

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

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Abstract

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

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

29 **1.Introduction**

30 Most viral diseases in humans have a zoonotic origin (Taylor et al., 2001; Jones et al,
31 2008; Morse et al., 2012) and current global change is increasing the risk of zoonotic
32 diseases emergence due to the growing use of bushmeat, deforestation and the loss of
33 biodiversity and habitats (Wolfe et al., 2005; Aguirre et al., 2008; Keesing et al., 2010).
34 To understand and quantify the risk of zoonotic disease emergence, it is fundamental to
35 gain knowledge about the ecology of the most important wildlife reservoirs and how
36 they interact with humans. The number and proportion of zoonotic viruses varies across
37 mammal taxa and those groups harboring higher viral richness also hold a higher
38 proportion of zoonotic viruses (Olival et al., 2017). Understanding the relationship
39 between hosts and viruses is important when studying the zoonotic potential of viruses
40 and their characteristics (Calisher et al., 2006; O’Shea et al., 2014), as well as essential
41 in the development of predictive models that forecast the risk of new zoonotic diseases
42 emergence (Brierley et al., 2010).

43 Bats (Chiroptera) is the taxonomic order of mammals with the greatest viral
44 richness and the highest proportion of zoonotic viruses (Olival et al., 2017; Luis et al.,
45 2012; Letko et al., 2020), including coronaviruses (Li et al., 2005), lyssaviruses (Pawan,
46 1936; Marston et al., 2017), filoviruses (Towner et al., 2009), Nipah and Hendra viruses
47 (Calisher et al., 2006; Drexler, et al., 2009; Letko et al., 2020). Although these viruses
48 rarely lead to signs of disease in bats (O’Shea et al., 2014), they can cause disease
49 emergence in other species (Calisher et al., 2006; Letko et al., 2020). The causes and
50 mechanisms that allow bats to maintain this high viral load remain under debate. Bats’
51 unique physiological and life-history traits such as flight and echolocation (Norberg and
52 Rayner, 1987), longevity (Wilkinson, 2002), population structure, hibernation, and daily
53 torpor (Calisher et al., 2006; Wang et al., 2020) could influence the unusually high viral
54 richness that has been documented for bats compared to other mammals (Calisher et al.,
55 2006; Wang et al., 2020). These singular adaptations and life strategies are thought to be
56 related to the need of bats to balance energy budgets while coping with high energy
57 demands for flight and metabolism, which may subsequently affect the functionality of
58 their immune response.

59 The recently proposed *flight as fever* hypothesis (FFH; O’Shea et al., 2014)
60 argues that the increase in body temperature of bats during flight might stimulate their
61 immune system, providing a selective force against virulence and promoting the

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

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

86 Biophysical models can quantify the amount of energy invested in flight as a
87 function of key morphological features such as body mass, wing surface area, and
88 wingspan (Pennycuick, 1968; Heerenbrink et al., 2015). Classically, animal's flight
89 models were based on the theory of the fixed wing describing airplanes and helicopters
90 (Pennycuick, 1968). Yet, these classic models do not consider the effect of flapping and
91 wingspan changes during flight (Heerenbrink et al., 2015). Thanks to wind tunnels
92 experiments, the vortices of turbulent air flows generated during flight were measured
93 (Heerenbrink et al., 2015; Hedenström, and Johansson 2015) allowing better
94 descriptions of the aerodynamic forces on the basis of Kelvin's circulation theorem

95 (Hedenström, and Johansson, 2015). In this context, Heerenbrink et al., (2015)
96 developed a biophysical model based on the Pennycuick models (1968; 2008), which
97 describes the geometry and vorticity of the turbulent flows generated in the flapping, as
98 well as wingspan changes during flight. Using these aerodynamic properties, the model
99 by Heerenbrink et al., (2015) calculates the minimum power speed, which can be used
100 to describe the activity of bats more realistically (Hedenström and Johansson, 2015).
101 Most of the work required to maintain minimum power speed is transformed into heat
102 because flight muscles have a limited efficiency (i.e., approximately 23%, Pennycuick,
103 1968). Although part of this heat is dissipated through the wing membranes, another
104 portion is retained in the body, which could increase body temperature during flight. By
105 describing heat production and dissipation from the wings, biophysical models offer the
106 opportunity to investigate the impact of flight mechanics on body temperature and its
107 relationship with viral richness within bats.

108 Here we used a biophysical model to investigate whether differences in the
109 amount of heat produced during flight and the resulting wing temperature excess can
110 explain the variation in viral richness across bat species. We examine the relationship
111 between wing temperature excess and viral richness while controlling for the possible
112 confounding effects of geographic range area, annual mean temperature, research effort,
113 phylogenetic relatedness among species, and differences in diet type. Thus, bats with
114 different diet types may differ in flight metabolism (Norberg and Rayner, 1987,
115 Dumont, 2008), and have different viromes and microbiomes (Li et al., 2010; Banskar
116 et al., 2016). Environmental factors such as ambient temperature could also affect the
117 heat of flight-viral richness relationship via its influence on metabolism (Fristoe et al.,
118 2015). In addition, bats with larger geographic ranges (McNab, 1963; Valen, 1973;
119 Brown and Maurer, 1987), could have more chances to get in contact with new viruses,
120 potentially increasing their viral richness. Using a model selection approach, we
121 investigated whether temperature excess during flight has the potential to explain the
122 variation in viral richness across bat species thus providing an exploration analysis of
123 the FFH.

124 **2. Methods**

125 **2.1 Data collection**

126 We collected body mass, wingspan, and wing surface area data from Norberg & Rayner
127 (1987), and only used species with available data for the three variables. Taxonomy of
128 the selected species was updated following the UICN red list. Information on viral
129 richness for each bat species was obtained from the VIRION database (Carlson et al
130 2021), which includes the most recent and complete compilation of virus-host
131 interaction data. Within VIRION database, we removed viral records that were
132 introduced as not taxonomically resolved either for the host or for the virus. For each
133 bat species, we used VIRION to calculate viral richness both at the species level (i.e., by
134 counting the number of different virus taxonomic IDs); and at the family level (i.e., by
135 counting the different virus families). Analyses at the family level were included to
136 assess the possible effect that difficulties in assigning viruses at the species level might
137 have on our results. In addition, to estimate research effort, we counted the total number
138 of viral records for each bat species. To determine diet types, we used the information
139 on Elton Traits (Wilman et al 2014), and classified each species as either insectivores,
140 frugivores, omnivores, carnivores, nectarivores, or sanguivores. To obtain the
141 geographic range area of each bat species, we used the Spatial Information for
142 Terrestrial Mammals from the IUCN red list (downloaded in March 2018). Finally,
143 annual mean temperature that each species experiences across its distributional range
144 was obtained by overlaying IUCN range maps with climatic data from Fick & Hijmans
145 (Fick & Hijmans, 2017). Thus, our final database contained morphological, ecological
146 and viral information of 107 bats species.

147 **2.2 Biophysical modelling**

148 Morphological data (body mass, wingspan, and wing surface area) were used to
149 estimate flight heat for each bat species. We used the Heerenbrink's et al. (2015) model
150 implemented in the R package "*afpt*" to calculate the minimum power speed and the
151 minimum work (W_{flight}) used for steady flight. Part of that work is transformed into heat,
152 depending on the efficiency with which flight muscles transform metabolic energy into
153 mechanical work ($\eta = 0.23$) (Pennycuick, 2008). For simplicity, we assumed that the
154 efficiency (η) remains constant across body sizes. Using the definition of muscle
155 efficiency by Hill (1938), we calculated the by-product heat of flight as:

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

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

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

158 where T_e (°C) represents the temperature excess of the wings with respect to the
159 environment, A_{wing} is wing surface area (m²) and h_c is the convection heat transfer
160 coefficient (W m⁻²°C⁻¹), which was estimated using the relationship:

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

161 (Reichard 2010) where Re is the Reynolds number ($\text{Re} = Vd/\nu$), V is wind velocity at
162 the wing surface (m s⁻¹), ν is the kinematic viscosity of air (15.69×10^{-6} m² s⁻¹ at 25 °C),
163 Pr is the Prandtl number (0.708 at 25°C), k_f the thermal conductivity of air (0.0262 Wm⁻¹
164 K⁻¹ at 25°C), and d is the characteristic dimension (m) estimated here as half of the total
165 wingspan. To calculate wind speed at the wing surface, we used the minimum power
166 velocity estimated with the *afpt* package.

167 **2.3 Statistical analyses**

168 We analyzed the relationship between viral species richness and wing temperature
169 excess using Phylogenetic Generalized Least Squares models (PGLS) and Pagel's
170 lambda to control the phylogenetic signal. Phylogenetic analyses were run using the
171 PHYLACINE_1.2.1 phylogeny (Faurby, 2018) with *ape* and *caper* R packages (Orme
172 et al., 2017; Paradis & Schliep, 2019). The models included geographical range area,
173 annual mean temperature within the species' range, research effort, and bat's diet as
174 covariates, we then performed a model selection analysis to obtain the best-fitting
175 model, i.e. the one with the lowest AIC, using the *MuMIn* R package (Bartoń, 2020). In
176 case of equal AIC, we selected the one with higher adjusted R squared estimated with
177 *caper* package.

178 **3. Results**

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

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

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

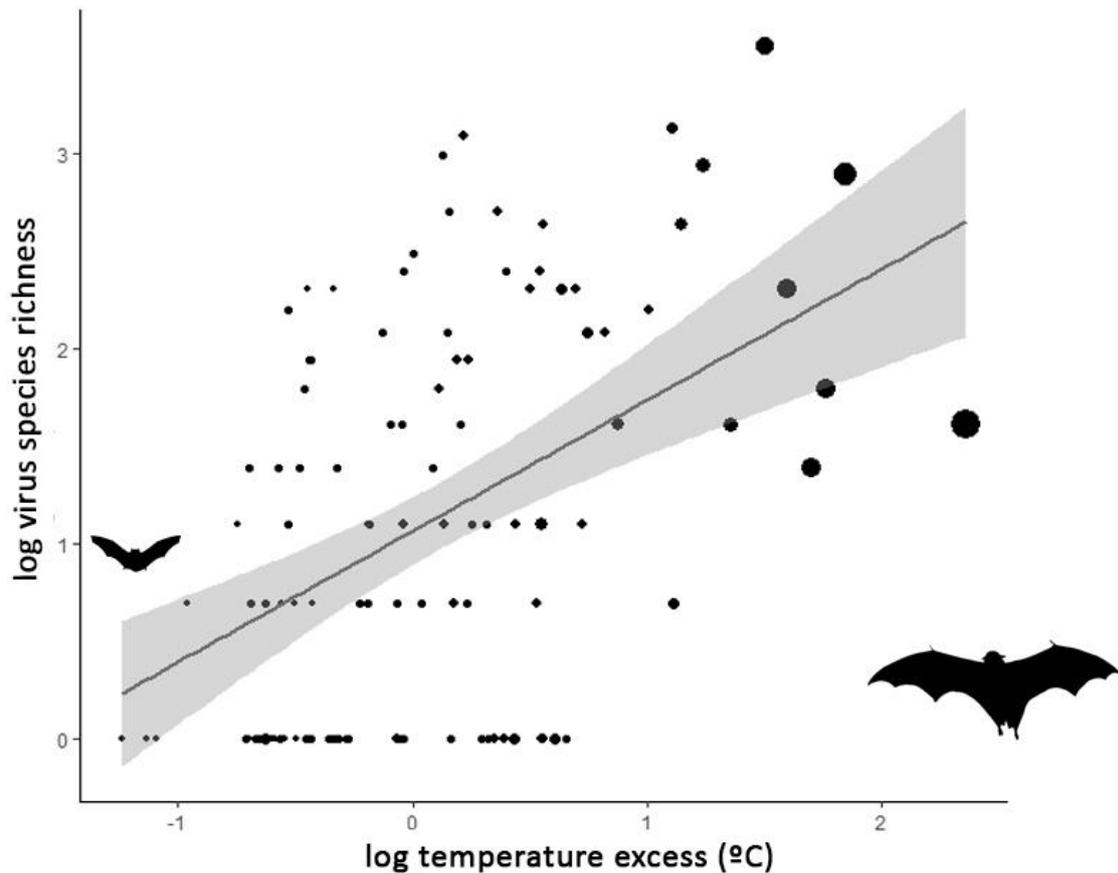
189 **Table 1:** Variables of the best fitting Phylogenetic Generalized Least Squares (PGLS)
 190 models to explain viral richness at the species (a) and family level (b). T.E= temperature
 191 excess, R.E=research effort, R.A=range area.

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

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

198 **4. Discussion**

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

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

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

237 A second argument questioning the validity of the FFH is that high flight
238 temperature may not necessarily stimulate bats' immune response (Brook & Dobson
239 2015, Schountz et al 2017, Levesque et al 2020). Thus, the fever response that occurs
240 during infections results from an immunological cascade involving inflammatory
241 cytokines and prostaglandins that cause an increase in body temperature after the
242 immune response has begun (Schountz et al. 2017). However, the increase in body
243 temperature during flight occurs due to an increase in muscle activity and metabolic
244 rate, which may not necessarily promote the immune response. For example, a higher

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

250 Body size influences multiple physiological traits including those affecting
251 hosts' exposure to different viruses and capacity to respond to infections (Downs et al.,
252 2019). For example, body size affects habitat utilization and home range area, group
253 density, and geographic range areas, and all these factors determine the level of
254 exposure and transmission rates of different viruses (Dobson and Hudson, 1986; Han et
255 al., 2015). Here, we found that viral richness was positively related with geographic
256 range area, suggesting that species with larger ranges were exposed to a greater
257 diversity of viruses. Since larger bat species also have larger geographic ranges, this
258 effect may in part explain the mass-scaling of viral richness in bats. In addition, body
259 size may influence hosts' susceptibility to viral infections and capacity to control viral
260 reproduction. This capacity ultimately depends on the host immune system and yet little
261 is known on how different immunological components scale with body mass
262 (Hechinger, 2013; Downs et al., 2020).

263 It has been suggested that the relationship between bats and viruses has an
264 evolutionary context (Wang et al, 2011). Bats are an ancient group of mammals, with
265 modern fossils dating from 52 million years ago (Jepsen 1966). Events such as the
266 Cretaceous extinction could have influenced the origin of virus-bats relationships
267 (Wang et al, 2011). The zoonotic potential of the viruses that bat species host may be
268 high because molecular receptors that allow viral infection may have been conserved
269 throughout the evolutionary history of the clade (Calisher et al, 2006). For this
270 relationship to have been maintained without causing damage in bats, there must be
271 mechanisms that control viral infections (O'Shea 2014, Brook & Dobson 2015,
272 Schountz et al 2017). Moreover, viruses may be beneficial for bats acting as a defense
273 mechanism against other species or preventing the spread of other viruses and
274 pathogens (Roossinck, 2011; Wang et al, 2011). Therefore, understanding their
275 relationship with viruses could be important in bats' ecology and conservation.

276 **5. Conclusions**

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

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

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