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Long-lived birds suffer less from oxidative stress

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Abstract

Background: Oxidative stress, caused by an imbalance between reactive oxygen species and antioxidants, is thought to be an important intrinsic mechanism for aging. Ecologists have tested this hypothesis in birds, although the evidence supporting the link between oxidative stress and lifespan has so far been ambiguous. Two previous studies based on a wide range of different free-living bird species provided contradictory findings: antioxidants were negatively associated with survival rate in one study, but positively associated with longevity in another.

Methods: In this study, we identified possible shortcomings in previous research, and then used the comparative methods to test whether long-lived birds experience less oxidative stress reflected by four blood redox state markers (total antioxidant status, uric acid, total glutathione, malondialdehyde) based on data for 78 free-living species.

Results: Relatively long-lived bird species had high levels of antioxidants (total antioxidant status, total glutathione) and low levels of reactive oxygen species (malondialdehyde). These associations were independent of statistical control for any effects of body mass, sampling effort and similarity among taxa due to common phylogenetic descent.

Conclusions: The direction of these associations is consistent with the oxidative stress theory of aging.

Keywords: Ageing, Antioxidant, Birds, Longevity, Oxidative stress, Sampling effort

Background

Human beings and members of other species, especially animals, necessarily experience ageing and mortality (Rose 1991). Current theories are assigned to the damage concept, whereby the accumulation of damage (such as DNA oxidation) may cause biological systems to fail, or to the programmed ageing concept, whereby internal processes (such as DNA methylation) may cause ageing (Sohal and Weindruch 1996; Finkel and Holbrook 2000). Toxicity of oxygen was linking to aging of cells at least one hundred years ago (Harman 1956; Gilbert 1963). The processes of aerobic metabolism produce a variety of reactive oxygen species (ROS), and organisms cope with such ROS by means of antioxidant defenses (Finkel and Holbrook 2000; Falnes et al. 2007). Oxidative stress occurs when the production of ROS exceeds antioxidant defenses, which damage biological macromolecules, such as proteins and DNA (Agarwal and Sohal 1994; Sohal et al. 1994; Falnes et al. 2007), and they consequently impair gene expression, and ultimately lead to cell death (Sohal and Weindruch 1996; Finkel and Holbrook 2000; Barja 2004).

Differences in aging and its causes are key features of life-history trade-offs (Ricklefs 2008; Martin 2015). For example, species with long lifespan should spend more energy on self-maintenance, while species with short lifespan should put more effort into reproduction (Martin 2002; Selman et al. 2012). The intuitive logic is that differential rates of aging among species may be due to differences in oxidative stress (Sohal and Weindruch 1996; Finkel and Holbrook 2000; Barja 2004). Ecologists have tested this hypothesis in birds during the last 20 years, although there is so far no consistent conclusion. Early research used a small number of domesticated species (typically less than ten), often including both birds and mammals, and found a weakly negative association between oxidative stress and lifespan (Sanz et al. 2006; Buffenstein et al. 2008). Based on 21 bird species, Delhaye

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et al. (2016) found that long-lived birds produced fewer blood cell mitochondrial ROS production. However, the levels of oxidative damage were mostly indistinguishable between quails (*Coturnix japonica* and *C. chinensis*) and parrots (*Melopsittacus undulatus*, *Agapornis roseicollis*, and *Nymphicus hollandicus*), despite the quails on average having an approximate fivefold lower maximum lifespan potential than parrots (Montgomery et al. 2012). There are only two studies based on a wide array of different free-living bird species. Surprisingly, the results from these two studies are contradictory. Cohen et al. (2008) found that plasma antioxidant capacity (total antioxidant status, uric acid) in 58 American bird species was negatively associated with survival rate, while Galván et al. (2012) found high liver antioxidant concentrations (carotenoids and vitamin E) being positively associated with maximum longevity in 125 European bird species. The contradictory findings of these studies has caused some scientists to doubt whether oxidative stress determines maximum lifespan of animals, as well as the general validity of oxidative stress in life-history (Buffenstein et al. 2008; Salmon et al. 2010).

Two deficiencies may weaken the conclusions from previous research. It is the imbalance between ROS and antioxidants, rather than biochemicals considered separately, that might contribute to cumulative oxidative damage to a variety of biological molecules eventually leading to aging (Finkel and Holbrook 2000; Falnes et al. 2007; Hulbert et al. 2007). However, only ROS or antioxidants were considered in previous research, e.g. only antioxidants were measured by Cohen et al. (2008) and Galván et al. (2012), while only ROS were measured by Delhaye et al. (2016). Furthermore, oxidative stress within species is unstable, varying with season and habitat (Cohen et al. 2009; Costantini 2016). For example, Adelie Penguins (*Pygoscelis adeliae*) increased their plasma antioxidant defenses when more reproductive effort input (Beaulieu et al. 2011), while Barn Swallows (*Hirundo rustica*) decreased their antioxidant defenses (total glutathione) during hatching period (Pap et al. 2018). The level of oxidative stress in Great Tit (*Parus major*) and Pied Flycatcher (*Ficedula hypoleuca*) is significant changed by heavy metal pollution (Stauffer et al. 2017). However, these factors were not controlled in previous research, e.g. Cohen et al. (2008) collected data from multiple sites (in Panama and Michigan), Galván et al. (2012) collected data from different seasons (both breeding and non-breeding), and Delhaye et al. (2016) collected data from both domesticated and free-living species. Thus, these factors could complicate relationships between oxidative stress and lifespan. Clearly, additional research is needed.

The objective of this study was to test whether long-lived bird species are associated with less oxidative stress based on data for 78 free-living bird species. All these species were caught from Romania during the breeding seasons 2011–2013 (Vágási et al. 2016). Large brain size is associated with less oxidative stress (higher total antioxidant status and less malondialdehyde levels) in these species, and an explanation for this link is that large-brained species exhibit slow-paced life histories. Therefore, they are expected to invest more in self-maintenance such as reduced oxidative stress (Vágási et al. 2016). However, the relationship between lifespan and oxidative stress has so far not been documented in these species. A test of this association is the first aim of this study.

Longevity records only provide reliable information on maximum lifespan if they are adjusted for sampling effort (Møller 2006). Statistical theory requires that the maximum value of a random sample should increase, on average, with sample size (Scharf et al. 1998). Thus, it is by definition easier to record an extremely old individual in a large than in a small sample of individuals. While this is obvious, only few previous comparative studies of lifespan have controlled statistically for such sampling effort (e.g. Møller 2006, 2007). The second aim of this study was to test whether maximum lifespan was positively correlated with sampling effort, and whether the relationship between maximum lifespan and oxidative stress was affected by sampling effort.

Methods

Oxidative stress

We used the dataset of oxidative stress from Vágási et al. (2016), which is the largest dataset containing information on both ROS and antioxidants in free-living bird species. In this dataset, Vágási et al. (2016) sampled 544 adult birds belonging to 85 species in Romania, and measured four blood redox state markers in these birds. Among these blood redox state markers, three markers describe the antioxidant defense (total antioxidant status, TAS, uric acid, UA and total glutathione, tGSH), while one marker shows oxidative damage (malondialdehyde, MDA). The markers were chosen for the following reasons (Costantini 2008, 2011; Vágási et al. 2016): (1) total antioxidant status, uric acid and total glutathione are nonenzymatic antioxidants deployed to combat free radical insults and might play a role in ageing; (2) glutathione is the most important intracellular, endogenous, nonenzymatic antioxidant with multifaceted physiological effects including integral to the ageing process; (3) malondialdehyde, which results from lipid peroxidation of polyunsaturated fatty acids, is a widely used marker for oxidative stress, can react with deoxyadenosine and deoxyguanosine in DNA and was also linked to ageing. Vágási et al. (2016) tested for species-specificity of these markers by partitioning variance into among- and within-species components, and found significantly larger variation among than within species. Thus, these markers were found to be species-specific, and averaged values of theses markers for each species are suitable for multispecies comparison. The age and sex was not controlled in the dataset, implying that our analyses are conservative because this random error would reduce the potential detection of any relationship between lifespan and oxidative stress.

Longevity records

We compiled information on longevities of above 85 bird species using information from three sources: Møller (2006), Wasser and Sherman (2010), and Animal Ageing and Longevity Database (Tacutu et al. 2013). If both longevity in the wild and longevity in captivity are provided, longevity in the wild was used. If longevity records for the same species differed among sources, the largest value was used. In total, we obtained longevity records from 78 species, 72 of these from the wild while 6 were from captivity.

Sampling effort

Records of longevity by necessity must be controlled for sampling effort because it is by definition easier to record an extremely old individual in a large than a small sample. Møller (2006) used longevity record and the recoveries reported by EURING (2018) (http://www.euring.org), and found longevities are positively related to the number of recoveries. We also included recoveries reported by EURING. However, using recoveries by EURING to reflect sampling effort in this study may be biased, as we collected longevity records from various sources, rather than only from EURING. As an alternative approach, we searched for the number of publications for each species at the Web of Science (http://apps.webofknowledge.com/) with scientific name of each species as the entry, and used the number of publications to reflect sampling effort. The logic underlying this approach is that the higher the sampling effort the more publications.

Body mass

As previous research has found that large species have greater longevity (e.g. Wasser and Sherman, 2010; Galván et al. 2015), we also included body mass in the analyses. Body mass data were collected from Dunning (2008).

The dataset used in this study is reported in Additional file 1: Table S1.

Statistical analyses

Four variables (longevity, body mass, number of recoveries, number of publication) were $\log_{10}$-transformed to meet the normality assumption. Pearson correlation was used to test for the relationship among longevity, and recoveries, number of publications. A z test was used to compare correlation coefficients. Both blood redox state markers and longevity showed a phylogenetic signal (Møller 2006, 2007; Vágási et al. 2016). To account for the dependence of observations due to shared evolutionary ancestry, we built Phylogenetic Generalized Least Squares (PGLS) models in which the phylogenetic signal (Pagel's λ) was estimated with maximum likelihood (Pagel 1999; Freckleton et al. 2002). To control for phylogeny and uncertainties in phylogenetic construction, we retrieved 1000 phylogenetic trees from birdtree.org (Jetz et al. 2012), with the backbone tree of Hackett et al. (2008), which were merged into a maximum clade credibility tree using Tree Annotator in BEAST v1.8.3 (Drummond et al. 2012). Longevity was the dependent variable in the model, and blood redox state markers (TAS, UA, tGSH, MDA), body mass, and number of publications were the independent variables in the model. The combinations of these 6 independent variables can generate 63 potential models (from one independent variable to 6 independent variables). Among these models, we choose the model based on the Akaike's Information Criterion (AIC) (Symonds and Moussalli 2011). We reported the model with the lowest AIC value. For reflecting the influence of sampling effort, we also reported the model with lowest AIC value without number of publications included. The AIC values for each model, and the details of two suboptimal model (delta AIC < 2) can be seen in Additional file 2: Table S2 and Additional file 3: Table S3.

All analyses were conducted using R 3.4.1 (R Core Team 2018). PGLS was performed using the "caper" package (David et al. 2013). Data was reported as mean ± standard error. Results were considered significant if $p < 0.05$ (two-tailed test).

Results

Among the 78 species, longevity ranged from 5.91 (*Merops apiaster*) to 35 years (*Columba livia*), with a mean of 14.16 ± 0.72 years across species. The mean number of publications was 353 ± 78, with a minimum of 5 in *Saxicola torquatus*, and a maximum of 3686 in *Columba livia*. The number of recoveries reported by EURING was on average 33,020 ± 6786 across species, with a minimum of 82 in *Falco vespertinus*, and a maximum of 375,858 in *Parus major*. The number of publications was significantly positively correlated with the number of recoveries (Pearson's $r = 0.540$, $p < 0.001$; Fig. 1a) and longevity (Pearson's $r = 0.579$, $p < 0.001$; Fig. 1b). Longevity was also significantly positively correlated with the number of recoveries (Pearson's $r = 0.340$, $p < 0.001$). However, this correlation

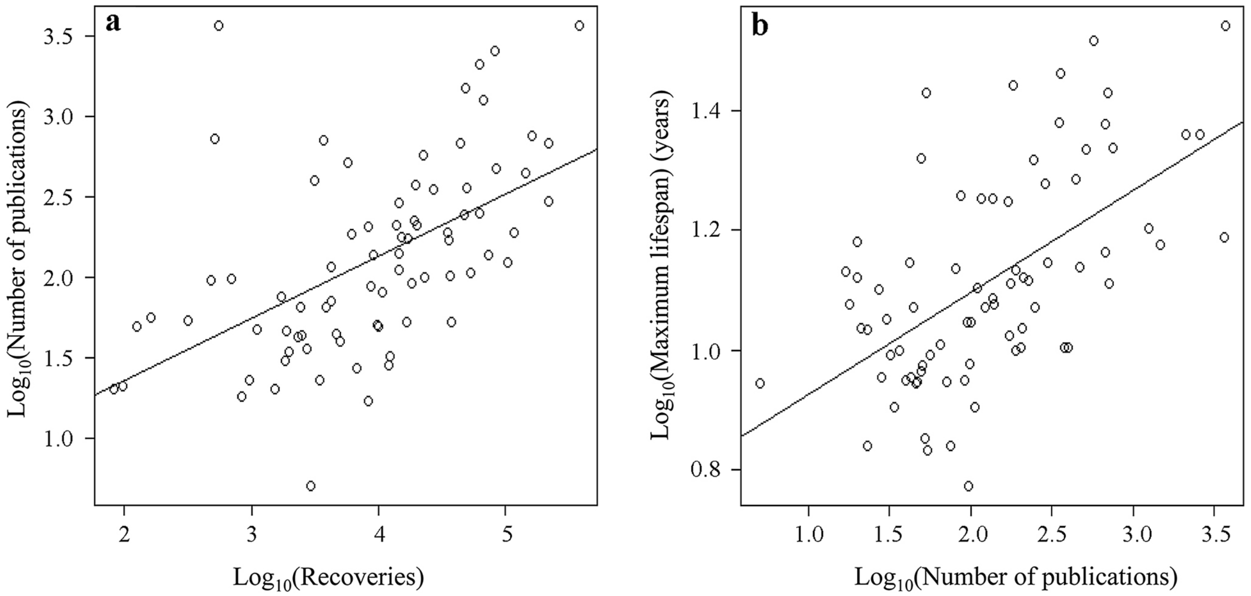

Fig. 1 Number of publications for different bird species is significantly positively correlated with the number of recoveries (**a**) (Pearson's $r = 0.540$, $p < 0.001$), and longevity is significantly positively correlated with number of publications (**b**) (Pearson's $r = 0.579$, $p < 0.001$). The lines are the regression lines

Table 1 The best PGLS model (with the lowest AIC value) for the relationship between longevity and oxidative stress based on 78 bird species

Variables	Coefficient	Standard error	*t*	*p*
Intercept	*0.534*	*0.112*	*4.751*	*< 0.001*
TAS	*0.075*	*0.029*	*2.592*	*0.012*
tGSH	0.004	0.003	1.723	0.089
MDA	*− 0.030*	*0.014*	*− 2.107*	*0.039*
Body mass	*0.110*	*0.033*	*3.313*	*0.001*
Number of publications	*0.158*	*0.024*	*6.445*	*< 0.001*

Values in italics are statistically significant at the 0.05 level

coefficient was lower than the correlation coefficient between longevity and number of publications (*z* test, $z = 1.880$, $p = 0.060$).

Generally, lifespan was positively correlated with the concentration of antioxidants, and negatively correlated with the concentration of ROS in these 78 species. In the best PGLS model ($F_{5,72} = 16.350$, $p < 0.001$, Adjusted $R^2 = 0.450$) (Table 1), longevity was positively correlated with TAS (Fig. 2a), tGSH (Fig. 2b) and body mass (Fig. 2d), and negatively correlated with MDA (Fig. 2c). If the sampling effort (number of publications) was not included, the above relationships remained almost unchanged. In the model ($F_{3,74} = 8.454$, $p < 0.001$, Adjusted $R^2 = 0.225$) (Table 2), longevity was positively correlated with TAS (Fig. 2a) and body mass (Fig. 2d), and negatively correlated with MDA (Fig. 2c). UA was not included in either model with or without inclusion of number of publications.

Discussion

In ecological research, much effort has been put into explaining extrinsic mortality, such as the link between lifespan and diet, sociality, breeding habitat, nest-site location and migratory behavior (e.g. Møller 2007; Ricklefs 2008; Wasser and Sherman 2010; Martin 2015). Intrinsic mechanisms of aging have also received attention. Oxidative stress is a possible link between extrinsic mortality and intrinsic mechanisms of senescence (Sohal and Weindruch 1996; Finkel and Holbrook 2000; Barja 2004). Based on data for 78 free-living bird species, we found that lifespan was positively correlated with the concentration of antioxidants (TAS, tGSH), and negatively correlated with the concentration of ROS (MDA), which means that long-lived birds generally suffer low levels of oxidative stress. The direction of these associations was consistent with the oxidative stress theory of aging (Sohal and Weindruch 1996; Finkel and Holbrook 2000). UA was not included in the models either with or without inclusion of the number of publications. Cohen et al. (2008) and Vágási et al. (2016) pointed out that UA significantly positively correlates with TAS in bird blood plasma. As there is collinearity between UA and TAS, the

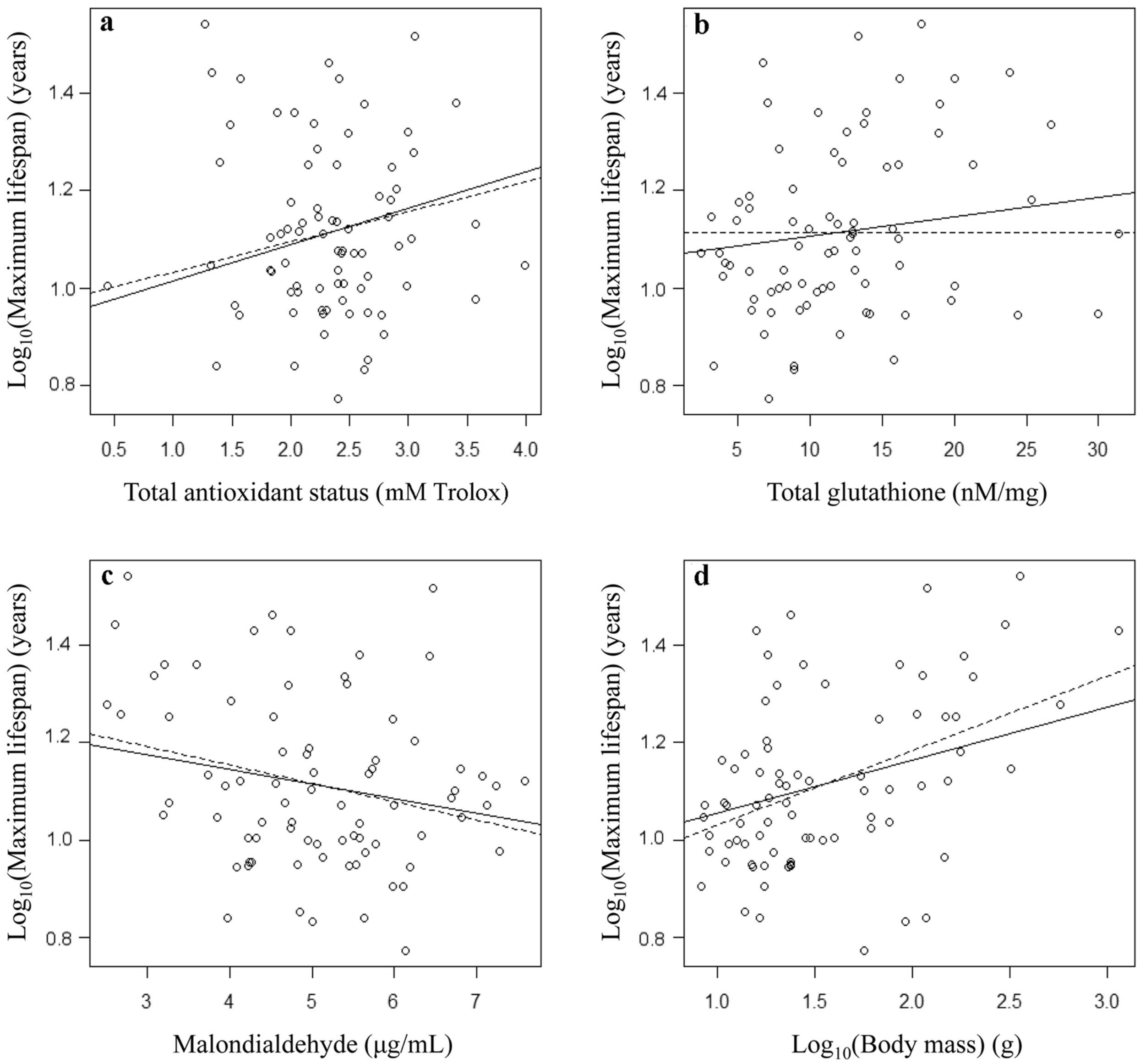

Fig. 2 Longevity in relation to total antioxidant status (**a**); total glutathione (**b**); malondialdehyde (**c**); and body mass (**d**). The slope of the solid line was extracted from the PGLS model presented in Table 1; the slope of the dashed line was extracted from PGLS model presented in Table 2. The slope of the dashed line in **b** was zero, as total glutathione was not included in the PGLS model presented in Table 2

Table 2 The best PGLS model (with the lowest AIC value) for the relationship between longevity and oxidative stress based on 78 bird species without including sampling effort (number of publications)

Variables	Coefficient	Standard error	*t*	*p*
Intercept	*0.922*	*0.118*	*7.819*	*< 0.001*
TAS	0.062	0.036	1.735	0.087
MDA	*− 0.038*	*0.017*	*− 2.176*	*0.033*
Body mass	*0.154*	*0.038*	*4.097*	*< 0.001*

Values in italics are statistically significant at the 0.05 level

relationship between UA and longevity could be covered by the effect of TAS.

Although the linkage between oxidative stress and lifespan has been proposed nearly half a century ago, e.g. free radical theory of aging (Harman 1956) and soma theory of aging (Kirkwood 1977), the evidence supporting this linkage has been ambiguous. For example, two studies based on a wide array of different free-living bird species obtained contradictory findings: antioxidants were negatively associated with survival rate in the study by Cohen et al. (2008), while it was positively associated with longevity in the study by Galván et al. (2012). We emphasize that two deficiencies may weaken the conclusions in these studies. There is an imbalance between ROS and antioxidants contributing to cumulative oxidative damage (Finkel and Holbrook 2000; Falnes et al. 2007; Hulbert et al. 2007). However, only one side, either ROS or antioxidants, was considered (Cohen et al. 2008; Galván et al. 2012; Delhaye et al. 2016). Covariates such as sampling season and habitat were not controlled, which could complicate relationships between oxidative stress and lifespan (Cohen et al. 2009; van de Crommenacker et al. 2017). In this study, we included both ROS and antioxidants, and based on the samples collected during the breeding season from a relatively small area within Romania (Vágási et al. 2016). Although the influence of covariates was not totally controlled, it is greatly reduced. However, there is also another possible explanation for the contradictory findings. There is no standardized protocol for measuring status of oxidative stress, and multiple assays were conducted (Costantini 2011, 2016), e.g. antioxidants (carotenoids and vitamin E) in liver were measured by Galván et al. (2012), while different types of plasma antioxidants were used by Cohen et al. (2008) and the present study. Different antioxidants may not covary with each other (Cohen and McGraw 2009), which may lead to contradictory findings among studies.

Two variables, survival rate and longevity record, were used to reflect maximum lifespan in birds. For example, survival rate was used by Cohen et al. (2008), longevity record was used by Galván et al. (2012, 2015) and Delhaye et al. (2016), while both were used in Møller (2006, 2007). Previous research has found that survival rate can readily change, e.g. survival rate increases as feeding conditions improve, while longevity remained constant (summarized in Buffenstein et al. 2008). Therefore, we considered longevity records rather than survival rate to reflect lifespan in this study. Longevity records only provide reliable information on maximum lifespan if records are adjusted for sampling effort, as it is by definition easier to record a maximum value in a large than a small sample (Scharf et al. 1998; Møller 2006). Møller (2006) described such bias in detail, and used the number of recoveries to adjust for sampling effort. However, it is difficult to obtain recoveries, especially when longevity records derive from multiple sources, and only a few comparative studies of lifespan have controlled for sampling effort (e.g. Møller 2006, 2007). In this study, we adopted an alternative approach, using the number of publications to reflect sampling effort. The logic underlying this approach is that sampling effort increases with the number of publications. Based on our data, we found that longevity was positively related to the number of publications, and the correlation coefficient was larger than that between longevity and number of recoveries. Although the general association remained consistent with or without inclusion of the number of publications, some details changed, e.g. tGSH was not included in the model without inclusion of the number of publications. When using longevity to reflect lifespan, we suggest sampling effort should be controlled, at least to test for the robustness of findings with or without sampling effort controlled.

Conclusions

The main finding of this study was that relatively long-lived bird species had high levels of antioxidants (TAS, tGSH) and low levels of MDA, which is a marker of oxidative damage. This association was independent of statistical control for effects of body mass, sampling effort and similarity among taxa due to common phylogenetic descent. At the broadest level, our results support the disposable soma theory of aging (Kirkwood 1977) and the free radical theory of aging (Harman 1956). The adjusted R^2 was less than 0.5 in the model, which implies there is still variation in lifespan that remains unexplained. Recent research has found other intrinsic mechanisms linked to lifespan in birds, such as monounsaturated fatty acids (Galván et al. 2015) and telomere erosion (Sudyka et al. 2016; Boonekamp et al. 2017). Pooling these factors may provide a better understanding of senescence.

Additional files

Additional file 1: Table S1. The dataset used in this study.

Additional file 2: Table S2. AIC values for each PGLS model.

Additional file 3: Table S3. Two suboptimal PGLS models (with delta AIC < 2) for the relationship between longevity and oxidative stress based on 78 bird species.

Authors' contributions

APM conceived this study. APM and CX collected the data. CX analyzed the data. CX and APM wrote the manuscript. Both authors contributed critically to the drafts. Both authors read and approved the final manuscript.

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Not applicable.

Competing interests

The authors declare that they have no competing interests.

Availability of data and materials

All data generated or analyzed during this study are included in this published article and its supplementary information files.

Consent for publication
Not applicable.

Ethics approval and consent to participate
Not applicable (All data used are from website or published paper).

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References

Agarwal S, Sohal RS. DNA oxidative damage and life expectancy in houseflies. Proc Natl Acad Sci USA. 1994;91:12332–5.

Barja G. Aging in vertebrates, and the effect of caloric restriction: a mitochondrial free radical production-DNA damage mechanism? Biol Rev. 2004;79:235–51.

Beaulieu M, Reichert S, Le Maho Y, Ancel A, Criscuolo F. Oxidative status and telomere length in a long-lived bird facing a costly reproductive event. Funct Ecol. 2011;25:577–85.

Boonekamp JJ, Bauch C, Mulder E, Verhulst S. Does oxidative stress shorten telomeres? Biol Lett. 2017;13:20170164.

Buffenstein R, Edrey YH, Yang T, Mele J. The oxidative stress theory of aging: embattled or invincible? Insights from non-traditional model organisms. Age. 2008;30:99–109.

Cohen AA, McGraw KJ. No simple measures for antioxidant status in birds: complexity in inter- and intraspecific correlations among circulating antioxidant types. Funct Ecol. 2009;23:310–20.

Cohen AA, McGraw KJ, Wiersma P, Williams JB, Robinson WD, Robinson TR, Brawn JD, Ricklefs RE. Interspecific associations between circulating antioxidant levels and life-history variation in birds. Am Nat. 2008;172:178–93.

Cohen AA, McGraw KJ, Robinson WD. Serum antioxidant levels in wild birds vary in relation to diet, season, life history strategy, and species. Oecologia. 2009;161:673–83.

Costantini D. Oxidative stress in ecology and evolution: lessons from avian studies. Ecol Lett. 2008;11:1238–51.

Costantini D. On the measurement of circulating antioxidant capacity and the nightmare of uric acid. Methods Ecol Evol. 2011;2:321–5.

Costantini D. Oxidative stress ecology and the d-ROMs test: facts, misfacts and an appraisal of a decade's work. Behav Ecol Sociobiol. 2016;70:809–20.

David O, Rob F, Gavin T, Thomas P, Susanne F, Nick I. caper: comparative analyses of phylogenetics and evolution in R. R package version. 2013.

Delhaye J, Salamin N, Roulin A, Criscuolo F, Bize P, Christe P. Interspecific correlation between red blood cell mitochondrial ROS production, cardiolipin content and longevity in birds. Age. 2016;38:433–43.

Drummond AJ, Suchard MA, Xie D, Rambaut A. Bayesian phylogenetics with BEAUti and the BEAST 1.7. Mol Biol Evol. 2012;29:1969–73.

Dunning JBJ. CRC handbook of avian body masses. 2nd ed. Boca Raton: CRC Press; 2008.

EURING. http://www.euring.org. Accessed 20 May 2018.

Falnes PO, Klungland A, Alseth I. Repair of methyl lesions in DNA and RNA by oxidative demethylation. Neuroscience. 2007;145:1222–32.

Finkel T, Holbrook NJ. Oxidants, oxidative stress and the biology of ageing. Nature. 2000;408:239–47.

Freckleton RP, Harvey PH, Pagel M. Phylogenetic analysis and comparative data: a test and review of evidence. Am Nat. 2002;160:712–26.

Galván I, Erritzøe J, Karadas F, Møller AP. High levels of liver antioxidants are associated with life-history strategies characteristic of slow growth and high survival rates in birds. J Comp Physiol B. 2012;182:947–59.

Galván I, Naudi A, Erritzøe J, Møller AP, Barja G, Pamplona R. Long lifespans have evolved with long and monounsaturated fatty acids in birds. Evolution. 2015;69:2776–84.

Gilbert DL. The role of pro-oxidants and antioxidants in oxygen toxicity. Radiat Res. 1963;3S:44–53.

Hackett SJ, Kimball RT, Reddy S, Bowie RCK, Braun EL, Braun MJ, Chojnowski JL, Cox WA, Han KL, Harshman J, Huddleston CJ, Marks BD, Miglia KJ, Moore WS, Sheldon FH, Steadman DW, Witt CC, Yuri T. A phylogenomic study of birds reveals their evolutionary history. Science. 2008;320:1763–8.

Harman D. Aging: a theory based on free-radical and radiation-chemistry. J Gerontol. 1956;11:298–300.

Hulbert AJ, Pamplona R, Buffenstein R, Buttemer WA. Life and death: metabolic rate, membrane composition, and life span of animals. Physiol Rev. 2007;87:1175–213.

Jetz W, Thomas G, Joy J, Hartmann K, Mooers A. The global diversity of birds in space and time. Nature. 2012;491:444–8.

Kirkwood TBL. Evolution of ageing. Nature. 1977;270:301–4.

Martin TE. A new view of avian life-history evolution tested on an incubation paradox. Proc Roy Soc B Biol Sci. 2002;269:309–16.

Martin TE. Age-related mortality explains life history strategies of tropical and temperate songbirds. Science. 2015;349:966–70.

Møller AP. Sociality, age at first reproduction and senescence: comparative analyses of birds. J Evol Biol. 2006;19:682–9.

Møller AP. Senescence in relation to latitude and migration in birds. J Evol Biol. 2007;20:750–7.

Montgomery MK, Buttemer WA, Hulbert AJ. Does the oxidative stress theory of aging explain longevity differences in birds? II. Antioxidant systems and oxidative damage. Exp Gerontol. 2012;47:211–22.

Pagel M. The maximum likelihood approach to reconstructing ancestral character states of discrete characters on phylogenies. Syst Biol. 1999;48:612–22.

Pap PL, Vincze O, Fulop A, Szekely-Beres O, Patras L, Penzes J, Vágási CI. Oxidative physiology of reproduction in a passerine bird: a field experiment. Behav Ecol Sociobiol. 2018;72:18.

R Core Team. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/. 2018. Accessed 25 Oct 2018.

Ricklefs RE. The evolution of senescence from a comparative perspective. Funct Ecol. 2008;22:379–92.

Rose MR. Evolutionary biology of aging. New York: Oxford University Press; 1991.

Salmon AB, Richardson A, Perez VI. Update on the oxidative stress theory of aging: does oxidative stress play a role in aging or healthy aging? Free Radic Biol Med. 2010;48:642–55.

Sanz A, Pamplona R, Barja G. Is the mitochondrial free radical theory of aging intact? Antioxid Redox Sign. 2006;8:582–99.

Scharf FS, Juanes F, Sutherland M. Inferring ecological relationships from the edges of scatter diagrams: comparison of regression techniques. Ecology. 1998;79:448–60.

Selman C, Blount JD, Nussey DH, Speakman JR. Oxidative damage, ageing, and life-history evolution: where now? Trends Ecol Evol. 2012;27:570–7.

Sohal RS, Weindruch R. Oxidative stress, caloric restriction, and aging. Science. 1996;273:59–63.

Sohal RS, Agarwal S, Candas M, Forster MJ, Lal H. Effect of age and caloric restriction on DNA oxidative damage in different tissues of C57BL/6 mice. Mech Ageing Dev. 1994;76:215–24.

Stauffer J, Panda B, Eeva T, Rainio M, Ilmonen P. Telomere damage and redox status alterations in free-living passerines exposed to metals. Sci Total Environ. 2017;575:841–8.

Sudyka J, Arct A, Drobniak S, Gustafsson L, Cichoan M. Longitudinal studies confirm faster telomere erosion in short-lived bird species. J Ornithol. 2016;157:373–5.

Symonds MRE, Moussalli A. A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. Behav Ecol Sociobiol. 2011;65:13–21.

Tacutu R, Craig T, Budovsky A, Wuttke D, Lehmann G, Taranukha D, Costa J, Fraifeld VE, de Magalhaes JP. Human ageing genomic resources: integrated databases and tools for the biology and genetics of ageing. Nucleic Acids Res. 2013;41:D1027–33.

Vágási CI, Vincze O, Patras L, Osvath G, Marton A, Barbos L, Sol D, Pap PL. Large-brained birds suffer less oxidative damage. J Evol Biol. 2016;29:1968–76.

van de Crommenacker J, Hammers M, van der Woude J, Louter M, Santema P, Richardson DS, Komdeur J. Oxidative status and fitness components in the Seychelles warbler. Funct Ecol. 2017;31:1210–9.

Wasser DE, Sherman PW. Avian longevities and their interpretation under evolutionary theories of senescence. J Zool. 2010;280:103–55.