# Are heat of flight and body mass related with zoonotic potential in bats?

Mario Gil Castro<sup>1</sup>, Juan Rubalcaba<sup>2</sup>, and Miguel Olalla-Tárraga<sup>3</sup>

<sup>1</sup>Universidad Rey Juan Carlos <sup>2</sup>McGill University <sup>3</sup>Rey Juan Carlos University

January 30, 2024

#### Abstract

Understanding the ecology, physiology, and interactions with humans of viral reservoirs such as bats – the mammalian order hosting the highest zoonotic viral richness– is key to forecast the emergence of new infectious diseases. The flight as fever hypothesis has been proposed to explain why bats host, without overt signs of illness, a high diversity of viruses that show high virulence in case of zoonotic spillover. High metabolic rates and the amount of heat produced during flight in bats would stimulate immune responses, thus allowing to control viral replication while promoting viral adaptation to febrile conditions and ultimately increasing viral richness. Here we use biophysical modelling to calculate the amount of heat produced during flight and examine if a relationship exists with observed viral richness across 75 bat species. As predicted by the flight as fever hypothesis, our phylogenetically-informed analyses detect a significant relationship between heat of flight and viral richness.

# Are heat of flight and body mass related with zoonotic potential in bats?

Mario G. Castro<sup>1\*</sup>, Juan G. Rubalcaba<sup>1,2</sup>, Miguel Á. Olalla-Tárraga<sup>1</sup>

1. Department of Biology and Geology, Physics and Inorganic Chemistry, Universidad Rey Juan Carlos, 28933, Móstoles, Madrid, Spain.

2. Department of Biology, McGill University, Montreal, QC H3A 1B1, Canada.

\* Correspondence: Mario G. Castro: mariogilcastro96@gmail.com

Running title: Flight and zoonotic potential in bats

**Key words:** Epidemiology, Viruses, Host ecology, Zoonosis, Reservoirs, Disease emergence, Biophysical Modelling, Flight aerodynamics, Chiroptera

Type of article: Letter

Number of total words: 3304

Number of words in the abstract: 150

References :47

### Authorship statement:

M. G. C. performed analyses and wrote the first draft of the manuscript,

J. G. R. contributed to data analyses and biophysical simulations,

M. Á. O-T. conceived the idea and designed the research.

All authors contributed to the writing of the manuscript

## Abstract

Understanding the ecology, physiology, and interactions with humans of viral reservoirs such as bats – the mammalian order hosting the highest zoonotic viral richness– is key to forecast the emergence of new infectious diseases. The *flight as fever* hypothesis has been proposed to explain why bats host, without overt signs of illness, a high diversity of viruses that show high virulence in case of zoonotic spillover. High metabolic rates and the amount of heat produced during flight in bats would stimulate immune responses, thus allowing to control viral replication while promoting viral adaptation to febrile conditions and ultimately increasing viral richness. Here we use biophysical modelling to calculate the amount of heat produced during flight and examine if a relationship exists with observed viral richness across 75 bat species. As predicted by the *flight as fever* hypothesis, our phylogenetically-informed analyses detect a significant relationship between heat of flight and viral richness.

# Introduction

Most viral diseases in humans have a zoonotic origin (Taylor et al. 2001, Jones et al. 2008; Morse et al. 2012) and current global change is increasing the risk of zoonotic diseases emergence due to the growing use of bushmeat, deforestation and the loss of biodiversity and habitats (Wolfe et al. 2005; Aguirre & Tabor 2008; Keesing et al. 2010). To understand and quantify the risk of zoonotic disease emergence, it is fundamental to gain knowledge about the ecology of the most important wildlife reservoirs and how they interact with humans. The number and proportion of zoonotic viruses varies across mammal taxa and those groups harboring higher viral richness also hold a higher proportion of zoonotic viruses (Olival et al. 2017). Understanding the relationship between hosts and viruses is important when studying the zoonotic potential of viruses and their characteristics (Calisher et al 2006, O'Shea et al 2014), as well as essential in the development of predictive models that forecast the risk of new zoonotic diseases emergence (Brierley et al 2016).

Bats (Chiroptera) is the taxonomic order of mammals with the greatest viral richness and the highest proportion of zoonotic viruses (Luis et al. 2012, Olival et al. 2017, Letko et al. 2020), including coronaviruses (Li et al. 2005), lyssaviruses (Pawan 1936; Marston 2017), filoviruses (Towner 2009), Nipah and Hendra viruses (Drexler 2009, Calisher et al. 2006; Letko et al. 2020). Although these viruses rarely lead to signs of disease in bats (O'Shea et al. 2014), they can cause disease emergence in other species (Calisher et al. 2006; Letko et al. 2020). The causes and mechanisms that allow bats to maintain this high viral load remain under debate. Bats' unique physiological and life-history traits such as flight and echolocation (Norberg & Raygner 1987), longevity (Wilkinson 2002), population structure, hibernation and daily torpor (Calisher et al 2006, Wang et al 2011) could influence the unusually high viral richness that has been documented for bats compared to other mammals (Calisher et al 2006, Wang et al 2011). These singular adaptations and life strategies are thought to be related to the need of bats to balance energy budgets while coping with high energy demands for flight and metabolism, which may subsequently affect the functionality of their immune response.

The *flight as fever* hypothesis proposes that high metabolic rate and increased body temperature during flight reduces the inherent costs of rising metabolism to activate immune response in bats (O'Shea et al. 2014). As a result, the heat produced during flight may allow bats to control viral load while also promoting viral adaptation to febrile conditions (O'Shea et al. 2014). Therefore, viruses that typically infect bats may be well-adapted to high body temperatures at flight and thereby more capable to cope with febrile conditions in other vertebrate hosts, which may enhance their zoonotic potential (O'Shea et al. 2014). As viral richness is related with zoonotic richness (Olival et al. 2017), species with higher viral richness would have in consequence a higher zoonotic potential. Testing the mechanisms behind the *flight* as *fever* hypothesis and how increased body temperatures influence bats' immune response remains a challenge (Schountz et al. 2017). An alternative to address this hypothesis is to investigate whether variations in the amount of heat

produced during flight are associated to variations in viral richness across bat species. Both flight heat and metabolic rates are strongly related with body mass (Winter & Helversen 1998, Speakman & Król 2010, Hudson et al. 2013) since larger bat species require more energy than smaller bats to maintain their lift, and part of this energy is transformed into by-product heat (Winter & Helversen 1998). Not only body mass but wingspan and wing surface area fundamentally determine flight mechanics (Norberg & Raygner 1987), and thus we expect that bat species that require higher mechanical power for flight also have higher viral richness. The relationship between viral richness and heat produced during flight might potentially differ among species with different lifestyles, across families, or even display a non-linear fashion if species that produce higher amount of heat also develop strategies for dealing with higher viral loads. So far, the existence and nature of the relationship between viral richness and heat production remains largely unexplored.

Biophysical models can quantify the amount of energy invested in flight as a function of key morphological features such as body mass, wing surface area, and wingspan (Pennycuick 1968, Heerenbrink et al. 2015). Classically, animal's flight models were based on the theory of the fixed wing describing airplanes and helicopters (Pennycuick 1968). Yet, these classic models do not consider the effect of flapping and wingspan changes during flight (Heerenbrink et al. 2015). Thanks to wind tunnels experiments, the vortices of turbulent air flows generated during flight were measured (Hendenstrom & Johansom 2015, Heerenbrink et al. 2015) allowing better descriptions of the aerodynamic forces on the basis of Kelvin's circulation theorem (Hendenstrom & Johansom 2015). In this context, Heerenbrink et al. (2015) developed a biophysical model based on the Pennycuick models (1968, 2008), which describes the geometry and vorticity of the turbulent flows generated in the flapping, as well as wingspan changes during flight. Using these aerodynamic properties, the model by Heerenbrink et al. (2015) calculates the minimum power speed, which can be used to describe the activity of bats more realistically (Hendenstrom & Johanson 2015). Most of the work required to maintain minimum power speed is transformed into heat because flight muscles have a limited efficiency (i.e. approximately 23%, Pennycuick 1968). Although part of this heat is dissipated through the wing membranes, another portion is retained in the body, which increases organismal temperature during flight. In this way, testing the relationship between heat produced to maintain steady flight and viral richness offers the opportunity to study the pattern expected under the *flight as fever* hypothesis in bats.

Here we investigate whether variations in the amount of heat produced during flight are related to variations in viral richness across bat species. We examine this relationship while controlling for the possible confounding effects of geographic range area, annual mean temperature, research effort and the phylogenetic relatedness of species. We also account for differences in the flight heat-viral richness relationship between feeding habits, as diets also reflect different life histories in bats. Therefore, our goals are: (1) test if there is a relationship between flight heat and viral richness and explore its linear or non-linear nature (2) test if the relationship remains significant after controlling for the effects of geographic range area, annual mean temperature, research effort, phylogenetic relatedness and diet of each species.

## Methods

We collected morphological data and information on viral richness across 75 bat species. Body mass, wingspan, and wing area data were taken from Norberg & Rayner (1987) and taxonomy was updated following the IUCN red list. For viral information, we used the database by Olival et al. (2017), which includes total viral richness (total number of viruses observed for each bat species), zoonotic viral richness (number of virus species described as zoonotic), and research effort (number of disease-related citations in the scientific literature per host species). To determine diet types, we used the information on Elton Traits (Wilman et al 2014), where bats are classified as either insectivorous, frugivorous, omnivorous, carnivorous, nectarivores, or sanguivorous. To obtain the geographic range area of each bat species, we used the Spatial Information for Terrestrial Mammals from the IUCN red list (downloaded on March 2018). Finally, annual mean temperature across the species geographical range was obtained from Fick & Hijmans (2017). We excluded sanguivore, nectarivore, and carnivore bats (n = 8 species) for preventing errors in the analyses of interaction and additive effect of bat's diet due to low sample sizes of these diet groups.

Morphological data (body mass, wingspan, and wing surface area) were used to estimate flight heat for

each bat species. We used the Heerenbrink's et al. (2015) model implemented in the R package "*afpt*" to calculate the minimum power speed and the minimum work used for steady flight. Part of that work is transformed into heat and the efficiency with which metabolic energy is transformed into work by flight muscles is estimated at 0.23 (Pennycuick 2008). For simplicity, we assumed that efficiency remains constant across body sizes.

To investigate the *flight as fever* hypothesis, we analyzed the relationship between total viral richness and heat produced during flight using Generalized Linear Models (GLM) assuming a negative binomial distribution to prevent overdispersion (using the R function glm.nb in the MASS package, Venables & Ripley 2002). Heat of flight was log-transformed to normalize the distribution and the models' residuals. We also explored potential nonlinear relationships between viral richness and heat of flight by testing goodness of fit of the quadratic model both using the Akaike Information Criterion (AIC) and comparing the squared deviances (Dsquared) of the linear and quadratic models. We also investigated how morphology affects heat of flight by testing the relationship between body mass and heat across bat species. Additionally, we analysed the influence of phylogenetic relatedness among species by fitting a Phylogenetic Generalized Least Squares (PGLS) model using Pagel's lambda for controlling the phylogenetic signal. PHYLACINE\_1.2.1 Phylogeny (Faurby et. al. 2018) was used for this model with *ape* and *phytools* R packages.

Then, we fitted another non-phylogenetic glm.nb model for 75 species with all predictors: geographical range area (logarithmically transformed), annual mean temperature, research effort, and heat of flight interacting with bat's diet. In this model, all predictors were introduced including their quadratic terms. Statistical significance of each predictor variable was tested with an ANOVA type III analysis. Another model was fitted removing non-significant variables and interactions. A post hoc analysis was performed to this model for testing viral richness differences between insectivorous, frugivorous, and omnivorous bats using *multcomp* R package.

Finally, we explored whether heat production and its relationship with body mass differs between bat species with different diet types. Also, we tested if larger bats have larger geographic range size or have been the focus of a more intense research effort.

#### Results

We found a significant quadratic relationship between viral richness and heat of flight using non-phylogenetic analyses for 75 species (Fig. 1). This quadratic model was preferred over the linear fit as shown by its lower AIC (quadratic AIC = 339.94, linear AIC = 350.18). Using PGLS models, the relationship between observed viral richness and heat of flight was also significant (Chisq = 12.14, Df = 1, Pr = 0.002) for both the linear and quadratic fits (lambda = 0.12, Df = 75).

The relationship between total viral richness and heat of flight remained significant after controlling for all predictor variables (LRChisq = 16.94; Df = 2; Pr = 0.0009). Geographic range area and the interaction between heat of flight and diet were not significant. The best-fitting model also included annual mean temperature (LRChisq = 9.18, Df = 2; Pr<0.001), research effort (LRChisq= 24.89; Df=2; Pr<0.001) and diet type (LRChisq= 17.87; Df=2; Pr<0.001) (Table 1). According to the post-hoc test, observed viral richness was significantly lower for insectivorous bats than for frugivorous and omnivorous (Fig 2, Table 1).

A strong relationship between observed viral richness and observed zoonotic richness was found, with adjusted  $R^2 = 0.96$  and a slope of 0.83 (Fig. 1 Supplementary Material). Body mass and heat of flight also showed a strong association ( $R^2 = 0.99$ , slope = 1.13; Fig. 2 Supplementary Material), suggesting that body mass variation underlies the observed differences in heat of flight among bats species. Heat of flight was significantly lower in insectivorous bats (Fig. 3 Supplementary Material). Body mass did not show a significant relationship with geographic range area and research effort (Figs. 4 and 5 Supplementary Material).

#### Discussion

Our analyses document a significant relationship between heat of flight and observed viral richness in bat species, thus supporting the *flight as a fever* hypothesis (O'Shea et al. 2014). As expected, heat of flight

also displayed a strong association with bat body mass (Winter & Helversen 1998, Speakman & Król 2010, Hudson et al. 2013). Phylogenetically-informed analyses (i.e. PGLS) are consistent with non-phylogenetic ones and show that the association between heat of flight and observed viral richness better fits a non-linear model even when other explanatory variables were included. The relationship is robust and remains significant in the presence of the effects of geographic range area, annual mean temperature, research effort, phylogenetic relatedness and diets of bat species. In agreement with Olival et al. (2017), higher viral richness also corresponds to higher richness of zoonotic viruses which, in the light of our findings, suggests that the zoonotic viral richness in bats is associated to the amount of heat produced during flight.

Observed viral richness increases with heat of flight from lowest to intermediate values and then decreases after reaching a certain threshold (Fig. 1). This nonlinearity suggests that small to intermediate sized bats (according to the body mass and heat of fight relationship) follow the pattern expected under the *flight as fever* hypothesis, whereas large-bodied species do the opposite. Different biological interpretations are possible for such nonlinearity. Heat of flight and the mechanism behind it could be enough for controlling virulence, but not to remove the presence of viruses in small to intermediate size classes, hence promoting the pattern of increasing viral richness detected for these bat species. At the opposite end of the size distribution, bigger bats may produce too much heat, which allows less virus species to persist. An alternative possibility is that large-sized bats such as pteropodids have evolved a different mechanism for dealing with viruses (Zhou et al. 2016, Schountz et al. 2017). This quadratic relationship does not seem to be due to differences in bat's feeding habits since we did not find a significant interaction between heat of flight and diet. Interestingly, a linear fit was only significant when heat of flight was the only predictor in the model.

A lower observed viral richness was found for insectivorous bats compared to frugivorous and omnivorous species. That also lends support to a pattern expected by the *flight as a fever* hypothesis since insectivorous bats are usually small (Barclay & Brigham 1991) and produce less heat compared to frugivorous and omnivorous species (see also Fig. 3 Supplementary Material). Yet we cannot discard that other unknown factors, beyond the set of predictors explored in this study, play a role in determining the low viral richness observed for insectivorous bats. Thus, further studies are warranted.

It has been suggested that the relationship between bats and viruses could have an evolutionary context (Wang et al 2011). Bats are an ancient group of mammals, with modern fossils dating from 52 million years ago (Jepsen 1966). Events such as the Cretaceous extinction could have influenced the origin of virus-bats relationships (Wang et al 2011). The zoonotic potential of the viruses that bat species host may be high because molecular receptors that allow viral infection may have been conserved throughout the evolutionary history of the clade (Calisher et al. 2006). For this relationship to have been maintained without causing damage in bats, there must be mechanisms that control viral replication (Schountz et al. 2017, O'Shea et al. 2014, Wang et al. 2011). Moreover, viruses may be beneficial to bats acting as a defense mechanism against other species or preventing the spread of other viruses and pathogens (Roossink 2011, Wang et al. 2011). Therefore, understanding their relationship with viruses could be important in bats' ecology and conservation. It could be possible that daily heat of flight and daily immune system activation is enough for controlling replication but not for removing viral presence. Thus, the mechanisms behind the *flight as fever* hypothesis could be driving the coexistence between bats and viruses through their shared evolutionary history.

Using heat of flight for investigating the *flight as fever* hypothesis in bats is challenging and requires considering a set of alternative variables that could also influence the variation in viral richness. For instance, it has been suggested that body mass is correlated with geographic range area, so that larger animals tend to have widespread distributions (McNab 1963, Van Valen 1973, Brown & Maurer 1987). Some authors have suggested that this relationship is triangular rather than linear (i.e. while small-bodied species can be either range-restricted or widespread, larger ones always need large geographic ranges to survive, see Gaston & Blackburn 1996, Blackburn & Gason 1996, Olifiers et al 2004). If larger bats had larger geographic ranges, they would have more chances to get in contact with new viruses, thus they will have a higher viral richness. Environmental characteristics, and especially thermal ambient conditions, could also affect the heat of flight-viral richness relationship via its influence on metabolism (Fristoe et al. 2015). Diet has also been found to be related to body mass and flight metabolism in bats (Norberg & Raygner 1987, Dumont 2007). Bats are an extremely diverse group in terms of feeding habits that reflect their lifestyles and flight performance (Norberg & Raygner 1987, Dumont 2007). Additionally, types of viruses can differ between diets in bats, for example, frugivorous and insectivorous bats have different viromes and microbiomes (Li et al 2010, Banskar et al 2016). Furthermore, research (sampling) effort could also influence viral richness in mammals (Olival et al. 2017). Our analyses were designed to account for this whole set of possible confounding factors (geographic range area, annual mean temperature, research effort, phylogenetic relatedness and diet), but their inclusion in the model did not alter our conclusions since heat of flight remained significant in all cases.

Several additional considerations should be considered when interpreting our findings. First, and perhaps more important, deepen our understanding on the *flight as fever* hypothesis (O'Shea et al. 2014) is a two-step process that ultimately demands assessing in detail how the metabolic costs of flight associate with the innate immune response. While our modelling exercise shows the unequivocal existence of a relationship between heat produced during flight and viral richness, in vivo and in vitro experiments that explore the link between flight capability and innate immunity are also necessary. So far, this link has received little attention (but see Wang et al. 2011) and requires the quantification and analysis of the adaptive immune system in bats including standard elements such as immunoglobulins, antibody responses, interleukins and other cytokines, and cell-mediated T-cell responses (O'Shea et al. 2014). The nonlinear nature of the relationship we detect between heat flight and viral richness also points towards the possibility that mechanisms to control viral replication differ between small and intermediate-size bat species vs. large-bodied ones, which deserves further scrutiny. Second, while our biophysical models are tools capable of capturing the complexity of flight in bats incorporating the effects of flapping and wingspan changes (Heerenbrink et al. 2015) future refinements to this modelling technique are still possible. For instance, more empirical data are needed to better understand the extent to which the efficiency of work transformation into heat varies with factors such as body mass and external temperature or remains constant.

# Conclusions

We found that heat of flight, which is mainly influenced by body mass, is related to observed viral richness among bat species worldwide. As predicted by the *flight as fever* hypothesis, our findings suggest that heat produced during flight in bats promotes their zoonotic potential. We document a non-linear relationship between heat of flight and virus richness that deserves further attention as it could involve that mechanisms to control viral replication differ between small and intermediate-sized bat species vs. large-bodied ones. Alternatively, too much heat of flight could be stressful for the persistence of some virus. Further studies are needed to continue investigating the validity of the *flight as fever* hypothesis. This would give us knowledge about those ecological and evolutionary mechanisms that have favoured the coexistence of bats and viruses and inform on its possible consequences in an epidemiological and conservation biology context.

## Data availability

All data used in the analyses and the R code used for biophysical simulations have been uploaded as Supplementary data files for review. All data and R codes used in this study will be uploaded to Zenodo and the DOI of the repository will be provided upon manuscript acceptance

#### References:

- Aguirre, A.A, Tabor G. Global Factors Driving Emerging Infectious Diseases. Acad. Sci. 1149. 10.1196/annals.1428.052. (2008).
- Banskar, S., Mourya, D.T. & Shouche, Y.S. Bacterial diversity indicates dietary overlap among bats of different feeding habits. *Microbiol. Res.* 182:99-108 (2016).
- 3. Barclay, R.M.R., Brigham R.M. Prey detection, dietary niche breadth, and body size in bats: why aerial insectivorous bats so small? *Am* . *Nat* 37:5. 693-703(1991).

- Blackburn, T. M., & Gaston, K. J. Spatial patterns in the geographic range sizes of bird species in the New World. *Philos Trans R Soc Lond B Biol Sci*, 351(1342), 897–912 (1996).
- Brierley, L., Vonhof, M.J., Olival, K.J., Daszak, P. & Jones, K.E. Quantifying global drivers of zoonotic bat viruses: A Process-based perspective. Am. Nat 187(2):E53-E64 (2016).
- Brown, J. H., and B. A. Maurer. Evolution of species assemblages: Effects of energetic constraints and species dynamics on the diversification of the American avifauna. Am. Nat 130:1-17 (1987).
- Calisher, C.H., Childs, J.E., Field, H.E., Holmes, K.V. & Schountz, T. Bats important reservoir host of emerging viruses. *Clin Microbiol*. Rev. 19: 531-545 (2006).
- 8. Drexler, J. F. et al. Henipavirus RNA in African bats. PLoS One . 4, e6367 (2009).
- 9. Dumont, E.R. Feeding mechanisms in bats: variation within the constraints of flight. *Comp. Biol*. 47(1): 137–146 (2007).
- Faurby, S., Davis, M., Pedersen, R.Ø., Schowanek, S.D., Antonelli1, A. & Svenning, J.-C. (2018) PHY-LACINE 1.2: The Phylogenetic Atlas of Mammal Macroecology. Ecology, 99: 2626-2626. (2018).
- Fick, S. & Hijmans, R. WorldClim 2: New 1-km spatial resolution climate surfaces for global land areas. Int J Climatol. 37. 10.1002/joc.5086 (2017).
- Fristoe, T.S., Burger, J.R., Balk, M.A., Khaliq, I., Hof, C. & Brown, J.H. Metabolic heat production and thermal conductance are mass-independent adaptations to thermal environment in birds and mammals. *PNAS* 112(52) :15934-15939 (2015).
- Gaston, K.J. & Blackburn, T.M. Conservation implications of geographic range size-body size relationships. *Conserv. Biol*10(2):538-646 (1996).
- Hedenstrom, A. & Johansson, L.C. Bat flight: aerodynamics, kinematics and flight morphology. J. Exp. Biol. 218:653-663 (2015).
- Heerenbrink, M.K., Johansson, L.C. & Hedenstrom, A. Power of wingbeat:modelling the effects of flapping wings in vertebrate flight. *R. Soc* A 471: 20140952 (2015).
- Hudson, L.N., Isaac, N.J.B. & Reuman D.C. The relationship between body mass and field metabolic rate among individual birds and mammals. *J Anim Ecol*. 82:1009-1020 (2013).
- 17. Jepsen, G.L. Early eocene bat from Wyoming. Sci . 154:1333-1339 (1966).
- Jones, K.E., Patel, N.G., Levy, M.A., Storeygard, A., Balk, D., Gittleman, J.L & Daszak, P. Global trends in emerging infectious diseases. *Nature* 451, 990-993. (2008).
- Keesing, F. et al. Impacts of biodiversity on the emergence and transmission of infectious diseases. Nature . 468. 647-52. (2010)
- Letko, M., Seifert, S.N., Olival, K.J., Plowright, R.K., & Munster, V.J. Bat-borne virus diversity, spillover and emergence. *Nat. Rev. Microbiol*. https://doi.org/10.1038/s41579-020-0394-z (2020).
- Li, L. et al. Bat guano virome: predominance of dietary viruses from insects and plants plus novel mammalian viruses. ASM.84(14):6955-6965 (2010).
- Li, W. et al. Bats Are Natural Reservoirs of SARS-Like Coronaviruses. Sci. 310. 676-9. 10.1126/science.1118391 (2005).
- Luis, A.D. et al. A comparison of bats and rodents as reservoirs of zoonotic viruses: are bats special? Proc. Royal Soc. B.280:20122753 (2012).
- Marston, D.A. et al. Complete genome sequence of Lleida Bat Lyssavirus. Genome Announc .https://doi.org/10.1128/genomeA.01427-16(2017).

- 25. McNab, B. K. Bioenergetics and the determination of home range size. Am. Nat 97:133-139 (1963).
- Morse, S.S. et al. Prediction and prevention of the next pandemic zoonosis. The Lancet 380, 1956-1965. (2012).
- Norberg, U.M., Rayner, J.M.V. Ecological morphology and flight in bats (Mammalia, Chiroptera) wing adaptations, flight performance, foraging strategy and echolocation. *Proc. Royal Soc. B* : Biological Sciences 316:337–419 (1987).
- Olifiers, N., Vieira, M. V., & Grelle, C. E. V. Geographic range and body size in Neotropical marsupials. Glob. Ecol. Biogeogr.13(5), 439–444 (2004).
- Olival, K.J., Hosseini, P.R., Zambrana-Torrelio, C., Noam, R. & Bogich, T.L., Daszak, P. Host and viral traits predict zoonotic spillover from mammals. *Nature*. 546: 646-612 (2017).
- 30. O'Shea, T.J. et al. Bat flight and zoonotic viruses. Emerg Infect Dis. 20(5):741–5. (2014).
- Pawan, M. B. The transmission of paralytic rabies in trinidad by the vampire bat (Desmodus Rotundus Murinus Wagner, 1840). Ann. Trop. Med. Parasitol .30, 101–103 (1936).
- Pennycuick, C.J. Power requirements for horizontal flight in the pigeon Columba livia. J. Exp. Biol. 49, 527–555 (1968).
- 33. Pennycuick, C.J. Modelling the flying bird. Amsterdam, The Netherlands: *Elsevier* (2008).
- 34. Roossinck, M.J. The good viruses: viral mutualistic symbioses. Nat Rev Microbiol 9:99-108 (2011).
- Scholander, P. F., Hock, R., Walters, V., Johnson, F., & Irving, L. Heat regulation in some artic and tropical mammals and birds. *Biol. Bull* 99(2), 237–258. doi:10.2307/1538741 (1950).
- 36. Schountz, T., Baker, M.L., Butler, J. & Munster, V. Inmunological control of viral infections in bats and the emergence of viruses highly pathogenic to humans. *Front. Immunol.* 8: 1098 (2017).
- 37. Speakman, J.R. & Krol, E. Maximal heat dissipation capacity and hyperthermia risk: neglected key factors in the ecology of endotherms. *J Anim Ecol.* 79:726-746. (2010)
- Taylor L.H, Latham S.M & Woolhouse M.E.J. Risk factors for human disease emergence. Proc. Royal Soc. B : Biological Sciences 356:983–989. (2001).
- Towner, J. S. et al. Isolation of genetically diverse Marburg viruses from Egyptian fruit bats. *PLoS Pathog*. 5, e1000536 (2009).
- 40. Van Valen, L. Body size and numbers of plants and animals. Evol. 27:27-35 (1973).
- 41. Venables & Ripley, Modern Applied Statistics with S. Springer .4th edition (2002)
- 42. Wang, L.F., Walker, P.J. & Poon, L.L.M. Mass extinctions, biodiversity and mitochondrial function: are bats 'special' as reservoirs for emerging viruses? *Curr Opin Virol* . 1:649–57 (2011).
- 43. Wilkinson, G.S. & South, J.M Life history, ecology and longevity and longevity in bats. Agin Cell . 1(2):124-131 (2002).
- 44. Wilman, H., Belmarker, J., Simpson, J. & de la Rosa, C. EltonTraits 1.0: Species-level foraging attributes of the world's birds and mammals. *Ecology* . 95(7) (2014).
- Winter, Y., & von Helversen, O.The energy cost of flight: do small bats fly more cheaply than birds? Syst. Environ. Physiol. 168(2), 105–111. doi:10.1007/s003600050126 (1998).
- Wolfe, N.D., Daszak, P., Kilpatrick, A.M. & Burke, D.S. Bushmeat hunting, deforestation, and prediction of zoonotic disease. *Emerg. Infect. Dis.* 11:1822–1827. (2005).

47. Zhou, P., Tachedjian, M., Wynne, J.W., Boyd, V., Cui, J., Smith, I. et al. Contraction of the type I IFN locus and unusual constitutive expression of IFN-alpha in bats. *Proc Natl Acad Sci*113(10):2696–701. doi:10.1073/pnas.1518240113 (2016).

# 48.

# Tables:

Table 1: Summary of coefficients of the best model and post hoc test viral richness differences among bats' diets (sp= 75, AIC=314.17, adjusted  $D^2=0.59$ ).

	Estimate	Std Error	z-value	$\Pr(> \mathbf{z} )$
Temperature	-1.40E-01	8.06E-02	-1.75	0.08
$Temperature^2$	5.30E-03	2.36E-03	2.24	0.02
Research effort	3.60E-03	1.05E-03	3.43	< 0.001
Research $effort^2$	-2.40E-06	1.19E-06	-2.01	0.044
log(heat of flight)	6.63E-02	7.10E-02	0.93	0.35
$\log(\text{heat of flight})^2$	-1.04E-01	3.38E-02	-3.07	0.002
Post-hoc				
Omnivores insectivores	0.85	0.24	3.62	< 0.001
Insectivores frugivores	-0.81	0.22	-3.66	< 0.001
Frugivores omnivores	0.05	0.23	0.2	0.97

# Figures:



