

# Heat of flight and body size are related with virus richness within bats

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## Abstract

Studying the ecology and physiology of key viral reservoirs such as bats is critical to understand host-pathogen relationships and to forecast the emergence of novel zoonotic diseases. The *flight as fever hypothesis* proposes that high metabolic rates and heat produced during flight stimulate immune functioning in bats, acting as a selective force against virulence and promoting the diversity of viruses associated with bat hosts. Testing this hypothesis has remained challenging due to the difficulty of measuring metabolic rate and heat produced by bats during flight. Here we use a biophysical model based on aerodynamic and heat-transfer principles to simulate heat production and wing temperature of flying bats as a function of body mass and wing morphology. We used these simulations to analyze the relationship between virus richness and wing temperature excess in a comparative study across 107 species of bats. Virus richness was significantly and positively related to wing temperature excess across bat species, and this relationship remained significant after controlling for the possible confounding effects of geographic range area, annual mean temperature, research effort, phylogenetic relatedness among species, taxonomic scale of virus richness, and differences in feeding habits. Our results suggest that body size and shape influence virus species richness through its effect on flight mechanics within bats.

**Key words:** Biophysical modelling, Chiroptera, Disease emergence, Flight aerodynamics, Host ecology, Viruses, Zoonosis.

## 1.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 et al., 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., 2010).

Bats (Chiroptera) is the taxonomic order of mammals with the greatest viral richness and the highest proportion of zoonotic viruses (Olival et al., 2017; Luis et al., 2012; Letko et al., 2020), including coronaviruses (Li et al., 2005), lyssaviruses (Pawan, 1936; Marston et al., 2017), filoviruses (Towner et al., 2009), Nipah and Hendra viruses (Calisher et al., 2006; Drexler, et al., 2009; 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 and Rayner, 1987), longevity (Wilkinson, 2002), population structure, hibernation, and daily torpor (Calisher et al., 2006; Wang et al., 2020) could influence the unusually high viral richness that has been documented for bats compared to other mammals (Calisher et al., 2006; Wang et al., 2020). 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 recently proposed *flight as fever* hypothesis (FFH; O' Shea et al., 2014) argues that the increase in body temperature of bats during flight might stimulate their immune system, providing a selective force against virulence and promoting the

diversity of viruses that infect bat populations (O’ Shea et al., 2014). Although FFH has attracted the attention of the media, where it has become especially popular during the global SARS-CoV-2 pandemic, empirical support for this theory is still limited and its mechanistic underpinnings remain poorly understood (Schountz et al., 2017). Levesque et al. (2021) recently argued that methodological limitations impede obtaining accurate measurements of flight temperature with which to evaluate whether bats really experience higher body temperatures than non-volant mammals. Therefore, a first approach to explore the FFH might require assessing the potential of heat of flight to affect body temperature and testing the relationship between this temperature excess and viral richness.

The flight power and the by-product heat produced during flight display considerable variation among bat species probably because flight heat and metabolic rates are strongly related to body mass (Winter and Helversen, 1998; Speakman and Król., 2010; Hudson et al., 2013); i.e., 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 and Helversen, 1998). Not only body mass but wingspan and wing surface area fundamentally affect flight mechanics, heat production and dissipation, and wing morphology also varies among species with different lifestyles and diets (Norberg and Rayner, 1987). In addition, both viral richness and zoonotic potential of viruses vary among different groups of bats (Guy et al., 2020). This variability in viral richness, morphological and ecological features of bats offer the opportunity to evaluate the relative importance of the heat of flight in explaining the interspecific variation in viral richness. To achieve this, it is critical to obtain accurate measurements or simulations of heat production and flight temperatures across bat species.

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 (Heerenbrink et al., 2015; Hedenström, and Johansson 2015) allowing better descriptions of the aerodynamic forces on the basis of Kelvin's circulation theorem

(Hedenström, and Johansson, 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 (Hedenström and Johansson, 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 could increase body temperature during flight. By describing heat production and dissipation from the wings, biophysical models offer the opportunity to investigate the impact of flight mechanics on body temperature and its relationship with viral richness within bats.

Here we used a biophysical model to investigate whether differences in the amount of heat produced during flight and the resulting wing temperature excess can explain the variation in viral richness across bat species. We examine the relationship between wing temperature excess and viral richness while controlling for the possible confounding effects of geographic range area, annual mean temperature, research effort, phylogenetic relatedness among species, and differences in diet type. Thus, bats with different diet types may differ in flight metabolism (Norberg and Rayner, 1987, Dumont, 2008), and have different viromes and microbiomes (Li et al., 2010; Banskari et al., 2016). Environmental factors such as ambient temperature could also affect the heat of flight-viral richness relationship via its influence on metabolism (Fristoe et al., 2015). In addition, bats with larger geographic ranges (McNab, 1963; Valen, 1973; Brown and Maurer, 1987), could have more chances to get in contact with new viruses, potentially increasing their viral richness. Using a model selection approach, we investigated whether temperature excess during flight has the potential to explain the variation in viral richness across bat species thus providing an exploration analysis of the FFH.

## **2. Methods**

### **2.1 Data collection**

We collected body mass, wingspan, and wing surface area data from Norberg & Rayner (1987), and only used species with available data for the three variables. Taxonomy of the selected species was updated following the UICN red list. Information on viral richness for each bat species was obtained from the VIRION database (Carlson et al 2021), which includes the most recent and complete compilation of virus-host interaction data. Within VIRION database, we removed viral records that were introduced as not taxonomically resolved either for the host or for the virus. For each bat species, we used VIRION to calculate viral richness both at the species level (i.e., by counting the number of different virus taxonomic IDs); and at the family level (i.e., by counting the different virus families). Analyses at the family level were included to assess the possible effect that difficulties in assigning viruses at the species level might have on our results. In addition, to estimate research effort, we counted the total number of viral records for each bat species. To determine diet types, we used the information on Elton Traits (Wilman et al 2014), and classified each species as either insectivores, frugivores, omnivores, carnivores, nectarivores, or sanguivores. To obtain the geographic range area of each bat species, we used the Spatial Information for Terrestrial Mammals from the IUCN red list (downloaded in March 2018). Finally, annual mean temperature that each species experiences across its distributional range was obtained by overlaying IUCN range maps with climatic data from Fick & Hijmans (Fick & Hijmans, 2017). Thus, our final database contained morphological, ecological and viral information of 107 bats species.

## 2.2 Biophysical modelling

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 ( $W_{flight}$ ) used for steady flight. Part of that work is transformed into heat, depending on the efficiency with which flight muscles transform metabolic energy into mechanical work ( $\eta = 0.23$ ) (Pennycuick, 2008). For simplicity, we assumed that the efficiency ( $\eta$ ) remains constant across body sizes. Using the definition of muscle efficiency by Hill (1938), we calculated the by-product heat of flight as:

$$Q_{flight} = W_{flight} \left( \frac{1}{\eta} - 1 \right) \quad (1)$$

We then estimated the impact of heat production on wing temperature using the ratio of  $Q_{flight}$  (W) to the rate of heat dissipation via convection at the wing surface:

$$T_e = \frac{Q_{flight}}{A_{wing} h_c} \quad (2)$$

where  $T_e$  (°C) represents the temperature excess of the wings with respect to the environment,  $A_{wing}$  is wing surface area (m<sup>2</sup>) and  $h_c$  is the convection heat transfer coefficient (W m<sup>-2</sup> °C<sup>-1</sup>), which was estimated using the relationship:

$$h_c = 0.664 \text{ Re}^{\frac{1}{2}} \text{ Pr}^{\frac{1}{3}} \frac{k_f}{d} \quad (3)$$

(Reichard 2010) where Re is the Reynolds number ( $\text{Re} = Vd / \nu$ ),  $V$  is wind velocity at the wing surface (m s<sup>-1</sup>),  $\nu$  is the kinematic viscosity of air ( $15.69 \times 10^{-6}$  m<sup>2</sup> s<sup>-1</sup> at 25 °C), Pr is the Prandtl number (0.708 at 25°C),  $k_f$  the thermal conductivity of air (0.0262 Wm<sup>-1</sup> K<sup>-1</sup> at 25°C), and  $d$  is the characteristic dimension (m) estimated here as half of the total wingspan. To calculate wind speed at the wing surface, we used the minimum power velocity estimated with the *afpt* package.

### 2.3 Statistical analyses

We analyzed the relationship between viral species richness and wing temperature excess using Phylogenetic Generalized Least Squares models (PGLS) and Pagel's lambda to control the phylogenetic signal. Phylogenetic analyses were run using the PHYLACINE\_1.2.1 phylogeny (Faurby, 2018) with *ape* and *caper* R packages (Orme et al., 2017; Paradis & Schliep, 2019). The models included geographical range area, annual mean temperature within the species' range, research effort, and bat's diet as covariates, we then performed a model selection analysis to obtain the best-fitting model, i.e. the one with the lowest AIC, using the *MuMIn* R package (Bartoń, 2020). In case of equal AIC, we selected the one with higher adjusted R squared estimated with *caper* package.

### 3. Results

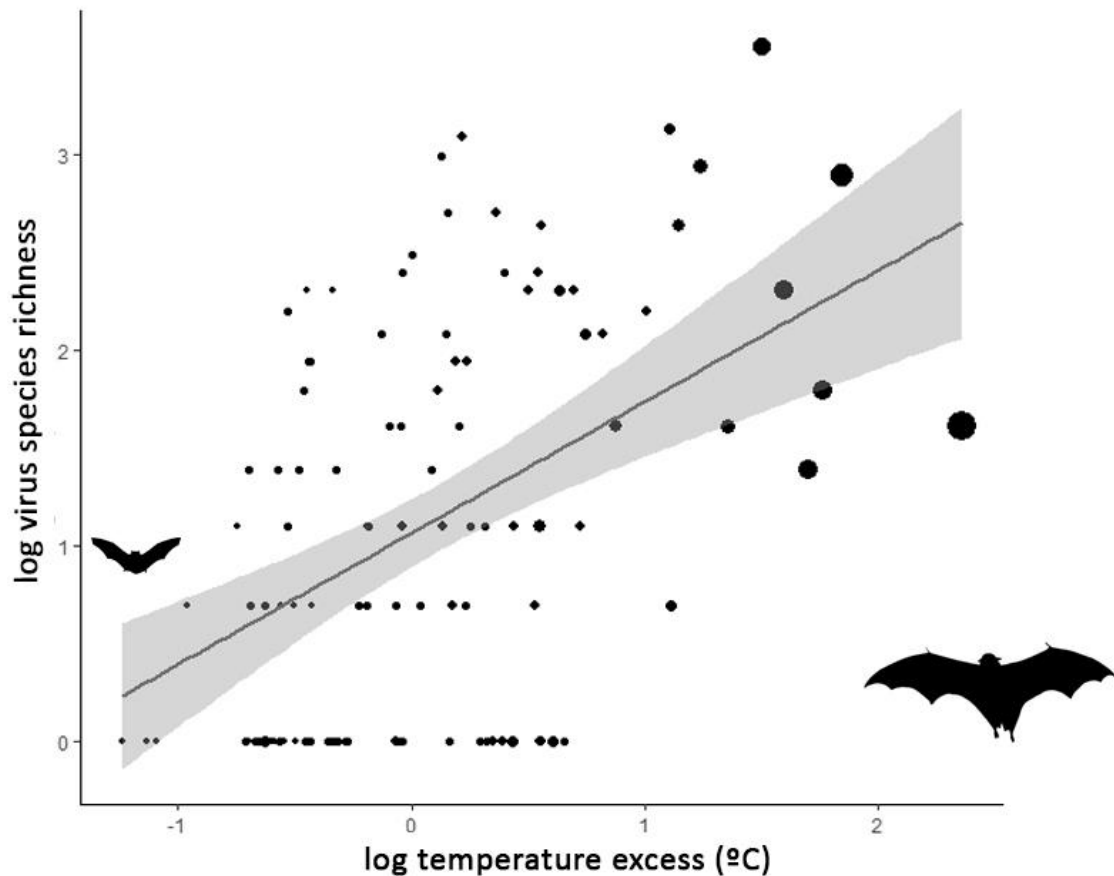
We found a significant relationship between viral species richness and temperature excess (Table 1, Fig 1). The best-fitting model included temperature excess, research effort, range area and bats' diet (adjusted r-squared: 0.62; AIC = 210; lambda=0.059, Table 1, Figure 1). While research effort and range area showed positive, significant

associations with viral species richness (Table 1, Figure 1), diet did not have a significant effect (Table 1).

The number of viral families was also significantly and positively related with temperature excess. The best-fitting model in this case included temperature excess, research effort and range area (adjusted r-squared = 0.56; AIC = 164.9; lambda=0.182, Table 1).

**Table 1:** Variables of the best fitting Phylogenetic Generalized Least Squares (PGLS) models to explain viral richness at the species (a) and family level (b). T.E= temperature excess, R.E=research effort, R.A=range area.

		Df	F-value	Pr(>0)	Estimate	Std Error
(a)	<b>Intercept</b>				-0.81	0.42
	<b>log (T.E)</b>	1	60.68	<b>&lt;0.001</b>	0.37	0.12
	<b>log(R.E)</b>	1	109.39	<b>&lt;0.001</b>	0.38	0.05
	<b>sqrt (R.A)</b>	1	4.03	<b>0.04744</b>	0.01	0.01
	<b>Diet</b>	5	2.05	0.07876		
	<b>Residuals</b>	98				
(b)	<b>Intercept</b>				-0.32	0.14
	<b>log (T.E)</b>	1	36.36	<b>&lt;0.001</b>	0.29	0.07
	<b>log (R.E)</b>	1	98.13	<b>&lt;0.001</b>	0.30	0.03
	<b>sqrt (R.A)</b>	1	4.29	<b>0.04085</b>	0.01	0.01
	<b>Residuals</b>	103				



**Figure 1:** Relationship between viral richness and wing temperature excess (log-transformed) across bat species. Point size varies depending on body mass (n=107).

#### 4. Discussion

Our analyses document a significant relationship between wing temperature excess resulting from heat produced during flight and virus richness within bats. The relationship between temperature excess and viral richness was robust and remained significant after controlling for the effects of geographic range area, annual mean temperature, research effort, phylogenetic relatedness and diet. Results were consistent between analyses including either the number of viral species or the number of viral families as a response variable. Differences in wing temperature excess were primarily related with differences in morphological traits such as body mass and wing size among species. Thus, larger bats produce more heat during flight and dissipate proportionally lower amounts of heat through the wings via convection, which may increase their body temperature at flight. According to the FFH, high flight temperature may act as a selective force against virulence and promote the diversity of viruses that affect bat species (O'Shea et al., 2014). Thus, in the light of the FFH, our results suggest the



higher temperature excess during flight may explain why larger bat species have associated higher viral richness. Understanding the mechanistic underpinnings of this relationship requires further research on the interplay between bat body temperature, immune function and body size and their influence on virus diversification across bat species.

The validity of the FFH to explain the high diversity of virus in bats has been questioned based on two main arguments. First, bats may not experience higher body temperatures than non-volant mammals because their large wing surface area allows dissipating the metabolic heat produced during flight (Levesque et al. 2021). When bats are captured and handled to measure their body temperature in the wild, heat dissipation rates drop drastically while metabolic rates remain elevated which may drive their body temperature up briefly (Levesque et al. 2021). Our model provides a means to estimate the temperature excess during flight and suggests that larger bats likely experience an excess in heat production relative to heat dissipation through the wings. Thus, while the flight power required for flapping scales near isometrically with body mass ( $b \sim 1$ ), heat dissipation rates are proportional to wing surface area, which scales with a smaller exponent,  $b \sim 2/3$  (the slope between wing area and body mass (both log-transformed) across the species represented in this study, was 0.60. As a result of this mismatch between the mass-scaling of flight power and the mass-scaling heat dissipation rates, larger bats may accumulate proportionally higher amounts of heat thereby experiencing higher temperatures. A further refinement of this analysis requires considering whether (1) the conversion efficiency of flight muscles is constant or scales with body size, and (2) whether wing temperature excess causes an increase in body temperature. Therefore, our biophysical approach supports the idea that the increased metabolic rate and by-product heat of flight can increase body temperature of bats.

A second argument questioning the validity of the FFH is that high flight temperature may not necessarily stimulate bats' immune response (Brook & Dobson 2015, Schountz et al 2017, Levesque et al 2020). Thus, the fever response that occurs during infections results from an immunological cascade involving inflammatory cytokines and prostaglandins that cause an increase in body temperature after the immune response has begun (Schountz et al. 2017). However, the increase in body temperature during flight occurs due to an increase in muscle activity and metabolic rate, which may not necessarily promote the immune response. For example, a higher

temperature did not allow a more efficient control of filovirus replication in bat cells (Miller et al., 2021). Whether increased body temperature from exertion triggers or facilitates immune response requires further research. Therefore, the effect of body temperature on viral richness through its effect on bats' immune response remains to be investigated.

Body size influences multiple physiological traits including those affecting hosts' exposure to different viruses and capacity to respond to infections (Downs et al., 2019). For example, body size affects habitat utilization and home range area, group density, and geographic range areas, and all these factors determine the level of exposure and transmission rates of different viruses (Dobson and Hudson, 1986; Han et al., 2015). Here, we found that viral richness was positively related with geographic range area, suggesting that species with larger ranges were exposed to a greater diversity of viruses. Since larger bat species also have larger geographic ranges, this effect may in part explain the mass-scaling of viral richness in bats. In addition, body size may influence hosts' susceptibility to viral infections and capacity to control viral reproduction. This capacity ultimately depends on the host immune system and yet little is known on how different immunological components scale with body mass (Hechinger, 2013; Downs et al., 2020).

It has been suggested that the relationship between bats and viruses has 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 infections (O'Shea 2014, Brook & Dobson 2015, Schountz et al 2017). Moreover, viruses may be beneficial for bats acting as a defense mechanism against other species or preventing the spread of other viruses and pathogens (Roossinck, 2011; Wang et al, 2011). Therefore, understanding their relationship with viruses could be important in bats' ecology and conservation.

## **5. Conclusions**

We found that wing thermal excess produced by heat of flight, is related to virus richness among bat species worldwide. Biophysical models were useful to calculate temperature excess of the wings during bats' flight using body size data: body mass, wingspan, and wing area. Thus, our results also suggest an interspecific scaling of virus richness.

Further studies are needed to explore how size and flight metabolism influence bats' competence as a host; if flight is related with immune responses in bats as proposed by the *flight as fever*; and any alternative hypotheses. That would give us knowledge about those ecological and evolutionary mechanisms that have favored the coexistence of bats and viruses and inform on its possible consequences in an epidemiological and conservation biology context.

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