has not yet been isolated from a bat, and the serological finding may be a result of antibodies to another lyssavirus, Lagos bat virus, which may cross-react with Mokola virus [1]. Therefore, some caution must be used in defining species based on serology alone. Other potential sources of bias may be a number of spillover hosts that are not important reservoirs, but are included in the analysis because infection has been detected in the species.

Supplementary Tables

Table S1. Loading values for principal components (PCs) summarizing life history traits of rodents.

	PC1	PC2	PC3	PC4
litter size	-0.374	0.774	-0.482	-0.168
litters per year	-0.428	-0.619	-0.659	-0.009
maximum longevity	0.591	-0.068	-0.310	-0.742
body mass	0.572	0.114	-0.488	0.649
proportion of variance	0.571	0.229	0.134	0.067

Table S2. Full set of generalized least squares rankings for rodents, including phylogenetic correction, considering species traits, with the number of zoonotic viruses identified in a species as the response variable.

Model	AICc	npar	Weight	p value	R	λ
~cit. + rodent sympatry + IUCN	356.4	5	0.213	9.80×10^{-08}	0.60	0.000
~cit. + rodent sympatry	356.4	4	0.213	6.26×10^{-08}	0.58	0.000
~cit. + rodent sympatry + torpor	357.6	6	0.114	2.24×10^{-07}	0.61	0.000
~cit. + rodent sympatry + PC2 _r	357.6	5	0.112	1.83×10^{-07}	0.59	0.000
~cit. + rodent sympatry + latitude	357.7	5	0.108	1.89×10^{-07}	0.59	0.000
~cit. + rodent sympatry + PC3 _r	358.6	5	0.070	2.90×10^{-07}	0.58	0.000
~cit. + IUCN	359.3	4	0.050	2.68×10^{-07}	0.56	0.000
~cit. + torpor	359.8	5	0.038	5.21×10^{-07}	0.57	0.000
~cit.	360.7	3	0.025	2.42×10^{-07}	0.53	0.000
~cit. + IUCN + PC3 _r	361.3	5	0.018	1.06×10^{-06}	0.56	0.000
~cit. + IUCN + PC1 _r	361.3	5	0.018	1.07×10^{-06}	0.56	0.000
~cit. + area	362.6	4	0.010	1.38×10^{-06}	0.53	0.000
~cit. + PC3 _r	362.8	4	0.008	1.60×10^{-06}	0.53	0.000
~cit. + area + latitude	364.5	5	0.004	4.98×10^{-06}	0.54	0.000
~rodent sympatry	379.0	3	0.000	3.99×10^{-03}	0.31	0.000
the null (intercept) model	385.2	2	0.000			0.017

Table S3. Loading values for principal components (PCs) summarizing life history traits of bats.

	PC1	PC2	PC3	PC4
litter size	-0.654	-0.104	-0.564	0.493
litters per year	0.295	0.721	0.070	0.624
maximum longevity	0.345	-0.681	0.246	0.597
body mass	0.605	-0.075	-0.785	-0.111
proportion of variance	0.378	0.328	0.176	0.119

Table S4. Full set of generalized least squares rankings for bats considering species traits, with the number of zoonotic viruses identified in a species as the response variable and λ showing the strength of the phylogenetic correction.

Model	AICc	npar	Weight	p value	R	λ
~cit. + bat sympatry + PC1 _b	290.5	5	0.787	1.06×10^{-8}	0.70	0.000
~cit. + bat sympatry + torpor	294.0	6	0.137	7.21×10^{-8}	0.69	0.000
~cit. + bat sympatry + latitude	297.3	5	0.026	2.96×10^{-7}	0.66	0.000
~cit. + bat sympatry	297.4	4	0.025	2.12×10^{-7}	0.64	0.000
~cit. + bat sympatry + IUCN	299.8	6	0.008	1.09×10^{-6}	0.66	0.000
~cit. + bat sympatry + PC2 _b	299.8	5	0.008	9.61×10^{-7}	0.64	0.000
~cit. + latitude + area	300.0	5	0.007	1.06×10^{-6}	0.64	0.000
~bat sympatry	301.7	3	0.003	8.55×10^{-7}	0.59	0.000
~cit. + PC1 _b	303.8	4	0.001	5.02×10^{-6}	0.58	0.188
~cit. + PC1 _b + migration	308.4	6	0.000	6.16×10^{-5}	0.58	0.178
~cit.	316.5	3	0.000	2.19×10^{-3}	0.36	0.254
~cit. + PC3 _b	318.7	4	0.000	8.87×10^{-3}	0.36	0.250
the null (intercept) model	323.7	2	0.000			0.295

Table S5. Loading values for principal components (PCs) summarizing life history traits of both rodents and bats.

	PC1	PC2	PC3	PC4
litter size	0.586	-0.235	0.413	0.657
litters per year	0.545	0.146	-0.822	0.083
maximum longevity	-0.598	-0.179	-0.358	0.694
body mass	0.052	-0.944	-0.162	-0.283
proportion of variance	0.511	0.267	0.137	0.085

Table S6. Generalized least squares rankings for rodents and bats together considering species traits, with response variable, number of zoonotic viruses identified in a species and λ showing the strength of the phylogenetic correction.

Model	AICc	npar	Weight	p value	R	λ
~order * taxon sympatry + cit. + torpor	643.2	8	0.366	8.88×10^{-16}	0.66	0.000
~order * taxon sympatry + cit. + torpor + latitude	643.8	9	0.269	1.55×10^{-15}	0.66	0.000
~order * taxon sympatry + cit. + PC3 _{rb} + torpor	645.2	9	0.132	3.11×10^{-15}	0.66	0.000
~order * taxon sympatry + order * cit. + torpor	645.4	9	0.120	3.33×10^{-15}	0.66	0.000
~cit. + order * taxon sympatry + order * torpor	646.7	10	0.062	7.66×10^{-15}	0.66	0.000
~order * taxon sympatry + cit. + PC3 _{rb}	649.6	7	0.014	1.34×10^{-14}	0.63	0.000
~order * taxon sympatry + cit.	649.9	6	0.012	9.77×10^{-15}	0.62	0.000
~order + cit. + taxon sympatry + torpor	650.3	7	0.010	1.80×10^{-14}	0.63	0.000
~order * taxon sympatry + cit. + area	651.8	7	0.005	3.74×10^{-14}	0.62	0.000
~order * torpor + cit. + taxon sympatry	651.9	9	0.005	7.09×10^{-14}	0.64	0.000
~order * taxon sympatry + cit. + latitude	652.1	7	0.004	4.43×10^{-14}	0.62	0.000
~order + cit. + taxon sympatry + PC3 _{rb}	658.2	6	0.000	5.34×10^{-13}	0.59	0.000
~order + cit. + taxon sympatry	659.3	5	0.000	5.30×10^{-13}	0.58	0.000
~order + cit. + taxon sympatry + PC4 _{rb}	661.1	6	0.000	2.17×10^{-12}	0.58	0.000
~order + cit. + taxon sympatry + PC1 _{rb}	661.4	6	0.000	2.58×10^{-12}	0.58	0.000
~order + cit. + latitude * torpor	662.6	9	0.000	1.02×10^{-11}	0.60	0.000
~order + cit. + taxon sympatry + IUCN	663.5	7	0.000	1.04×10^{-11}	0.58	0.000
~cit. + taxon sympatry	672.6	4	0.000	1.93×10^{-10}	0.52	0.001
~order + cit.	680.5	4	0.000	9.80×10^{-9}	0.47	0.000
~order + taxon sympatry	686.9	4	0.000	2.39×10^{-7}	0.44	0.000
the null (intercept) model	713.2	2	0.000			0.037

* indicates the two variables and their interaction, "cit." indicates logged citations

Table S7. Details of the best GLS model for bats and rodents combined (number of zoonotic viruses \sim order * taxon sympatry + citations + torpor).

	coefficients	std. error	p value
(Intercept)	-1.650	0.741	0.028
order Rodentia	-0.432	0.678	0.525
sympatry	0.014	0.003	<0.001
citations	0.867	0.133	<0.001
some torpor use	-1.080	0.528	0.043
true hibernation	-1.395	0.4751	0.002
Rodentia:sympatry	-0.010	0.003	0.003

Table S8. Generalized least squares model rankings for rodents considering species traits, with the total number of viruses identified in a species as the response variable.

Model	AICc	npar	Weight	p value	R
~cit. + rodent sympatry + torpor	429.3	6	0.237	9.22×10^{-10}	0.68
~cit. + area + latitude	429.9	5	0.178	8.64×10^{-10}	0.66
~cit. + rodent sympatry	430.1	4	0.159	5.51×10^{-10}	0.65
~cit. + rodent sympatry + PC3 _r	431.0	5	0.101	1.50×10^{-09}	0.66
~cit. + torpor	431.7	5	0.074	2.03×10^{-09}	0.65
~cit. + rodent sympatry + PC2 _r	432.1	5	0.059	2.55×10^{-09}	0.65
~cit. + rodent sympatry + latitude	432.4	5	0.052	2.89×10^{-09}	0.65
~cit. + rodent sympatry + IUCN	432.4	5	0.051	2.93×10^{-09}	0.65
~cit. + rodent sympatry + IUCN + PC3 _r	433.3	6	0.033	6.09×10^{-09}	0.66
~cit. + PC3 _r	434.2	4	0.021	4.18×10^{-09}	0.62
~cit.	434.6	3	0.017	2.03×10^{-09}	0.61
~cit. + IUCN + PC3 _r	435.9	5	0.009	1.64×10^{-08}	0.63
~cit. + IUCN	436.6	4	0.006	1.40×10^{-08}	0.61
~cit. + IUCN + PC1 _r	438.1	5	0.003	4.80×10^{-08}	0.62
~rodent sympatry	462.7	3	0.000	5.15×10^{-03}	0.31
~1	468.4	2	0.000		

* indicates the two variables and their interaction, cit. indicates logged citations
For all models, λ (strength of the phylogenetic correction) was estimated to be < 0.01

Table S9. Generalized least squares model rankings for bats considering species traits, with the total number of viruses identified in a species as the response variable.

Model	AICc	npar	Weight	p value	R	λ
~cit. + bat sympatry + PC1 _b	335.8	5	0.857	9.89×10^9	0.69	0.000
~cit. + bat sympatry + torpor	340.9	6	0.065	1.47×10^7	0.68	0.000
~cit. + PC1 _b	342.4	4	0.032	1.64×10^7	0.62	0.165
~cit. + bat sympatry	343.6	4	0.017	3.09×10^7	0.63	0.000
~cit. + bat sympatry + lat	344.7	5	0.010	7.71×10^7	0.64	0.000
~cit. + bat sympatry + PC3 _b	345.5	5	0.007	1.11×10^6	0.63	0.000
~cit. + bat sympatry + PC2 _b	346.0	5	0.005	1.39×10^6	0.63	0.000
~cit. + PC1 _b + migration	346.8	6	0.004	2.32×10^6	0.63	0.157
~cit. + lat + area	347.2	5	0.003	2.59×10^6	0.62	0.000
~bat sympatry	354.0	3	0.000	3.14×10^5	0.51	0.000
~cit.	355.6	3	0.000	7.20×10^5	0.45	0.211
~1	369.1	2	0.000			0.244

Table S10. Generalized least squares model rankings for both bats and rodents considering species traits, with the total number of viruses identified in a species as the response variable.

Model	AICc	npar	Weight	p value	R
~order * taxon sympatry + cit. + torpor	762.5	8	0.334	0.00	0.68
~order * taxon sympatry + cit. + PC3 _{rb} + torpor	763.7	9	0.180	1.11×10^{-16}	0.68
~order + cit. + taxon sympatry + torpor	764.2	7	0.147	0.00	0.67
~order * taxon sympatry + cit. + torpor + latitude	764.6	9	0.121	1.11×10^{-16}	0.68
~order * taxon sympatry + order * cit. + torpor	764.6	9	0.117	1.11×10^{-16}	0.68
~cit. + order * taxon sympatry + order * torpor	766.7	10	0.041	3.33×10^{-16}	0.68
~order * torpor + cit. + taxon sympatry	767.7	9	0.025	3.33×10^{-16}	0.67
~order * taxon sympatry + cit. + PC3 _{rb}	769.2	7	0.012	3.33×10^{-16}	0.65
~order * taxon sympatry + cit.	770.4	6	0.007	4.44×10^{-16}	0.64
~order + cit. + taxon sympatry + PC3 _{rb}	770.8	6	0.005	4.44×10^{-16}	0.64
~order * taxon sympatry + cit. + latitude	772.0	7	0.003	1.44×10^{-15}	0.64
~order * taxon sympatry + cit. + area	772.1	7	0.003	1.55×10^{-15}	0.64
~order + cit. + taxon sympatry	772.6	5	0.002	6.66×10^{-16}	0.63
~order + cit. + latitude * torpor	773.5	9	0.001	5.88×10^{-15}	0.65
~order + cit. + taxon sympatry + PC1 _{rb}	773.9	6	0.001	2.33×10^{-15}	0.63
~order + cit. + taxon sympatry + PC4 _{rb}	774.5	6	0.001	3.00×10^{-15}	0.63
~order + cit. + taxon sympatry + IUCN	776.5	7	0.000	1.31×10^{-14}	0.63
~cit. + taxon sympatry	783.4	4	0.000	5.78×10^{-14}	0.58
~order + cit.	789.7	4	0.000	1.37×10^{-12}	0.56
~order + taxon sympatry	820.0	4	0.000	5.23×10^{-6}	0.39
~1	840.1	2	0.000		

* indicates the two variables and their interaction, cit. indicates logged citations

For all models, λ (strength of the phylogenetic correction) was estimated to be < 0.01

Table S11. χ^2 tests comparing traits of zoonotic and non-zoonotic viruses.

	<u>nucleic acid</u>				<u>num. segments</u>				<u>replication site</u>			
	RNA	DNA	χ^2	p	single	mult.	χ^2	p	nucl.	cyto.	χ^2	p
Zoonotic	107	2	42.7	< 0.001	69	40	12.3	< 0.001	2	107	41.8	< 0.001
Non-zoonotic	141	77			178	40			76	142		

Table S12. χ^2 tests comparing traits of viruses in rodents and bats.

	<u>nucleic acid</u>				<u>num. segments</u>				<u>replication site</u>			
	RNA	DNA	χ^2	p	single	mult.	χ^2	p	nucl.	cyto.	χ^2	p
Rodents	148	51	2.45	0.118	139	60	6.89	0.008	47	152	0.69	0.407
Bats	123	27			124	26			29	121		

Table S13. Estimates for λ , indicating the strength of the effect of phylogeny on the given variables, in the null (intercept) model. If λ is near one, this indicates that the relationship between species traits was proportional to their shared branch lengths. If $\lambda = 0$, then species traits were not related to their shared branch lengths.

Model	Rodents	Bats	Both
zoonotic viruses	0.017	0.295	0.037
citations	0.620	0.000	0.000
area	0.000	0.135	0.297
sympatry	0.313	0.434	0.487
latitude	0.780	0.265	0.000
torpor	1.000	0.607	0.670
PC1	0.970	0.137	0.550
PC2	0.712	0.078	0.172
PC3	0.687	0.000	0.088

See separate supplemental file for Table S14: species traits used in the analysis.

Supplemental Figures

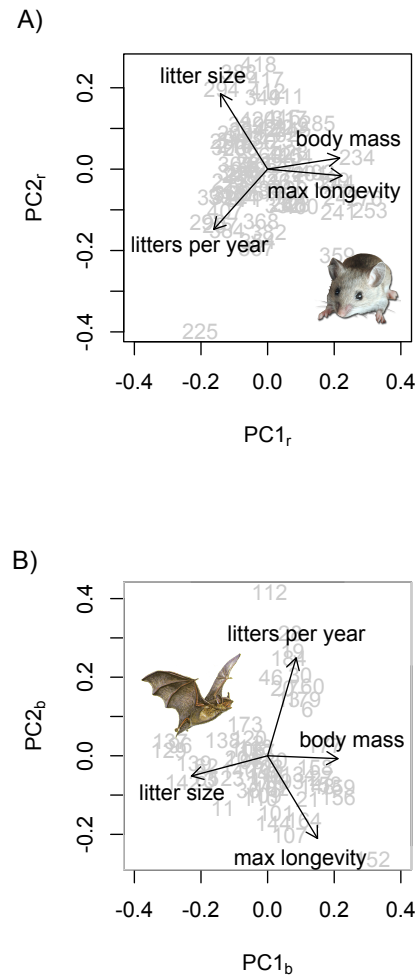


Fig. S1. Principal components analysis (PC) of (a) rodent (r) life history data showing PC1_r and PC2_r and (b) bat (b) life history data showing PC1_b and PC2_b.

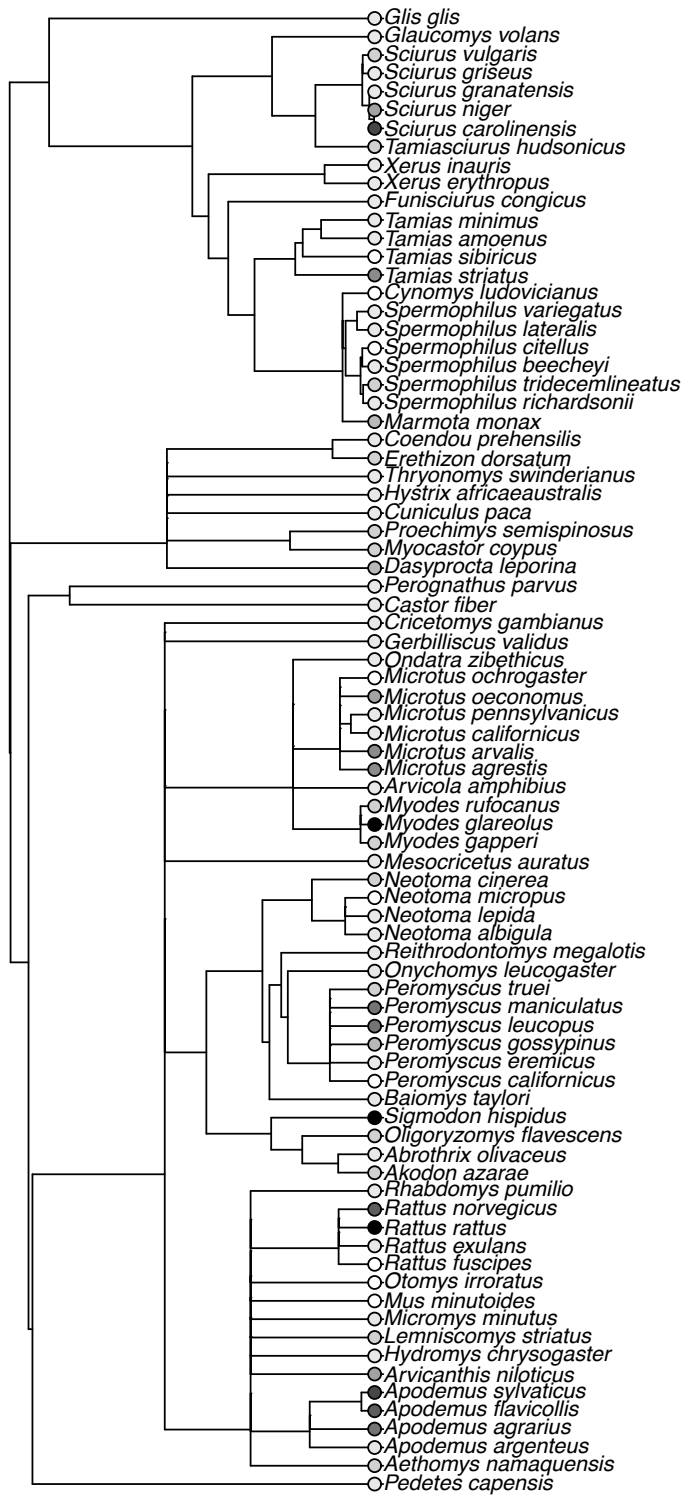


Fig. S2. The rodent species in our traits analysis in the mammalian supertree [2], with darker shades of gray indicating more zoonotic viruses.

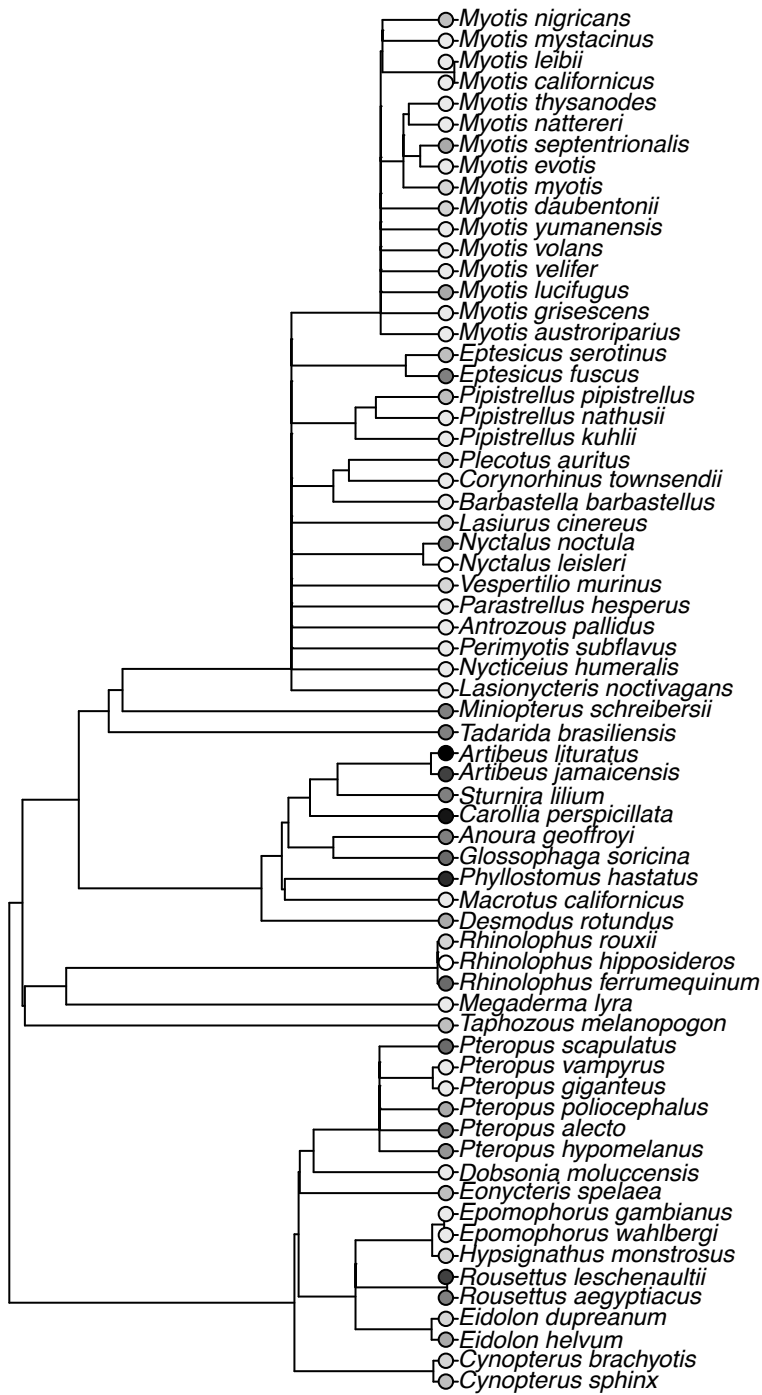


Fig. S3. The bat species in our traits analysis in the mammalian supertree [2], with darker shades of gray indicating more zoonotic viruses.

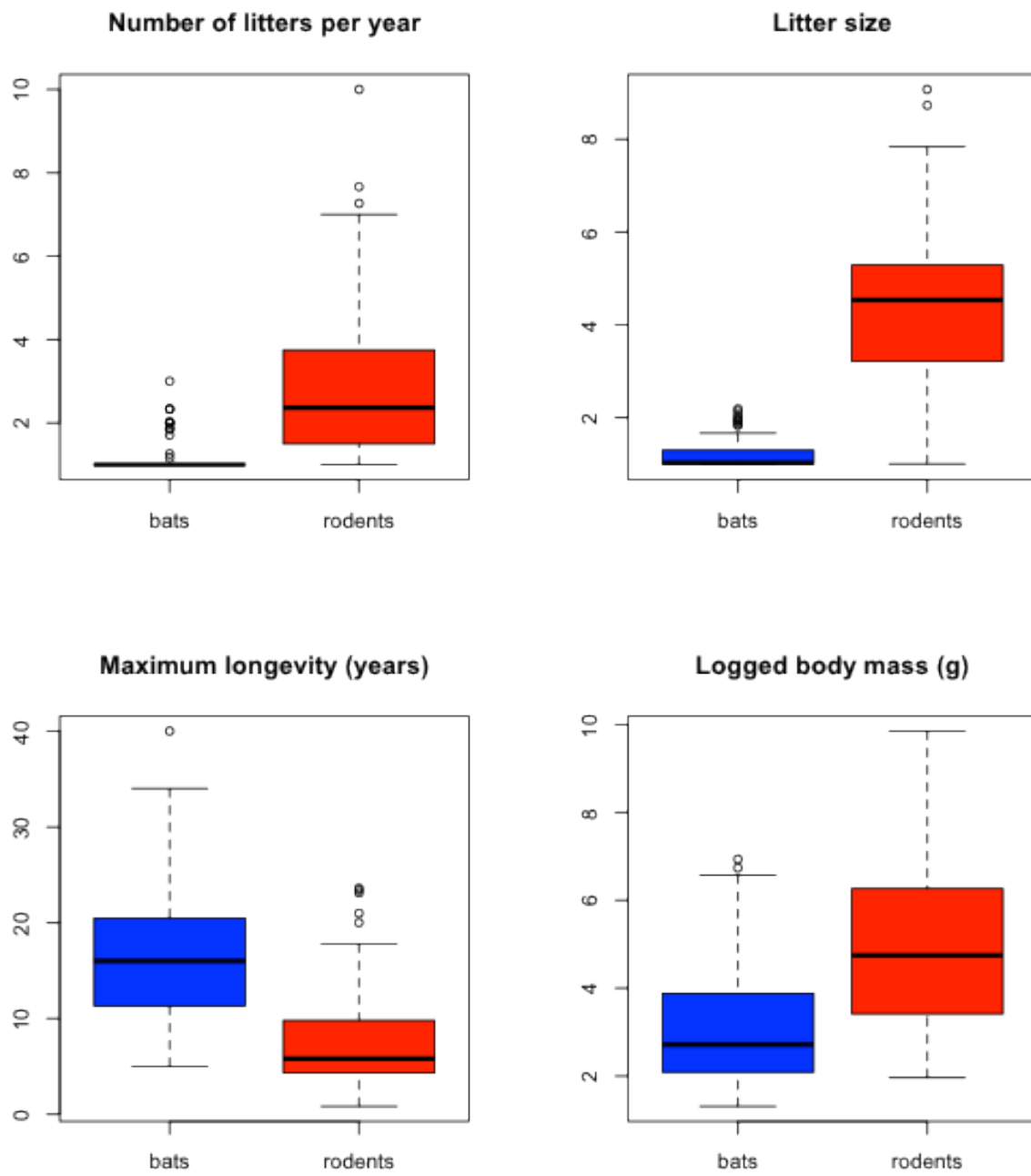


Fig. S4. Raw data for life history traits in rodents and bats.

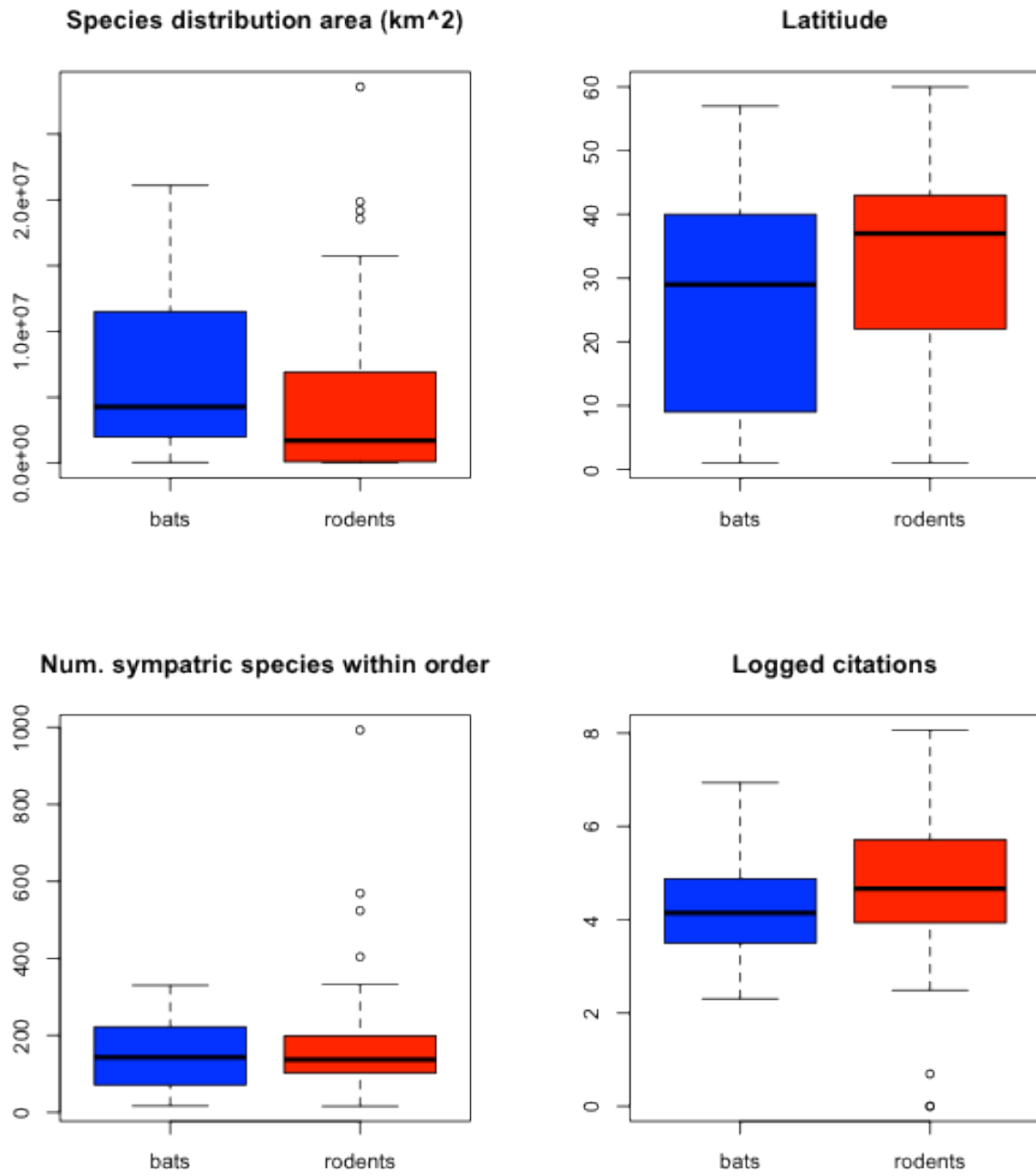


Fig. S5. Raw data for life history traits in rodents and bats (cont).

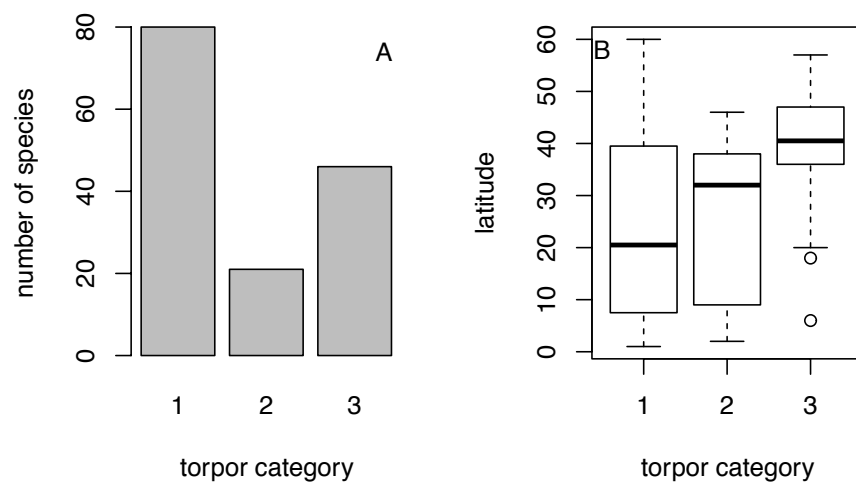


Fig. S6. a) Number of bat and rodent species using each of the 3 torpor categories, (1) no torpor use reported, (2) some torpor use but not true hibernation, and (3) hibernation. b) Latitude of midpoint of species distribution for the 3 torpor categories.

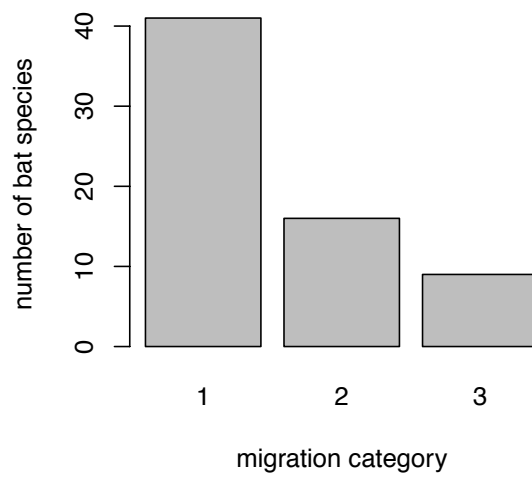


Fig. S7. Number of bats using each of the 3 migration categories, (1) sedentary or only local (< about 100km) migrations, (2) regional migrants (about 100-500 km), and (3) long-distance migrants (>500 km).

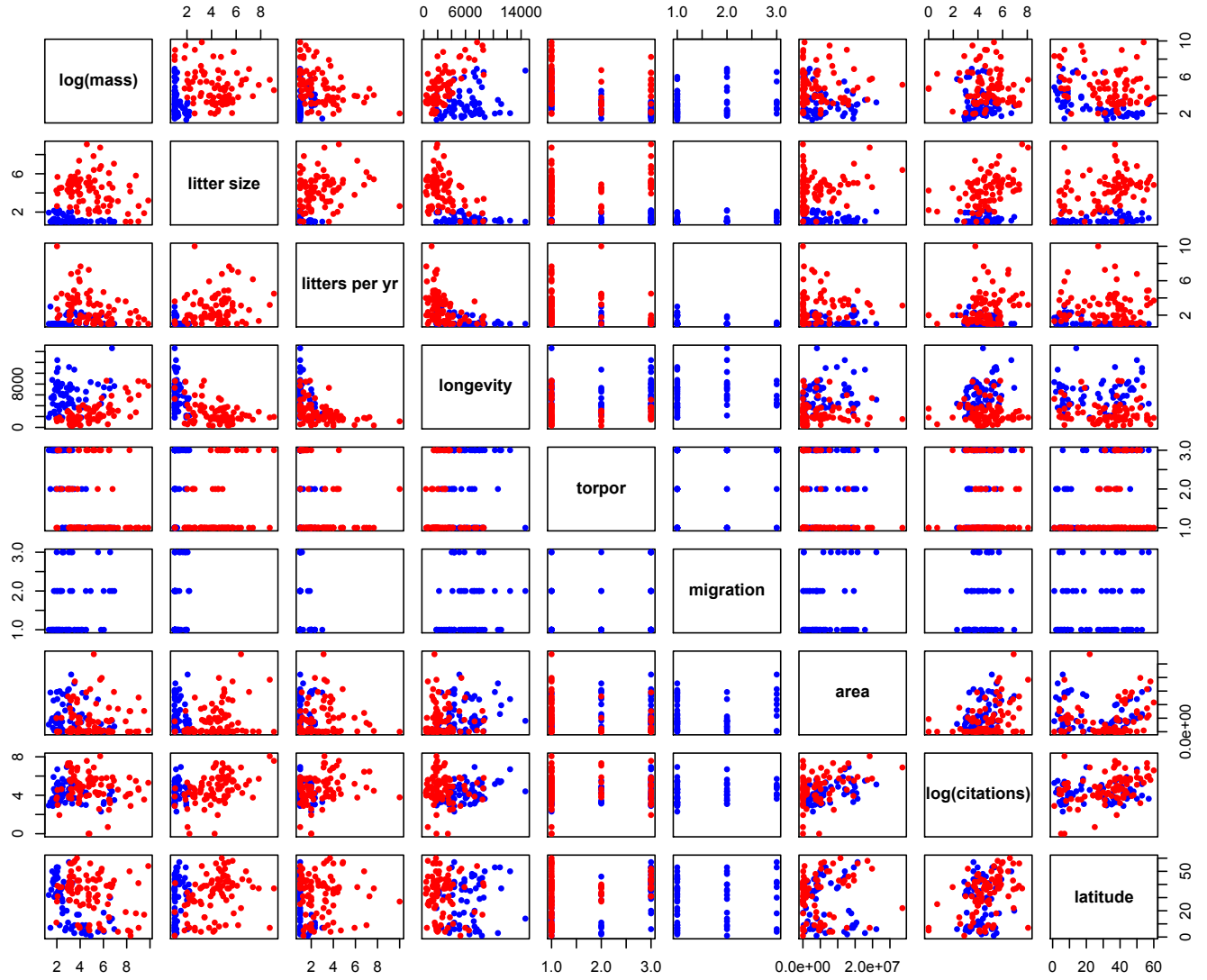


Fig. S8. Pairwise plots of all the variables examined. The bat data points are in blue, and the rodents in red.

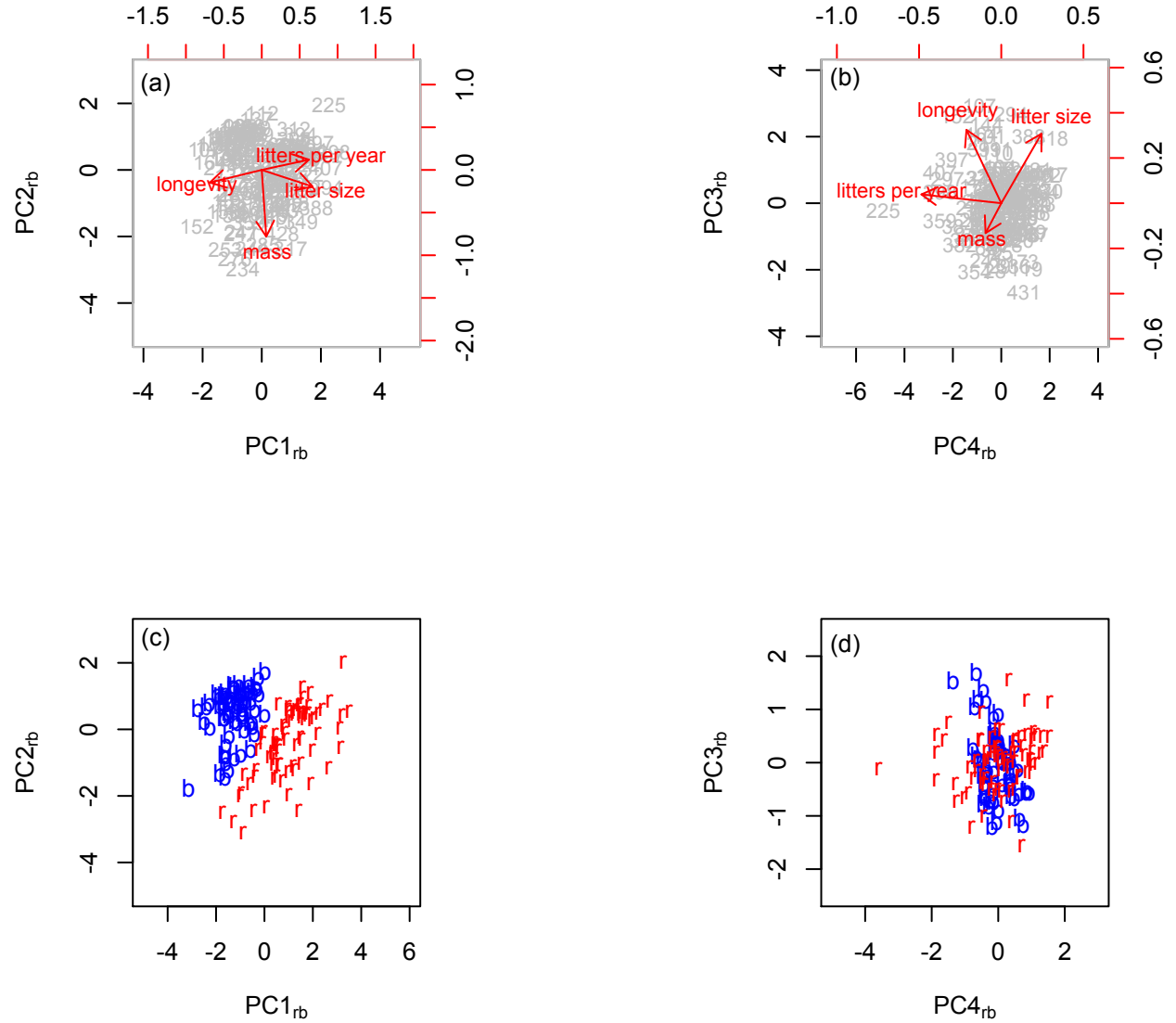


Fig. S9. Principal components analysis (PCA) for bats and rodents combined. Panel (a) shows PC1 and PC2, and panel (b) shows PC3 and 4. Panels (c) and (d) are the same principal components with bat data points as blue b's, and rodents as red r's.

References

- [1] Wright, E., Hayman, D., Vaughan, A., Temperton, N., Wood, J., Cunningham, A., Suu-Ire, R., Weiss, R. & Fooks, A., 2010 Virus neutralising activity of african fruit bat (*Eidolon helvum*) sera against emerging lyssaviruses. *Virology* **408**, 183–189.
- [2] Bininda-Emonds, O., Cardillo, M., Jones, K., MacPhee, R., Beck, R., Grenyer, R., Price, S., Vos, R., Gittleman, J. & Purvis, A., 2007 The delayed rise of present-day mammals. *Nature* **446**, 507.

Table S14. Species traits used in the study.

Order	Genus	Species	mass	lit.sz	lit.yr	longev	torp	mig	IUCN	area	lat	sympatry	cit	viruses	zoon	refs
Chiroptera	Anoura	geoffroyi	15.100	1.000	1.000	3650	1	1	LC	8665212	5	293	25	9	6	[1, 2, 3]
Chiroptera	Antrozous	pallidus	20.800	2.000	1.000	5406	2	1	LC	4506699	28	115	106	1	1	[1, 4, 2, 5, 6, 7, 8, 4]
Chiroptera	Artibeus	jamaicensis	41.800	1.000	2.000	7013	1	1	LC	1997429	17	262	163	12	9	[1, 5, 2, 9, 10]
Chiroptera	Artibeus	lituratus	65.600	1.025	1.879	3979	1	1	LC	15442170	9	300	77	14	12	[1, 5, 2, 9, 11, 12, 13]
Chiroptera	Barbastella	barbastellus	8.029	1.833	1.000	8401	3	1	NT	3924018	45	51	48	1	1	[1, 5, 14, 15, 16, 17, 18, 19, 20]
Chiroptera	Carollia	perspicillata	16.400	1.045	2.033	6209	1	1	LC	14606378	7	287	225	15	11	[1, 5, 2, 9, 21, 22, 23]
Chiroptera	Corynorhinus	townsendii	9.920	1.000	1.000	7487	3	1	LC	4849204	37	116	44	1	1	[1, 5, 24]
Chiroptera	Cynopterus	brachyotis	34.082	1.000	2.333	3689	1	1	LC	2861168	9	213	41	5	2	[1, 5, 25, 26]
Chiroptera	Cynopterus	sphinx	62.938	1.156	1.846	3650	2	1	LC	6858556	3	266	103	3	3	[1, 14, 27, 28, 29]
Chiroptera	Desmodus	rotundus	33.041	1.056	1.263	10665	2	1	LC	19150173	-3	302	246	7	4	[1, 5, 30, 31, 18, 3]
Chiroptera	Dobsonia	moluccensis	381.437	1.000	1.000	4490	1	1	LC	898926	-6	141	0	1	1	[1, 25, 9, 5, 32, 33]
Chiroptera	Eidolon	dupreanum	286.563	1.000	1.000	7300	1	1	V	460031	-17	38	6	3	2	[1, 34, 35, 36]
Chiroptera	Eidolon	helvum	252.840	1.020	1.167	7961	1	3	NT	12561712	-4	200	60	7	4	[1, 37, 38, 39, 40]
Chiroptera	Eonycteris	spelaea	59.887	1.000	2.333	1825	1	1	LC	3648868	7	296	21	5	3	[1, 37, 25, 26, 41]
Chiroptera	Epomophorus	gambianus	148.231	1.000	1.667	2849	1	1	LC	4800140	9	132	7	1	1	[1, 5, 42]
Chiroptera	Epomophorus	wahlbergi	89.538	1.000	2.000	3689	1	1	LC	5089184	-5	160	20	1	1	[1, 5, 43]
Chiroptera	Eptesicus	fuscus	17.221	1.500	1.000	7305	3	1	LC	14020198	20	280	1032	7	5	[1, 5, 14, 15, 44]
Chiroptera	Eptesicus	serotinus	22.859	1.375	1.000	6940	2	1	LC	27959853	46	187	104	4	3	[1, 5, 14, 45, 19, 20, 18]
Chiroptera	Glossophaga	soricina	9.400	1.000	2.000	4018	2	1	LC	16158143	9	310	128	8	7	[1, 5, 2, 46, 47, 48]
Chiroptera	Hypsignathus	monstrosus	328.294	1.143	2.000	4383	1	1	LC	3098273	6	150	10	2	2	[1, 5, 49, 50, 51]
Chiroptera	Lasionycteris	noctivagans	12.134	1.840	1.000	4383	2	3	LC	10473443	38	65	133	1	1	[1, 5, 14, 52, 53]
Chiroptera	Lasiurus	cinereus	25.279	2.053	1.000	5115	3	3	LC	23416663	6	274	168	2	2	[1, 5, 54, 53, 55]
Chiroptera	Macrotus	californicus	11.990	1.033	1.000	6209	1	1	LC	644039	27	71	46	1	1	[1, 5, 56, 14, 9, 57]
Chiroptera	Megaderma	lyra	48.709	1.100	1.000	5115	1	1	LC	6322216	17	218	100	2	1	[1, 5, 22]
Chiroptera	Miniopterus	schreibersii	11.609	1.001	1.000	8036	3	2	NT	4027214	29	154	161	12	6	[1, 5, 14, 58, 59, 60, 61, 62, 63, 19]
Chiroptera	Myotis	austroriparius	6.838	1.942	1.000	2190	2	1	LC	835458	33	17	25	1	1	[1, 64, 65, 66]
Chiroptera	Myotis	californicus	4.600	1.000	1.000	5479	3	1	LC	4188639	36	130	24	2	1	[1, 67, 68, 7, 8, 69]
Chiroptera	Myotis	daubentonii	7.373	1.125	1.000	10227	3	2	LC	34589751	53	90	175	3	2	[1, 5, 14, 70, 19, 71, 72]
Chiroptera	Myotis	evotis	6.875	1.000	1.000	8036	3	1	LC	3211018	44	34	38	2	1	[1, 5, 14, 73, 74, 75]
Chiroptera	Myotis	griseus	10.371	1.000	1.000	6026	3	2	NT	854076	36	17	40	1	1	[1, 5, 14, 76, 77]
Chiroptera	Myotis	leibii	5.210	1.000	1.000	4380	3	1	LC	1444356	42	17	18	1	1	[1, 5, 78, 79]
Chiroptera	Myotis	lucifugus	7.677	1.106	1.000	12419	3	2	LC	12664800	50	37	816	8	4	[1, 5, 14, 15, 80, 81, 82, 83, 18, 84]
Chiroptera	Myotis	myotis	22.925	1.375	1.000	7962	3	2	LC	3981498	40	43	279	7	2	[1, 14, 15, 85, 23, 86]
Chiroptera	Myotis	mystacinus	4.988	1.167	1.000	8766	3	1	LC	5217604	50	48	38	2	1	[1, 5, 14, 76, 18, 87, 88, 19]
Chiroptera	Myotis	nattereri	7.127	1.000	1.000	7305	3	1	LC	6190453	47	52	74	6	1	[1, 5, 14, 76, 89, 90, 19]
Chiroptera	Myotis	nigricans	4.252	1.000	3.000	2557	2	1	LC	15129223	-7	289	27	3	3	[1, 5, 14, 91, 92]
Chiroptera	Myotis	septentrionalis	6.268	1.000	1.000	6940	3	2	LC	5168594	48	23	81	4	4	[1, 5, 14, 93, 83]
Chiroptera	Myotis	thysanodes	8.191	1.000	1.000	6685	3	1	LC	3661784	35	123	21	1	1	[1, 5, 14, 91, 94, 95]
Chiroptera	Myotis	velifer	10.097	1.000	1.000	4128	3	2	LC	1967504	32	139	32	1	1	[1, 5, 14, 96, 97]
Chiroptera	Myotis	volans	8.765	1.000	1.000	1159	3	1	LC	4845574	32	94	22	2	1	[1, 98, 99, 100, 101]
Chiroptera	Myotis	yumanensis	9.158	1.000	1.000	3217	3	1	LC	4205191	38	86	27	2	1	[1, 5, 14, 102, 103]
Chiroptera	Nyctalus	leisleri	13.280	1.667	1.000	5844	3	3	LC	5868175	42	87	63	1	0	[1, 5, 104, 105, 19, 22]
Chiroptera	Nyctalus	noctula	27.967	1.439	1.000	4383	3	3	LC	13146436	41	173	132	9	5	[1, 5, 14, 54, 19, 62, 106]
Chiroptera	Nycticeius	humeralis	8.989	2.188	1.000	2192	3	2	LC	2910364	35	70	62	1	1	[1, 5, 14, 54, 107, 108]
Chiroptera	Parastrellus	hesperus	3.700	1.942	1.000	1840	3	1	LC	2680623	32	99	19	1	1	[1, 68, 7, 8, 109]
Chiroptera	Perimyotis	subflavus	5.737	2.140	1.000	5406	3	2	LC	4370640	40	143	105	1	1	[1, 5, 14, 76, 110]

Chiroptera	Phyllostomus	hastatus	90.022	1.000	1.000	6575	2	1	LC	13235754	2	262	73	13	10	[1, 5, 14, 111]
Chiroptera	Pipistrellus	kuhlii	5.934	1.300	1.000	2922	3	1	LC	12479184	31	115	41	1	1	[1, 5, 14, 112, 22]
Chiroptera	Pipistrellus	nathusii	7.309	1.900	1.000	4018	3	3	LC	6115801	53	43	53	4	1	[1, 5, 14, 113, 19, 114, 115, 116, 106]
Chiroptera	Pipistrellus	pipistrellus	5.557	1.281	1.000	5844	3	1	LC	34836390	44	168	365	8	3	[1, 5, 14, 15, 19, 20, 117, 118] [119, 19, 120, 121, 122]
Chiroptera	Plecotus	auritus	8.148	1.250	1.000	10958	3	1	LC	6895907	53	44	209	3	2	[1, 5, 14, 76, 18, 19, 85, 123]
Chiroptera	Pteropus	alecto	686.928	1.200	1.000	7191	1	2	LC	1404130	-12	172	55	7	6	[1, 5, 124]
Chiroptera	Pteropus	giganteus	842.349	1.000	1.000	14610	1	2	LC	4058065	14	132	82	2	1	[1, 5, 9, 125]
Chiroptera	Pteropus	hypomelanus	421.069	1.000	1.000	7410	1	1	LC	550427	4	183	27	5	5	[1, 5, 9, 126, 127, 32, 128]
Chiroptera	Pteropus	poliocephalus	718.814	1.000	1.000	8614	1	3	V	249713	-30	36	111	4	4	[1, 5, 9, 129, 22]
Chiroptera	Pteropus	scapulatus	412.179	1.000	1.000	5770	1	2	LC	3126765	-19	78	22	8	7	[1, 5, 9, 130]
Chiroptera	Pteropus	vampyrus	1027.955	1.000	1.000	7629	1	2	NT	1985718	6	219	33	1	1	[1, 5, 9, 124, 131]
Chiroptera	Rhinolophus	ferrumequinum	21.061	0.984	1.000	11140	3	1	LC	25129304	37	178	233	12	7	[1, 5, 14, 132, 18, 19, 133]
Chiroptera	Rhinolophus	hipposideros	4.958	1.137	1.000	5338	3	1	LC	7260478	39	84	69	1	0	[1, 132, 19, 134, 135, 136, 134]
Chiroptera	Rhinolophus	rouxii	11.788	1.000	1.000	1825	1	1	LC	870083	22	116	95	3	2	[1, 22]
Chiroptera	Rousettus	aegyptiacus	134.774	1.021	1.706	8359	1	2	LC	4450539	-1	211	196	10	7	[1, 9, 137]
Chiroptera	Rousettus	leschenaultii	89.181	1.040	1.875	5114	1	2	LC	7194098	9	222	55	14	9	[1, 5, 14, 138, 139, 140, 141, 142]
Chiroptera	Sturnira	lilium	19.343	1.000	2.333	4383	2	1	LC	16647201	11	303	68	8	6	[1, 5, 143, 144, 13, 145, 146]
Chiroptera	Tadarida	brasiliensis	11.978	1.031	1.000	4383	3	3	LC	15746797	18	330	300	5	5	[1, 5, 15, 147]
Chiroptera	Taphozous	melanopogon	27.568	1.000	1.000	7300	2	2	LC	5988880	8	311	23	4	3	[1, 148, 149, 150]
Chiroptera	Vespertilio	murinus	20.786	1.375	1.000	4380	3	3	LC	29699591	57	81	38	2	2	[1, 151, 19, 152, 153, 154, 155, 106]
Rodentia	Abrothrix	olivaceus	23.645	5.323	2.000	360	1		LC	1086786	-42	60	53	1	1	[1]
Rodentia	Aethomys	namaquensis	55.025	3.900	2.000	1717	1		LC	3375275	-24	99	53	2	2	[1, 5]
Rodentia	Akodon	azarae	24.500	4.680	2.000	549	1		LC	1231751	-36	93	106	2	2	[1, 156, 157]
Rodentia	Apodemus	agrarius	24.575	5.706	3.125	1460	1		LC	14443824	41	233	223	8	6	[1]
Rodentia	Apodemus	argenteus	21.000	4.077	4.000	1826	1		LC	367845	35	22	51	1	1	[1, 5]
Rodentia	Apodemus	flavicollis	32.260	5.367	4.875	1644	1		LC	6298880	57	122	407	11	7	[1, 5, 9]
Rodentia	Apodemus	sylvaticus	26.914	5.057	4.000	2301	1		LC	5399377	56	91	952	16	8	[1, 5]
Rodentia	Arvicanthis	niloticus	120.900	5.146	3.500	2447	1		LC	6772138	9	242	196	9	4	[1, 5]
Rodentia	Arvicola	amphibius	129.557	5.022	4.843	1338	1		LC	18522732	56	181	371	2	1	[1]
Rodentia	Baiomys	taylori	7.475	2.623	10.000	1127	2		LC	1280182	27	166	44	2	1	[1, 15]
Rodentia	Castor	fiber	19000.000	3.208	1.000	7665	1		LC	3812235	54	79	200	1	1	[1]
Rodentia	Coendou	prehensilis	4154.000	1.000	1.300	5268	1		LC	10484553	1	332	18	1	1	[1, 5, 158, 9]
Rodentia	Cricetomys	gambianus	1403.200	3.136	3.750	3068	1		LC	9019456	-4	263	98	4	1	[1, 5, 9]
Rodentia	Cuniculus	paca	8309.333	2.639	1.750	5954	1		LC	13382516	7	524	96	1	1	[1, 5, 9]
Rodentia	Cynomys	ludovicianus	883.587	4.536	1.000	3103	2		LC	1824941	40	114	355	1	0	[1, 159]
Rodentia	Dasyprocta	leporina	3339.300	1.800	1.300	6497	1		LC	2040718	5	81	61	3	3	[1, 160]
Rodentia	Erethizon	dorsatum	8144.400	1.032	1.000	8547	1		LC	12649972	41	210	113	3	2	[1, 5, 9]
Rodentia	Funisciurus	congius	112.120	2.200	2.000	3468	1		LC	1750122	-7	104	1	1	1	[1, 5, 9]
Rodentia	Gerbilliscus	validus	121.000	4.250	2.000	1826	1		LC	4675845	-5	186	1	1	1	[1, 5]
Rodentia	Glaucomys	volans	70.346	3.169	1.800	4137	1		LC	3926064	25	175	135	1	1	[1, 9]
Rodentia	Glis	glis	166.700	4.500	1.000	3114	3		LC	3811259	44	118	170	1	1	[1, 161, 15]
Rodentia	Hydromys	chrysogaster	651.125	3.437	2.209	2666	1		LC	4299391	-15	127	35	1	1	[1, 5, 9]
Rodentia	Hystrix	africaeauralis	13309.005	1.884	1.500	8437	1		LC	7729424	-17	205	35	1	1	[1, 5, 9]
Rodentia	Lemniscomys	striatus	50.400	4.609	1.500	1753	1		LC	4773339	8	242	30	4	2	[1, 5]
Rodentia	Marmota	monax	3795.903	4.767	1.000	5114	3		LC	8064664	50	77	347	5	3	[1, 5, 15]
Rodentia	Mesocricetus	auratus	97.125	9.076	4.500	1947	3		V	4702	37	16	1960	7	1	[1, 15]
Rodentia	Micromys	minutus	7.793	5.669	2.667	1278	1		LC	24127199	39	288	94	2	1	[1]
Rodentia	Microtus	agrestis	41.633	4.831	3.700	1753	1		LC	13088085	60	112	728	10	5	[1, 5]

Rodentia	Microtus	arvalis	25.117	4.841	6.786	1753	1	LC	8014045	50	160	629	7	5	[1, 5, 9]
Rodentia	Microtus	californicus	56.424	5.425	7.665	365	1	LC	288183	37	97	87	3	1	[1, 162]
Rodentia	Microtus	ochrogaster	43.210	4.160	4.000	1936	1	LC	3279550	36	82	967	2	0	[1, 5]
Rodentia	Microtus	oeconomus	34.647	5.709	3.413	584	1	LC	370998862	58	154	269	5	4	[1]
Rodentia	Microtus	pennsylvanicus	42.136	5.369	3.919	1423	1	LC	12643410	43	137	937	5	1	[1, 5]
Rodentia	Mus	minutoides	7.120	4.257	4.000	1571	1	LC	4269469	-11	218	37	1	0	[1, 5, 9]
Rodentia	Myocastor	coypus	6559.575	5.801	2.479	2784	1	LC	46600750	18	268	242	2	2	[1, 9]
Rodentia	Myodes	gapperi	22.100	5.296	2.366	600	1	LC	8792882	46	138	265	2	2	[1, 9]
Rodentia	Myodes	glareolus	22.829	4.362	3.150	1790	1	LC	9836202	56	113	1549	16	11	[1, 5, 9]
Rodentia	Myodes	rufocanus	30.333	4.930	3.750	1205	1	LC	14280106	46	102	317	2	2	[1, 5, 9]
Rodentia	Neotoma	albigula	200.258	2.144	2.000	3470	1	LC	835143	30	122	75	1	1	[1, 5, 9]
Rodentia	Neotoma	cinerea	254.125	3.590	1.773	2118	1	LC	3732149	48	146	56	2	2	[1, 5, 9]
Rodentia	Neotoma	lepida	236.000	3.083	3.333	3835	1	LC	988729	27	125	72	2	1	[1, 5, 9]
Rodentia	Neotoma	micropus	247.000	2.456	1.750	1205	2	LC	1066915	32	123	59	1	0	[1, 5, 163]
Rodentia	Oligoryzomys	flavescens	21.300	5.200	2.000	1403	1	LC	3209722	-28	238	50	2	2	[1, 157]
Rodentia	Ondatra	zibethicus	997.121	7.051	2.601	2118	1	LC	15517661	43	195	250	5	1	[1, 5, 9]
Rodentia	Onychomys	leucogaster	26.207	3.974	2.667	1825	1	LC	4156363	41	185	104	1	1	[1, 164]
Rodentia	Otomys	irroratus	117.113	1.810	4.000	730	1	LC	557001	-24	67	55	1	0	[1, 5, 9]
Rodentia	Pedetes	capensis	2727.500	1.001	3.600	7305	1	LC	3847276	-19	117	48	1	1	[1, 5, 9]
Rodentia	Perognathus	parvus	21.400	5.140	1.440	1460	3	LC	922281	42	110	42	1	1	[1, 132]
Rodentia	Peromyscus	californicus	43.606	2.021	4.375	2009	2	LC	132681	34	75	206	2	0	[1, 5, 9]
Rodentia	Peromyscus	eremicus	22.636	2.509	3.250	2703	2	LC	1227317	28	162	47	1	1	[1, 5, 15]
Rodentia	Peromyscus	gossypinus	27.998	4.094	4.000	300	2	LC	1163524	33	39	71	3	3	[1, 132]
Rodentia	Peromyscus	leucopus	18.400	4.309	4.300	2885	2	LC	6141145	37	199	1202	7	6	[1, 5, 15]
Rodentia	Peromyscus	maniculatus	19.333	4.892	3.248	3032	2	LC	13623312	39	293	1528	6	6	[1, 5, 15]
Rodentia	Peromyscus	truei	25.913	3.600	3.000	1972	2	LC	1567435	39	157	39	3	2	[1, 5, 9]
Rodentia	Proechimys	semispinosus	406.409	2.650	4.680	2118	1	LC	374844	5	104	62	2	2	[1, 5]
Rodentia	Rattus	exulans	52.450	3.800	5.920	450	1	LC	2279381338	-7	404	180	4	1	[1]
Rodentia	Rattus	fuscipes	115.300	4.844	3.300	1936	1	LC	524290	-33	28	145	1	0	[1, 5, 9]
Rodentia	Rattus	norvegicus	305.717	8.735	3.192	1825	1	LC	180534351	7	569	3182	20	7	[1, 5]
Rodentia	Rattus	rattus	176.612	6.394	3.117	1534	1	LC	62945738	22	993	987	15	11	[1, 5, 9]
Rodentia	Reithrodontomys	megalotis	10.968	4.545	4.500	1315	2	LC	5308921	38	280	103	2	1	[1, 5, 15]
Rodentia	Rhabdomys	pumilio	44.838	6.162	7.000	1644	1	LC	3304974	-9	170	123	1	1	[1, 5, 9]
Rodentia	Sciurus	carolinensis	527.738	3.384	1.885	8620	1	LC	4162786	39	85	333	15	8	[1, 5]
Rodentia	Sciurus	granatensis	279.000	2.029	2.000	4200	1	LC	995652	10	175	13	1	1	[1, 5]
Rodentia	Sciurus	griseus	714.000	2.670	1.000	4018	1	LC	377346	40	103	24	1	1	[1, 5]
Rodentia	Sciurus	niger	810.443	3.222	1.563	5844	1	LC	4408246	38	122	147	4	4	[1, 5]
Rodentia	Sciurus	vulgaris	348.500	4.600	2.333	5406	1	LC	43680564	52	185	310	4	2	[1, 5]
Rodentia	Sigmodon	hispidus	114.395	5.645	7.267	1899	1	LC	2676280	31	126	647	18	11	[1, 5, 9]
Rodentia	Spermophilus	beecheyi	648.025	6.075	1.000	3650	3	LC	463741	39	104	139	2	1	[1, 132, 165]
Rodentia	Spermophilus	citellus	290.000	6.500	1.250	2447	3	V	443576	44	45	69	2	0	[1, 5, 15]
Rodentia	Spermophilus	lateralis	192.033	5.292	1.000	3799	3	LC	1713233	37	150	267	1	1	[1, 5, 15]
Rodentia	Spermophilus	richardsonii	329.300	6.800	1.000	2192	3	LC	904070	50	48	163	2	1	[1, 5, 15]
Rodentia	Spermophilus	tridecemlineatus	172.168	7.841	1.333	2885	3	LC	3799232	37	111	304	2	2	[1, 5, 166]
Rodentia	Spermophilus	variegatus	673.430	4.946	1.250	3579	3	LC	2327898	31	209	33	2	1	[1, 5, 132]
Rodentia	Tamias	amoenus	49.800	5.315	1.071	1899	3	LC	1152398	43	102	89	1	1	[1, 5, 15]
Rodentia	Tamias	minimus	48.058	5.092	1.200	3653	3	LC	5585611	52	145	24	1	1	[1, 5, 166]
Rodentia	Tamias	sibiricus	92.227	5.046	1.143	3506	3	LC	16750695	47	164	51	1	0	[1, 5, 167]
Rodentia	Tamias	striatus	108.501	4.715	1.563	3470	3	LC	4321942	43	53	281	5	5	[1, 5, 15]

Rodentia	Tamiasciurus	hudsonicus	215.535	4.034	1.625	3579	1	LC	10942922	43	147	314	4	2	[1, 5, 9]
Rodentia	Thryonomys	swinderianus	4053.347	4.144	2.250	1972	1	LC	8119945	-4	260	64	1	1	[1, 5]
Rodentia	Xerus	erythropus	649.133	3.417	3.000	3762	1	LC	10427903	15	248	12	2	1	[1, 5, 168]
Rodentia	Xerus	inauris	588.000	2.048	1.000	580	1	LC	1519144	-25	66	2	1	1	[1, 5, 166]

abbreviations and units:

‘mass’ – body mass in grams

‘lit.sz’ – mean litter size

‘lit.yr’ – mean number of litters per year

‘longev’ – maximum longevity in days

‘torp’ - torpor category, 1=no evidence of torpor use; 2=some torpor use with minimum body temperature > 11°C; 3=true hibernation with min Tb < 11°C)

‘mig’ – migration category, 1=only local movement; 2=regional migration, 3=long distance migration (see main text)

‘IUCN’ – IUCN conservation status. LC= least concern; V=vulnerable; NT=near threatened

‘area’ – area in km² of the species’ distribution

‘lat’ – absolute value of the latitude at the midpoint of the species distribution

‘sympatry’ – number of other species in the same taxonomic order whose distributions overlap with the species of interest

‘cit’ – number of citations on Web of Science for the species name

‘viruses’ – the number of viruses identified in the species in the attached database

‘zoon’ – the number of zoonotic viruses

All of the data for IUCN status, species distribution area, latitude and number of range overlaps (sympatry) came from ref[169].

References

- [1] Jones, K., Bielby, J., Cardillo, M., Fritz, S., O’Dell, J., Orme, C., Safi, K., Sechrest, W., Boakes, E., Carbone, C. *et al.*, 2009 Pantheria: a species-level database of life history, ecology, and geography of extant and recently extinct mammals. *Ecology* **90**, 2648–2648.
- [2] Eisenberg, J., 1989 *Mammals of the Neotropics, Vol. 1, The Northern Neotropics: Panama, Colombia, Suriname, French Guiana*. Chicago, Illinois, USA: The University of Chicago Press.
- [3] Fraser, K., McKinnon, E. & Diamond, A., 2010 Migration, diet, or molt? interpreting stable-hydrogen isotope values in neotropical bats. *Biotropica* **42**, 512–517.
- [4] Hermanson, J. & O’Shea, T., 1983 *Antrozous pallidus*. *Mammalian Species* pp. 1–8.
- [5] de Magalhaes, J. & Costa, J., 2009 A database of vertebrate longevity records and their relation to other life-history traits. *Journal of Evolutionary Biology* **22**, 1770–1774.
- [6] Marom, S., Korine, C., Wojciechowski, M., Tracy, C. & Pinshow, B., 2006 Energy metabolism and evaporative water loss in the european free-tailed bat and hemprich’s long-eared bat (microchiroptera): Species sympatric in the negev desert. *Physiological and Biochemical Zoology* **79**, 944–956.
- [7] O’Farrell, M. & Bradley, W., 1970 Activity patterns of bats over a desert spring. *Journal of Mammalogy* pp. 18–26.
- [8] O’Farrell, M., Bradley, W. & Jones, G., 1967 Fall and winter bat activity at a desert spring in southern nevada. *The Southwestern Naturalist* **12**, 163–171.
- [9] McNab, B., 2008 An analysis of the factors that influence the level and scaling of mammalian bmr. *Comparative Biochemistry and Physiology-Part A: Molecular & Integrative Physiology* **151**, 5–28.
- [10] Ortega, J. & Castro-Arellano, I., 2001 *Artibeus jamaicensis*. *Mammalian species* **662**, 1–9.
- [11] Duarte, A. & Talamoni, S., 2010 Reproduction of the large fruit-eating bat artibeus lituratus (chiroptera: Phyllostomidae) in a brazilian atlantic forest area. *Mammalian Biology-Zeitschrift für Säugetierkunde* **75**, 320–325.
- [12] Mendes, P., Vieira, T., Oprea, M. & Ditchfield, A., 2009 Long-distance movement of artibeus lituratus (chiroptera: Phyllostomidae) in the state of espírito santo, brazil. *Ecotropica* **15**, 43–46.
- [13] Sánchez, F., Alvarez, J., Ariza, C. & Cadena, A., 2007 Bat assemblage structure in two dry forests of colombia: Composition, species richness, and relative abundance. *Mammalian Biology* **72**, 82–92.
- [14] Wilkinson, G. & South, J., 2002 Life history, ecology and longevity in bats. *Aging Cell* **1**, 124–131.
- [15] Geiser, F., 2004 Metabolic rate and body temperature reduction during hibernation and daily torpor. *Annual Reviews in Physiology* **66**, 239–274.

- [16] Gottfried, I., 2009 Use of underground hibernacula by the barbastelle (*barbastella barbastellus*) outside the hibernation season. *Acta Chiropterologica* **11**, 363–373.
- [17] Rydell, J. & Bogdanowicz, W., 1997 *Barbastella barbastellus*. *Mammalian species* **557**, 1–8.
- [18] Baker, R., 1978 The evolutionary ecology of animal migration. *The Evolutionary Ecology of Animal Migration* .
- [19] Hutterer, R., Ivanova, T., Meyer-Cords, C. & Rodrigues, L., 2005 Bat migrations in europe: A review of literature and analysis of banding data. *Natur. Biol. Vielfalt* **28**, 1–172.
- [20] Dietz, C., von Helversen, O. & Nill, D., 2009 *Bats of Britain, Europe & Northwest Africa*. A & C Publishers LTD. London.
- [21] Cloutier, D. & Thomas, D., 1992 *Carollia perspicillata*. *Mammalian species* pp. 1–9.
- [22] Fleming, T. & Eby, P., 2003 Ecology of bat migration. In *Bat Ecology* (eds. T. Kunz & M. Fenton), pp. 156–208. University of Chicago Press, Chicago, Illinois.
- [23] Rodrigues, L., Ramos Pereira, M., Rainho, A. & Palmeirim, J., 2010 Behavioural determinants of gene flow in the bat *miniopterus schreibersii*. *Behavioral Ecology and Sociobiology* **64**, 835–843.
- [24] Kunz, T. & Martin, R., 1982 *Plecotus townsendii*. *Mammalian Species* pp. 1–6.
- [25] McNab, B. & Bonaccorso, F., 2001 The metabolism of new guinean pteropodid bats. *Journal of Comparative Physiology B: Biochemical, Systemic, and Environmental Physiology* **171**, 201–214.
- [26] Hodgkison, R., Balding, S., Zubaid, A. & Kunz, T., 2004 Temporal variation in the relative abundance of fruit bats (megachiroptera: Pteropodidae) in relation to the availability of food in a lowland malaysian rain forest. *Biotropica* **36**, 522–533.
- [27] Banerjee, A., Meenakumari, K. & Krishna, A., 2007 Relationship between delayed embryonic development and metabolic factors and fat deposition in fruit bat *cynopterus sphinx*. *Reproduction, Fertility and Development* **19**, 626–633.
- [28] Storz, J. & Kunz, T., 1999 *Cynopterus sphinx*. *Mammalian Species* **613**, 1–8.
- [29] Storz, J., 2002 Contrasting patterns of divergence in quantitative traits and neutral dna markers: analysis of clinal variation. *Molecular Ecology* **11**, 2537–2551.
- [30] Lyman, C. & Wimsatt, W., 1966 Temperature regulation in the vampire bat, *desmodus rotundus*. *Physiological Zoology* **39**, 101–109.
- [31] Trajano, E., 1996 Movements of cave bats in southeastern brazil, with emphasis on the population ecology of the common vampire bat, *desmodus rotundus* (chiroptera). *Biotropica* **28**, 121–129.
- [32] Bonaccorso, F., 1998 *Bats of Papua New Guinea*. Tropical Field Guide Series. Conservation International, Washington, DC.
- [33] Mickleburgh, S., Hutson, A. & Racey, P., 1992 Old World fruit bats: an action plan for their conservation. .
- [34] Goodman, S., Andriafidison, D., Andrianaivoarivelo, R., Cardiff, S., Ifticene, E., Jenkins, R., Kofoky, A., Mbohoahy, T., Rakotondravony, D., Ranivo, J. *et al.*, 2005 The distribution and conservation of bats in the dry regions of madagascar. *Animal Conservation* **8**, 153–165.
- [35] MacKinnon, J., Hawkins, C. & Racey, P., 2003 Pteropodidae. In *The natural history of Madagascar* (eds. S. Goodman & J. Benstead), pp. 1299–1302. The University of Chicago Press, Chicago, IL.
- [36] Cardiff, S., Ratrimomanarivo, F., Rembert, G. & Goodman, S., 2009 Hunting, disturbance and roost persistence of bats in caves at ankarana, northern madagascar. *African Journal of Ecology* **47**, 640–649.
- [37] Krutzsch, P., 1979 Male reproductive patterns in nonhibernating bats. *Reproduction* **56**, 333.
- [38] DeFrees, S. & Wilson, D., 1988 *Eidolon helvum*. *Mammalian species* pp. 1–5.
- [39] Richter, H. & Cumming, G., 2008 First application of satellite telemetry to track african straw-coloured fruit bat migration. *Journal of Zoology* **275**, 172–176.
- [40] Thomas, D., 1983 The annual migrations of three species of west african fruit bats (chiroptera: Pteropodidae). *Canadian Journal of Zoology* **61**, 2266–2272.
- [41] Krutzsch, P., 2005 Reproductive anatomy and cyclicity of the bat *eonycteris spelea* dobson (chiroptera: Pteropodidae) in west malaysia. *Acta Chiropterologica* **7**, 51–64.
- [42] Thomas, D. & Marshall, A., 1984 Reproduction and growth in three species of west african fruit bats. *Journal of Zoology* **202**, 265–281.
- [43] Acharya, L., 1992 *Epomophorus wahlbergi*. *Mammalian Species* pp. 1–4.
- [44] Neubaum, D., O'Shea, T. & Wilson, K., 2006 Autumn migration and selection of rock crevices as hibernacula by big brown bats in colorado. *Journal of Mammalogy* **87**, 470–479.
- [45] Harbusch, C. & Racey, P., 2006 The sessile serotine: the influence of roost temperature on philopatry and reproductive phenology of *Eptesicus serotinus* (Schreber, 1774) (Mammalia : Chiroptera). *ACTA CHIROPTEROLOGICA* **8**, 213–229. ISSN 1508-1109.
- [46] Kelm, D. & von Helversen, O., 2007 How to budget metabolic energy: torpor in a small neotropical mammal. *Journal of Comparative Physiology B: Biochemical, Systemic, and Environmental Physiology* **177**, 667–677.

- [47] Alvarez, J., Willig, M., Jones Jr, J. & Webster, W., 1991 *Glossophaga soricina*. *Mammalian Species* pp. 1–7.
- [48] Fleming, T., Nuñez, R. & Sternberg, L., 1993 Seasonal changes in the diets of migrant and non-migrant nectarivorous bats as revealed by carbon stable isotope analysis. *Oecologia* **94**, 72–75.
- [49] Bradbury, J., 1977 Lek mating behavior in the hammer-headed bat. *Zeitschrift für Tierpsychologie* **45**, 225–255.
- [50] Langevin, P. & Barclay, R., 1990 *Hypsignathus monstrosus*. *Mammalian Species* **357**, 1–4.
- [51] King, T. & Dallimer, M., 2010 The fruit bats (chiroptera: Pteropodidae) of the lesio-louna reserve, bateke plateau, republic of congo. *Mammalia* **74**, 63–69.
- [52] Dunbar, M., 2007 Thermal energetics of torpid silver-haired bats *lasiurus noctivagans*. *Acta theriologica* **52**, 65–68.
- [53] Cryan, P., 2003 Seasonal distribution of migratory tree bats (*lasiurus* and *lasiurus*) in north america. *Journal of Mammalogy* **84**, 579–593.
- [54] Genoud, M., 1993 Temperature regulation in subtropical tree bats. *Comparative Biochemistry and Physiology Part A: Physiology* **104**, 321–331.
- [55] Findley, J. & Jones, C., 1964 Seasonal distribution of the hoary bat. *Journal of Mammalogy* pp. 461–470.
- [56] Bell, G., Bartholomew, G. & Nagy, K., 1986 The roles of energetics, water economy, foraging behavior, and geothermal refugia in the distribution of the bat, *macrotus californicus*. *Journal of Comparative Physiology B: Biochemical, Systemic, and Environmental Physiology* **156**, 441–450.
- [57] Anderson, S., 1969 *Macrotus waterhousii*. *Mammalian species* pp. 1–4.
- [58] HALL, L., 1982 The effect of cave microclimate on winter roosting behaviour in the bat, *miniopterus schreibersii* *blepotis*. *Australian Journal of Ecology* **7**, 129–136.
- [59] Rodrigues, L., 1999 *Miniopterus schreibersii*. In *The Atlas of European Mammals* (ed. A. e. a. Mitchell-Jones), pp. 154–155. Academic Press, London, UK.
- [60] Rodrigues, L. & Palmeirim, J., 2008 Migratory behaviour of the schreiber's bat: when, where and why do cave bats migrate in a mediterranean region? *Journal of Zoology* **274**, 116–125.
- [61] Paunovic, M., 1998 New results of bat marking (mammalia, chiroptera) in eastern serbia vi. naučno-stručni skup o prirodnim vrednostima i zaštiti zivotne sredine, zbornik radova. *Zbornik Radova* **27**, 243–246.
- [62] Holland, R., 2007 Orientation and navigation in bats: known unknowns or unknown unknowns? *Behavioral Ecology and Sociobiology* **61**, 653–660.
- [63] Serra-Cobo, J., Sanz-Trullén, V. & Martínez-Rica, J., 1998 Migratory movements of *miniopterus schreibersii* in the north-east of spain. *order* .
- [64] McNab, B., 1974 The behavior of temperate cave bats in a subtropical environment. *Ecology* pp. 943–958.
- [65] Jones, C. & Manning, R., 1989 *Myotis austroriparius*. *Mammalian species* pp. 1–3.
- [66] Rice, D., 1957 Life history and ecology of *myotis austroriparius* in florida. *Journal of Mammalogy* **38**, 15–32.
- [67] Duke, S., Bateman, G. & Bateman, M., 1979 Longevity record for *myotis californicus*. *The Southwestern Naturalist* **24**.
- [68] Hirshfeld, J. & O'Farrell, M., 1976 Comparisons of differential warming rates and tissue temperatures in some species of desert bats. *Comparative Biochemistry and Physiology Part A: Physiology* **55**, 83 – 87. ISSN 0300-9629. (doi:DOI: 10.1016/0300-9629(76)90127-4).
- [69] Simpson, M., 1993 *Myotis californicus*. *Mammalian Species* **428**, 1–4.
- [70] Dietz, M. & Kalko, E., 2006 Seasonal changes in daily torpor patterns of free-ranging female and male *daubenton's* bats (*myotis daubentonii*). *Journal of Comparative Physiology B: Biochemical, Systemic, and Environmental Physiology* **176**, 223–231.
- [71] Tress, J., Tress, C., Schorcht, W., BIEDERMANN, M., Koch, R. & Iffert, D., 2004 Mitteilungen zum wanderverhalten von wasserfledermäusen (*myotis daubentonii*) und rauhhaufledermäusen (*pipistrellus nathusii*) aus mecklenburg. *Nyctalus (NF)* **9**, 236–248.
- [72] Bogdanowicz, W., 1994 *Myotis daubentonii*. *Mammalian species* pp. 1–9.
- [73] Chruszcz, B. J. & Barclay, R. M. R., 2002 Thermoregulatory ecology of a solitary bat, *myotis evotis*, roosting in rock crevices. *Functional Ecology* **16**, 18–26. ISSN 1365-2435. (doi:10.1046/j.0269-8463.2001.00602.x).
- [74] Lausen, C. & Barclay, R., 2006 Winter bat activity in the canadian prairies. *Canadian journal of zoology* **84**, 1079–1086.
- [75] Manning, R. & Jones, J., 1989 *Myotis evotis*. *Mammalian Species* pp. 1–5.
- [76] Webb, P., Speakman, J. & Racey, P., 1996 How hot is a hibernaculum? a review of the temperatures at which bats hibernate. *Oecologia* **98**, 40–47.
- [77] Decher, J. & Choate, J., 1995 *Myotis grisescens*. *Mammalian Species* pp. 1–7.

- [78] Best, T. & Jennings, J., 1997 *Myotis leibii*. *Mammalian species* pp. 1–6.
- [79] Johnson, J. & Gates, J., 2008 Spring migration and roost selection of female *myotis leibii* in maryland. *Northeastern Naturalist* **15**, 453–460.
- [80] Davis, W. & Hitchcock, H., 1965 Biology and migration of the bat, *myotis lucifugus*, in new england. *Journal of Mammalogy* pp. 296–313.
- [81] Griffin, D., 1940 Migrations of new england bats. *Bulletin of The Museum of Comparative Zoology* **86**, 217–246.
- [82] Griffin, D., 1945 Travels of banded cave bats. *Journal of Mammalogy* **26**, 15–23.
- [83] Britzke, E., Loeb, S., Hobson, K., Romanek, C. & Vonhof, M., 2009 Using hydrogen isotopes to assign origins of bats in the eastern united states. *Journal of Mammalogy* **90**, 743–751.
- [84] Fenton, M. & Barclay, R., 1980 *Myotis lucifugus*. *Mammalian Species* pp. 1–8.
- [85] Furmankiewicz, J. & Altringham, J., 2007 Genetic structure in a swarming brown long-eared bat (*plecotus auritus*) population: evidence for mating at swarming sites. *Conservation Genetics* **8**, 913–923.
- [86] Simon, M., Hüttenbügel, S. & Smit-Viergutz, J., 2004 Ecology and conservation of bats in villages and towns. *Schriftenr. Landschaftspfl. Natursch.* **77**, 1–264.
- [87] Gerell, R., 1999 *Myotis mystacinus* (kuhl, 1817). In *Atlas of European Mammals* (eds. A. J. Mitchell-Jones, G. Amori, W. Bogdanowicz, B. Krystufek, P. J. H. Reijnders, F. Spitzenberger, M. Stubbe, J. B. M. Thissen, V. Vohralík & J. Zima), pp. 116–117. The Academic Press, London, UK.
- [88] Gaisler, J., Hanák, V., Hanzal, V. & Jarský, V., 2003 Výsledky kroužkování netopýru v české republice a na slovensku, 1948–2000. *Vespertilio* **7**, 3–61.
- [89] Rivers, N., Butlin, R. & Altringham, J., 2006 Autumn swarming behaviour of natterer’s bats in the uk: population size, catchment area and dispersal. *Biological conservation* **127**, 215–226.
- [90] Masing, M., Poots, L., Randla, T. & Lutsar, L., 1999 50 years of bat-ringing in estonia: methods and the main results. *Plecotus et al. Moskva* **2**, 20–35.
- [91] Studier, E. & O’Farrell, M., 1972 Biology of *myotis thysanodes* and *m. lucifugus* (chiroptera: Vespertilionidae)–i. thermoregulation. *Comparative Biochemistry and Physiology Part A: Physiology* **41**, 567–595.
- [92] Wilson, D. & LaVal, R., 1974 *Myotis nigricans*. *Mammalian Species* **39**, 1–3.
- [93] Caceres, M. C. & Barclay, R. M. R., 2000 *Myotis septentrionalis*. *Mammalian Species* pp. 1–4. (doi:10.1644/1545-1410(2000)634i0001:MSi2.0.CO;2).
- [94] Geluso, K., 2007 Winter activity of bats over water and along flyways in new mexico. *The Southwestern Naturalist* **52**, 482–492.
- [95] O’Farrell, M. & Studier, E., 1980 *Myotis thysanodes*. *Mammalian species* pp. 1–5.
- [96] Reisen, W., Kennedy, M. & Reisen, N., 1976 Winter ecology of ectoparasites collected from hibernating *myotis velifer* (allen) in southwestern oklahoma (chiroptera: Vespertilionidae). *The Journal of Parasitology* pp. 628–635.
- [97] Fitch, J., Shump, K. & Shump, A., 1981 *Myotis velifer*. *Mammalian Species* pp. 1–5.
- [98] Warner, R. & Czaplewski, N., 1984 *Myotis volans*. *Mammalian species* pp. 1–4.
- [99] Armstrong, D. M., Fitzgerald, J. P. & Meaney, C. A., 2011 *Mammals of Colorado*. University of Colorado Press, Boulder, CO, second edition.
- [100] Schowalter, D., 1980 Swarming, reproduction, and early hibernation of *myotis lucifugus* and *m. volans* in alberta, canada. *Journal of Mammalogy* **61**, 350–354.
- [101] CRYAN, P., BOGAN, M. & YANEGA, G., 2001 Roosting habits of four bat species in the black hills of south dakota. *Acta Chiropterologica* **3**, 43–52.
- [102] Milligan, B. & Brigham, R., 1993 Sex ratio variation in the yuma bat (*myotis yumanensis*). *Canadian journal of zoology* **71**, 937–940.
- [103] Geluso, K. & Mink, J., 2009 Use of bridges by bats (mammalia: Chiroptera) in the rio grande valley, new mexico. *The Southwestern Naturalist* **54**, 421–429.
- [104] Nagel, A. & Nagel, R., 1991 How do bats choose optimal temperatures for hibernation? *Comparative Biochemistry and Physiology Part A: Physiology* **99**, 323–326.
- [105] Ohlendorf, B., Hecht, B., Strassburg, D. & AGIRREMENDI, P., 2000 Fernfund eines kleinabendseglers (*nyctalus leisleri*) in spanien. *Nyctalus* **7**, 239–242.
- [106] Popa-Lisseanu, A. & Voigt, C., 2009 Bats on the move. *Journal of Mammalogy* **90**, 1283–1289.
- [107] Humphrey, S. & Cope, J., 1968 Records of migration of the evening bat, *nycticeius humeralis*. *Journal of Mammalogy* **49**, 329–329.
- [108] Watkins, L., 1969 Observations on the distribution and natural history of the evening bat (*nycticeius humeralis*) in northwestern missouri and adjacent iowa. *Transactions of the Kansas Academy of Science* **72**, 330–336.
- [109] Ruffner, G., Poche, R., Meierkord, M. & Neal, J., 1979 Winter bat activity over a desert wash in southwestern utah. *The Southwestern Naturalist* **24**, 447–453.

- [110] Cryan, P. Unpublished .
- [111] Santos, M., Aguirre, L., Vázquez, L. & Ortega, J., 2003 *Phyllostomus hastatus*. *Mammalian Species* **722**, 1–6.
- [112] Andreuccetti, P., Angelini, F. & Taddei, C., 1984 The interactions between spermatozoa and uterine epithelium in the hibernating bat, *pipistrellus kuhli natt*. *Gamete research* **10**, 67–76.
- [113] Flaquer, C., Ruiz-Jarillo, R., Torre, I. & Arrizabalaga, A., 2005 First resident population of *pipistrellus nathusii* (keyserling and blasius, 1839) in the iberian peninsula. *Acta Chiropterologica* **7**, 183–188.
- [114] Petersons, G., 2004 Seasonal migrations of north-eastern populations of *nathusius*' bat *pipistrellus nathusii* (chiroptera). *Myotis* **41/42**, 29–56.
- [115] Bogdanowicz, W., 1999 *Pipistrellus nathusii* (keyserling and blasius, 1839). In *The Atlas of European Mammals* (eds. A. Mitchell-Jones, G. Amori, W. Bogdanowicz, B. Kryštufek, P. Reijnders, F. Spitzenberger, M. Stubbe, J. Thissen, V. Vohralík *et al.*), pp. 124–125. The Academic Press, London, UK.
- [116] Russ, J., O'Neill, J. & Montgomery, W., 1998 *Nathusius*' pipistrelle bats (*pipistrellus nathusii*, keyserling & blasius 1839) breeding in ireland. *Journal of Zoology* **245**, 345–349.
- [117] Avery, M., 1991 Pipistrelle. In *Handbook of British Mammals* (eds. G. Corbet & S. Harris), pp. 124–128. Blackwell Scientific Publications, Oxford, UK.
- [118] Bryja, J., Kaňuch, P., Fornůsková, A., Bartonička, T. & Řehák, Z., 2009 Low population genetic structuring of two cryptic bat species suggests their migratory behaviour in continental europe. *Biol. J. Linn. Soc.* **96**, 103–114.
- [119] Buresh, I., 1941 The bats (chiroptera) migrate like the migrating birds. *Bulg. Akad. Nauk. Iskustv.* **61**, 4–72.
- [120] Benda, P., Ivanova, T., Horáček, I., Hanák, V., Červený, J., Gaisler, J., Gueorguieva, A., Petrov, B. & Vohralík, V., 2003 Bats (mammalia: Chiroptera) of the eastern mediterranean. part 3. review of bat distribution in bulgaria. *Acta Soc. Zool. Bohem* **67**, 245–357.
- [121] Park, K., Altringham, J. & Jones, G., 1996 Assortative roosting in the two phonic types of *pipistrellus pipistrellus* during the mating season. *Proceedings: Biological Sciences* **263**, 1495–1499.
- [122] Sachteleben, J. & Von Helvesen, O., 2006 Songflight behaviour and mating system of the pipistrelle bat (*pipistrellus pipistrellus*) in an urban habitat. *Acta Chiropterologica* **8**, 391–401.
- [123] Burland, T., Barratt, E., Beaumont, M. & Racey, P., 1999 Population genetic structure and gene flow in a gleaning bat, *plecotus auritus*. *Proceedings of the Royal Society of London. Series B: Biological Sciences* **266**, 975–980.
- [124] Breed, A., Field, H., Smith, C., Edmonston, J. & Meers, J., 2010 Bats without borders: long-distance movements and implications for disease risk management. *EcoHealth* pp. 1–9.
- [125] Epstein, J. H. Personal communication .
- [126] Jones, D. & Kunz, T., 2000 *Pteropus hypomelanus*. *Mammalian Species* pp. 1–6.
- [127] Heideman, P. & Heaney, L., 1989 Population biology and estimates of abundance of fruit bats (pteropodidae) in philippine submontane rainforest. *Journal of Zoology* **218**, 565–586.
- [128] McNab, B. & Armstrong, M., 2001 Sexual dimorphism and scaling of energetics in flying foxes of the genus *pteropus*. *Journal of mammalogy* **82**, 709–720.
- [129] Tidemann, C. & Nelson, J., 2004 Long-distance movements of the grey-headed flying fox (*pteropus poliocephalus*). *Journal of Zoology* **263**, 141–146.
- [130] Sinclair, E., Webb, N., Marchant, A. & Tidemann, C., 1996 Genetic variation in the little red flying-fox *pteropus scapulatus* (chiroptera: Pteropodidae): implications for management. *Biological Conservation* **76**, 45–50.
- [131] Epstein, J., Olival, K., Pulliam, J., Smith, C., Westrum, J., Hughes, T., Dobson, A., Zubaid, A., Rahman, S., Basir, M. *et al.*, 2009 *Pteropus vampyrus*, a hunted migratory species with a multinational home-range and a need for regional management. *Journal of Applied Ecology* **46**, 991–1002.
- [132] Geiser, F. & Ruf, T., 1995 Hibernation versus daily torpor in mammals and birds: physiological variables and classification of torpor patterns. *Physiological Zoology* **68**, 935–966.
- [133] De Paz, O., Fernández, R. & Benzal, J., 1986 El anillamiento de qirópteros en el centro de la península ibérica durante el periodo 1977-1986. *Central de Ecología* **30**, 113–138.
- [134] Gaisler, J. & Chytil, J., 2002 Mark-recapture results and changes in bat abundance at the cave of Na Turoldu, Czech Republic. *FOLIA ZOOLOGICA* **51**, 1–10. ISSN 0139-7893.
- [135] Roer, H., 1995 60 years of bat-banding in europe-results and tasks for future research. *Myotis* **32-33**, 251–261.
- [136] Schober, W. & Grimmberger, E., 1998 *Die Fledermäuse Europas*. Kosmos Publishing House, Stuttgart, Germany.
- [137] Kwiecinski, G. & Griffiths, T., 1999 *Rousettus egyptiacus*. *Mammalian Species* pp. 1–9.
- [138] He, L., Pan, Y., He, G., Lin, B., Liao, C., Zuo, X. & Yuan, L., 2010 Structural and functional studies of leptins from hibernating and non-hibernating bats. *General and comparative endocrinology* **168**, 29–35.
- [139] Roberts, T., 1977 *The mammals of Pakistan*. Cambridge Univ Press.

- [140] Advani, R., 1982 Distribution and status of chiroptera species in rajasthan, india. *Saeugetierkundliche Mitteilungen* **30**, 49–52.
- [141] Brosset, A., 1962 The bats of central and western india. part 1. *Bombay Nat. Hist. Soc.* **59**, 1–57.
- [142] Chen, J., Rossiter, S., Flanders, J., Sun, Y., Hua, P., Miller-Butterworth, C., Liu, X., Rajan, K. & Zhang, S., 2010 Contrasting genetic structure in two co-distributed species of old world fruit bat. *PloS one* **5**, e13903.
- [143] Audet, D. & Thomas, D., 1997 Facultative hypothermia as a thermoregulatory strategy in the phyllostomid bats, *Carollia perspicillata* and *Sturnira lilium*. *Journal of Comparative Physiology B: Biochemical, Systemic, and Environmental Physiology* **167**, 146–152. ISSN 0174-1578.
- [144] Timm, R. & LaVal, R., 2000 Mammals. In *Monteverde: ecology and conservation of a tropical cloud forest* (eds. N. Nadkarni & N. Wheelwright), pp. 223–244. Oxford University Press, Oxford, UK.
- [145] Mello, M., Kalko, E. & Silva, W., 2008 Diet and abundance of the bat *sturnira lilium* (chiroptera) in a brazilian montane atlantic forest. *Journal of Mammalogy* **89**, 485–492.
- [146] Giannini, N., 1999 Selection of diet and elevation by sympatric species of *sturnira* in an andean rainforest. *Journal of Mammalogy* pp. 1186–1195.
- [147] Cockrum, E., 1969 Migration in the guano bat, *tadarida brasiliensis*. In *Contributions in Mammalogy* (ed. J. Jones Jr), volume 51. Museum of Natural History, University of Kansas Miscellaneous Publications, Lawrence, KS.
- [148] Geiser, F. & Stawski, C., 2011 Hibernation and torpor in tropical and subtropical bats in relation to energetics, extinctions, and the evolution of endothermy. *Integrative and Comparative Biology* **51**, 337–348.
- [149] Gopalakrishna, A., 1986 Migratory pattern of some indian bats. *Myotis* **23/24**, 223–227.
- [150] Badwaik, N., 1991 Seasonal migration of two species of microchiroptera in relation to breeding cycles. *Mammalia* **55**, 625–628.
- [151] Rydell, J. & Baagøe, H., 1994 *Vespertilio murinus*. *Mammalian species* pp. 1–6.
- [152] Kawai, K., Fukui, D., Satō, M., Harada, M. & Maeda, K., 2010 *Vespertilio murinus* linnaeus, 1758 confirmed in japan from morphology and mitochondrial dna. *Acta Chiropterologica* **12**, 463–470.
- [153] Markovets, M., Zelenova, N. & Shapoval, A., 2004 Beringung von fledermäusen in der biologischen station rybachy, 1957-2001. *Nyctalus (NF)* **9**, 259–268.
- [154] Strelkov, P., 1969 Migratory and stationary bats (chiroptera) of the european part of the soviet union. *Acta Zoologica Cracoviensia* **14**, 393–440.
- [155] Masing, M., 1989 A long-distance flight of *vespertilio murinus* from estonia. *Myotis* **27**, 147–150.
- [156] Suarez, O. V., Busch, M. & Kravetz, F. O., 2004 Reproductive strategies in *akodon azarae* (rodentia, muridae). *Canadian Journal of Zoology* **82**.
- [157] Parera, A. & Erize, F., 2002 *Los mamíferos de la Argentina y la región austral de Sudamérica*. El Ateneo Buenos Aires.
- [158] Roberts, M., Brand, S. & Maliniak, E., 1985 The biology of captive prehensile-tailed porcupines, *coendou prehensilis*. *Journal of mammalogy* pp. 476–482.
- [159] Lehmer, E., Van Horne, B., Kulbartz, B. & Florant, G., 2001 Facultative torpor in free-ranging black-tailed prairie dogs (*cynomys ludovicianus*). *Journal of Mammalogy* **82**, 551–557.
- [160] Dubost, G., Henry, O. & Comizzoli, P., 2005 Seasonality of reproduction in the three largest terrestrial rodents of french guiana forest. *Mammalian Biology-Zeitschrift für Saugetierkunde* **70**, 93–109.
- [161] Fietz, J., Pflug, M., Schlund, W. & Tataruch, F., 2005 Influences of the feeding ecology on body mass and possible implications for reproduction in the edible dormouse (*glis glis*). *Journal of Comparative Physiology B: Biochemical, Systemic, and Environmental Physiology* **175**, 45–55.
- [162] Pearson, O., 1960 Habits of *microtus californicus* revealed by automatic photographic recorders. *Ecological Monographs* **30**, 232–250.
- [163] Raun, G., 1966 Rectal body temperatures of the woodrat (*neotoma micropus*) in southern texas. *The Southwestern Naturalist* **11**, 467–475.
- [164] McCarty, R., 1978 *Onychomys leucogaster*. *Mammalian species* pp. 1–6.
- [165] MacClintock, D. & Ferguson, W., 1970 *Squirrels of North America*. Van Nostrand Reinhold New York.
- [166] Lovegrove, B. G., 2003 The influence of climate on the basal metabolic rate of small mammals: a slow-fast metabolic continuum. *Journal of Comparative Physiology B: Biochemical, Systemic, and Environmental Physiology* **173**, 87–112.
- [167] Kawamichi, M., 1996 Ecological factors affecting annual variation in commencement of hibernation in wild chipmunks (*tamias sibiricus*). *Journal of mammalogy* **77**, 731–744.
- [168] Hardouin, J., 1995 Minilivestock: from gathering to controlled production. *Biodiversity and Conservation* **4**, 220–232. ISSN 0960-3115.
- [169] IUCN, 2010. Iucn red list of threatened species. version 2010.4. <http://www.iucnredlist.org>.