Variation in albumin glycation rates in birds suggests resistance to relative hyperglycaemia rather than conformity to the pace of life syndrome hypothesis

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ABSTRACT

The pace of life syndrome hypothesis (POLS) suggests that organisms' life history, physiological and behavioural traits should co-evolve. In this framework, how glycaemia (i.e., blood glucose levels) and its reaction with proteins and other compounds (i.e. glycation) covary with life history traits remain relatively under-investigated, despite the well documented consequences of glucose and glycation on ageing, and therefore potentially on life history evolution. Birds are particularly relevant in this context given that they have the highest blood glucose levels within vertebrates and still higher mass-adjusted longevity when compared to organisms with similar physiology as mammals. We thus performed a comparative analysis on glucose and albumin glycation rates of 88 bird species from 22 orders, in relation to life history traits (body mass, clutch mass, maximum lifespan and developmental time) and diet. Glucose levels correlated positively with albumin glycation rates in a non-linear fashion, suggesting resistance to glycation in species with higher glucose levels. Plasma glucose levels decreased with increasing body mass but, contrary to what is predicted to the POLS hypothesis, glucose levels increased with maximum lifespan before reaching a plateau. Finally, terrestrial carnivores showed higher albumin glycation compared to omnivores despite not showing higher glucose, which we discuss may be related to additional factors as differential antioxidant levels or dietary composition in terms of fibres or polyunsaturated fatty acids. These results increase our knowledge about the diversity of glycaemia and glycation patterns across birds, pointing towards the existence of glycation resistance mechanisms within comparatively high glycaemic birds.

INTRODUCTION

The pace of life (POL) hypothesis [1-3] postulates that organisms behavioural/physiological characteristics and life histories have co-evolved in answer to specific ecological conditions forming pace of life syndromes (POLS) along a fast-slow continuum (but see [4] for the more recent consideration of other axes). According to the classical approach from life history theory, slower organisms would have, e.g. large body mass, late maturation, slow growth rate, small number of large offspring and high longevity, whit faster ones representing the opposite trait values (see [5-8]) within this continuum. Pace of life hypothesis added physiology to this continuum, with studies testing its predictions focusing often on metabolic rate (i.e. higher or lower metabolic rate corresponding to faster or slower pace of life, respectively; see e.g. [9-12]). However, key energy substrates related to metabolic performance, such as glucose

concentrations in tissues, have been largely overlooked (but see [13-16]). Notably, glucose, a central energy source for many organisms, plays a pivotal role in metabolism and there are some indications that its circulating blood or plasma levels correlate positively with metabolic rate per gram of mass at the interspecific level [13,17], and with whole body metabolism at the intraspecific level ([18] for the case of non-diabetic humans).

Research focusing on plasma glucose becomes highly relevant as high glycaemia can entail costs that accelerate ageing. Along with other reducing sugars, glucose can react non-enzymatically with free amino groups of proteins, lipids or nucleic acids, a reaction known as glycation [19][20]. This reaction, after several molecular reorganizations, can lead to the formation of a plethora of molecules called Advanced Glycation End-products (AGEs) [21]. AGEs can form aggregates in tissues that are well known to contribute to several age-related diseases related, such as diabetes (e.g., reviews by [22-25]). AGEs are also known to promote a proinflammatory state through their action on specific receptors called RAGEs [26-27].

Remarkably, birds show circulating glucose levels much higher than other vertebrate groups, on average almost twice as high as mammals [28]. These relatively high glucose levels might support the higher metabolic rates [29, 11] and body temperatures observed in birds compared to mammals [30-31]. In addition, elevated glycaemia is thought to be an adaptation to flight, providing birds with rapid access to an easily oxidizable fuel during intense bursts of aerobic exercise (see [32-33]), such as during take-off and short-term flapping flights [34-35]). However, the presence of high glycaemia in birds is also paradoxical, given their remarkable longevity compared to their mammalian counterparts — living up to three times longer than mammals of equivalent body mass [36, 11].

Several non-excluding hypotheses have been proposed to explain how birds apparently resist the pernicious effects of a high glycaemic state. One possibility is that birds might resist protein glycation through a lower exposure of lysine residues at the surface of their proteins [37]. Another hypothesis suggests that increased protein turnover may play a role [38-39]. Additionally, birds might benefit from more effective antioxidant defences [40-42] (although within Passeriformes, [16] shows no coevolution between glycaemia and antioxidant defences) or even the presence of “glycation scavengers” such as polyamines which circulate at high concentration [35]. Moreover, it is generally considered that RAGEs are not present in avian tissues, suggesting possible adaptive mechanisms that would allow birds to avoid the inflammatory consequences associated with RAGE activation [43-44]. However, a putative

88 candidate for RAGE and a case of AGE-induced inflammation were identified by Wein et al. [45],
89 warranting further investigation on the occurrence of RAGEs in birds.
90 To date, although protein glycation levels have been measured in birds in several species, these
91 results were mostly descriptive and concerned a small number of species [46-54]. Additionally,
92 many of these studies employ commercial kits that were not specifically designed for avian
93 species, making it challenging to interpret the results [53]. These limitations restrict our ability
94 to draw general conclusions from these studies. Here, we performed a comparative analysis on
95 88 species belonging to 22 orders (see ESM6) and assessed whether and how bird glycaemia and
96 glycation rates are linked to ecological and life-history traits (including body mass). While doing
97 this, we also checked whether glycation levels are influenced by circulating plasma glucose
98 concentrations. Finally, as diet can influence glycaemia (see e.g. [15, 55-56] but [14] found no
99 significant effects) and glycation, we included it in our analyses. We hypothesized that
100 carnivorous birds would exhibit higher glycaemia and glycation levels than omnivorous or
101 herbivorous species, as diets with low-carbohydrates, high-proteins and high-fat are associated
102 with comparatively high glycaemia and reduced insulin sensitivity in some vertebrates (e.g.; [57-
103 59]). Accordingly, a recent comparative study in birds showed higher blood glucose levels in
104 carnivorous species [56]. This may be attributed to high levels of constitutive gluconeogenesis,
105 which has been confirmed in certain raptors [60-61]. Conversely, bird species with high sugar
106 intake, such as frugivores or nectarivores, are expected to exhibit high glycaemia, as observed
107 in hummingbirds [49] and Passeriformes with such diet [15] (although the opposite was found
108 in [56]). In line with POLS hypothesis, we also hypothesized that species with a slower POL should
109 exhibit a lower glycaemia and higher glycation resistance (glycation levels for a given glycaemia)
110 compared to species with a faster POL. Hence, we included the following four parameters in our
111 analyses of glycaemia and glycation levels: body mass, maximum lifespan, clutch mass and
112 developmental time. Body mass is one of the main factors underlying life history, with higher
113 body mass associated with "slower" strategies and vice versa [62]. Previous studies have
114 reported a negative relationship between body mass and glycaemia [63, 34, 13-14, 56](but see
115 [49, 64] with non-significant trends in birds, and [15] only for temperate species within
116 Passeriformes). Therefore, we predicted that bird species that live longer, develop more slowly
117 and invest less per reproductive event (see ESM6 for further justification of the chosen variables)
118 should show lower plasma glucose levels and albumin glycation rates (after controlling for body
119 mass, phylogeny, diet and glucose in the case of glycation; see methods).

MATERIALS AND METHODS

Species and sample collection

A total of 484 individuals from 88 species measured were included for this study (see **Table ESM6. 1**). A detailed list with the provenance of the samples is provided in ESM3, with a textual description in ESM6.

Blood samples were collected from the brachial or tarsal vein, or from the feet in the case of swifts, using heparin-lithium capillaries or Microvette® (Sarstedt). Samples were centrifuged at 4°C, 3500 g for 10 min and plasma was aliquoted when a large volume was available. Subsequently, they were transported on dry ice to the IPHC (Institut Pluridisciplinaire Hubert Curien) in Strasbourg and stored at -80º C until analysis. Glycaemia was measured in the laboratory on the remaining plasma after taking an aliquot for glycation assessment, using a Contour Plus® glucometer (Ascensia diabetes solutions, Basel, Switzerland) and expressed in mg/dL. These of point-of-care devices have previously been assessed for its usage in birds [65-66], with several examples of its usage in recent literature related to the topic presented here (e.g. [14, 67-69]. We also performed an assay with this particular brand on a subset of 46 samples from this study, coming from 9 species distributed across the whole range of glucose values (3 “low”, 3 “medium” and 3 “high”, from both captive and wild populations), confirming a positive linear correlation ($R^2_{marginal}$=0.66; $R^2_{conditional}$=0.84, for a model including the species as random factor) of this device with Randox GLUC-PAP colourimetry kits (P-value<0.001, unpublished data). Due to methodological constraints, we could not measure glycaemia values of 95 individuals of those that we sampled and in which glycation levels were assessed (belonging to 40 species coming from different sources). For these species, if not a single individual had a glucose measurement (which was the case in 13 species), we obtained mean plasma glucose values reported for the species from the ZIMs database from Species360 (Species360 Zoological Information Management System (ZIMS) (2023), zims.Species360.org). This database provides plasma glucose data measured by colorimetric glucose kits on zoo specimens not neccessary corresponding to those in which we measured glycation values. The sample sizes for both glucose and glycation measurements, either from our measured individuals or from the ones from ZIMs, are reported on the ESM5.

Glycation levels

Glycation levels for each individual were determined using liquid chromatography coupled to mass spectrometry (LC-MS), which is considered the gold standard for the assessment of protein glycation levels (see e.g. [70]) and has previously been used for birds [52-53, 71]. The samples were analysed across several instances within a period of less than 2 years (2021-2023). Only one sample from each individual was measured, given logistic limitations on the total number of samples that could be processed. Briefly, 3 µl of plasma were diluted with 22 µl of distilled water containing 0.1% of formic acid, followed by injection of 5 µl into the system. The glycation values used in the analyses represent the total percentage of glycated albumin, obtained by adding the percentages of singly and doubly glycated albumin. These percentages were calculated by dividing the areas of the peaks corresponding to each glycated molecule form (albumin plus one or two glucose) by the total albumin peak area (sum of the areas of glycated plus non-glycated molecules) observed in the spectrograms obtained from the mass spectrometry outcomes. These spectrograms represent the different intensities of signal for the components differentiated in the sample by their TOF (Time Of Flight), which depends on the mass to charge ratio (m/z) of the ionized molecules. More detailed information regarding functioning of the method and data processing can be found in [53]. In cases where albumin glycation values dropped below the limit of detection, resulting in missing data, these individuals (10 individuals from 4 species) were excluded from the statistical analyses, as outlined below.

Data on ecology and life-history

Diets of individual species were extracted from the AVONET dataset ([72], coming from [73], and those adapted from [74]) and life history traits from the Amniote Database [75]. After realizing that diet classifications from AVONET were not always suitable for our purposes, minor changes were made after consulting the original Wilman et al. [74] database (see ESM6).

For missing data after this stage, we extracted values, in order of preference, from the AnAge database [76] or the Birds of the World encyclopaedia [77], by calculating mean values if an interval was given, and then averaging if male and female intervals were provided separately. For European species, longevity records have always been checked against the most recent Euring database [78]. Maximum lifespans from *Chionis minor* and *Eudyptes chrysolophus* (not available from the previous sources) were extracted from the Centre d'Etudes Biologiques de Chizé, Centre National de la Recherche Scientifique (CNRS-CEBC) database. Several species from

181 the zoo had maximum lifespan values available on the ZIMs from Species 360 (Species360
182 Zoological Information Management System (ZIMS) (2023), zims.Species360.org), so these were
183 also compared with the data we had from other sources.
184 In the case of variables for which two different sources provided different records, an average
185 value was calculated. For the maximum lifespan value, available sources were cross-checked
186 and the highest value was always used. In the absence of satisfactory support from another
187 source, values for maximum lifespan indicated as being anecdotal and of poor quality have been
188 excluded from the analyses. A table with the adequate citations for each value is provided as
189 part of the online available data (see Data accessibility section). When the source is AVONET
190 [72], this database is cited, and when it is Amniote Database [75], we cite the sources provided
191 by them, so the references can be checked in [75]. A list with all the additional references not
192 coming from any of these databases or not provided by their authors (and that are not already
193 in the main text) is given as ESM4.

194 Statistical analyses

195 All analyses were performed in R v.4.3.2 [79]. Alpha (α) ≤0.05 was reported as significant, and
196 0.05<α≤0.1 as trends. General Linear Mixed Models with a Bayesian approach (*MCMCglmm*
197 function in R; [80]) were performed. All models were run with 6×10^6 iterations, with a thinning
198 interval of 100 and a burn-in of 1000. The models were simplified by eliminating quadratic terms
199 where they were not significant and selecting models with lower AIC (Akaike Information
200 Criterion) and BIC (Bayesian Information Criterion). Gaussian distribution of the response
201 variables was assumed (after $\log_{10}$ conversion for glucose; see ESM6 for further discussions). The
202 priors were established assuming variance proportions of 0.2 for the G matrix and 0.8 for the R
203 matrix, with ν=2. For the phylogenetically controlled analyses, consensus trees (each with the
204 species included in the model) were obtained by using the *consensus.edges* function (from the
205 *phytools* package from R [81] from a total of 10,000 trees downloaded from Birdtree.org (option
206 "Hackett All species" [82]). For such purpose, a list of species with the names adapted to the
207 synonyms available in such website was used (see ESM5), including the change of *Leucocarbo*
208 *verrucosus* for *Phalacrocorax campbelli*, as the former was not available and it was the only
209 species from the order Suliformes in our dataset, so that neither the position in the tree nor the
210 branch length would be affected by this change. The consensus trees were included as *pedigree*
211 in the models. We performed models with either glucose or glycation as dependent variables
212 and with the diet, body mass and life history traits as predicting variables (and glucose in the

models with glycation as a response to assess glycation resistance; see introduction). Variance Inflation Factors (VIFs) were calculated for all the models with more than one predictor variable to assess the collinearity of them, as it may be expected for life history traits (see results on ESM1). Models testing the effects of age and sex on glucose and glycation levels and the number of exposed lysine residues on glycation were also carried. Finally, we performed models on glucose and glycation values controlling for the taxonomic orders included in the dataset (see ESM5). The effects of phylogeny on all models was determined by calculating the ratio of the variance estimated for the "animal" variable, representing the *pedigree* (see ESM6) by the total variance (all random factors plus *units*). A thorough description of all of the models, including transformations of the variables and other details is given on the ESM6.

RESULTS

Plasma glucose and albumin glycation variability across the birds' tree

Plasma glucose and albumin glycation values varied considerably across species (**Figure 1**). Considerable within species repeatability (see ESM6) was observed (Glucose: R = 0.716, SE = 0.043, CI_{95} = [0.621, 0.786], P-value <0.0001; Glycation: R = 0.703, SE = 0.039, CI_{95} = [0.621, 0.766], P-value <0.0001).

We found significant differences between some orders for both glucose and albumin glycation. ESM1 shows the raw outcomes of the models, showing such significant differences to the intercept and the Confidence Intervals to perform the pairwise comparisons across all groups. To explore some of the details, we can see for example how Apodiformes showed the highest average glucose values (species average model: Estimated mean=351.8 mg/dL, CI_{95}[238.9, 514.2]; model with individuals: Estimated mean=349.8 mg/dL, CI_{95}[251.8, 476.7], n=39 individuals, 1 species), followed by Passeriformes (species average model: Estimated mean=349.2 mg/dL, CI_{95}[279.6, 438.6]; model with individuals: Estimated mean=337.6 mg/dL, CI_{95}[274.5, 414.5], n=84 individuals, 8 species), while the Suliformes (species average model: Estimated mean=172 mg/dL, CI_{95}[117.6, 252.9]; model with individuals: Estimated mean=169.5 mg/dL, CI_{95}[120.9, 239.7], n=5 individuals, 1 species), Rheiformes (species average model: Estimated mean=173.7 mg/dL, CI_{95}[118, 254.7]; model with individuals: Estimated mean=172 mg/dL, CI_{95}[123.7, 239.8], n=9 individuals, 1 species) and Phoenicopteriformes (species average model: Estimated mean=176 mg/dL, CI_{95}[130, 241.1]; model with individuals: Estimated mean=141.2 mg/dL, CI_{95}[100.4, 198.2], n=5 individuals, 1 species) show the lowest average

values (for the species average models, the pattern is Suliformes<Rheiformes<Phoenicopteriformes, while for the individual models is Phoenicopteriformes<Suliformes<Rheiformes).

For glycation, Strigiformes (species average model: Estimated mean=25.6 %, CI_{95}[20, 31]; model with individuals: Estimated mean=25.3 %, CI_{95}[19.1, 31.5], n=7 individuals, 2 species), Apodiformes (species average model: Estimated mean=25.5 %, CI_{95}[18.6, 32.4]; model with individuals: Estimated mean=24.8 %, CI_{95}[17.9, 32], n=40 individuals, 1 species) and Coraciiformes (species average model: Estimated mean=24.5 %, CI_{95}[17.9, 31.6]; model with individuals: Estimated mean=23.9 %, CI_{95}[15.8, 32], n=2 individuals, 1 species), all terrestrial carnivores as by our sampled species (see discussion below), had the highest average.

On the other hand, Casuariiformes (species average model: Estimated mean=10.8 %, CI_{95}[3.7, 18.1]; model with individuals: Estimated mean=11.4 %, CI_{95}[2.7, 20.6], n=1 individuals, 1 species), Phoenicopteriformes (species average model: Estimated mean=11.2 %, CI_{95}[5.6, 16.7]; model with individuals: Estimated mean=10.5 %, CI_{95}[4.6, 16.3], n=22 individuals, 2 species) and Suliformes (species average model: Estimated mean=13.8 %, CI_{95}[7, 20.7]; model with individuals: Estimated mean=13.2 %, CI_{95}[5.6, 20.5], n=5 individuals, 1 species) had the lowest average levels for the species average models, the pattern is Casuariiformes<Phoenicopteriformes<Suliformes, while for the individual models is Phoenicopteriformes<Casuariiformes<Suliformes). Graphs with raw data on species average and individual glucose and glycation values by order are shown on ESM2 (**Figure ESM2.3**). Estimates of phylogeny effects on glucose and glycation values differ if we consider the models with intraspecific variability or without it, but not so much between the models with and without life history traits (within the previous categories). In the case of species averages, the effect of the tree on glucose is lower and the estimation is less precise than for glycation, while for the models considering individual values, it is glycation what shows lower levels of tree-related variance than glucose (see ESM1).

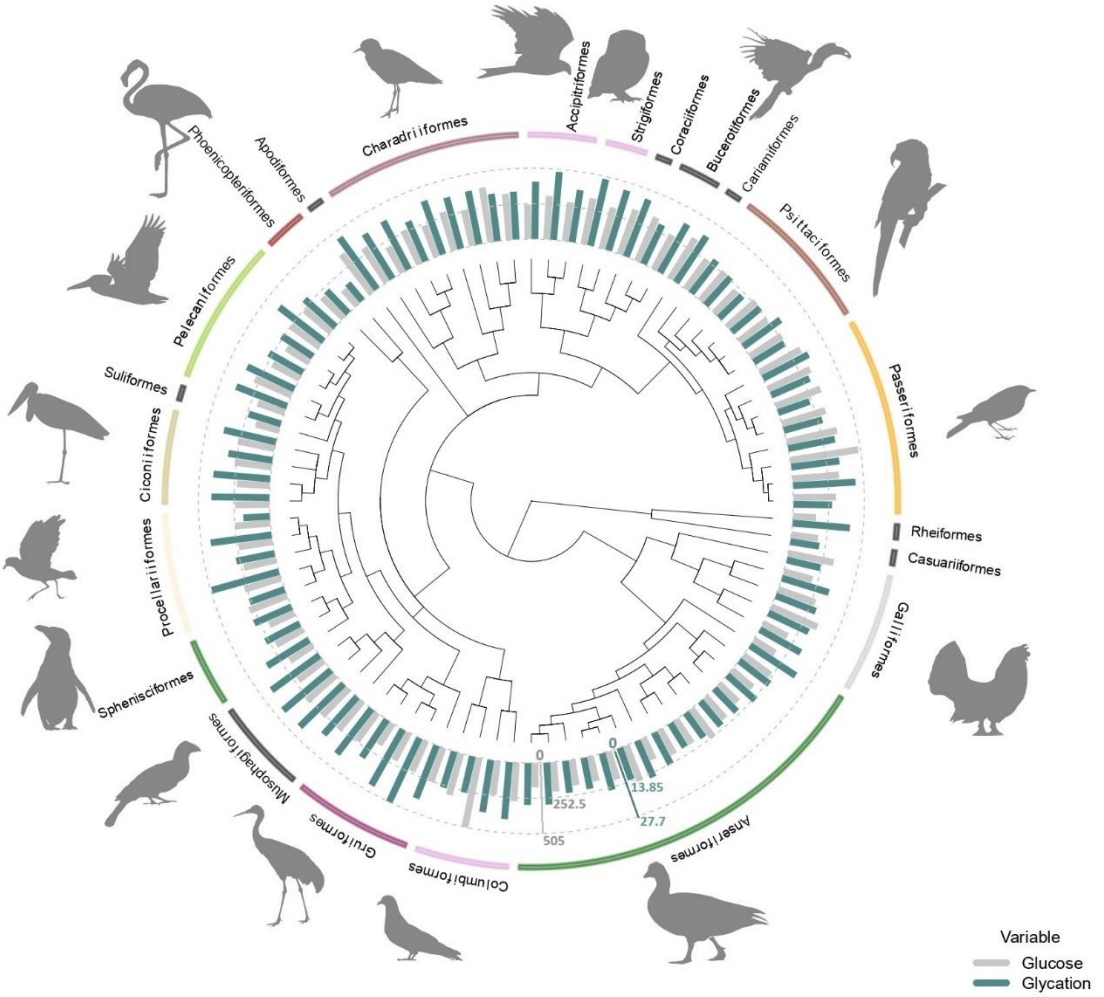

Figure 1. Average plasma glucose values in mg/dL (in grey) and average albumin glycation rate as a percentage of total albumin (in blue) from all the species used in this study (some of them with glucose values coming from ZIMs database; see methods) with the orders they belong to. Glucose and glycation values are standardized in order to be compared, with the dotted lines representing half the maximum and maximum values for each variable (as indicated by the axes in their corresponding colours), from inside out. Tree from a consensus on 10,000 trees obtained from "Hackett All species" on Birdtree.org, including 88 species from 22 orders (see methods).

Bird glycemia appears related to body mass and maximum lifespan

After controlling for intraspecific variation in our analyses, we found that variation in glucose levels were significantly explained by variations in body mass and both the linear and quadratic component of mass-adjusted maximum lifespan, but not by variations in diet (**Figure 4.A** with predictions from the model without life history traits and **Figure ESM2.2.A** with raw individual data from the same dataset), clutch mass and developmental time (see **Table 1** for the model

284 including life-history trait variables). Heavier species had lower glucose levels (see **Figure 2.A**,
285 drawn with the estimates from the model without life history traits, which includes more
286 species). Glucose levels increase with increasing mass-adjusted lifespan until reaching a plateau
287 (**Figure 2.B**). Models that did not consider intraspecific variability show no significant effect of
288 any of the aforementioned variables on glucose levels (see ESM1).

289 **Table 1.** Final glucose model with diet, body mass, and life history traits as explanatory variables, including
290 the significant quadratic effect of maximum lifespan. Posterior means, CI_{95} and pMCMC from a
291 phylogenetic MCMC GLMM model including n=326 individuals of 58 species. Both glucose and body mass
292 are log_{10} transformed and life history traits are residuals from a pGLS model of log_{10} body mass and log_{10}
293 of the trait in question (see ESM6). Body mass was also centred to better explain the intercept, as 0 body
294 mass would make no biological sense. The intercept corresponds to the Omnivore diet, being used as the
295 reference as it is considered the most diverse and "neutral" group for this purpose. Significant predictors
296 are indicated in bold.

	Estimates	Lower 95% CI	Upper 95% CI	Sampling effort	pMCMC
Intercept (Omnivore)	2.407181	2.309	2.506	59900	<0.001
Diet: Carnivore terrestrial	0.025121	-0.047	0.095	59900	0.475
Diet: Aquatic predator	0.028388	-0.044	0.0989	59900	0.424
Diet: Herbivore	-0.054	-0.167	0.058	60726	0.328
Diet: Frugivore/granivore	-0.01	-0.158	0.14	57618	0.89
Centred Log_{10}Body mass	**-0.051**	**-0.087**	**-0.014**	**59178**	**0.009**
Maximum lifespan	**0.13**	**0.002**	**0.253**	**59900**	**0.042**
Maximum lifespan^2	**-0.627**	**-1.122**	**-0.141**	**59900**	**0.014**
Clutch mass	-0.079	-0.233	0.066	59900	0.292
Developmental time	-0.012	-0.191	0.167	59041	0.891

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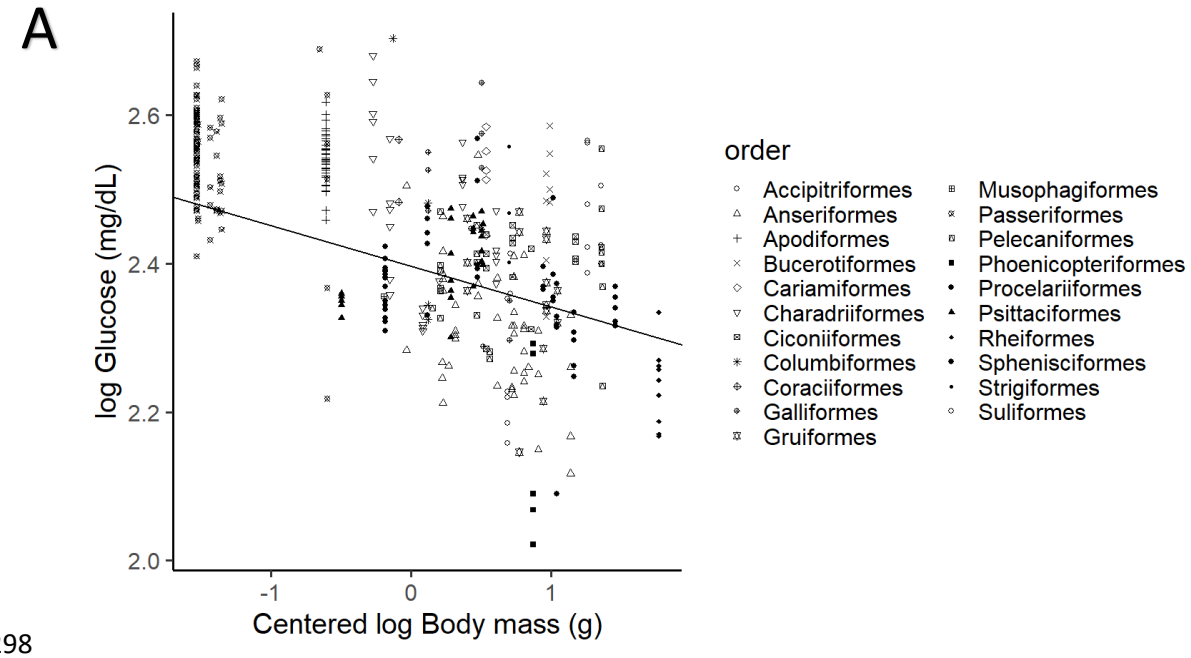

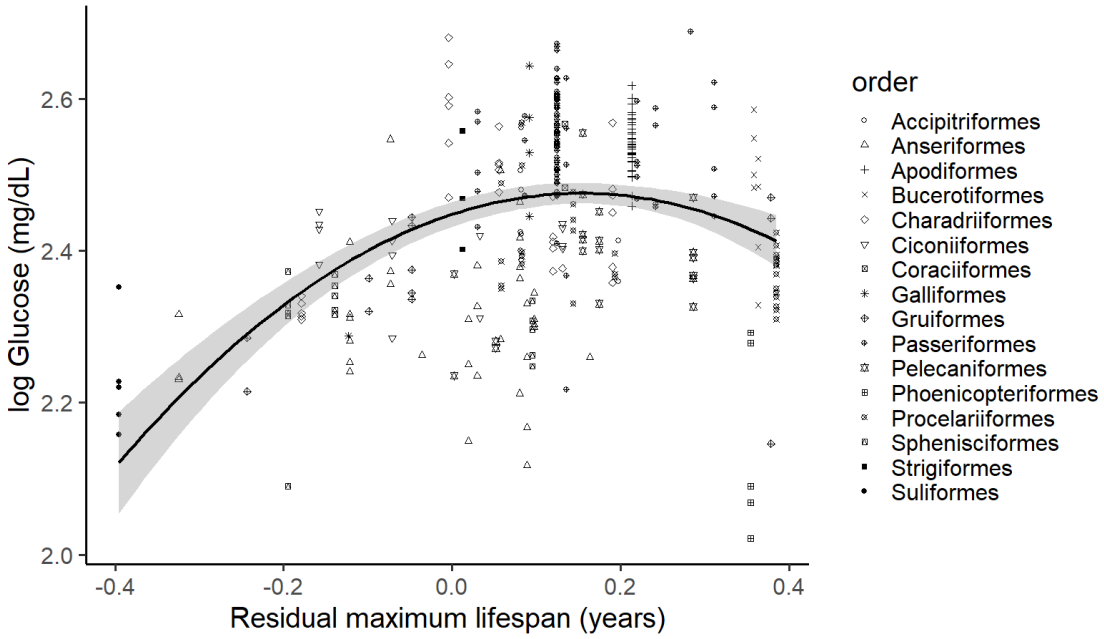

Figure 2. Plasma glucose levels (in mg/dL) variation as a function of **A** species mean centred body mass and **B** residual maximum lifespan. Both glucose and body mass are log transformed. Maximum lifespan (in years) is given as the residues of a pGLS model with body mass (in grams), both $\log_{10}$ transformed, so the effects of body mass on longevity are factored out (see ESM6). Different bird orders, are indicated by symbols, as specified on the legends at the right side of the graphs. **Figure 2.A** uses the values and estimates from the glucose model without life history traits (n=389 individuals from 75 species), while **Figure 2.B** uses only the data points employed on the complete model (n=326 individuals of 58 species).

Bird albumin glycation is related to glycemia and diet

After controlling for intraspecific variability, we found that diet was affecting variation in albumin glycation rates, with terrestrial carnivorous species having higher glycation levels than omnivorous species (**Table 2** for complete model; see **Figure 4.B** with predictions of the model without life history traits and **Figure ESM2.2.B** with raw individual data from the same dataset). However, for the models for species averages, there was only a trend on this pattern in the one including life history traits, and no effect in the other (see ESM1). The relation between glycation and glucose levels was positive and significant in all but the model that included life history traits but not intraspecific variation (see **Table 2** for the outcome of the model with individual values and life history traits and ESM1 for the rest; see **Figure 3** with estimates from the model including individual variation but no life history traits, as it contains more species and the estimates are similar). Given that plasma glucose is logarithm transformed and the estimated slope of their relationship is lower than one, this implies that birds with higher glucose levels have relatively lower albumin glycation rates for their glucose, fact that we would be referring as higher glycation resistance.

Additional analyses looking at the number of exposed lysines in the albumin sequence of a species show no effect of this variable on albumin glycation rates (α=10.39: CI_{95} [-3.713, 24.993], β=0.246: CI_{95}[-0.144, 0.629], P_{MCMC}=0.196; ESM1).

335 **Table 2.** Final glycation model with diet, body mass, glucose and life history traits as explanatory variables.
336 Posterior means, CI_{95} and pMCMC from a phylogenetic MCMC GLMM model including n=316 individuals
337 of 58 species. Both glucose and body mass are log_{10} transformed and life history traits are residuals from
338 a linear model of log_{10} body mass and log_{10} of the trait in question (see ESM6). Body mass and glucose
339 were also centred to better explain the intercept. The intercept corresponds to the Omnivore diet, being
340 used as the reference as it is considered the most diverse and "neutral" group for this purpose. Significant
341 predictors are indicated in bold and the confidence intervals are considered for making pairwise
342 comparisons between the groups.

	Estimates	Lower 95% CI	Upper 95% CI	Sampling effort	pMCMC
Intercept	18.066	13.743	22.38274	59900	<0.001
Diet: Carnivore terrestrial	**4.18**	**0.673**	**7.82346**	**59900**	**0.023**
Diet: Aquatic predator	1.037	-2.704	4.645	59557	0.577
Diet: Herbivore	-1.301	-6.798	4.266	60677	0.634
Diet: Frugivore/granivore	2.77	-5.88	11.189	59900	0.523
Centred log_{10}Body mass	0.015	-1.954	1.908	62211	0.985
Log_{10}Glucose	**6.498**	**1.111**	**11.8**	**59900**	**0.017**
Maximum lifespan	1.564	-5.5	8.391	59900	0.657
Clutch mass	5.064	-2.84	13	59900	0.203
Developmental time	3.551	-5.935	13.226	60780	0.455

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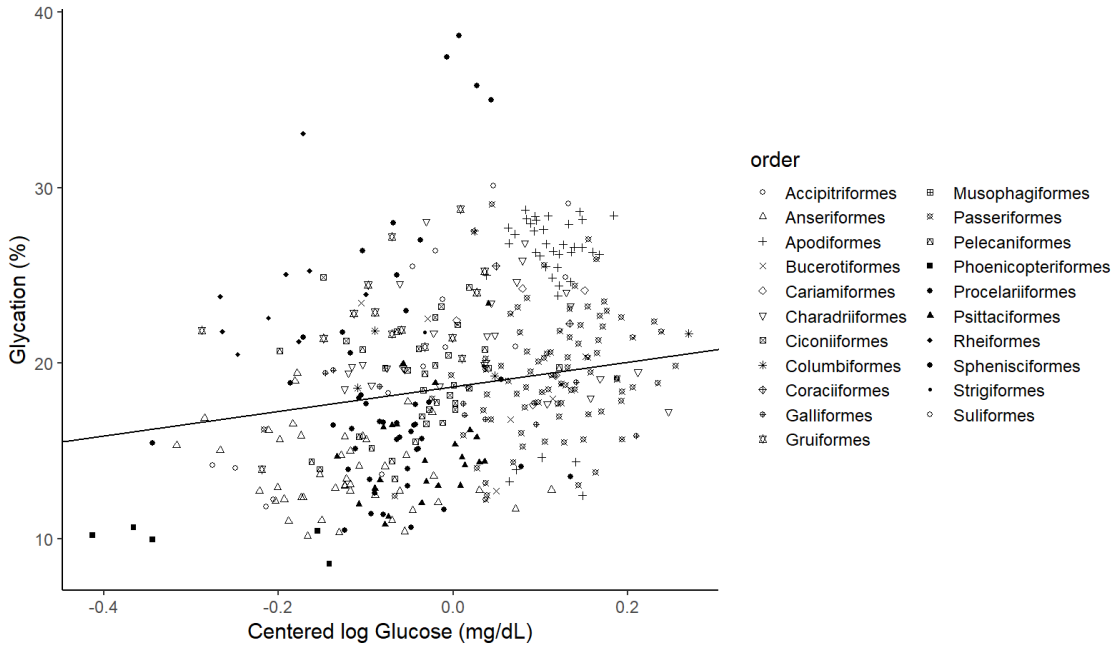
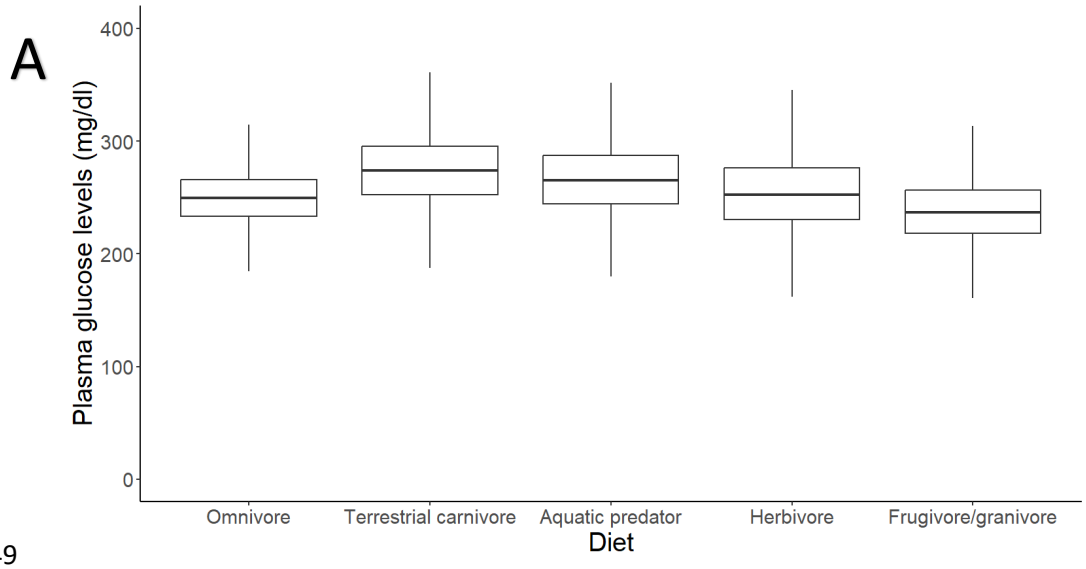


Figure 3. Albumin glycation rates (as a percentage of total albumin) variation as a function of individual plasma glucose values (mg/dL). Different bird orders are indicated by symbols, as specified on the legends at the right side of the graphs. The values and estimates used are from the glycation model without life history traits (n=379 individuals from 75 species).



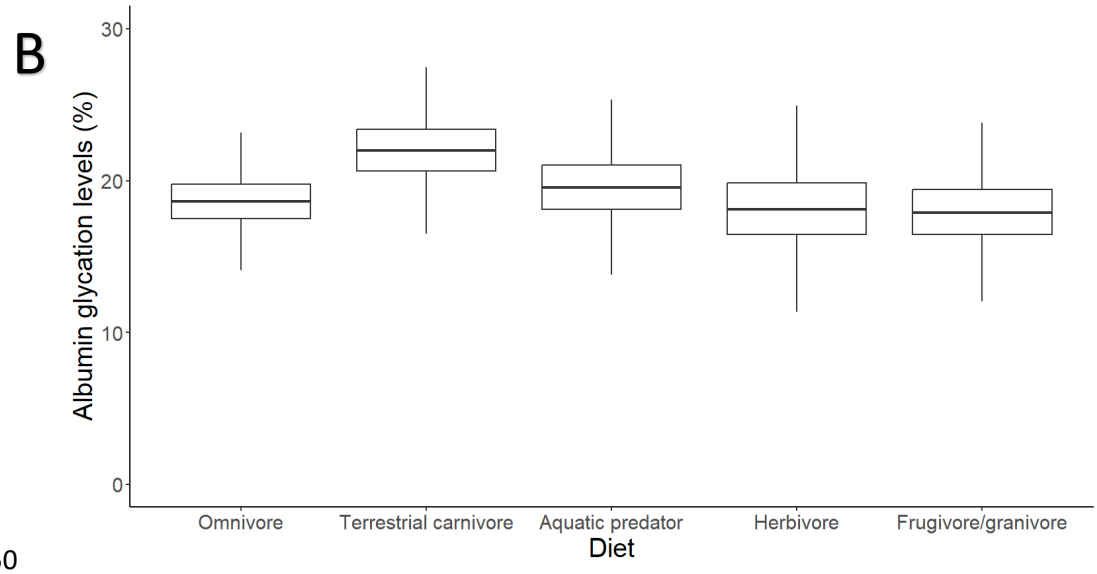


Figure 4. Outcomes of the models on individual data on effects of diet on (**A**) plasma glucose levels and (**B**) albumin glycation in birds. Glucose levels are given in mg/dL, while glycation levels are a percentage of total plasma albumin which is found to be glycated. Terrestrial carnivores showed significantly higher glycation levels than omnivores (Estimate=22.01 %, CI_{95}[18.77, 25.15], p_{MCMC}=0.039). Models without life history traits, including more individuals, are represented, but the models with life history traits do not show differences in their qualitative predictions (i.e. higher albumin glycation in terrestrial carnivores than in omnivores; see ESM1).

We observed no significant effect of age relative to maximum lifespan nor sex on either glycaemia or glycation (see ESM1).

DISCUSSION

Plasma glucose level and albumin glycation rate (co)variation patterns suggests resistance mechanisms

Our findings show that glucose levels vary widely among different bird groups. Interspecific differences are partly explained by the allometric relationship of glycaemia with body mass (**Figure 2.A**), which has already been reported in previous studies [56, 63, 34, 13, 14]. Indeed, Passeriformes, Apodiformes and some Columbiformes (e.g. *Nesoenas mayeri* holds the highest value in our dataset) are found at the higher end of the glucose level continuum, in accordance with their relatively small body mass and powered flight, while groups of larger birds such as Phoenicopteriformes, Anseriformes, Rheiformes and Suliformes tend to show low glycaemia

371 levels. This pattern is similar for glycation, with some groups of large birds (such as
372 Phoenicopteriformes, Anseriformes and Suliformes) showing the lowest levels of glycated
373 albumin, while small birds (such as Apodiformes) had the highest values. Nevertheless, glycation
374 remains high in some birds in relation to their glucose levels, as in Rheiformes, or low as in
375 Psittaciformes or Passeriformes. The case of Procellariiformes, which are typically long-lived
376 birds, is particularly striking, with some species exhibiting some of the highest glycation levels
377 (*Calonectris diomedea* and *Macronectes giganteus*) and others some of the lowest (*Procellaria*
378 *aequinoctialis*). This suggests that, if birds are protected against the deleterious effects of high
379 glycaemia, certain species may have evolved mechanisms to efficiently prevent proteins to be
380 glycated at high rates while others may have evolved mechanisms to resist the consequences of
381 protein glycation. We should also bear in mind that some taxonomic groups may be
382 underrepresented in our study, or biases in species selection due to availability contingencies
383 (e.g. species common in zoos or present in European countries) may exist, so further studies
384 should target this underrepresented groups in order to confirm our predictions.
385 As expected for a non-enzymatic reaction, just by the law of mass action, bird albumin glycation
386 rates increase with plasma glucose concentration. However, the logarithmic nature of the
387 relationship, suggests that species with higher plasma glucose levels exhibit relatively greater
388 resistance to glycation. This finding aligns with previous research indicating that *in vitro* glycation
389 levels of chicken albumin increase at a slower rate than those of human albumin when glucose
390 concentration is elevated [82]. Moreover, these levels are consistently lower than those of
391 bovine serum albumin regardless of glucose concentration and exposition time [37]. As
392 discussed in previous studies comparing chicken to bovine serum albumin [37], or zebra finch to
393 human haemoglobin [53], the lower glycation rates observed in bird proteins may result from a
394 lower number of glycatable amino acids (e.g. lysines) in their sequence and/or their lesser
395 exposure at the protein surface.
396 Our analyses do not succeed in indicating a significant positive relationship between average
397 glycation levels and the number of glycatable lysines in the albumin sequence. This may be
398 attributed to the limited number of species employed or the weak variation in the number of
399 glycatable lysine residues, which are mostly ranging from 33 to 39. An interesting exception are
400 the 18 glycatable lysine residues of flamingos (*Phoenicopterus ruber*), which also shows very low
401 glycation levels (mean=10.1%). However, the exceptions of 44 in zebra finches and 20 in godwits
402 (*Limosa lapponica*, used in place of *Limosa limosa*) are nevertheless associated with very similar
403 average glycation levels of 20.2% and 20.7% respectively.

404 **Plasma glucose relates with longevity and may be influenced by reproductive**
405 **strategies**

406 Our results were only in minor agreement with predictions from POLS theory: it holds for body
407 mass, but not for the other life history variables tested. The only previous comparative study of
408 glycaemia and life history traits to our knowledge [14] shows no relationship with mass-adjusted
409 maximum lifespan in passerines. However, our study over 88 bird species on 22 orders revealed
410 an increase in glucose with mass-adjusted longevity up to a plateau (see **Figure 2.B**). Thus, the
411 relationship between glucose and maximum lifespan may depend on differences between bird
412 orders or be tied to specific species particularities not explored in our study. Such species
413 particularities might involve additional undetermined ecological factors that modify the
414 relationship of glycaemia with longevity. Further exploration of glucose metabolism in relation
415 with lifestyle will bring further light on species-specific life-history adaptations concerning
416 glucose. For example, the species with the lower mass-adjusted maximum lifespan here was a
417 cormorant (*Leucocarbo verrucosus*), which have quite low glucose values for birds.
418 Regarding reproductive investment (i.e. clutch mass), our results show no relationship with
419 glycation (see **Table 2**), while previous studies reported positive relationships with glycaemia in
420 passerines [14, 83]. Interestingly, most of the species with high clutch mass included in our study
421 belong to the Anseriformes (**Figure ESM2.1**). While these species exhibit very low glycaemia and
422 albumin glycation rates, they are also characterized by a particular reproductive strategy
423 compared to passerines, for whom clutch mass does not imply the same in terms of parental
424 investment. For instance, Anseriformes, unlike Passeriformes, are precocial and their offspring
425 are not very dependent on parental care. Furthermore, they are capital breeders, accumulating
426 the energetic resources required for reproduction in advance rather than collecting them during
427 reproduction. These species typically have large clutch sizes and incubation is usually carried out
428 by females, who store internal fat resources to support this main part of the parental
429 investment. In addition, ducklings are born highly developed, reducing the amount of care
430 required post-hatching (see e.g. [84-85]). Consequently, their dependence on glucose as a rapid
431 energy source for reproduction may be lower, with investment in this activity likely more closely
432 linked to lipid accumulation. This could explain why we did not detect previously reported
433 effects of clutch mass on glucose levels.
434

435 **Terrestrial carnivores show a paradoxically increased albumin glycation rate without**
436 **increased plasma glucose levels**

437 Contrary to our expectation of finding differences across dietary groups, plasma glucose did not
438 significantly vary with species diet. This aligns with results previously reported by [14] for
439 Passeriformes or by [55] for 160 species of vertebrates among which 48 were birds, but not with
440 [15], that showed glycaemia to be increased with the proportion of fruits/seeds in the diet, or
441 with [56], that showed higher (mass-adjusted) glucose levels for terrestrial carnivores and
442 insectivores (those included in our terrestrial carnivores' category) and lower for
443 frugivorous/nectarivorous. On the other hand, intraspecific data indicates that changes in diet
444 composition hardly affects glycaemia in birds [86]. These studies suggest that glycaemia is tightly
445 regulated independently of dietary composition within species, while it probably varies across
446 species depending on the diet they are adapted to, although depending on the bird groups
447 included in the analyses and the way of assessing it.
448 Although terrestrial carnivore species did not have significantly higher glycaemia levels in our
449 study, they nonetheless demonstrated significantly higher albumin glycation rates, suggesting a
450 potential susceptibility to protein glycation. Besides unique structural features, this
451 phenomenon could be due to lower albumin turnover rates in terrestrial carnivores. Studies in
452 humans have linked higher oxidative damage to albumin with lower turnover rates (reviewed in
453 [87]), which may extend to other species and post-translational modifications of albumin, such
454 as bird's albumin glycation. However, the contrary outcome would be anticipated if protein
455 intake were high as seen in carnivorous species [87-88].
456 Interestingly, the contrast between terrestrial and aquatic predators, which did not show such
457 high glycation rates, suggests the beneficial influence of a substantial difference in food
458 composition or the pre-eminence of another ecological factor, yet to be determined, which may
459 explain lower glycation levels in aquatic predators. In terms of food composition, the proportion
460 of essential n-3 PUFA (polyunsaturated fatty acids), particularly long-chain ones such as DHA and
461 EPA compared with n-6 PUFA and short-chain n-3 PUFA, is different in aquatic and terrestrial
462 environments [89] and therefore in the diet of predators in each environment (e.g. [90]). For
463 instance, low n-6 PUFA/n3- PUFA ratio have been shown to decrease insulin levels and improve
464 insulin resistance in humans [91]. On the other hand, while some studies report that an increase
465 in dietary n3-PUFA reduces the levels of glycated haemoglobin (HbA1c) in humans, this effect
466 was not detected in many other studies and therefore remains inconclusive (reviewed in [92]).

467 The detailed study of the fat composition of the diets of terrestrial and aquatic predators, in
468 particular the ratio between different types of PUFA, merits more attention. In addition,
469 micronutrient content, such as circulating antioxidant defences, should also be taken into
470 consideration. Indeed, a positive relationship between oxidative stress and glycated levels of
471 bovine serum albumin has been reported [93]. One hypothesis is that terrestrial predators have
472 higher systemic oxidative stress levels compared to other species, which may be explained by
473 defects in their antioxidant defences. Uric acid is one of the main non-enzymatic antioxidants in
474 birds [94-96]**,** and uric acid levels are especially high in carnivore species that have a rich protein
475 diet [95, 97-100]. We should therefore take into account other important antioxidants such as
476 vitamin E, vitamin A and carotenoids, which may be less abundant in the diets of terrestrial
477 carnivores (e.g. [101], but see [52]). The question of whether the diet of aquatic carnivores
478 provides a better intake of antioxidants would therefore requires a more detailed description of
479 dietary habits. The herbivorous diet, meanwhile, despite the expected possibility contributing
480 to lower glycaemia and glycation levels due to higher levels of PUFA compared to SFA (saturated
481 fatty acids) (effects reviewed in [92] for humans) and higher fibre content (see [102]), did not
482 lead to significantly lower levels of either of these two parameters. However, the relatively low
483 sample size in that group or the presence of outliers as *Nesoenas mayeri*, with the highest
484 glucose levels of this dataset, makes the interpretation of the obtained results somehow limited.
485 Therefore, further research should be carried out on these species to determine if the expected
486 pattern would emerge with a better sampling.
487 Finally, differences between captive and wild populations could be considered as a source of
488 variation in glucose or glycation levels, due to a more sedentary lifestyle in captivity, with lower
489 activity levels and a higher food intake likely to lead to increased circulating glucose levels in
490 captive individuals. Additionally, differences in nutrient intake, such as antioxidants, specific
491 fatty acids or amino acids, between captive and wild populations could contribute to variations
492 in glycation levels, as we saw above. Nevertheless, we think that this factor is unlikely to
493 significantly affect our findings regarding diet categories, because our study encompasses
494 species from both captive and wild populations across various diet groups, particularly those
495 exhibiting significant differences (e.g., omnivores versus terrestrial carnivores).

496 **CONCLUSION AND PERSPECTIVES**

497 In conclusion, the avian plasma glucose levels measured here are generally higher or in the high
498 range of values recorded for mammalian species [28]. Our study also concludes that there is

499 considerable variation in plasma glucose levels and albumin glycation rates between bird
500 species, with those with the highest glucose levels showing greater resistance to glycation. The
501 correlation between plasma glucose and life history traits are primarily influenced by its inverse
502 association with body mass, along with non-linear, mass-independent effects of longevity.
503 Finally, although diet does not explain plasma glucose levels in our study, terrestrial carnivores
504 have higher albumin glycation rates than omnivores. Whether these intriguing results are
505 explained by specific effects of certain dietary components, such as PUFAs and/or antioxidants,
506 remains to be determined. Differences in plasma glucose levels and albumin glycation rates
507 across bird species do not seem consistent with predictions according to the POL hypothesis,
508 except for body mass. Further investigation is needed to elucidate the correlation between
509 these traits and specific life conditions, such as reproductive strategy, migration patterns, flight
510 mode or more detailed diet composition. In addition, more in-depth exploration of glycation
511 levels within high glycaemic groups such as the Passeriformes and other small birds, which make
512 up a significant proportion of avian species, could provide valuable new insights. Similarly,
513 investigating groups such as the Phoenicopteriformes or Anseriformes, which are at the other
514 end of the glycaemic-glycation spectrum, could shed light on the origin of differences between
515 avian orders. Furthermore, notable variations were observed between species within orders, as
516 in the Procellariiformes, which with their high mass-adjusted longevity, and particularly given
517 that some of the age known individuals in our dataset (indeed, two specimens of snow petrels,
518 *Pagodroma nivea*, showed ages higher than the maximum lifespan reported in the sources we
519 explored, determining a new record) have still relatively low levels of glycation, may suggest that
520 some species (the ones that do show higher glycation levels) are not intrinsically resistant to
521 glycation, but rather to its adverse consequences for health. As the main limitations from this
522 study, the usage of individuals from both wild and captive populations, sampled at different
523 periods of the year, and the low sample size for some species, due to logistic constraints, may
524 have introduced noise in the values reported that should be addressed in future studies by
525 implementing a stricter sampling protocol. Also, a more thorough and accurate report and
526 compilation of life history traits from multiple species would allow to increase the number of
527 species included in this kind of analyses. Future research should also focus on specific species to
528 unravel the physiological mechanisms mediating the effects of blood glucose and protein
529 glycation on life-history trade-offs, in particular mechanisms that may vary between taxa and
530 contribute to characteristic adaptations in birds to mitigate the potentially negative effects of
531 comparatively high glycaemia.

CONFLICTS OF INTEREST

None declared.

DATA ACCESSIBILITY

All data used, including references for the values taken from bibliography or databases, will be available as Electronic Supplementary Material (ESM5).

ETHICS STATEMENT

This study followed all the legal considerations, with the ethic authorisations from the French Ministry of Secondary Education and Research, n°32475 for the zebra finches sampling, the Swiss Veterinary Office (FSVO) nº 34497 for the Alpine swifts, the Ethics Committee of the University of Extremadura (licenses112//2020 and 202//2020) and the Government of Extremadura (licenses CN0012/22/ACA and CN0063/21/ACA) for the godwits and terns from Spain, and Sampling in Terres Australes et Antarctic Françaises was approved by a Regional Animal Experimentation Ethical Committee (French Ministry of Secondary Education and Research permit APAFIS #31773-2019112519421390 v4 and APAFIS#16465–2018080111195526 v4) and by the Comité de l'Environnement Polaire and CNPN (A-2021-55). The samples from the Mulhouse zoo were taken by its licensed veterinary with capacity number: 2020-247-SPAE-162.

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AUTHORS' CONTRIBUTIONS

F. Criscuolo and F. Bertile conceived the idea, directed most of the sample collection and logistics and contributed significantly to the writing. A. Moreno-Borrallo contributed to the development of the questions, gathered the diet and life-history data, performed the statistical analyses, and led the writing. S. Jaramillo Ortiz and C. Schaeffer performed the mass spectrometry analyses for protein glycation measurements, and S. Jaramillo Ortiz contributed to the glucose measures and commented on the manuscript. T. Boulinier. and V. A. Viblanc coordinated the ECONERGY and ECOPATH polar programs, organised the collection of samples on subantarctic seabirds, and commented on the manuscript. Olivier Chastel collaborated collecting marine bird samples and commented on the manuscript. B. Rey contributed with the collection of samples from Parc des Oiseaux (Villars-les-Dombes, France) and commented on the manuscript. P. Bize leads the monitoring of Alpine swifts' populations from which the samples were obtained, he helped collecting them and commented on the manuscript. J. S Gutiérrez and J. A. Masero contributed with samples from Spain and part of the statistic scripts and commented on the manuscript. B.

589 Quintard leads the health monitoring of Mulhouse zoo bird collection, organized and realized
590 most of Mulhouse zoo samplings and commented on the manuscript. All authors gave their
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